Report

Current Biology

Resource Ephemerality Drives Social Foraging in Bats

Highlights

- Miniature GPS-microphone tags allow monitoring wild bats' movement and interactions
- Bats foraging on ephemeral resources move in groups in variable movement patterns
- Bats foraging on predictable resources move alone and in fixed movement patterns
- Results support the hypothesis that resource predictability shapes group foraging

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In Brief

Using miniature tags, Egert-Berg et al. record bats' movement and social interactions. Whereas species foraging on ephemeral resources search in groups, switching foraging sites, species foraging on predictable resources search alone, returning to the same sites. The results suggest a connection between resource predictability and group foraging.

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Resource Ephemerality Drives Social Foraging in Bats

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SUMMARY

Observations of animals feeding in aggregations are often interpreted as events of social foraging, but it can be difficult to determine whether the animals arrived at the foraging sites after collective search [1–4] or whether they found the sites by following a leader [5, 6] or even independently, aggregating as an artifact of food availability [7, 8]. Distinguishing between these explanations is important, because functionally, they might have very different consequences. In the first case, the animals could benefit from the presence of conspecifics, whereas in the second and third, they often suffer from increased competition [3, 9–13]. Using novel miniature sensors, we recorded GPS tracks and audio of five species of bats, monitoring their movement and interactions with conspecifics, which could be inferred from the audio recordings. We examined the hypothesis that food distribution plays a key role in determining social foraging patterns [14–16]. Specifically, this hypothesis predicts that searching for an ephemeral resource (whose distribution in time or space is hard to predict) is more likely to favor social foraging [10, 13–15] than searching for a predictable resource. The movement and social interactions differed between bats foraging on ephemeral versus predictable resources. Ephemeral species changed foraging sites and showed large temporal variation nightly. They aggregated with conspecifics as was supported by playback experiments and computer simulations. In contrast, predictable species were never observed near conspecifics and showed high spatial fidelity to the same foraging sites over multiple nights. Our results suggest that resource (un)predictability influences the costs and benefits of social foraging.

RESULTS AND DISCUSSION

We compared the movement and social foraging behavior of five bat species (representing four families), which cover a wide range of foraging styles and exploit different resources (see Table 1). Two species rely on ephemeral resources (henceforth the "ephemeral foragers"): (1) the greater mouse-tailed bat (*Rhinopoma microphyllum*, Rhinopomatidae), an open-space insectivorous bat that preys on ephemeral insect swarms [17], and (2) the Mexican fish-eating bat (*Myotis vivesi*, Vespertilionidae), which forages primarily over marine waters [18, 19], where it feeds on local upwellings of fish and crustaceans [18, 19] whose exact location is difficult to predict on any given night. Indeed, our analysis of the spatial distribution of marine chlorophyll (a proxy of marine food availability [20, 21]) indicates low predictability of food spatial distribution over consecutive nights (Figure S1). Two additional species rely on plants which provide predictable stationary food resources (henceforth the "predictable foragers"): (1) the lesser long-nosed bat (*Leptonycteris yerbabuenae*, Phyllostomidae), a nectarivorous (and occasionally frugivorous) bat foraging on cactus pollen and nectar, which are predictably available at the same plants during our monitoring periods [22], and (2) the Egyptian fruit bat (*Rousettus aegyptiacus*, Pteropodidae), which feeds at trees that offer fruit continuously for weeks [23]. Our fifth species, the greater mouse-eared bat (*Myotis myotis*), gleans terrestrial insects

Table 1. Number of Bats per Analysis

Species	Resource Predictability	Bats with Movement Data (No.)	Mean Number of Nights (No.)	Bats with Movement Data of More Than Two Nights (No.)	Bats with Audio (No.)
Myotis vivesi	ephemeral	39	2.9	15	10
Rhinopoma microphyllum	ephemeral	12	1.7	6	8
Myotis myotis	predictable	18	2.7	15	14
Rousettus aegyptiacus	predictable	15[a]	2.6	15	10
Leptonycteris yerbabuenae	predictable	10	2.5	7	7

[a]We also used data of additional 150 *Rousettus* bats for which we either had GPS data or colony emerging times (STAR Methods).

(e.g., beetles and crickets) from the ground [24] and can therefore also be considered a predictable forager because these insects commonly occur in large numbers in the same patches over many consecutive nights [25]. We first use GPS data to compare the movement of these five species and then use on-board audio recordings to test the hypothesis that ephemeral foragers use group searching whereas predictable foragers do not. For further support, we model the foraging behavior of the ephemeral forager (*M. vivesi*) and the predictable forager (*M. myotis*) with the most data and use playback experiments to determine whether these two species differ with regard to conspecific attraction [26, 27].

Food Predictability Shapes Foraging Patterns

Individuals of all five species flew many kilometers each night, spending several hours foraging outside the roost (Table 2), but several movement patterns varied in accordance with their reliance on ephemeral or predictable resources (Figures 1 and S2):

(1) The spatial fidelity—the distance between the two closest foraging sites visited on consecutive nights—was large (>1 km) in bats relying on ephemeral food and small (<50 m) in bats relying on predictable food (Figure 1B; $F_{1,4} = 22.1$, $p = 0.01$, nested ANOVA with species nested within foraging style and defined as a random effect; see STAR Methods for how foraging sites were inferred). Whereas ephemeral foragers had to search nightly for feeding sites, predictable foragers returned to the same sites night after night. For example, a mouse-eared bat returned to the same site on seven consecutive nights (Figure S3), and an Egyptian fruit bat returned to the same tree 20 nights in a row.

(2) Predictable and ephemeral foragers also differed in temporal variability, estimated as the coefficient of variation (CV) of activity time (total time spent away from the roost) on consecutive nights. We calculated the CV of the activity time, that is, the SD of the activity time over all nights divided by the mean activity time. Ephemeral foragers exhibited a substantial CV, $\geq$50%, whereas predictable foragers were significantly more consistent, spending very similar amounts of time on the wing night after night (mean CV < 15%, $F_{1,4} = 22.7$, $p < 0.01$, nested ANOVA; Figure 1C). In a previous study, we used audio recordings on board *Rhinopoma* to show that the number of attacks on prey often varies between nights and does not correlate with searching time, thus demonstrating the uncertainty faced by ephemeral foragers [28].

(3) Predictable foragers visited fewer foraging sites per night than ephemeral foragers (Table 2; fewer than six versus more than eight sites per night, respectively; $F_{1,4} = 9.0$, $p < 0.06$, nested ANOVA).

Although predictable foragers repeatedly visited the same foraging sites, they still flew as far as ephemeral foragers in order to obtain food (Figure 1 and Table 2). Even mouse-eared bats never started foraging near the cave. Instead, they flew far, often passing above foraging grounds that seemed suitable. The median distance to foraging sites in this species was 14.8 km (n = 15 bats), with one bat flying ~32 km to a site. In contrast to ephemeral foragers, however, fidelity to a foraging site over several nights was high for mouse-eared bats (Figure S3), with some bats repeatedly foraging in a 100 m radius area (Figure S3). Relying on a predictable resource thus does not necessarily mean commuting less. When good roosting sites are rare, predictable foragers will often prefer to roost together and commute far.

Bats that Rely on an Ephemeral Resource Searched in a Group

Because the studied species all roost in colonies with hundreds to thousands of individuals (Table 2), the chances of tracking two bats that moved together was very low. On-board audio recording offered a unique window into the sociality of these species, as we could detect when bats encountered conspecifics from their calls. There was a clear difference in the social foraging behavior of the ephemeral and the predictable foragers. In brief, ephemeral foragers moved in groups, and predictable foragers did not (all results below are based on data from all bats from which we had audio; Table 1). Fish-eating bats commuted with conspecifics during the entire night (*cf.* Video S1, which presents the encounters for several bats). They commuted very close to conspecifics at least 6.5% of the time (median; quartiles 4.2%–8.2%; conspecific percentage was defined as the percentage of audio files with conspecific calls, and we did not differentiate between files with few or many conspecific calls). Note that due to the limited sensitivity of our on-board microphone, we could only record conspecifics when they came as close as 12 m to the bat carrying a microphone [29]. Because the bats' hearing range for conspecific calls is far larger (can reach up to 185 m), there were most likely many more conspecifics within eavesdropping range that we did not detect. Indeed, when using a new tag version (Vesper) with

Table 2. Movement and Ecological Characteristics of Five Bat Species

Species	Average Colony Size (N)	Body Mass (g)	Main Food	Food Predictability	Maximum Distance (km)	Activity Time (hr)
Myotis vivesi	5–1,000[a]	30	fish and crustaceans	ephemeral	25.1 (21.1–29.9)	3.7 (3.1–4.3)
Rhinopoma microphyllum	1,000	30	flying insects	ephemeral	9.8 (8.3–13.5)	5.5 (2.8–6.8)
Myotis myotis	4,000	30	terrestrial arthropods	predictable	20.9 (12.7–25.4)	5.4 (5.0–5.8)
Rousettus aegyptiacus	500	130	fruit	predictable	12.6 (7.3–22.8)	5.8 (5.4–6.8)
Leptonycteris yerbabuenae	100,000	25	nectar (and fruit)	predictable	53.5 (46.7–59.0)	6.6 (4.8–7.6)

Medians and quartiles are presented for all parameters. Colony size is typical for the areas where we worked. The maximal distance was defined as the distance to the farthest foraging site. Activity time was defined as the period during which the animal was away from its daytime roost.
[a]Hundreds of small groups of approximately five individuals can be found under neighboring rocks.

better audio sensitivity (and a detection range of ~50 m), we estimated a conspecific encounter rate of 55% (n = 1 bat). Moreover, as we recorded a 0.5 s sound file every 5 s, an encounter rate of 6.5% means that on average there was a nearby conspecific every 1.25 min, suggesting that there were many more conspecifics beyond the reach of our microphone. We observed a similar encounter rate (~8%) in the second ephemeral forager (*Rhinopoma microphyllum*) in a previous study [28]. For comparison, in all three predictable species, we detected no conspecific calls during commutes (absolute zero). To make sure that this was not due to technical limitations, such as the different sensitivity of our microphone at different frequencies used by the predictable species, we recorded bats from these three species with our new and more sensitive Vesper tag, thus assuring that the detection range of conspecifics was higher for the three predictable species than for the two ephemeral species (see STAR Methods). Even with these more sensitive tags, we never recorded any conspecifics near the predictable species. Moreover, because *Rousettus* bats do not always echolocate while commuting, we used the movement data of bats in our colony, including 3,605 GPS tracks collected from 96 individuals and 15,551 events of bats entering and leaving the colony (collected from 150 individuals), to determine whether bats ever depart or travel together. Analysis of this immense dataset strongly suggests that *Rousettus* do not leave the colony in groups and do not commute in groups when searching for food (see STAR Methods).

Foraging Patterns Deviate from Random

For the two species with the most tracking data (39 fish-eating bats and 18 mouse-eared bats; Table 1), we simulated independently moving bats with random conspecific encounters to test whether the observed conspecific encounter rates could be explained purely by the bats' density and movement patterns. We used observed data to characterize the movement patterns and the foraging areas of these two species (Figures S2C and S2D). In fish-eating bats (ephemeral foragers), the observed conspecific encounter rate was four times higher than expected by chance during commuting (medians: 6.5% versus 1.6%, $p < 0.0001$; permutation test on the median, n = 100 simulations of 10,000 bats), supporting the hypothesis that fishing bats intentionally search in groups (Figures 2A and 2B). The observed conspecific encounter rate at foraging sites was more than two times higher than expected by chance (medians: 27.5% versus 12.8%, $p < 0.0001$; permutation tests on the median, n = 100 simulations of 10,000 bats), which further supports our inference that these bats move in groups because distant unpredictable feeding sites would not be found by multiple bats simultaneously unless they commuted together. In mouse-eared bats (predictable foragers), conspecific encounter rate was significantly smaller both during commuting and foraging than expected by a random process (medians: 0.0% versus 0.1%, quartiles 0%–0% and 0%–0.2%, $p = 0.001$; and 0.0% versus 0.2%, quartiles 0%–0% and 0.3%–0.5%, $p = 0.0001$, respectively; permutation tests on the median, n = 100 simulations of 4,000 bats). Unlike the ephemeral forager, mouse-eared bats thus do not aggregate, and in contrast, most likely actively avoid conspecifics.

For the fish-eating bat, we also compared the temporal variation in conspecific encounter rate (i.e., how encounter rate changes over time during a night) between observed and simulated data. Observed bats encountered conspecifics at a constant rate during the entire night (Figure 2C, gray line), as would be expected if the bats intentionally moved together. Because bats often foraged while returning to the island, as evidenced by recorded echolocation attack sequences, it is reasonable that the conspecific encounter rate remained high when heading home (Figure 2C, gray line). In contrast, the conspecific encounter rate for simulated flights was greatest early in the evening (when bats emerge from their roost) and decayed to nearly zero within ~1.5 hr, as the bats dispersed (Figure 2C, black line).

Eavesdropping Is Limited to Social Foragers

Finally, we performed a playback experiment with the two species that we modeled to confirm that ephemeral foragers eavesdrop and follow a searching conspecific, whereas predictable foragers do not. We placed an ultrasonic speaker at locations where we previously observed individuals commuting to foraging sites. We measured attraction to the playback speaker using echolocation sequences of flying bats to score approaches and passes (see STAR Methods). We compared attraction to three playback treatments: (1) conspecific search calls, or recordings of calls emitted by conspecifics that are searching for prey; (2) conspecific feeding buzzes, or recordings of calls emitted by conspecifics that have found prey and are attacking it; and (3) noise, or pulses of noise with the same duration, rate, and bandwidth as the search calls of each species.

The two species clearly differed in their responses to the playbacks (Figures 2D and S4). Fish-eating bats were significantly more attracted to playbacks of conspecific search and buzz calls in comparison to noise (~5 and ~15 times more, $p < 0.04$, for the

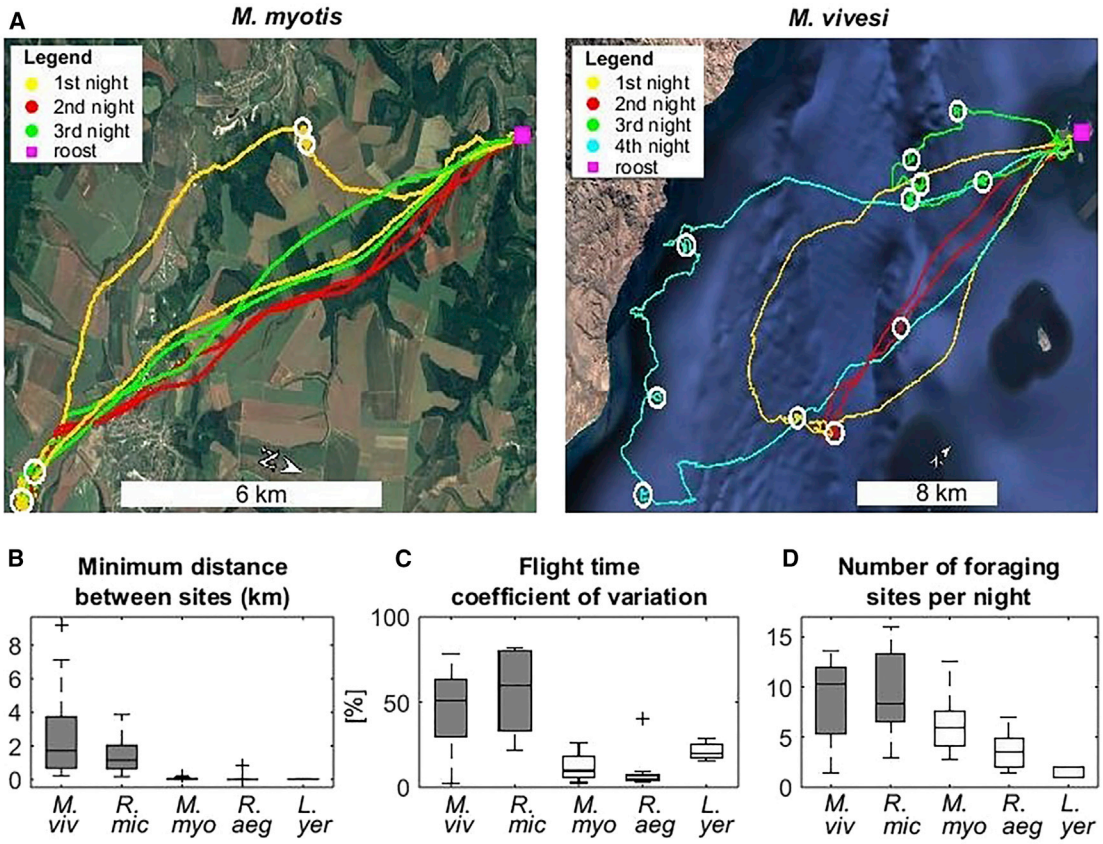

Figure 1. Foraging Movement Patterns of Five Bat Species

(A) The complete foraging movement of two individual bats over several consecutive nights. The mouse-eared bat (left) used a few foraging sites per night (white circles) and returned to the same foraging sites on consecutive nights, whereas the Mexican fish-eating bat (right) covered large areas and switched foraging sites nightly.

(B–D) Movement parameters of five bat species (only individuals with at least two nights were used in the analysis; Table 1) relying on ephemeral (gray bars) or predictable (white bars) resources.

(B) Spatial fidelity—the distance between the closest foraging patches visited on consecutive nights.

(C) Temporal variability—the coefficient of variation of the activity time.

(D) The number of foraging sites per night. Boxplots show median, quartiles, and whiskers extending to the most extreme data points not considered outliers (see MATLAB for outlier definition).

See also Figures S1–S3.

comparisons of search versus noise and buzz versus noise, respectively; Wilcoxon signed-rank test, after Bonferroni correction). Likewise, we have previously shown that *R. microphyllum* (the other ephemeral species) is also attracted to conspecific search and buzz calls to a similar degree [28]. In both cases, many bats flew close to inspect the speaker. In contrast, mouse-eared bats did not approach any playback ($p > 0.1$ for all comparisons, Wilcoxon signed-rank test).

Conclusions

Our data indicate that resource predictability correlates with foraging style. Of the five bat species that we studied, the two species relying on ephemeral resources intentionally aggregated while searching for food, whereas the three that rely on predictable resources were never observed near conspecifics during search. Neither body mass nor colony size could explain these differences in social foraging (Table 2). Why should ephemeral bats search in groups? In a previous study, we used a computer simulation to show that group foraging bats can gain information about the location of prey by remaining within eavesdropping range of conspecifics [28]. Interestingly, the terminal frequency of the fish-eating bat's echolocation signal (~18 kHz) is surprisingly low for a *Myotis* bat. Because low frequencies attenuate less, this should enable conspecific eavesdropping up to ~185 m (assuming a dynamic range of 120 dB between the emitter's intensity and the receiver's detection threshold).

Importantly, the advantage of group searching as described above would hold for any animal that can estimate the positions of neighboring conspecifics (to some degree) using any sensory system. Bats' reliance on sound is not a prerequisite, and visual animals could benefit from similar behavior. For example, scavenging birds of prey [30, 31] can visually detect a conspecific circling a carcass from many kilometers, and marine birds can spot diving neighbors [16]. Likewise, a bird searching for seeds can observe pecking behavior of a conspecific from a greater

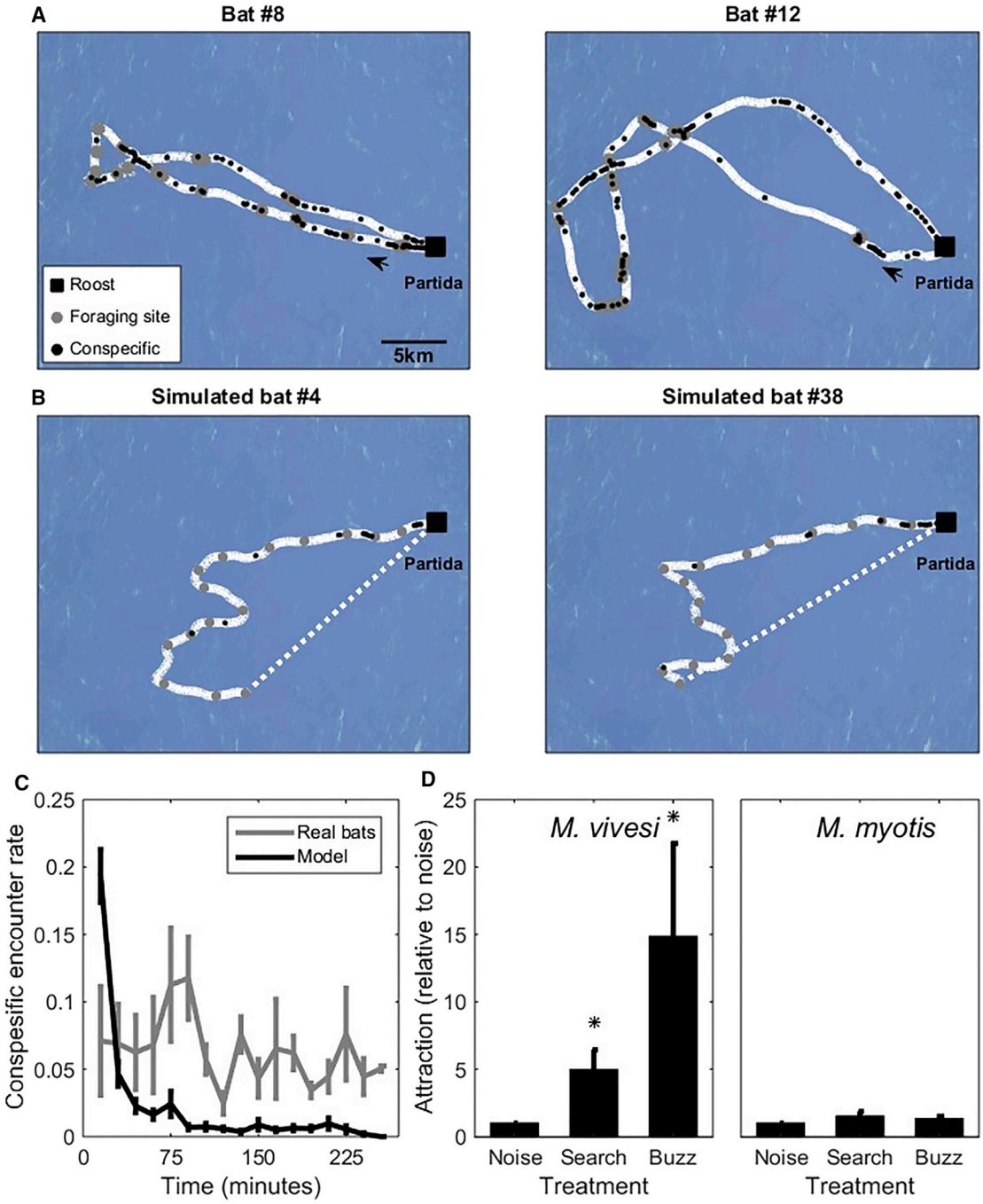

Figure 2. Mexican Fish-Eating Bats Intentionally Aggregate to Search in a Group

(A and B) Two examples of nightly flight trajectories of real bats (A) and simulated bats (B), showing encounters with conspecifics (black circles) and detection of foraging sites (gray circles). The black arrows indicate the flight direction of the real bats. The scaling of all maps is equal. Note how the simulated bats encounter far fewer conspecifics (black circles) and mostly at the beginning of the night (near the roost), whereas the real bats encounter conspecifics during the entire night. Real and simulated bats detected on average the same number of foraging sites). White dotted lines represent the return to the island, which we did not simulate because we stopped the simulation after the period of time observed in reality (STAR Methods).

(C) Encounter rate of conspecifics over time (15 min bins) in real fish-eating bats (gray) versus simulated independently moving fish-eating bats (black).

(D) Fish-eating bats are significantly attracted to playbacks of conspecific search and buzz echolocation calls, compared to the noise control, whereas mouse-eared bats are not attracted to any playback.

In (C) and (D), data are shown as means and SEs. See also Figure S4.

distance than it can detect an individual seed. This can sometimes also lead to producer-scrounger dynamics [32].

The relationship that we found between resource ephemerality and foraging sociality does not demonstrate causation. In addition to the unpredictability of the resource (in time and or space), several additional conditions (which often, but not always, correlate with resource ephemerality) should influence social foraging patterns. These include (1) patch abundance, i.e., a patchy resource with food that it is sufficient to provide food for many foragers once found, and (2) sparseness, which means that the resource is rare and necessitates exhaustive searching. Note that in theory, a resource could be ephemeral but not sparse. In the case of the fish-eating bat, not only is the resource patchily distributed and hard to predict in space, but it is also time limited, as it appears at the surface for a short time and then can quickly dive beyond the bat's reach. Perhaps this is why bats spent 9 min, on average, in a patch before departing. Such a short-lasting resource might also encourage social foraging because a single individual only has time to consume a portion of the patch before it disappears, so competition between individuals should be reduced [2]. Nevertheless, even when all of these conditions are met, social foraging may not occur. Moreover, other forms of social interactions can influence foraging. For example, mouse-eared bats were solitary both when flying to foraging sites and when searching for prey at foraging sites. Field researchers have reported observing individuals of this species actively defending foraging sites (C. Dietz, personal communication). Such behavior is only economically beneficial when the resource is defendable. In comparison, the nectarivorous and frugivorous species that we monitored exhibited different forms of social foraging. These two species did not search for food collectively, but they were observed at foraging sites in groups, occasionally interacting on a fruit tree (*Rousettus*) or chasing each other around a cactus (*Leptonycteris*). Such social interactions do not influence searching, but they could enable information transfer [33, 34] or result in competition [35]. Social foraging can have different causes and more field data are required in order to reveal its origin and underlying functions. This study illustrates how new technologies can shed new light onto fundamental questions in behavioral ecology, such as social foraging, and how bat diversity can serve as a comparative and representative toolbox for mammals in general.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures and one video and can be found with this article online at https://doi.org/10.1016/j.cub.2018.09.064.

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AUTHOR CONTRIBUTIONS

K.E.-B. conceived and designed the research, carried out the data analysis, was responsible for the modeling, collected the field data, and wrote the manuscript. E.R.H. and S.G. conceived and designed the research, collected the field data, carried out the playback experiments, and wrote the manuscript. L.H. conceived and designed the research and carried out the data analysis. A.G., L.G.H.M., J.J.F.-M., A.T.V., R.A.M., D.S.J., O.E., I.B., J.R.S., G.S.W., and H.R.G. contributed to field data collection and helped write the manuscript. Y.Y. conceived and designed the research, contributed to field data collection, and wrote the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Analyzed data	This paper	https://doi.org/10.17632/rb7r4cb74r.1
Experimental Models: Organisms/Strains		
Rhinopoma microphyllum	Northern Israel	Taxonomy ID: 173903
Myotis vivesi	Partida Norte Island, Mexico (28°52′30″N, 113°02′17″W)	Taxonomy ID: 233766
Myotis myotis	Orlova Chuka cave in northeastern Bulgaria	Taxonomy ID: 51298
Leptonycteris yerbabuenae	El Pinacate y Gran Desierto de Altar Biosphere Reserve, Sonoran Desert, Mexico	Taxonomy ID: 700936
Rousettus aegyptiacus	Two caves in central Israel (Beit Govrin and Herzelia)	Taxonomy ID: 9407
Software and Algorithms		
MATLAB	N/A	https://www.mathworks.com/downloads/; RRID: SCR_001622
Avisoft Recorder USGH	Avisoft Bioacoustics	http://www.avisoft.com/downloads.htm; RRID: SCR_014436
R	The R project for statistical computing	https://cran.r-project.org/mirrors.html
Batalef	In-house script for audio analysis	https://doi.org/10.17632/f6mvhj5gj9.3
Other		
Ultrasonic Dynamic Speaker Vifa	Avisoft Bioacoustics	Ultrasonic Dynamic Speaker Vifa Avisoft Bioacoustics, http://www.avisoft.com/usg/vifa.htm
Avisoft player 116 DA converter	Avisoft Bioacoustics	https://www.avisoft.com/usg/usgplayer116.htm
GPS - Robin	lucid Inc. Israel	http://www.yossiyovel.com/index.php/component/content/article?id=86
GPS - Vesper	asd Inc. Israel	N/A

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Yossi Yovel (yossiyovel@gmail.com).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Data acquisition and analysis

Animal capture and experiments in Bulgaria, Mexico and Israel were conducted under permits of the responsible authorities (Bulgaria: MOEW-Sofia and RIOSV-Ruse, permit # 465/29.06.2012 and 639/28.05.2015. Mexico (*M. vivesi*): permits # 7668-15 and 2492-17 from Dirección General de Vida Silvestre, and permits # 17-16 and 21-17 from Secretaría de Gobernación, and the University of Maryland Institutional Animal Care and Use Committee protocol FR-15-10; Mexico (*L. yerbabuenae):* permit # 04019/15, 03946/15 14509/16 from Dirección General de Vida Silvestre. Israel: (*R. microphyllum* and *R. aegyptiacus*): permits # 2011/38346 and 2012/38346 from the NPA, and # L-11-054 from the Tel-Aviv University IACUC.

METHOD DETAILS

Animal monitoring

M. vivesi data acquisition in Mexico took place during May and June of 2015-2016 in Partida Norte Island, Mexico (28°52′30″N, 113°02′17″W). Lactating females that had pups were tagged. Moreover, the pups did not lose weight over this short period (pup

weight increased (non-significantly) by 0.02 r, on average, $p > 0.9$, Wilcoxon signed rank test, $n = 10$ pups). All bats were captured in their roost in the morning (around 10.00AM), mounted with the devices within an hour from capture, and released where they were caught. Data acquisition for *L. yerbabuenae* bats was performed in El Pinacate y Gran Desierto de Altar Biosphere Reserve, Sonoran Desert, Mexico, during May-June 2015-2017 where we tracked post-lactating females. In Bulgaria, post-lactating females of *M. myotis* were tracked between July and August of 2013 and 2015. They were caught with a harp trap at Orlova Chuka cave in north-eastern Bulgaria when exiting the cave in the evening, tagged at the site and released. We collected data for *R. microphyllum* bats in northern Israel during the summers of 2012-2013 (see ref [28]). The *R. aegyptiacus* bats that we tracked were males captured in two caves in central Israel (Beit Govrin and Herzelia). We collected data for this species during February-June 2012-2015. All bats were processed and tagged within 2 hr and released at the cave. Additional bats from all species were tagged with light telemetry tags for comparison (see details below). Tags in all sites were retrieved by recapturing the bats after several days or by retrieving them from the ground after they fell off the animals.

In Mexico, Bulgaria and Israel the microphone and tracking device (30 × 20 × 4 mm) consisted of a GPS data-logger (Lucid Ltd., Israel) and a synchronized ultrasonic microphone (FG-23329, Knowles). The device's total weight (including battery, coating and a telemetry unit—LB-2X 0.3 g, Holohil Systems Ltd. Carp, Ontario, Canada) was 4.3 g on average (see discussion of weight effects below). The telemetry unit was attached to the device helping the experimenters to locate it. The devices were wrapped in colored balloons for water proofing and were attached to the bats using medical cement glue (Perma-Type Surgical Cement, AC103000, McKesson Patient Care Solutions, Inc., Moon Township, PA, USA). After gluing, bats were held for about 5 min to allow the glue to dry, and then placed in a cloth bag for another 15 min before releasing (see ref [28, 29] for full details). In case of recapture, the device was gently removed from the recaptured bats by cutting the fur that was attached to the tag. The tags remained on the animals for < 4 days on average (and up to 9 days at most). The microphone was positioned on the bat's back in between the shoulders, *ca.* 2 cm behind the bat's mouth, thus ensuring very high signal-to-noise ratio. Audio was sampled at 192 kHz. Due to the limited battery life and memory capacity when operating the microphone, we recorded a 0.5 s audio window every 5 s (10% recording duty cycle). GPS points were sampled at 15 s intervals. One L. *yerbabuenae* and one *M. vivesi* were sampled with a new tag (Vesper, ASD inc. Israel) with audio recorded at 200 kHz (using an on-board microphone, FG-23329, Knowles) in segments of 20 s every 30 s.

Because *Rousettus* bats do not always echolocate while commuting, we also analyzed GPS tracking data collected over 14 months in our in-house wild colony of fruit-bats. Bats in this colony (N = 30-50 individuals) roost in Tel-Aviv University and fly out to forage in the wild. They behave like bats in the nearby wild colonies. They fly similar distances, visit nearby colonies and occasionally switch roosts [36]. Similarly, bats from nearby colonies visit and join our colony. Each of the bats was tracked over dozens of nights with many tracked simultaneously on the same nights. We analyzed a total of 3605 tracks collected from 96 individuals (bats come and go and thus we have a total of more than 50 bats). On average, we tracked 5 bats simultaneously on a given night, but we often tracked 10 on the same night. Despite this huge dataset, we never observed two bats flying together – not when emerging, not during foraging and not when returning. Moreover, we monitored the exit times of all individuals in the colony over a period of 14 months (in total we monitored the exit of 150 individuals, while we only had GPS data for 96 individuals). Of the 15,551 events of bats exiting or entering the colony only in 48 cases (~0.3%) did another bat follow within a time-period of 5 min which might suggest following behavior.

The definition of foraging versus commuting

We used a union of two movement indices, the Straightness index [37] and the First passage time [38], to detect foraging events and separate them from commuting periods. In brief, the Straightness index is the ratio between the distance from the starting point to an end-point and the actual path length traveled between these two points (a value of 1 means moving straight). The straightness index was calculated at each point along the trajectory with a window of 15 min (and an almost complete overlap – a 1 point shift). An index value of max. 0.5 was set for foraging following manual scrutiny of part of the data. The First passage time is a measure of the time an animal spends within a given radius along the path. The First passage time was estimated for each location along the trajectory with a radius of interest of 60 m. The minimum First passage time for defining foraging was set to 50 s. Any point along the trajectory that crossed one of the two thresholds (had a straightness index of less than 0.5 or a first passage time of more than 50 s) was defined as a moment of foraging. After identifying all potential foraging sites (i.e., connecting all locations in which foraging occurred), we omitted sites in which bats spent less than 30 s in total, and we merged sites that were less than 60 m apart. We only performed this analysis on bats that were farther than 100 m from their roost. We used the on-board audio recordings where we could detect echolocation attack sequences to confirm that this algorithm was performing well (this could only be done in *M. vivesi* as *M. myotis* is a gleaner and does not emit attack sequences).

Simulation of independently moving bats

In the simulations of both species, the bats moved according to the movement parameters of the real bats, that is, with the same average speed and the same distribution of turning angles, but as independent individuals without any intention to aggregate in groups. We used a permutation test to compare the simulated data to the real data. To this end, 10,000 random samples of 10 bats were drawn from each model and the median of the real data (e.g., conspecific rate median) was compared to these 10,000 simulated groups.

Fish-eating bat model

The aim of the simulations was to examine whether the rate of encountering conspecifics observed in the fish-eating bat could be explained by random encounters of conspecifics when moving independently in the foraging areas (i.e., due to the number of bats moving through the area). We simulated 10000 bats independently flying in a rectangle area of 34 × 17 km^2 - the area was estimated by taking the convex hull of the areas covered by all 39 searching bats (90 nights in total) which were tracked in the study. This area was probably an underestimation of the actual area covered by the bats – the more bats we followed the more the area increased. The number of bats we used was a maximum estimate of the number of bats on Isla Partida Norte which is by far the largest colony in the area [30]. The simulated bats left the island dueing 30 min (like the real bats) flying toward the same range of angles relative to the Island as the real bats (165-245 degrees, relative to north defined as 0). The simulated island was positioned at the same position relative to the foraging rectangle as the real island – this means that the simulated bats spread a triangular area within the foraging sites (like the real bats) while the complete rectangle only defined their maximal borders – they never crossed these borders (see turning heuristics below). The simulated bats flew for 3.5 hr (the average observed flight duration of the real bats) at a constant velocity of 5.9 m/s (the average speed of searching bats according to the real data). They stopped at foraging sites for 9 ± 2 min on average (see details below).

Simulated bats that were farther than 1 km from the borders of the foraging area performed a correlated walk movement, changing their direction relative to the previous heading every 5 s, according to a (zero-centered) normal distribution of possible angles with a standard deviation of 0.1 rad. This distribution was estimated based on the turning angles of the real 39 bats (over all 90 nights). When a simulated bat came as close as 1 km to the borders of the foraging area, it altered its turning behavior by adding a bias to the angle-distribution turning it back into the area. The bias aimed to turn the bats back into the foraging area (as the real bats did). The bias was randomly negative or positive, and it was added as follows:

a) Between 1 to 0.68 km from the borders, the bat turned based on the same distribution above but with a bias of 12 degrees thus turning back into the foraging area.
b) Between 0.68 to 0.36 km from the borders, the bat turned based on the same distribution above but with a bias of 21 degrees.
c) Bats that still reached one of the borders of the area turned back (according to a physical reflection model).

In all cases a-c the bat either turned like in the general search model or it turned as defined in a-c with increasing probabilities (40-70%–80% in a-c respectively). A bat that reached the border without turning bounced back in with the impinging angle equal to reflected angle. These parameters were chosen such that the turning angle distribution of the simulated bats will resemble the distribution of the real bats (Figure S4). The overall movement of the simulated bats captured the essence of that of the real bats crossing through the foraging areas in an ellipse-like trajectory (compare Figure 2A and Figure 2B).

Because we did not want to assume anything about the distribution of the resource that might influence our results, we used the bats' behavior to model the resource. The probability of finding a foraging site at a given time-point was a Poisson process with an average Lambda of 0.045 sites per minute (based on the observed data). When a simulated bat detected a foraging site, based on this probability, this was now a foraging site for all bats encountering it. The bats remained within the site for 9 ± 2 min (the exact time was drawn from a normal distribution with a mean and standard deviation based on the real data). We used the estimated detection range (185 m) to model the attraction of other bats to this discovered site. When a bat passed within 185 m from a bat that found a foraging site, it was immediately attracted to the site. This assumption aimed to model the aggregation of (independently moving) bats at foraging sites, a process which could have influenced the encounter rate of conspecifics right after leaving the site. Indeed even independent bats aggregated at foraging sites (but to a much lesser degree than the real bats, see main text). The bat's movement inside the foraging site was modeled as a random walk (see below). The simulation stopped after 3.5 hr wherever the bat was – we did not simulate the final return to the island, because we only aimed to examine the encounter-rate of conspecifics. Importantly, all of the simulation assumptions intended to increase the encounter-rate of conspecifics in the simulation. We used the maximum number of bats roosting on the island, and we assumed that they all left every night flying in the same direction (in reality bats occasionally did not leave the island). We probably underestimated the foraging area (see above), and we used the maximum range (185 m) for detecting foraging conspecifics (which in the real bats is only achieved when the bat is facing the center of the beam of another bat and is otherwise shorter). This approach of increasing the encounter-rate of conspecifics in the simulations aimed to set an upper-bound on the potential encounter-rate of bats that were moving independently. If the real bats encountered conspecifics more than this upper-bound, they were probably intentionally aggregating.

The analysis of the simulated bats was identical to that of the real bats to allow a fair comparison. To this end, during the commute periods of each simulated bat, we measured its distance from all other simulated bats. We registered every distance to another bat that was smaller than 12 m as an encounter event, as we would have recorded by our microphone in reality (because our microphone could only record bats from up to 12 m). This was also an over-estimation because of the directionality of the echolocation beam (see above). We only quantified interactions occurring more than 1 km from the island (in both the real and simulated bats) in order to avoid overestimations due to the synchronized emergence.

We also modeled the encounter rate within foraging sites. The number of bats arriving at the foraging sites was determined based on the model of independently moving bats and the attraction between them (see above). The sites themselves were modeled as 210 m-radius circles (the average size of the foraging sites estimated based on a convex-hull of foraging bats). The first bat arriving

at the site left after 9 ± 2 min (see above) and the other bats left within 1 min after the first one. Bats moved through the foraging site in a Brownian movement and their encounter rate was calculated as above.

Mouse-eared bat model

The model for *M. myotis* was similar with a few adaptations to the behavior of this species. Four thousand bats emerged from a central location (their cave) flying in straight lines in all directions (as we observed in the data, Figure S2). The bats stopped at a distance from the cave, which was sampled from the distribution of the distances of the real foraging sites. We did not model the behavior in the foraging sites in this case as these bats showed no tendency to aggregate. For this species, we assumed a detection range of a conspecific by our microphone as 8 m – according to the emission level of these bats and the sensitivity of the microphone at the most intense frequency of the bats' signal.

Validation of conspecific recordings

The fact that we did not detect conspecifics in the three predictable foragers did not result from a technical artifact for two main reasons. First, for the predictable foragers we also used recordings from our new and much more sensitive device (Vesper, ASD Inc. Israel). We used Vesper recordings of 4 *M. myotis*, 4 *L. yerbabuenae* and 10 *R. aegyptiacus*. We calibrated the Vesper's microphone estimating the recording range for these species at ca. 30 m, 20 m and 25 m respectively. In all cases, this is much more than the 12 m recording range for the two ephemeral species (with the old device). We therefore strongly biased our recordings in favor of the predictable species and still found that they do not encounter conspecifics. Second, in the models of independently moving bats (above) we took into account the exact detection range of our microphone (which was 12 m for *M. vivesi* but only 8 m for *M. myotis* with the old device). The comparison was therefore fair and we found that *M. myotis* encountered conspecifics in reality less than expected by chance.

Playback Experiments

To test if bats are attracted to foraging conspecifics, we performed playbacks of *M. vivesi* and *M. myotis* search and attack echolocation calls (using the Avisoft UltraSoundGate Player D/A converter connected to a Vifa speaker, Vifa, Copenhagen, Denmark). The sequences we used (i.e., a search sequence and an approach sequence which ended with a buzz) were composed of signals that were recorded on-board wild bats using our miniature sensors. A third white noise control-treatment included a train of noise pulses. As our main comparison was between the search and the noise treatments, these two playbacks had the same pulse duration, pulse interval and bandwidth. The amplitude for all playbacks was normalized so that the peak intensity of all treatments was identical (the total energy was higher in the approach sequence because the calls were more frequent). In the case of *M. vivesi*, the playbacks were performed from an anchored boat roughly 100 m off Isla Partida Norte while in *M. myotis* it was ca. 10 m from the entrance of the cave (in the past, we used a similar position near the cave of *R. microphyllum* which showed clear attraction to the playback of searching conspecifics even at such a short distances [23]). Playbacks were made when the bats were emerging from their roosts, but after the majority of bats have already left so that mostly single bats were passing by to ease the analysis of the behavior. Playbacks were performed along 6 consecutive nights in Mexico and 5 consecutive nights in Bulgaria. All three treatments were played back twice on each night but their order varied haphazardly between nights. Each treatment-playback lasted 5 min before the next treatment-playback was played.

Playback recordings were analyzed using "Batalef," a custom-made in-house MATLAB program for sound analysis. Calls were automatically detected using a peak detection filter based on the local noise in the channel. Signals were bandpass-filtered between 30 - 50 kHz to ensure that only loud high frequency calls will be detected. This allowed automatic recognition of bats, which approached the microphone and distinguishing them from passing bats and from our own playback (Figure S4). High frequencies are more directional and attenuate more rapidly and thus they will be picked up by the microphone only when the bat points its emission toward it. A total of ~29,000 and ~9,000 calls were analyzed in Mexico and Bulgaria respectively. At least 30% of the data (of each species) were scrutinized manually to confirm high performance of the automatic algorithm. Because individual bats were hard to identify, we quantified the number of calls per session (night) per treatment (search, buzz, noise) and we ran a non-parametric paired test on the search versus noise and buzz versus noise comparisons (and corrected the p values for multiple comparisons using the conservative Bonferroni correction).

Controlling for the effects of the extra-loading on the bats

The extra-weight loaded on the bats reached a maximum of 15% of body mass (14 ± 0.5% In *M. myotis* and 14 ± 1.0% in *M. vivesi*). The analyzed GPS-tagged bats from both species left their roosts as usual together with the non-tagged individuals. Tagged individuals flew directly to their foraging sites and engaged in foraging, suggesting that they behaved as usual. To validate that the bats could forage with this extra weight we performed several controls for both species:

(1) We trained bats to forage in a room / tent to confirm that they could do so with the extra-weight. *M. vivesi* bats successfully learned to rake a small artificial pool and catch food items that were on the water (e.g., beetles) while *M. myotis* quickly learned to glean mealworms from a plate positioned on the floor in a flight room when carrying the extra-weight.

(2) Light telemetry tags (ca. 1% of the bats body mass) were mounted on bats of both species and the time they spent foraging (out of the roost) was compared to that of the GPS bats. For a fair comparison we used a telemetry logger (DataSika, Biotrack, New Market, Ontario, Canada) that was placed in the roost of each species and thus picked up the telemetry signals of the bats

when they were in the roost (the logger checked the presence of each tag on average once every minute). The GPS bats also had telemetry tags so we used an identical method for both treatments. Foraging flights were defined as events in which a bat was not detected by the logger for at least 20 min (between 20:00 and 7:00 local time). The amount of time that the *M. myotis* control bats, tagged with light tags, spent out of the roost did not differ from the amount of time spent by bats tagged with the GPS tags (5.8 ± 0.9 versus 5.5 ± 1.0 hr respectively, p = 0.37, permutation t test; n = 15 GPS bats and n = 8 telemetry tags). The same result was obtained for *M. vivesi* where control bats, tagged with light tags, flew for 4.3 ± 2.1 hr on average while the GPS tagged bats flew 3.8 ± 1.8 hr (p = 0.4, permutation t test n = 20 GPS bats and n = 15 telemetry tags).

(3) When we had a chance to recapture bats, we compared the weight loss of bats that were tagged with GPS to that of bats tagged with light telemetry tags. In *M. myotis*, both GPS-tagged bats and bats tagged with light telemetry tags lost weight, but there was no significant difference between the two treatments (on average the GPS and telemetry bats lost 1.3 ± 1.3 versus 0.9 ± 0.5 g, mean ± SD respectively, p = 0.5, permutation t test; n = 8 GPS bats and n = 6 telemetry tags). There was also no difference when accounting for the time period of the tagging (ANCOVA hypothesis of parallel slopes: *M. myotis* adults – $F_{1,44}$ = 0.005, p = 0.95, N = 28 and 20 Telemetry bats). In *M. vivesi* weight loss was slightly higher in GPS bats in comparison to the telemetry tagged bats (bats lost 1.8 ± 1.3 versus 0.9 ± 0.9 gr, mean ± SD respectively, p = 0.05, permutation t test; n = 12 GPS bats and n = 10 telemetry tags). However, when time since first capture was taken into account and the loss of weight per day was estimated, we found no significant difference between telemetry and GPS tagged bats (ANCOVA hypothesis of parallel slopes: *M. myotis* adults – $F_{1,7}$ = 3.866, p = 0.09, N = 7 GPS and 4 telemetry bats; *M. vivesi* adults – $F_{1,63}$ = 1.549, p = 0.218, N = 47 GPS and 20 telemetry bats). This suggest that the difference resulted from the capture of GPS bats after more nights than the telemetry bats (GPS bats were tagged for significantly more time than telemetry bats – 2.5 versus 1.6 days; p = 0.0001, Wilcoxon rank sum test, N = 47 GPS and 20 telemetry bats).

In both species, both GPS and telemetry bats lost weight over the period of the few days that they carried the tags. Telemetry units were tiny, adding only ~1% to the body mass, so it was probably not the weight of the tags that caused the bats' weight loss. One possibility is that the nuisance of carrying a foreign body stressed the bats. Another explanation is regression to the mean as we always tried to select the heaviest bats for tagging, so these bats could have been above their typical average weight. Loss of weight could also be a result of the normal seasonal trend, because we had tagged (currently or recently) lactating bats that probably lose weight during this time of the season (after reaching a peak weight during pregnancy).

In terms of the pups' health, there was no significant difference in the weight to forearm ratio between *M vivesi* pups whose mothers were GPS or telemetry tagged (ANCOVA hypothesis of parallel slopes: F = 2.306, p = 0.204, N = 8, 5 GPS and 3 telemetry pups).

Importantly, the tags stayed on the animals for an average period of < 3days (in the most extreme case 9 days) so their effect of the animals' welfare was extremely limited in time. Note that as we are comparing two species in this work, even if the bats behavior was somewhat affected by the tags' weight (e.g., their foraging success declined), the comparison of foraging and social behavior between the two species is still valid as it is hard to imagine that the huge differences that we observed between the two species could be an artifact of the extra loading – it is hard to imagine that the weight made a social bat suddenly solitary in such a short time. For similar controls in Rhinopoma see [28].

QUANTIFICATION AND STATISTICAL ANALYSIS

For analyzing the differences in movement between ephemeral and predictable foragers, we ran a nested ANOVA test with species nested within foraging style (i.e., ephemeral versus predictable) and species defined as a random effect. This test was run for each movement parameter separately.

The comparison of the model to the real bats (the conspecific encounter rate), we used a permutation test because the sample size of the model (i.e., the number of simulations) was a parameter we could control, thus influencing the power of our analysis.

We used a non-parametric Wilcoxon rank sum test to examine the attraction of bats to playbacks because of the small sample size and because the tests were run within the species, (so there was no need for an ANOVA structure). All statistical analyses were done in MATLAB.

Current Biology, Volume *28*

Supplemental Information

Resource Ephemerality Drives Social Foraging in Bats

Katya Egert-Berg, Edward R. Hurme, Stefan Greif, Aya Goldstein, Lee Harten, Luis Gerardo Herrera M., José Juan Flores-Martínez, Andrea T. Valdés, Dave S. Johnston, Ofri Eitan, Ivo Borissov, Jeremy Ryan Shipley, Rodrigo A. Medellin, Gerald S. Wilkinson, Holger R. Goerlitz, and Yossi Yovel

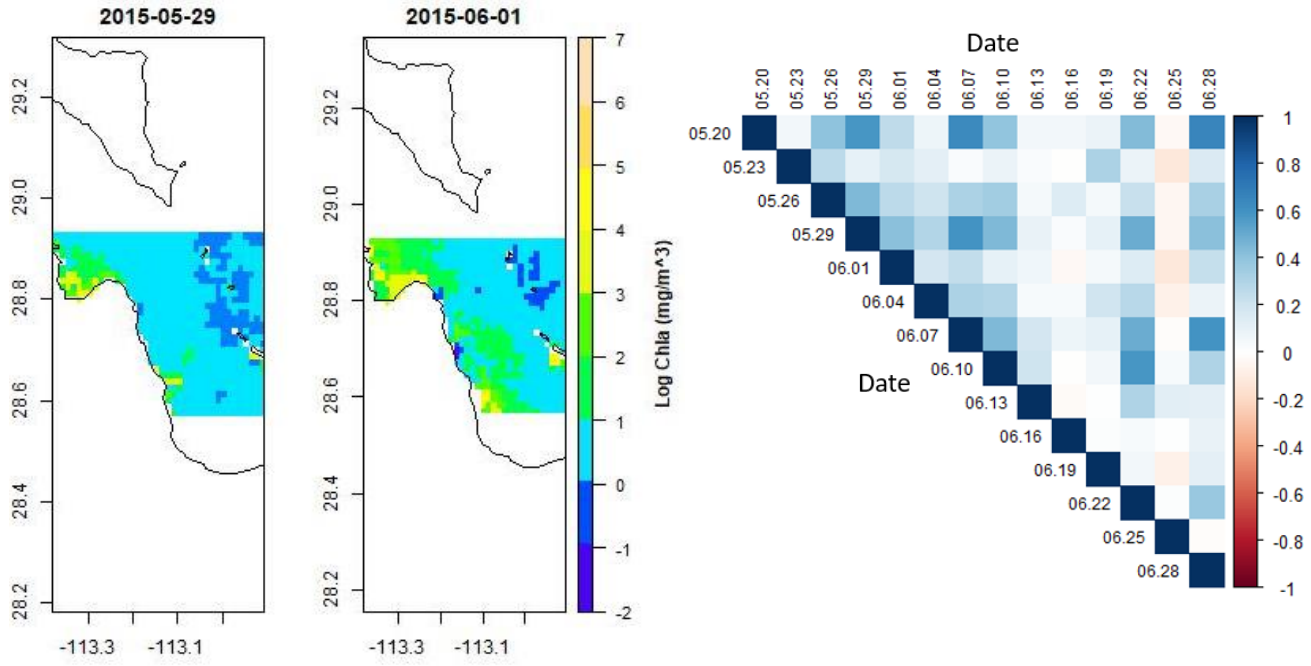

Figure S1. Food is difficult to predict in the foraging areas of the Fish-eating bat as can be learnt from an analysis of ocean chlorophyll concentrations. Related to Figure 1.Top - Two maps of chlorophyll concentrations (on May 29 and June 6) in the foraging area around Isla Partida Norte, between May 20 and June 30, 2015 (axes show dates). Each spatial map of chlorophyll concentration (mg/m^3) was generated for the foraging areas of our bats (X min: -113.3862, X max: -112.9022, Y min: 28.5709, Y max: 28.9277). Chlorophyll concentration strongly correlates with the concentration of plankton, which should predict the concentration of fish and crustaceans eaten by the bats. **Bottom** - Each cell in the matrix depicts the Pearson's correlation between the spatial distribution of chlorophyll concentrations on a pair of days (3-days apart). The dates are depicted on the axes (a total of 14 days were sampled). Chlorophyll concentration had low spatial correlation over time, suggesting that chlorophyll abundance and probably also fish abundance was spatially stochastic over the study period. Data was obtained from NOAA ERDDAP data server at 0.0125 degree (~1 km^2) spatial resolution: (http://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMWchla3day.graph).

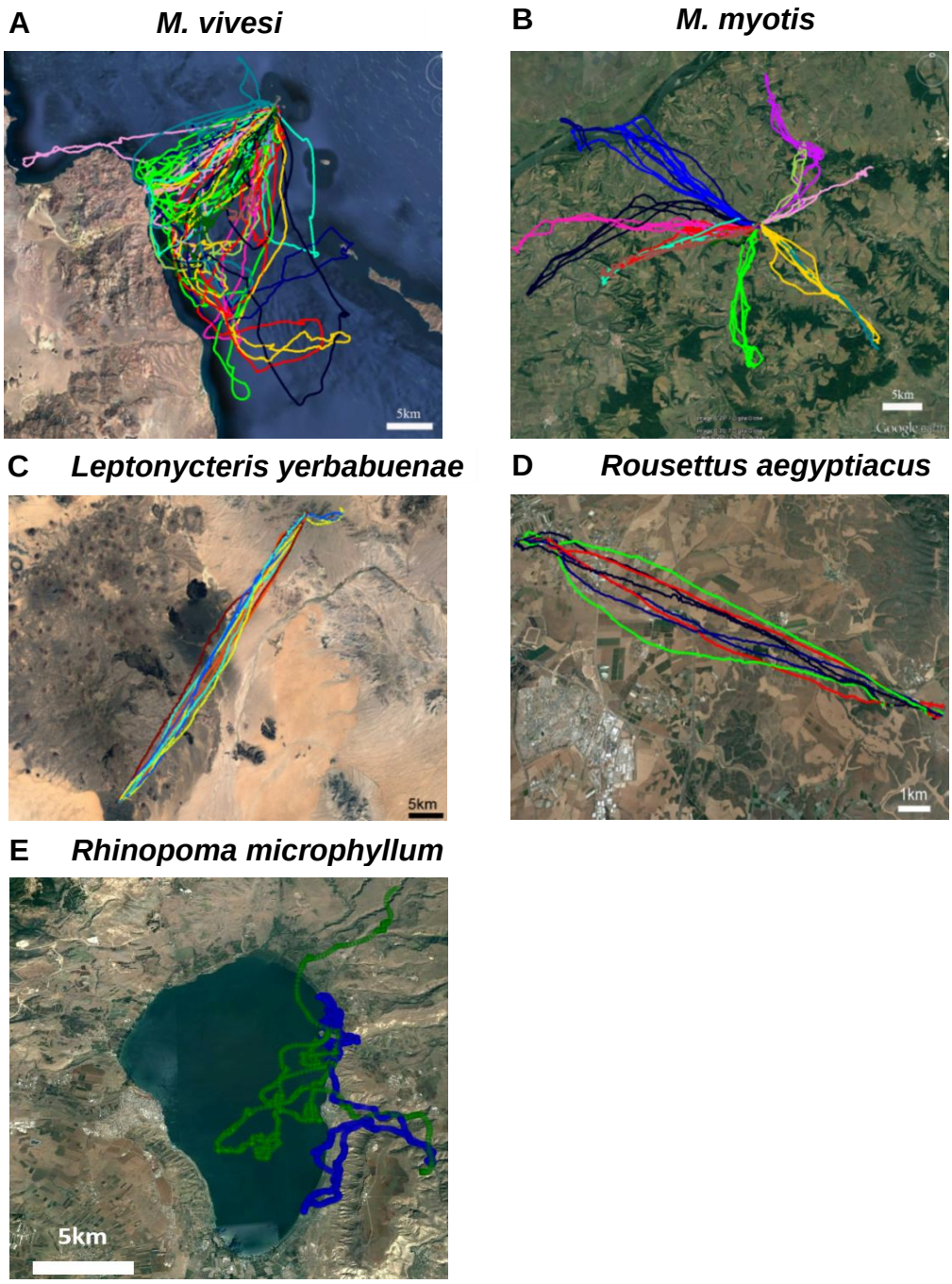

Figure S2. Flight trajectories of all five bat species. Related to Figure 1. A - *M. vivesi*, B - *M. myotis*, C - *Leptonycteris yerbabuenae*, D - *Rousettus aegyptiacus* and E - *Rhinopoma microphyllum.* For *M. myotis and M. vivesi* the trajectories of different individuals (15 individuals per species) are presented in different colors (some individuals are masked by others). Note the straight flight trajectories of *M. myotis* bats vs. the wandering movement in *M. vivesi* bats. Several nights of one individual are presented for the other three species (C-E). In *Leptonycteris* nights are ordered: blue, turquoise, yellow, orange and brown. *Rousettus* nights are ordered: black, red, green and blue. *Rhinopoma* nights are ordered: blue, green. All maps in the supplementary figures are presented with the north pointing up.

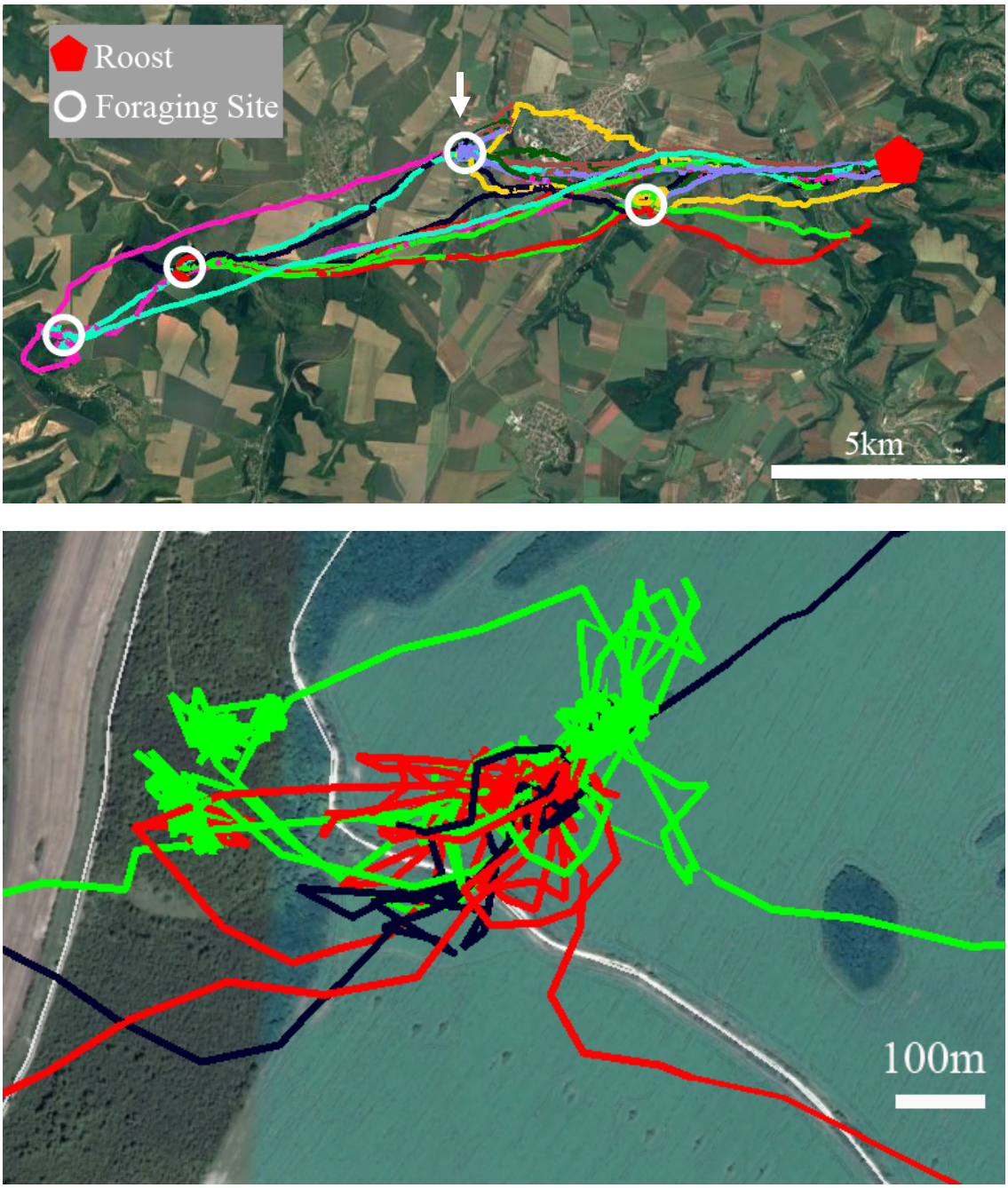

Figure S3. Foraging trajectories of *M. myotis*. Related to Figure 1. Top, the flight trajectories of a single *M. myotis* bat that visited 4 foraging sites (white circles) over a period of 9 nights (1-10/8/2015). Each color depicts a different night. All sites were visited for at least 3 nights consecutively, and the one most visited (white arrow) was visited on 7 nights in a row. **Bottom,** three consecutive foraging nights (color coded) of one *M. myotis*. Note how in all three nights, the bat returned to the exact same patch in the field (note scale). In two of the nights (red and green) it also returned to the same patch in the nearby forest (to the left).

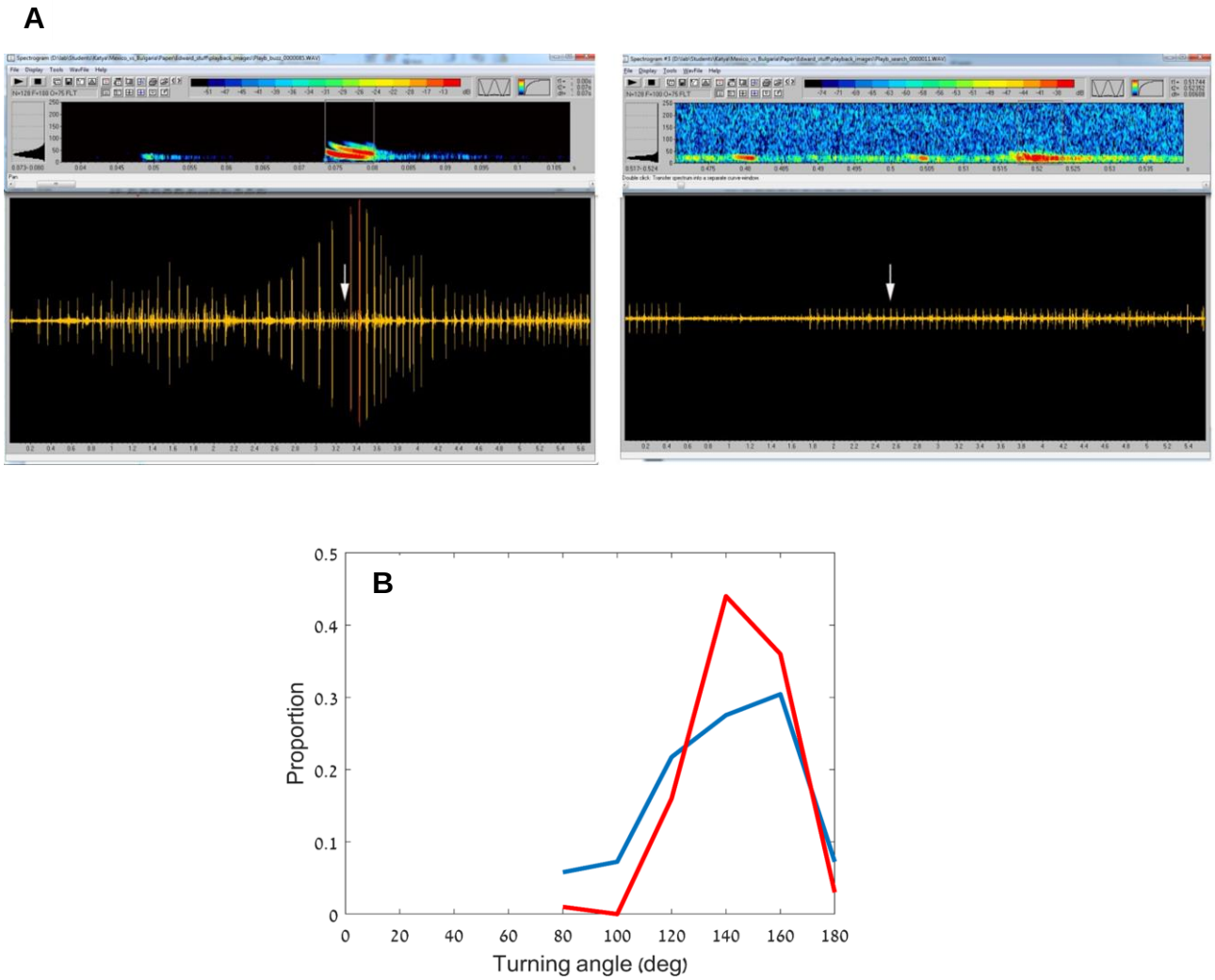

Figure S4. Validation experiments. Related to Figure 2. A - Recordings of Playback experiments. Left – a recording of a *M. vivesi* bat that approached the speaker in response to a 'search' playback and was detected by our analysis. Right – a recording of a *M. vivesi* bat that passed above the system during the 'search' playback. Bottom panels show the time signals while the top ones show a spectrogram of a single call. Note the second harmonic that appears in the call of the approaching bat (Left) because its calls are directed towards the playback system (and microphone). This phenomenon allowed us to distinguish approaching bats from passing bats, and to detect the calls of approaching bats automatically. White arrows depict the playback signals. Playback signals are weak in the recordings because of the relative position of the speaker, which was behind the microphone. Screen shots are taken from Avisoft saslab. **B - Turning angles of modeled bats (blue) and real bats (red).** The turning angles were defined by three points – the turning points and two points at a distance of 1km from the turning point (one before and one after the turn).