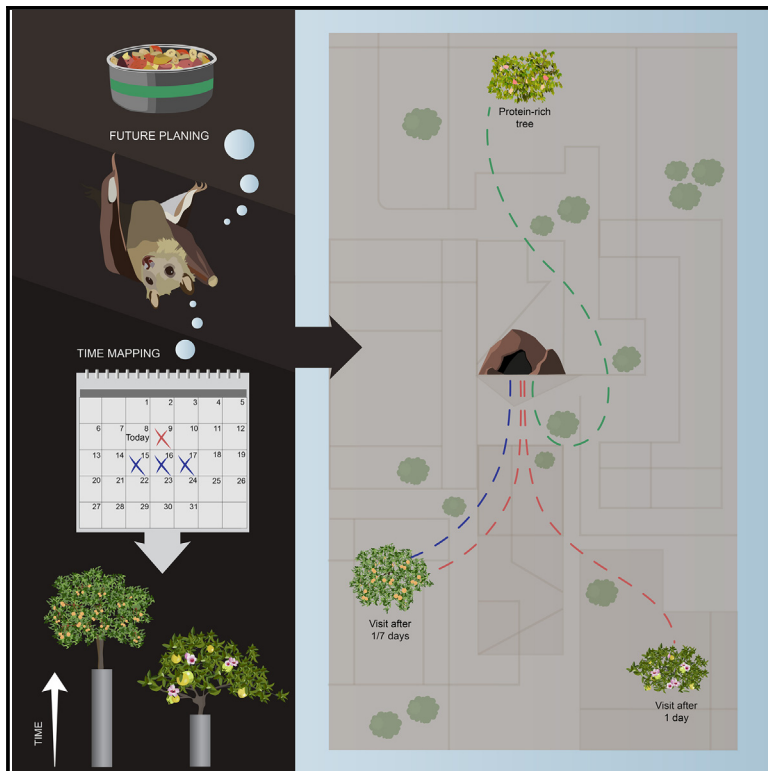


Current Biology

Time-mapping and future-oriented behavior in free-ranging wild fruit bats

Graphical abstract



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In brief

Harten et al. use GPS tracking and captive manipulations to demonstrate that wild Egyptian fruit bats map the temporal availability of food sources and the time since their last visit to a tree, then plan their foraging accordingly as well as according to their nutritional requirements.

Highlights

- Fruit bats track tree phenology and estimate fruit availability since the last visit
- Young bats must learn tree phenology through experience
- Bats exhibit future-oriented behavior and fly to specific protein-rich trees
- When doing so, bats pass and skip over many familiar sugar-rich trees

Report

Time-mapping and future-oriented behavior in free-ranging wild fruit bats

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SUMMARY

Episodic memory and mental time travel have been viewed as uniquely human traits.^{1–3} This view began to shift with the development of behavioral criteria to assess what is referred to as “episodic-like memory” in animals.^{4,5} Key findings have ranged from evidence of what-where-when memory in scrub-jays, rats, and bees; through decision-making that impacts future foraging in frugivorous primates; to evidence of planning based on future needs in scrub-jays and tool use planning in great apes.^{4,6–13} Field studies of these issues have been rare, though there is field-based evidence for future-oriented behaviors in primates.^{8,10,14,15} We report evidence that free-ranging wild fruit bats rely on mental temporal maps and exhibit future-oriented behaviors when foraging. We tracked young bats as they navigated and foraged, documenting every tree they visited over many months. We prevented the bats from foraging outside for different time periods and monitored their foraging decisions, revealing that the bats map the spatiotemporal patterns of resources in their environment. Following a long period in captivity, the bats did not visit those trees that were no longer providing fruit. We show that this time-mapping ability requires experience and is lacking in inexperienced bats. Careful analysis of the bats’ movement and foraging choices indicated that they plan which tree to visit while still in the colony, thus exhibiting future-oriented behavior and delayed gratification on a nightly basis. Our findings demonstrate how the need for spatiotemporal mental mapping can drive the evolution of high cognitive abilities that were previously considered exclusive to humans.

RESULTS AND DISCUSSION

In our study, we examined episodic-like memory and future-oriented behavior in wild free-foraging Egyptian fruit bats (*Rousettus aegyptiacus*). Bats, especially frugivorous species like the Egyptian fruit bat, represent an interesting model because their survival and reproductive success heavily depend on foraging decisions, which necessitate understanding and following temporal and spatial changes in food resources.^{16–19} Equipped with their cognitive spatial maps,^{20–22} these bats navigate through landscapes with numerous fruit and nectar trees, which they would need to mentally track in order to revisit over time.^{20–22}

We thus hypothesized that these bats plan their foraging not only based on their knowledge of what and where food is available, but that they also rely on mental time-mapping to decide when to visit specific trees. Specifically, we predicted that (1) bats learn tree phenology and track the time passed since their last visit to a tree and that (2) on most nights, bats know where they are heading the moment they leave the colony. To test these hypotheses, we employed high-resolution GPS tracking and nutritional analysis, combined with experimental manipulations

involving controlled periods in captivity, to uncover the underlying decision-making process.

Experiment 1: Time-mapping

Egyptian fruit bats are opportunistic and feed on a wide variety of trees (often dozens of tree species per individual bat) that provide food for different periods of time, basing their choice on tree phenology and attractiveness; i.e., some tree species offer fruit (or nectar) for longer periods, while others are more attractive to the bats and are thus depleted faster. Indeed, when examining the total duration in which a tree was visited by the bats from our colony, it was evident that some trees offer food for much longer periods than other trees (many weeks versus a few days; [Figure 1A](#)). Moreover, individual bats repeatedly returned to long-fruited trees over more consecutive nights, demonstrating that they exploit such trees for longer periods ([Figure 1B](#)).

To determine whether bats possess a temporal understanding of tree phenology and whether they track the time since they last visited a tree, we performed a controlled manipulation, keeping 19 bats in captivity and preventing them from foraging outside for a short period (one night) or a long period (4/7 consecutive nights) ($n = 29$ trials in total; [STAR Methods](#); [Table S1](#)).

We hypothesized that if bats kept track of time, they would revisit different tree species at different frequencies according to their either short or extended periods in captivity. Namely, they would not visit short-fruited trees after long periods in captivity because these trees will likely no longer offer food. We separated the bats into two groups (experienced and inexperienced) based on their experience outdoors (STAR Methods), as assessed from our continuous tracking of the same individuals from their first nights outdoors.

There was a clear and significant difference between experienced and inexperienced bats. Experienced bats behaved in line with our predictions and were more likely to revisit long-fruited trees than short-fruited trees after 4/7 nights in captivity, but not after one night in captivity. This was evident when examining the trees at both the specimen and the species levels (Figure 1C, left column; there was a significant positive interaction between the fruiting period and the captivity period, $p = 0.03$ and $p = 0.0004$ for the tree species and specimen levels, respectively; mixed-effect generalized linear model (GLMM) with the revisit rate set as the explanatory parameter, the above interaction as a fixed effect, and the individual bat as a random effect). Visiting more long-fruited trees after longer periods in captivity suggests an understanding of both the time that has passed and tree phenology.

Because episodic memory is defined as a memory of a specific event, we examined whether bats exhibit this behavior even for individual trees that they only visited once before, and indeed we found a very similar pattern (Figure S1B). An alternative hypothesis to explain what-where-when behavior suggests that animals' memory decays at various rates depending on the stimulus (i.e., the different trees in our case, a.k.a. the familiarity hypothesis).²³ Because the bats returned to dozens of different trees after spending time in captivity, including trees they only visited once before, it seems less likely that they have an individual clock for each of these stimuli and more likely that they recall the previous event (Figure S1A).

In inexperienced bats, we did not observe this pattern (Figure 1C, right column; there was no significant interaction between the fruiting period and the bat captivity period, $p = 0.26$ and $p = 0.42$ for the tree species and specimen levels, respectively; GLMM as above). This suggests that bats must learn tree phenology in order to time their visits effectively.

Our findings cannot be explained by seasonal shifts in the availability of food because pups were introduced into the colony throughout the entire season (December–March)—thus experiencing different resources—and the age of the bats did not affect our findings (see seasonality and age section in STAR Methods).

Experiment 2: Future planning

Previous findings^{20,22} along with the above results suggest that individual fruit bats memorize the locations of (at least) dozens of trees and possess some knowledge of their phenology. We thus next sought to elucidate how these bats decide between the many foraging options available to them and, specifically, whether they plan their foraging ahead before exiting the roost. For this part, we tracked 15 bats (45 nights per bat on average; Table S2). We took advantage of the fact that some bats leave our roost early in the evening, whereas others, for up to a few hours before leaving, choose to feed from the bowl of fruit that

we place in the roost at the beginning of every evening to supplement the bats' natural diet (STAR Methods). We confirmed that the bats that ate more inside foraged less outside (Figure S2A). Because the fruits we offer in the colony are rich in sugar and water and poor in protein (0.6% protein on average inside versus up to 8.5% outside), we hypothesized that the bats that leave the colony at different times will exhibit different food choices outdoors. Specifically, we hypothesized that after not drinking for ~ 12 h, early-leaving bats that had not eaten much from the bowl would seek water-rich fruit, while late-leaving bats would seek protein-rich fruit. Notably, because fruits are typically low in protein, finding protein-rich fruiting trees presents a fundamental foraging challenge for fruit bats.²⁴ Consequently, flying to specific protein-rich trees probably requires planning ahead (less than 5% of all trees in the area are protein-rich, and these trees are located around the colony in various directions and distances; Figure 2E1). Indeed, there was a significant positive correlation between the time of bat emergence and the average protein content of the first visited tree, in contrast to a significant negative correlation between the time of bat emergence and the water content of the first visited tree (Figures 2A and 2B; $p = 0.022$ and $p = 0.001$, for protein and water, respectively; GLMM with either protein or water content of the first visited fruit set as the explained variable, exit time relative to sunset and tree distance from the colony set as fixed factors, and bat ID and visit date as random effects).

The model's estimates suggested an increase of 2.4% and a decrease of 2.2% per hour in the protein and water content of the visited fruits, respectively. It is known that animals adjust their decisions according to their current motivational state.²⁵ Here, however, we had an opportunity to demonstrate that bats already initiate movement toward a familiar desirable resource up to 30 min before reaching it. Such data are rare for animals in the wild. Sugar did not seem to play a key role in the bats' decisions (Figure S2B).

Moreover, when running the same analysis only on unfamiliar trees that were visited by the bats for the first time, no significant relation was found between the protein or water content of the tree and the time of the bats' emergence from the colony, strongly suggesting that the bats rely on memory of previous events when deciding where to forage (GLMM as above, with nutrition [protein/water] as a function of emergence time: protein, $p = 0.69$; water, $p = 0.66$).

These findings suggest that the bats had chosen *what* to eat before exiting the roost. Their behavior also suggested that they had planned *where* to fly to before leaving the roost. The bats' flight toward familiar targets was characterized by high straightness indices (0.59 ± 0.16 ; see examples in Figures 2E1–2E3 and S3), demonstrating that they flew directly to their planned destination. Moreover, the bats adjusted their flight speed according to the distance to the target—flying faster when the target was farther from the colony—suggesting that they aimed for a specific tree at a location already known before they left the roost (Figures 2C, 2D, 2E1, and 2E2; $p < 0.005$, GLMM with either the average flight speed [Figure 2C] or the initial flight speed set as the explained variable [Figure 2D], the distance to the first visited tree and the time of exit set as a fixed factors, and bat ID and visit date as random factors).

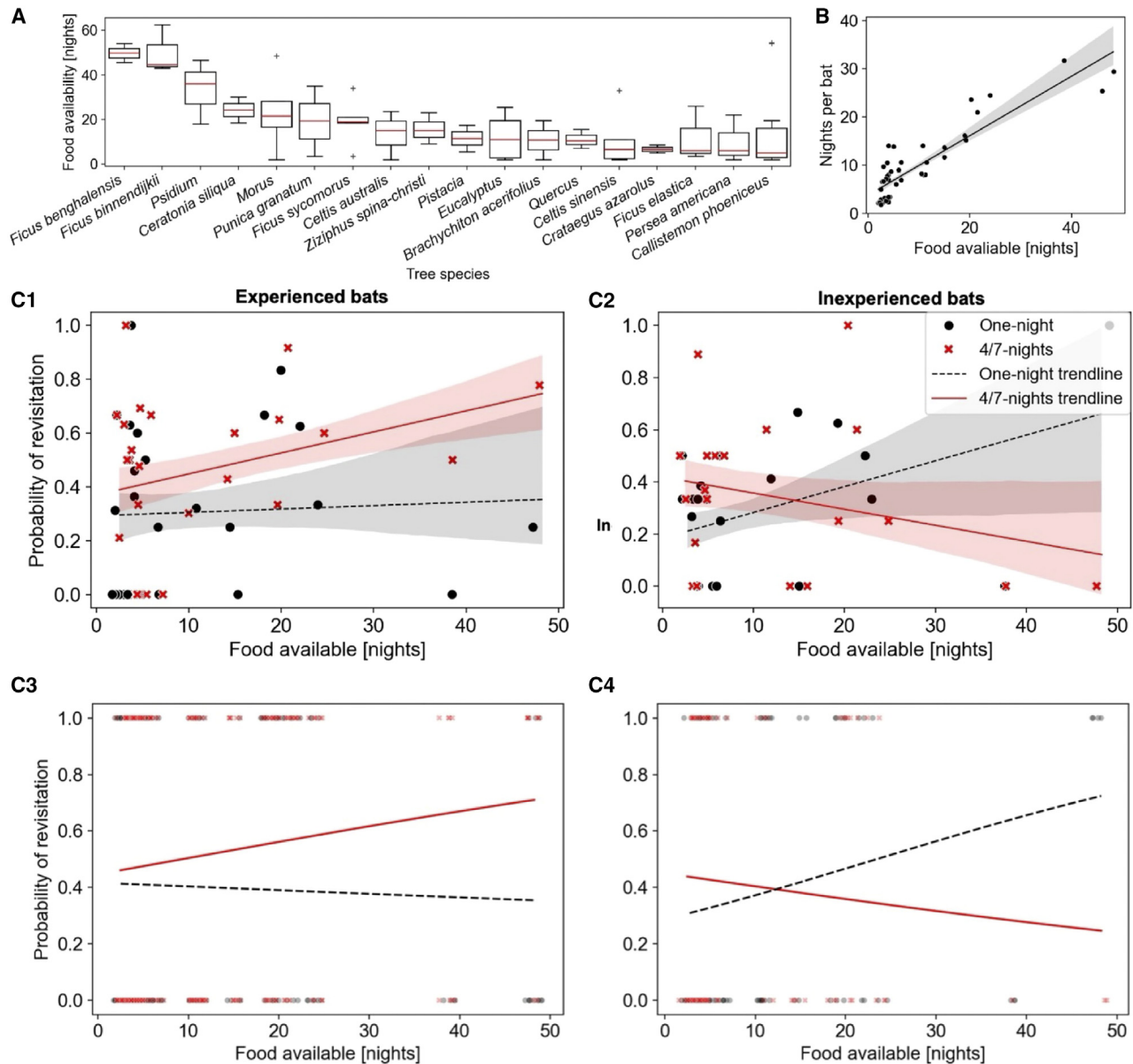


Figure 1. Bats revisit trees based on their learning of tree phenology and experience

(A) Visit duration to different tree species by the bats in our colony. The 20 species with the longest visit durations are presented. We include only those trees that were examined by us and were fruiting during the research period (STAR Methods). Boxplots show medians and quartiles.

(B) Trees that were visited during more consecutive nights by the population were also visited longer by individual bats. Linear model: $y = 3.78 + 0.62x$, $R^2 = 0.80$. The gray area indicates the 75% confidence intervals (CIs) around the linear model.

(C) The revisit rate as a function of the fruiting period after one night in captivity (gray) or 4/7 nights in captivity (red). Top row shows the results when pooling all trees from the same species together (i.e., each dot represents a tree specimen), while the bottom row shows the results per specimen (i.e., each dot represents a tree specimen). At the species level, the revisit probability was estimated as the probability of revisiting familiar trees of that species after a period in captivity, while at the specimen level revisiting was binary (1/0), depending on whether the bat returned to a specific individual tree specimen after captivity. The left column shows the results for experienced individuals while the right column shows the results for the inexperienced individuals. The gray and red areas indicate the 75% CI around the mean of the models for the 1 and 4/7 nights, respectively. We also examined an alternative visiting criterion setting a 1-min time threshold per visit, and the findings remain the same (Figure S1C).

The effect of the distance to the target tree was also significant in the above analysis, but the effect size was negligible. While, on average, the bats flew 52 m closer to the first tree for every hour of delay in their exit time, this accounted for only a tiny proportion (~0.5%) of the mean cumulative distance these bats fly per hour.

In contrast, the change in protein consumption, i.e., a huge increase of 2.4% per hour, accounted for a nearly 100% increase in the nightly average protein intake of these bats.

Importantly, previous research, in which we tracked all the individuals in the colony over many months, totaling

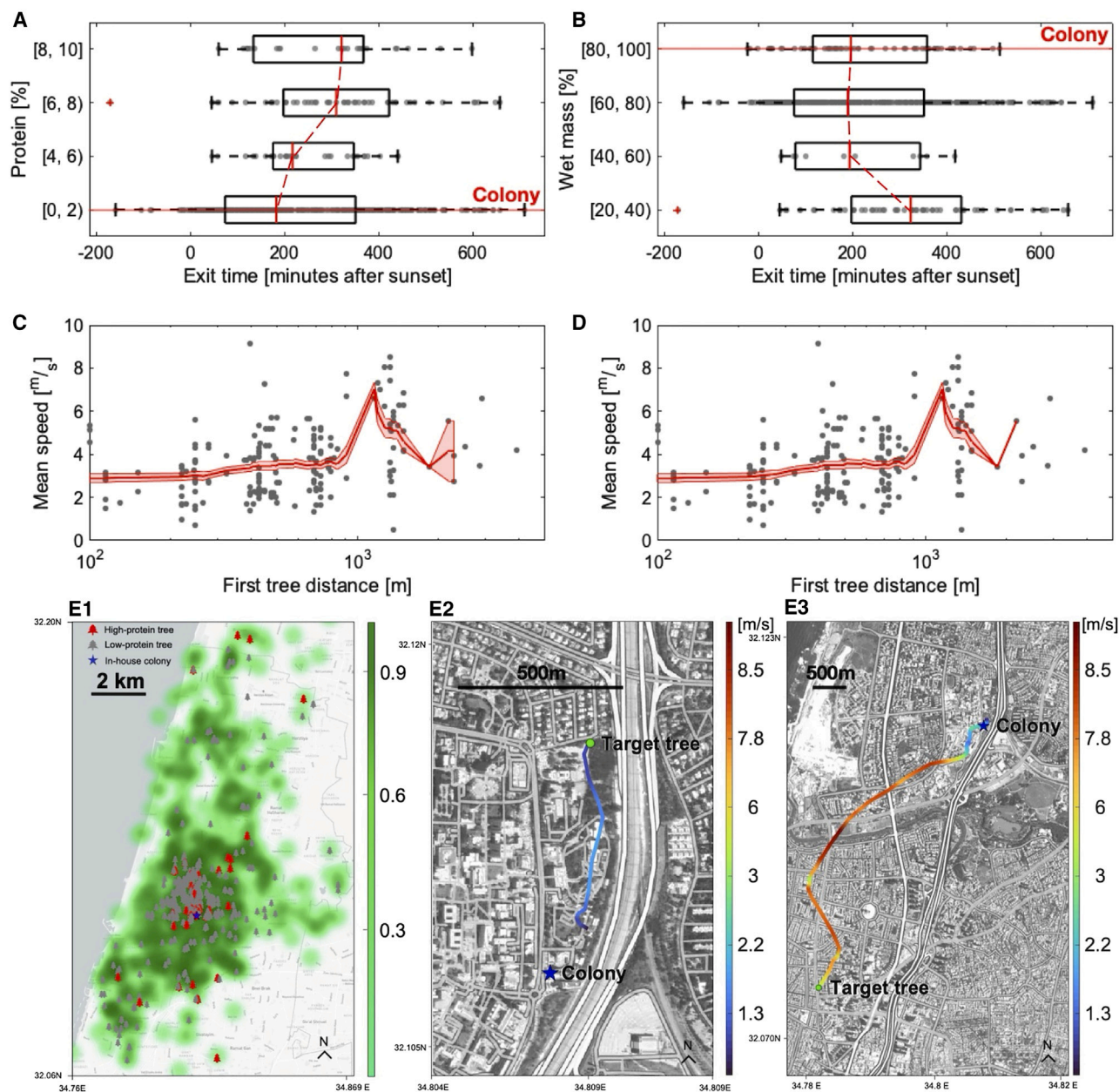


Figure 2. Bats determine what and where to eat before emerging from the roost

(A and B) Protein/water content as a function of the emergence time. The red line denotes the protein/water content of the food offered in the colony. Significant differences were determined using mixed-effect generalized linear models (GLMMs) for (A) ($p = 0.022$) and (B) ($p = 0.001$).

(C and D) Flight speed as a function of the distance of the first visited tree averaged along the entire route until arriving at the tree and (C) for the first 3 min after emerging from the colony starting at a distance of 100 m from the colony (D). The red line shows the mean speed smoothed with a moving window size of 150 m. The red-shaded area denotes the standard error. Two samples in (C) and one sample in (D) are not shown due to the limits of the y axis.

(E) Examples of flight trajectories.

(E1) Heatmap of the 15 bats' activity and the 974 mapped trees (including 47 high-protein trees) located in the study research area. Shades of green depict bat activity density (map based on a random selection of 3% of the data points). High-protein trees are rare and color-coded red, while regular trees are depicted in gray. On average the farthest tree visited by the bats was 7.4 ± 2.8 km from the colony.

(E2 and E3) Two examples of flight trajectories to the first tree at a short (E2) and far (E3) distance from the colony, colored according to flight speed (m/s, smoothed with a moving average with a window size of five GPS points).

See also [Figure S2](#).

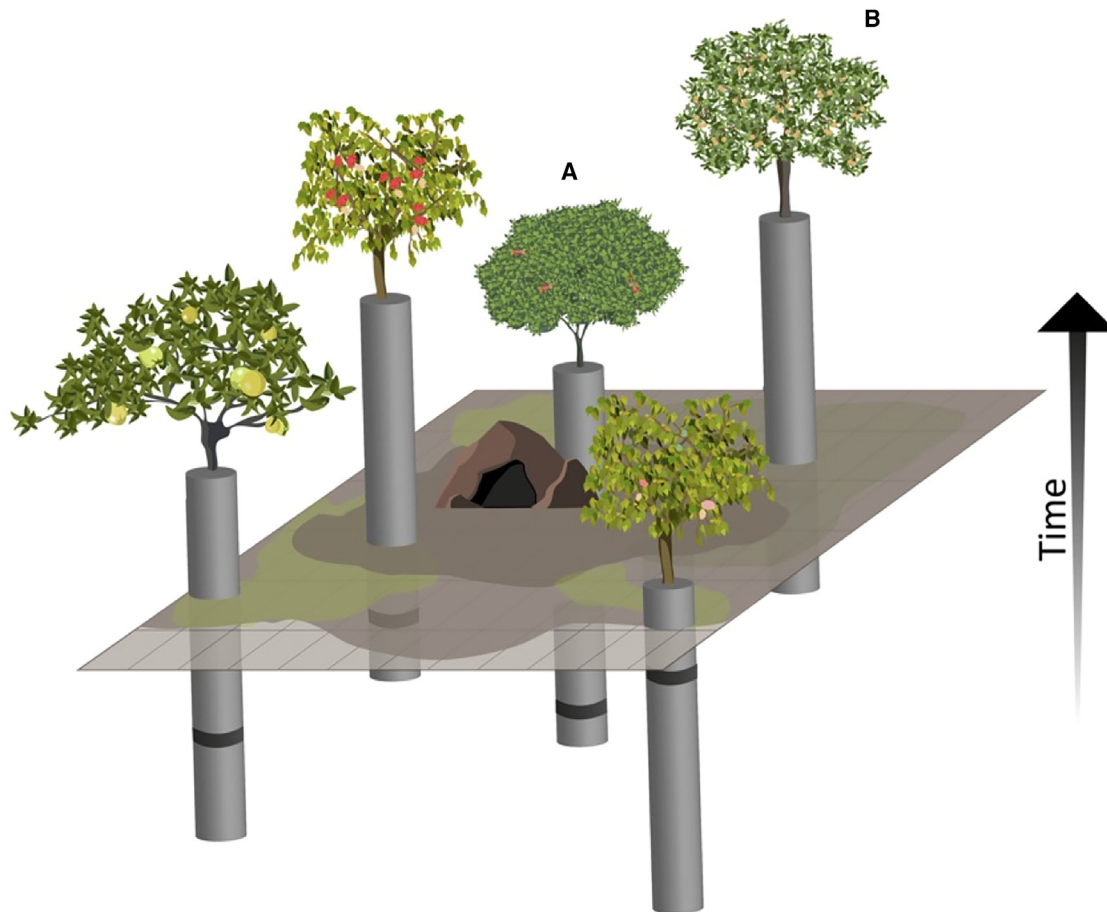


Figure 3. Bats maintain spatiotemporal mental maps

The illustration depicts a hypothetical food availability map that a bat stores in its brain; the z axis represents time. The map depicts the type and location of dozens of trees. Each cylinder protrudes vertically according to the fruiting time of the tree. The lower part of the gray cylinders depicts the beginning of the fruiting period estimated by the bat, e.g., tree “A” started fruiting before tree “B” and will end earlier. We hypothesize that fruit bats maintain such a spatiotemporal mental map. The 2D surface represents the current moment in time and the black rings on the cylinders represent the bat’s last visit to each tree.

thousands of flights, revealed no evidence of tandem flight in fruit bats that exited the roost.^{20,26} In conclusion, the findings from the two experiments described above indicate a complex decision-making process that includes future-oriented behavior based on dietary needs (experiment 2), which are weighed by the bats based on a spatiotemporal map of the resources, which they constantly updated (experiment 1; see Figure 3 for a schematic). Previous work also excluded the possibility that the bats rely on olfactory navigation.²⁶ There we showed that bats’ navigation is not impacted by wind direction. Moreover, there are thousands of trees from each species in the area, making it very unlikely that the bats can smell an individual tree from afar.

We posit that the bats’ tendency to fly to specific protein-rich trees when exiting the colony late offers evidence of future-oriented behavior even if it is driven by their momentary motivation to acquire protein. In many of these events, the bats flew for many minutes (sometimes even dozens of minutes), targeting a specific tree, while bypassing many familiar sugar-rich fruit trees (see Figure S2C for examples). Such long periods of delayed gratification have to date only been

demonstrated for a few animals, including primates, corvids, and cuttlefish.^{27–30}

As animals cannot be “asked” about their mental time-travel, episodic memory and future planning are extremely difficult to assess. Our findings highlight the advantage of outdoor experiments in the natural environment and the need for better quantitative methods when studying animals in the wild.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2024.05.046>.

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AUTHOR CONTRIBUTIONS

L.H. and Y.Y. designed the experiment; Y.Y., X.C., and L.D.M. conceived the analysis; L.H., M.H., and A.R. conducted the experiment; and Y.Y., X.C., L.D.M., and A.G. conducted the analysis. M.F.L. and S.R. carried out the nutritional analysis. L.H. wrote the manuscript, and Y.Y., A.G., X.C., L.D.M., and M.H. reviewed it. L.H., X.C., and L.D.M. contributed equally to this work.

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://www.dropbox.com/sh/54fk1s7qav4z234/AAD1H5hF5bxLMZ7JdQbQ9IxRa?dl=0
Experimental models: Organisms/strains		
Egyptian fruit bat: <i>Rousettus aegyptiacus</i>	Herzliya cave, Beit Govrin, Tinshemet, Israel	Taxonomy ID: 9407
Software and algorithms		
MATLAB R2021a	MathWorks	https://www.mathworks.com/downloads/
Python 3.10	Python Software Foundation	https://www.python.org/downloads/release/python-3100/
Other		
GPS - Robin	lucid, Israel	N/A

RESOURCE AVAILABILITY

Lead contact

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

Materials availability

This study did not generate new unique reagents.

Data and code availability

All datasets included in the paper are available at: <https://www.dropbox.com/sh/54fk1s7qav4z234/AAD1H5hF5bxLMZ7JdQbQ9IxRa?dl=0>.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Experimental model

Fifty neonate Egyptian fruit bat (*Rousettus aegyptiacus*) pups were captured together with their mothers before they became volant, from the “Herzliya cave” (Herzliya, Israel, 32°10'3.62"N, 34°48'51.54"E); or Beit Govrin (31°36'45.8"N, 34°53'41.7"E) and Tinshemet (31°59'43.2"N, 34°57'19.2"E), Israel, between 2016 and 2021. The pups were first held in an indoor flight room at the Zoological Garden of Tel-Aviv University. The flight room was 2.5 × 2 × 2.5 m³, under a 12:12 light:dark cycle and a controlled temperature of ~27°C. Bats were individually marked using commercial hair bleach and their weight and forearm length were measured. The 50 pups' average age on arrival was estimated based on their forearm length to be 34 ± 23 days. The pups were divided into groups of eight based on their size. After all the members in a group were able to fly, they were tagged with RFID chips (Trovan, Ltd.) and introduced into our in-house wild colony (see below). Groups of juvenile bats were gradually added to the in-house colony throughout the season (October-May of each study year).

All experiments were performed with capture permits from the Israel Nature and Parks Authority and were approved by the IACUC committee (permit number L-12-031).

The in-house colony

Our in-house wild colony holds several dozens of wild-caught fruit bats that roost in our cave-like facility but behave as wild bats, flying nightly out to forage.^{20,31} They are free to enter and leave as they wish. The colony's diet is supplemented with a fruit plate containing apples (50%), melons (25%) and bananas (25%) that is placed nightly in the colony; this does not prevent the bats from foraging in the wild.³¹ Moreover, we have previously validated that the movement of our bats is similar to that of bats in nearby natural colonies.²⁰ The entrance to the colony is monitored via surveillance video-cameras (GeoVision Inc. and Imagingsource Inc.), allowing us to monitor the time of exit and entrance of each bat. The colony is situated at Tel Aviv University and surrounded by hundreds of fruit and nectar trees scattered around the colony within a 2-km radius. The pups were introduced into the colony at an average age of 86 ± 12 days old, when they could already fly and forage independently. When the pups (caught between 2016

and 2019) were introduced to the in-house colony, the mothers were released back into nature at the site where they had been caught when their pups. The pups from 2020 were released in the in-house colony with their mothers, but most of these mothers flew out immediately and never returned, while the remaining mothers did not carry their pups, which had grown by this stage.

METHOD DETAILS

Tracking

The bats were tracked continuously annually following their release during winter to late spring, between December and May. After exiting the colony for two nights in succession and then returning, each pup was equipped with a miniature GPS device (Robin, Lucid Ltd or Vesper, ASD inc., between 2016 and 2018 telemetry devices were added as well LB-2X, weight 0.3gr, Holohil Systems Ltd or PicoPip Ag379, weight 0.42gr, Biotrack). The mean weight mounted on a bat (including GPS, telemetry, and coating) was ~ 6 gr, which constituted $8.0\% \pm 1.8$ of the pups' weight upon release into the colony in 2016-2018; and 6 gr, which constituted $5.6\% \pm 0.6\%$ of the pups' weight upon release into the colony in 2019-2021. The tag was coated with Parafilm (Heathrow Scientific) and duct tape and was fitted onto the bat's neck using a chain necklace coated with Heat-shrink tube. The pack was glued to the pup's back using medical cement glue (Perma-Type Surgical Cement, AC). The monitoring devices were programmed to start a few hours before sunset and run until 06:00 a.m., recording location fixes every 15-30 s, allowing a battery life of up to one week. Every 2 days on average, the pups' physical conditions were examined in parallel to replacing the battery when necessary. On average we managed to track the bats activity outside 84% of the time. All bats had tracking data after the release from captivity and during the week before captivity.

Fruiting-tree identification and food availability validation

We surveyed all fruiting trees visited by the 50 bats. The sites were surveyed for eight days on average and no later than two weeks after the bats' visit. This period is long enough to assess that the trees had provided fruit/nectar when the bats visited them. Because fruit bats typically masticate and then spit out the remains, we used these remains on the ground below the tree to infer whether the bats had foraged on that tree. When we were unsure whether a specific tree product had been consumed, potential food items from that location were sampled and offered to captive bats in the lab, enabling us to confirm or reject the species as a food source.

We examined 974 individual trees that our bats had visited between the years 2016-2021. These trees belonged to 26 species – 23 fruit-bearing trees and three nectar-producing species, two of which were visited the most frequently – *Eucalyptus camaldulensis* and *Callistemon phoeniceus*. The most visited fruit trees were species of *Ficus* (e.g., *F. macrocarpa* and *F. rubiginosa*). As the fruit on these trees ripen gradually, the same tree can provide fruit over a period of several weeks.

Fruit sample collection and nutritional analysis

Food items were collected from fruit trees visited by the bats. A total of 60 samples were obtained from 15 tree species. Food items were picked from the trees, sealed in plastic bags, and brought to the lab within 3 h. If fruits were not accessible due to the height of the tree, ripe fruits were collected from the ground (we ensured that the chosen fruits had only recently fallen from the tree, based on their color and texture). Fruit samples were treated in accordance with the feeding habits of the fruit bat, by removing the seeds. We collected at least 80 gr of material per sampled tree. All samples were stored at -20°C for chemical analysis. Crude protein was determined using the Kjeldahl method (ISO 1871:2009); sugar content was determined using an In-House HPLC-ELSD method; and wet mass was determined according to the standard chemical procedures, AOAC (Association of Official Analytical Chemists): AOAC 930.15 for leaves and AOAC 934.06 for fruit. All chemical analyses were conducted by the National Public Health Food Laboratory in Tel Aviv. As the inter-individual variability of tree nutritional values showed low variability, we used the above analysis to calculate the mean percentage of each nutritional component for each tree species (Table S3). In the statistical analysis, we used the natural logarithm of those percentages. Notably, although we used the mean nutritional values of the species in our analysis (rather than the values of individual trees), a comparison of several specimens from each species revealed relatively low variation (Table S3).

Experiment 1: Episodic-like memory

Overall, this experiment analyzed GPS data of 2,314 nights from 50 bats (an average of 46.3 nights per bat for 673 individual nights) recorded during the years 2016-2021. The data from these 50 bats are provided in Figure 1.

The captive manipulation was performed on 19 of the 50 bats between February and May in 2020 and 2021 (Table S1). When possible, each bat underwent two periods of captivity during which they could not leave the colony for either 1 or 4/7 nights. The order of the two treatments was randomly assigned to each individual. The first captive period took place 2-3 weeks after the bats' first exit from the colony, followed by an interval of 2-3 weeks before the second captivity period. As several bats abandoned the colony before their second captive period, and several of the GPS devices failed to function, we had both long-term and short-term data for only 13 of the 19 bats (although data from all 19 bats were used in the analysis).

We analyzed the captivity trials in two cohorts based on the bats' foraging experience. To estimate the experience of a specific bat when performing a specific trial, we calculated the total accumulated time it spent near foraging trees times the total visits to these

trees prior to each of its captivity trials (Equation 1). This parameter accounts for foraging time together with the number of visited trees together as a measure of experience: Equation 1. $\text{Exp} = \ln(n \cdot T)$, where n is total number of visits (including repeated visits to the same tree) and T is the total time spent foraging near trees.

Note that the two trials of the same individual could be assigned to different experience groups if the bat acquired much additional experience between its two captive trials (Table S1). Moreover, bats in both the experienced and inexperienced groups were on average more than 250 days old, and therefore the age difference between the groups was not significant ($p = 0.08$, t-test), so that age-dependent dietary differences could not explain the difference in foraging behavior between the groups.

Effects of tree seasonality and bat age

We validated that seasonality could not explain our results statistically by adding the month of the year as a fixed factor to the specimen level GLMM, and the above-noted interaction remained significant ($p = 0.009$). We also validated that age could not explain the foraging behavior of the experienced bats. We added the bats' age as a fixed factor to the specimen level GLMM. The interaction between the tree fruiting period and the bat captivity period remained positively significant ($p = 0.0001$). Age significantly increased the probability of revisiting productive trees ($p = 0.04$), which is rational because aged bats are more experienced.

Identifying tree revisits

We present two visit criteria in Figure 1: (1) we chose all trees located within 20 m or less of the GPS points recorded in the bats' trajectories. (2) we set no minimum time threshold for a visit in order to include all cases in where the bats even passed near a tree – potentially assessing it. We also set a minimum time threshold of spending at least 1 min near a tree – ensuring that the bat had actually visited it (Figure S1C).

Food-available nights for the fruiting trees

As above, we initially identified fruiting-tree specimens based on food remains on the ground. We then determined the longest consecutive period in which the bats from our colony visited these tree specimens (without any night-gap). When the same tree (specimen) was visited over two years (or more) we took an average of longest consecutive periods (Figure 1A).

Experiment 2: Future-planning

Overall, we collected GPS data between October 2016 and December 2018 from 15 bats and 674 nights (177 individual nights), with an average of ~ 45 nights per bat (Table S2). All 15 bats took part in both the episodic and future-planning experiments.

Detection of foraging trees

The GPS trajectories in this part were divided into commute and foraging segments based on straightness index (SI) – the ratio between the direct distance and the actual path length between two points (for additional details see Harten et al.²⁰). This procedure was first carried out over the entire trajectory commute and foraging in windows of 12 GPS points, which were previously found suitable for this species.^{20,26} Points with higher SI values were defined as commute (Figure S3). If the bat flew above a height of 70 m, this segment was classified as commute regardless of its straightness index. The location of the foraging site was defined as the average position of all points within a foraging segment. The existence of a foraging tree in these locations was validated by a survey of the sites (see above). The first visited tree was defined when the center of a foraging segment was at a distance of less than 30 m from one of the identified trees.

The mean flight speed was estimated by calculating the derivative of the GPS movement. When estimating speed for the first 3 min after a bat's exit, the exit time was defined as the first GPS point farther than 70 m (Euclidian X-Y distance) from the colony. This threshold was determined in order to overcome the bats' tendency to sometimes exit and re-enter the colony but not leave to forage.

Exclusion criteria: Overall, we obtained a total of 674 trajectories for the nutrition part of the study (Table S2). We removed trajectories in which: (1) we were unable to identify the first tree visited (eight trajectories); (2) the first tree was a new tree never visited by the bat previously, and thus we could not assume that the bat knew where it was heading (121 trajectories). These new unvisited trees were used for the control analysis that we present here; (3) the first tree did not belong to one of the species whose dietary composition we analyzed (78 trajectories); (4) the species of the first tree was documented as a first tree in fewer than three trajectories (four trajectories). In total, we were left with 463 trajectories for this analysis (note that there might be some overlap between criteria and hence the sum of the exclusions is larger than 463).

In the speed analysis, we removed trajectories using the same criteria as above, with the exception of criterion number (3), which was replaced by: (3b) the average flight speed in the relevant section was more than 15 m per second, which is on the higher side of flight speed for a bat in an urban environment (205 trajectories were removed from the average-speed analysis and 214 trajectories from the 3-min analysis). Finally, the trajectories were excluded if the bat didn't pass 150 m from the first point detected out of colony within 3 min (405 trajectories). This was done to remove flights where bats circled around the colony for several minutes before commuting. In total, we were left with 198 trajectories for the first analysis and 197 trajectories for the second analysis.

QUANTIFICATION AND STATISTICAL ANALYSIS

GLMMs were fitted to the data using MATLAB (fitglme function). The date and bat identity were used as random factors in all models. When analyzing speed, we used the distance of the first tree as a fixed factor, and the response factor was the mean speed before the first visit or the mean speed in the first 3 min. When analyzing nutrition, we ran a separate GLMM for each nutrition type (Wet Mass, Protein, or Glucose). In each of these GLMMs, the distance to the first tree and the exit time were used as fixed factors and the response factor was the log nutritional value (e.g., protein percentage). When analyzing the effect of exit time on the distance to the first tree, the exit time was set a fixed factor and the distance to the first tree was the response.