Article

Mother bats facilitate pup navigation learning

Highlights

- Simultaneous GPS tracking of mothers and pups revealed bats' navigation ontogeny

- Mothers facilitate navigation learning by repeatedly placing pups on specific trees

- Independent pups first fly to the same sites they were carried to by their mothers

- Pups learn to navigate while passively being transported upside down by their mothers

Authors

Aya Goldshtein, Lee Harten, Yossi Yovel

Correspondence

yossiyovel@gmail.com

In brief

Goldshtein et al. document bats' navigation ontogeny. Results suggest that mothers facilitate learning of navigation by repeatedly placing their pups on specific trees, which the pups later fly to on their first independent flights. Pups seem to learn navigation routes while being transported upside down by their mothers.

CelPress

Current Biology

 CellPress

Article

Mother bats facilitate pup navigation learning

Aya Goldshtein,[1,4,5] Lee Harten,[1,5] and Yossi Yovel[1,2,3,6,*]
[1]School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 6997801, Israel
[2]Sagol School of Neuroscience, Tel Aviv University, Tel Aviv 6997801, Israel
[3]Wissenschaftskolleg zu Berlin, Berlin 14193, Germany
[4]Present address: Department of Collective Behaviour, Max Planck Institute of Animal Behavior, Konstanz 78464, Germany
[5]These authors contributed equally
[6]Lead contact
*Correspondence: yossiyovel@gmail.com
https://doi.org/10.1016/j.cub.2021.11.010

SUMMARY

Learning where to forage and how to navigate to foraging sites are among the most essential skills that infants must acquire. How they do so is poorly understood. Numerous bat species carry their young in flight while foraging. This behavior is costly, and the benefits for the offspring are not fully clear. Using GPS tracking of both mothers and bat pups, we documented the pups' ontogeny from being non-volant to foraging independently. Our results suggest that mothers facilitate learning of navigation, assisting their pups with future foraging, by repeatedly placing them on specific trees and by behaving in a manner that seemed to encourage learning. Once independent, pups first flew alone to the same sites that they were carried to by their mothers, following similar routes used by their mothers, after which they began exploring new sites. Notably, in our observations, pups never independently followed their mothers in flight but were always carried by them, suggesting that learning occurred while passively being transported upside down.

INTRODUCTION

Acquiring crucial skills such as navigation in early life is essential for both immediate survival of the young and long-term fitness of parents.[1–9] Colonial central place foragers, like most bats and many birds,[10,11] rely on a specific form of spatial navigation: they must leave a roost to forage and return to it on time every day.[12] Relying on patchily distributed predictable food sources, such as fruit trees, further enhances the need for efficient spatiotemporal navigation, as animals must remember the positions of multiple targets and often their temporal seasonality as well.[13,14] Indeed, the need to remember the location and seasonal changes of fruiting trees for extended periods of time as fruit bats probably do requires fast spatiotemporal long-term memory, which, in primates for instance, has been hypothesized to play a major role in the evolution of cognition.[15]

The acquisition of navigational skills may be innate, as documented for some long-distance migrants, which follow innate compass headings on their first migrations, demonstrated by some birds[16] and insects for example.[17] Alternatively, navigational skills can be acquired through various forms of passive or active learning.[18] For young dependent offspring, parents or experienced conspecifics often present the main source of learning opportunities.[1] Parental guidance in the acquisition of essential skills can take numerous forms, ranging from local enhancement to active teaching.[5,19–22] Periods of strong maternal dependency have been correlated with the need for offspring learning.[14,23,24] Baleen whale calves (*Megaptera novaeangliae*), for example, follow their mothers to feeding areas on their first migration and later return independently to these

same sites.[25] Acquiring foraging, navigation, and other essential skills from parents has received much interest in evolutionary biology, yet the overall roles of innate, learned, and social factors in these processes are poorly understood in most taxa,[18] with only a few well-documented examples in non-humans[24] and very few examples in the wild.[5,21,26–28]

With ~1,400 known species,[29] bats exhibit a wide range of different foraging strategies and social behaviors.[30–38] However, how offspring acquire essential foraging and navigational skills and the role of maternal investment and social learning in this process are severely understudied in bats,[39–45] with only one clear example suggesting maternal facilitation of learning what to eat in offspring[46] (but see Bunkley and Barber[47] for anecdotal evidence of teaching in the Pallid bat). Many bat species carry their non-volant and volant young[48] while foraging[40,41,49–52] and switching roosts.[45,53,54] This behavior is costly for mothers[55,56] in comparison to leaving pups in their day roost as seen in other bat species;[41] however, the benefits for offspring are still not clear. The observation of adults and newly independent offspring foraging at the same sites suggests that parental tutoring may play a role in offspring's learning to navigate to and from the foraging sites.[40,51,52,57]

Acquisition of spatial information by pups can theoretically occur either passively in the non-volant stage or actively by volant young following their parents.[58] Anecdotal evidence in *Uroderma bilobatum* suggest that mothers might transport non-volant pups to secondary roosts while they forage, possibly returning to provision them.[42,59] We hypothesize that carrying offspring while foraging should provide an advantage for developing pups, mothers, or both. The miniaturization of tracking
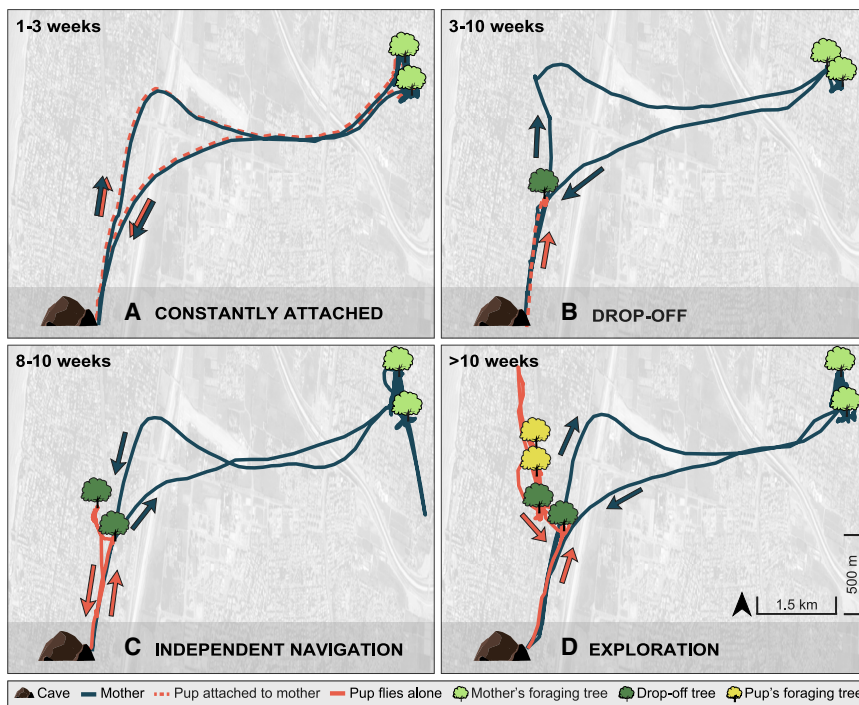
Figure 1. Four stages in the development of independent foraging

GPS tracks from a single mother-pup pair.

(A) The pup is attached to its mother continuously (as opposed to the following stages, this track is for illustrative purposes alone, as this stage was not tracked via GPS).

(B) The mother carries her pup to a drop-off tree where she leaves it, flies alone to a farther foraging site, and picks her pup up on the way back to the cave.

(C) The mother leaves the cave to forage alone, and the pup flies independently to previous drop-off sites.

(D) The pup flies independently and begins exploration from its previous drop-off site. In all panels, the mother's GPS tracks are depicted by blue lines. The pup's GPS tracks, while being passively transported and while flying independently, are depicted by orange dashed and solid lines, respectively. Drop-off trees are depicted by green trees, mother's and pup's foraging trees are depicted by light green and yellow, respectively. The pup's age range during each stage is presented. Note that the X scale and Y scale are different (see bars) to ease reading of the behavior. See also Table S1.

technology allowed us to monitor the movement of both mothers and pups for the first time by simultaneously tracking mother-pup pairs using a high-resolution global positioning system (GPS) and acceleration data loggers in combination with radio-telemetry. These detailed behavioral data allowed us to document the transformation of Egyptian fruit bats (*Rousettus aegyptiacus*) from being non-volant to becoming fully independent and to shed light on the role mothers play in the acquisition of navigation.

RESULTS

High-resolution tracking of mother-pup pairs allowed us to define four distinct stages in the development of independent navigation by pups (Figure 1).

Stage 1. Constantly attached (1–3 weeks old)—the pup is constantly attached to its mother

As previously documented[60–62] and as we also validate, pups in this stage are non-volant, constantly attached to their mothers, and still suckling, completely dependent on their mothers nutritionally (Figure 1A; Table S1; see detailed explanation for how we confirmed this in the "Stage 1" section in STAR Methods; n = 17 mother-pup pairs; hereafter, "pairs" refers to mother-pup pairs).

Stage 2. Drop-off (3–10 weeks old)—pups are left by mothers on specific trees

In this stage, mothers carry their pups to a drop-off tree, where they leave them while they are foraging (n = 26 pairs; Figure 1B; Table S1). Mothers typically then fly alone to a farther foraging site and return to the drop-off site to pick their pup up on their way back to the cave (6.7 ± 2.3 h later; mean ± SD; n = 10 pairs;

Figure 1B). In our study, mothers repeatedly carried the pups to the same drop-off trees, which sometimes housed a few additional pups that were not clustered together. Mothers dropped their pups off on the same tree in 66% of the consecutive nights that we monitored (n = 29 consecutive nights). In all other cases, pups were dropped off on a nearby tree within 300 m from the drop-off site of the previous night. Mothers often visited their pups during the night between drop-off and pick up. The accumulated visiting time reached as much as ~5 h per night (1.7 ± 1.2 h; mean ± SD; n = 15 pairs). Acceleration recordings on both mothers and pups simultaneously (n = 3 pairs) revealed that pups re-attached to their mothers at least in some of these visits, suggesting lactation or thermoregulation. As the pups grew larger and heavier, mothers dropped off pups significantly closer to the cave (pups' forearm and body mass were found to significantly explain drop-off distance; generalized linear model [GLM] test; see Figure S1). We hypothesize that this shift in drop-off distance is a result of the high energetic cost associated with transporting the pups as they get heavier.[55,56,63,64]

Notably, our observations suggest that the mothers always carried the pups to the drop-off sites, even at the later phase of this stage, when the pups could already fly independently. That is, in our observations, pups never followed their mothers, as we verified using flight speed and acceleration (based on a total of five pairs). Pups flew much slower when flying alone without their mothers for the first time than when flying with their mothers, suggesting that they were carried by their mothers as opposed to flying alongside them (2.9 ± 0.3 m/s versus 5.7 ± 0.08 m/s, respectively; n = 2 pairs; GLM with flight speed set as explained variable, the developmental stage set as a fixed factor, and pair index set as a random effect: $R^2 = 0.64$, p < 0.001; Figures 2A and S2A–S2D). At this stage, pups cannot reach flight speeds of more than 6 m/s as the mothers did (see

Current Biology
Article

CellPress
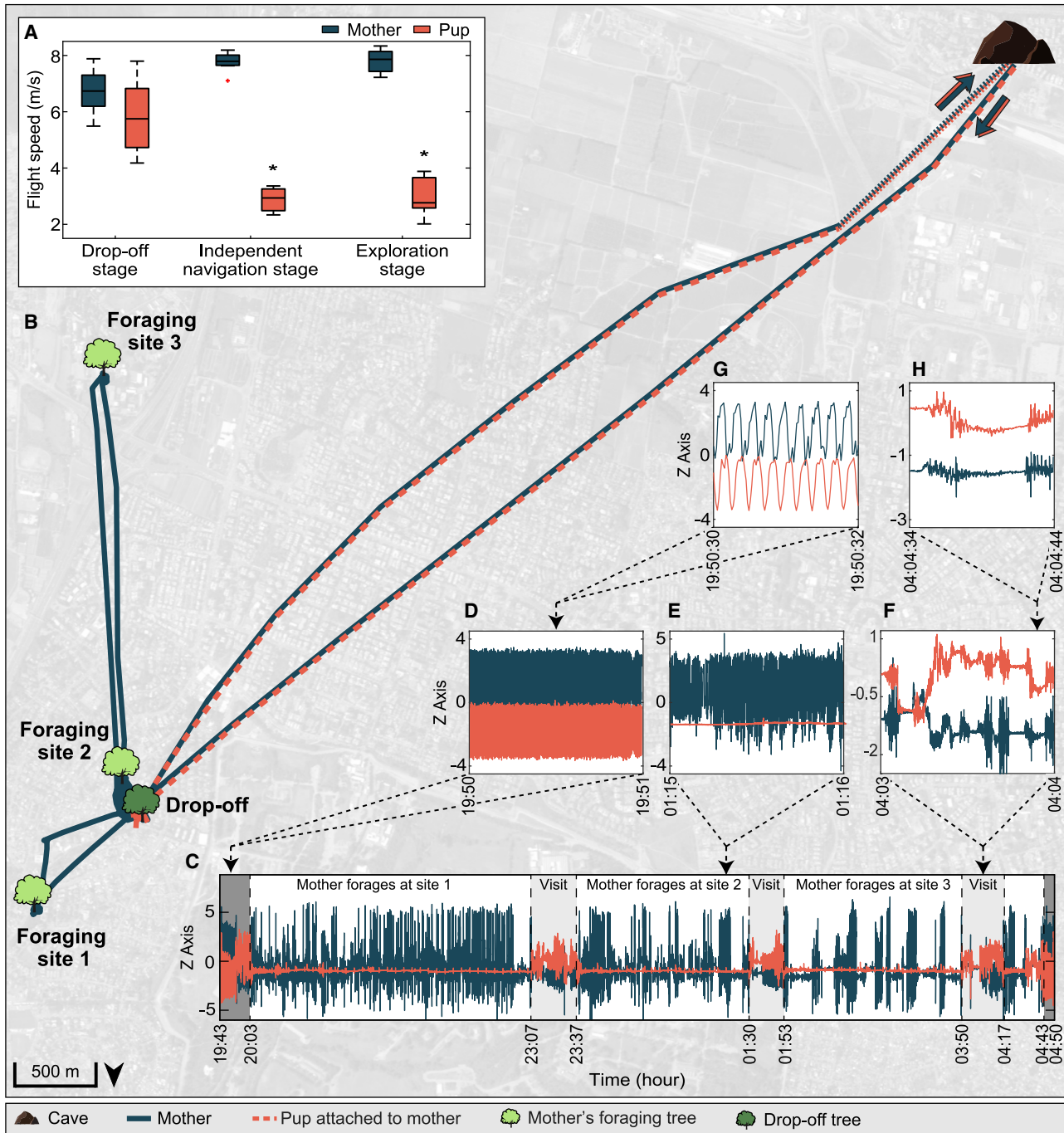
Figure 2. Mothers carry pups and provide parental care at drop-off sites

(A) Average flight speed per stage, n = 2 pairs. Pups flew significantly slower when flying independently (i.e., in the independent navigation and exploration stages) than when flying with their mother (in the drop-off stage).

(B) GPS tracks of a mother (blue) that flew with her pup attached (dashed orange line). The last 500 m before the return to the cave were extrapolated (dotted blue and orange lines). The pup, which was at the beginning of the drop-off stage, was dropped off, and the mother visited it occasionally throughout the night.

(C) Full-night z axis acceleration recording of the mother (blue) and pup (orange). Dark-gray-shaded parts represent periods when mother flew with the pup attached. Light-gray-shaded periods depict the mother's visits at the drop-off site.

(D) The pup's acceleration pattern is synchronized with the mother's wing beating on the way to the drop-off site, with mirrored acceleration indicating that the pup was positioned belly up while the mother is flying (belly down) as expected if mothers carry the pups.

(E) Wingbeat synchronization disappeared once the mother departed from the drop-off site.

(legend continued on next page)

STAR Methods). Moreover, the acceleration recordings of another three mother-pup pairs revealed that mothers' and pups' acceleration is perfectly synchronized during flights from the cave to the drop-off site, but not after the drop-off (Figures 2B–2H), once again suggesting that the mothers carried their pups.

In the later phases of the drop-off stage, the pups were semi-volant, occasionally moving within drop-off sites (n = 2; see acceleration data in Figure 3A; personal observations) and, on one observed occasion, even traveling independently to a previous nearby drop-off site (∼300 m away; Figures 3B and 4A).

To assure that the drop-off behavior was not a consequence of the extra GPS weight, we carried out a few control experiments, including tagging bats with lighter telemetry tags and visually monitoring trees in search of non-tagged bats. These controls suggested that dropping off the pups is the typical mother behavior at this stage (see STAR Methods; Figures S2E and S2F).

Stage 3. First independent navigation (8–10 weeks old)—pups exit the cave alone and fly independently to known sites where their mothers previously dropped them off

At the beginning of this stage, the fully volant pups are left in the cave while the mothers leave to forage alone (we observed this in n = 8 pairs; Table S1). At this stage, bats can stay in the cave or at the entrance of the cave or fly to a tree within a few meters away. We did not consider such short <50-m movements as navigation because they do not require spatial orientation capabilities. Although the mothers stopped transporting their pups, they actually increased the rate of which they visited the cave during the night in comparison to when the pups were not left in the cave (n = 5 pairs; Table S2). Notably, the mothers did not return to the cave in the middle of the night during the early drop-off stage. In general, Egyptian fruit bats without pups do not return to their cave during the night, so this behavior was unusual, suggesting a specific effort on the mothers' side.[65] Moreover, several behaviors suggest that mothers actively supervised pups' progress during their first independent foraging bouts (Table S3; Figures 4B–4D). For example, when a pup did not emerge from the cave, mothers occasionally reverted to dropping it off at the beginning of the night and picking it up at its end, as we observed on several occasions (Figures 4B and 4C).

In another example, when a pup flew independently to a previous drop-off site but failed to return to the cave before sunrise, its mother flew between the cave and the drop-off site, eventually transporting the pup back to the cave (see Figures 4A and 4D). At this developmental stage, the pups still remain nearby the mothers in the day roosts,[60] therefore allowing the mothers to notice their absence and to retrieve pups that fail to return to the cave before dawn. Learning when to return to the cave is a crucial skill, as remaining outside the cave in daylight can be deadly for bats due to predation and ambient temperature.[66] Notably, by placing the pups on specific trees, the mothers then know where to search for them, easing the task of monitoring.

To assure that the pups did not remain in the cave as a result of the GPS weight, we validated that non-tagged bats of the appropriate age (i.e., forearm length > 73; Table S1) were left alone in the cave by regularly surveying the cave after bats left to forage and measuring the forearm of the bats that were inside (see STAR Methods).

At the average age of 63 ± 3 days, pups flew out independently, first navigating to the last tree where they were dropped off by their mothers (n = 6 pairs; Figure 1C; Table S1). Moreover, the pups used similar paths to those that were used by their mothers while transporting them (see examples in Figure 5). Notably, there are thousands of fruiting and non-fruiting trees in a square kilometer around the cave (Figure S3A), and thus, flying to a specific tree, which was introduced by the mother, cannot be explained by random navigation. The fact that pups were carried to these sites prior to their first independent navigation (Figures 2A and S2A–S2D) suggests that they have learned to navigate while passively being transported upside down. Note that following other bats cannot explain this result, as bats leaving the cave disperse in all directions while the pups flew specifically in the direction of their drop-off trees (Figures S3B and S3C).

Stage 4. Exploration—pups leave the cave alone and explore new sites (>10 weeks)

The pups always began their exploration from their previous drop-off site and not, for example, directly from the cave (on the first night of exploration, pups reached a maximum exploration distance of 317 ± 147 m from their previous drop-off site; mean ± SD; n = 3 pairs; Figure 1D; Table S1). Moreover, the pups continued visiting their previous drop-off sites multiple times during the first nights of exploration, even after finding new food trees (Figure 6).

### The cost of maternal investment

Previous studies discuss the increased energetic cost of transporting a pup to secondary sites in terms of wing loading, maneuverability, foraging efficiency, and energetics, in comparison to leaving the pup in the cave, as other bat species do.[55,56,63,64] As the pups grew older, mothers gradually shifted from carrying them constantly to transporting them up to a few km to a drop-off site near their foraging site and finally to transporting them to drop-off sites within 1.5 km of the cave (0.49 ± 0.43 km; mean ± SD; n = 18 pairs). At this later stage, when pups weigh up to 41% of the mothers' weight (n = 19 pairs), it should be more efficient for the foraging mothers to leave the pups in the cave and fly back to the cave to visit them.

Moreover, transferring the pups out of the warm cave and leaving them alone on a branch probably comes with additional costs for the pups, such as increasing the pups' thermoregulation costs. The daily minimum ambient night temperature in this area was 13.3°C ± 2°C during April 2019, while the temperature in the cave was ∼15°C higher.

(F) Mother's and pup's accelerations were synchronized when the pup was attached to the mother during her visit at the drop-off site.
(G and H) High-resolution zoom in on the synchronized acceleration pattern of the mother and pup during (G) 2 s of commute flight and (H) 10 s of the mother's visit at the drop-off site.
See also Figures S2 and S4.

Current Biology
Article

CellPress
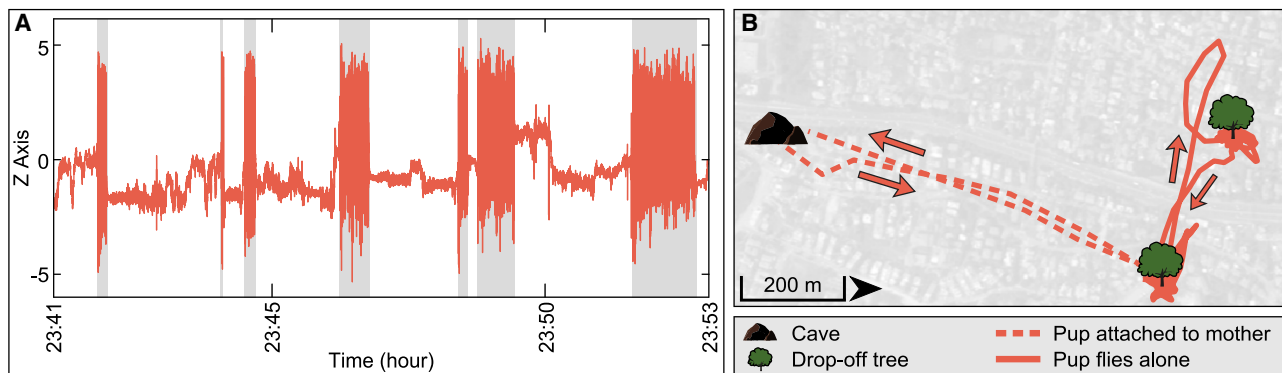
Figure 3. Pup flies within drop-off site and between close-by drop-off trees in the late phase of the drop-off stage

(A) A pup's movement inside the foraging site is depicted by z axis acceleration (orange line), with flight bouts highlighted in gray. These data correspond to a time frame where the pup was alone at the drop-off site.

(B) GPS trajectory of another pup that flew between two close-by drop-off trees while the mother was foraging elsewhere. Note that the pup is moving between two trees where it has already been dropped off in previous nights; thus, it is not exploring new territories. The mother carried the pup between these two trees on one of the previous nights. Pup's GPS tracks, while being passively transported and while flying independently, are depicted by orange dashed and solid lines, respectively.

In addition to the energetic cost of carrying the pups, during the drop-off stage, mothers spent significantly more time at the drop-off sites visiting their pups more frequently than in the following stages, when pups emerged independently (Figures S4A and S4B; GLM for visit duration and visit frequency, respectively: $R^2 = 0.37$, p = 0.001, n = 17 pairs and $R^2 = 0.16$, p = 0.053, n = 15 pairs, with stage set as a fixed factor and pair index as a random effect). As drop-off sites were typically not "food trees" (71% of the 31 identified sites were not edible or non-fruiting trees), the time spent there was not rewarding nutritionally for the mother.

In total, mothers spent 7.8 ± 2.2 h outside the cave during the drop-off stage versus 6.8 ± 2.1 h in the following stages (GLM: $R^2 = 0.56$, p = 0.004, n = 18 pairs), even though they effectively spent the same time at foraging sites (5.3 ± 2.4 h in the drop-off stage versus 4.9 ± 2.5 h during the independent navigation and exploration stage; GLM: $R^2 = 0.86$, p = 0.156, n = 16 pairs).

The cost of leaving the pups at the drop-off sites potentially increased as the pups became more independent and began moving around the drop-off sites. For example, we documented a mother that returned from foraging to the drop-off site where she left her volant pup to discover that the pup was no longer there. The mother then proceeded to visit the cave and flew to the drop-off site where she left the pup on a previous night, the pup arrived shortly after, and the mother took it home (Figure 4A). Once again, if the mothers left the pups in the cave, they would not have had to face such situations.

Taken together, our results suggest that the mothers change their typical foraging behavior and pay a cost during the drop-off stage. By repeatedly placing pups on specific trees and monitoring them, mothers facilitate situations conducive to learning of several essential skills, including (1) independent navigation to key trees up to ~1.5 km from the cave and (2) an ability to independently return to the cave before sunrise. We use the term facilitating rather than active teaching because we cannot show that the mothers clearly intend to teach the pups, only that the pups learn. For example, we cannot fully exclude that carrying the pups out

of the cave has additional benefits, such as reducing predation risk or parasite load.

DISCUSSION

Our study reveals the first steps in the ontogeny of foraging and navigation of young Egyptian fruit bats, transitioning from non-volant fully dependent pups to volant independent foragers. We find that the process of learning how to navigate is facilitated by maternal investment, with mothers repeatedly transporting non-volant pups to specific trees, which later become the first sites that pups independently navigate to. To our knowledge, this is the first concrete validation of such drop-off behavior in bats (which was suggested anecdotally before).[42,59]

Comparing the pups' behavior described above to a previous study revealed that the mothers actively placed pups in situations conducive to learning of essential skills. In a previous experiment, we brought 54 very young newborn pups independently into the lab long before they could fly. When they became volant, we released them without their mothers in our open colony that adult bats routinely fly in and out from, exhibiting similar patterns to wild colonies.[65,67] This manipulation thus allowed us a direct comparison of the ontogeny of navigation with and without mothers, that is, to compare drop-off pups to no-drop-off pups. The differences were clear. (1) The first trees visited by the no-drop-off pups were significantly closer to the colony than those of the drop-off pups (Figure S3D); that is, the no-drop-off pups began their exploration right near the roost. (2) The first trees visited by the no-drop-off pups were in the same direction relative to the roost—about half of them (10 of 22) flew to the nearest concentration of fruit-trees within <100 m from the roost. This was in contrast to the drop-off pups that flew in all directions (Figures S3B–S3E). (3) The no-drop-off pups often failed to return to the colony before sunrise. 33% of the 54 no-drop-off pups failed to return home on time at least once during their first week of foraging independently. Drop-off pups never failed to return before sunrise; although, mothers transported pups back to the cave on rare occasions
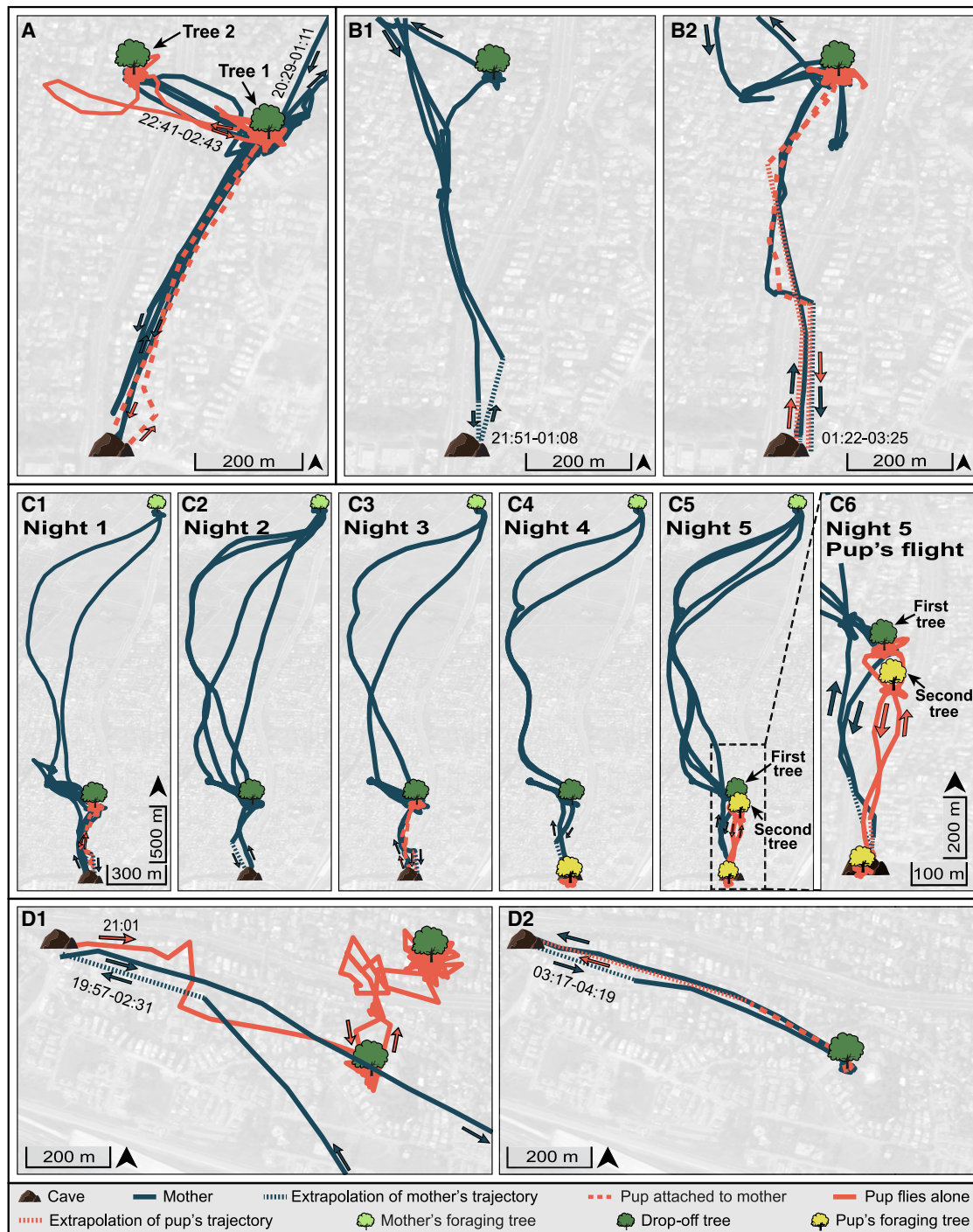
Figure 4. Examples of maternal investment

In all panels, the mother's GPS tracks are depicted by blue lines. The pup's GPS tracks, while being passively transported and while flying independently, are depicted by orange dashed and solid lines, respectively. Drop-off trees are depicted by green trees; mother's and pup's foraging trees are depicted by light green and yellow, respectively. Extrapolation of mother's and pup's trajectories between the first or last GPS point and cave is depicted by blue and orange dotted lines.

(A) Mothers heavily monitor the pups during the drop-off stage. The mother visited a drop-off site where she left her volant pup (tree 1). The pup was absent at this time, and the mother then proceeded to visit the cave and a drop-off site from the previous night (tree 2) and returned without her pup to the drop-off tree where she left it (tree 1). The pup then returned to the drop-off tree where she left it, and the mother found it and took it home.

(B) Mothers seem to encourage pups to exit the cave independently for the first time. (B1) The pup was left in the cave and failed to emerge while its mother flew to forage and returned to the cave at 1 am. (B2) A few minutes later, the mother picked up her pup in the cave, transported it to the drop-off site, and picked it up again at the end of the night and brought it back to the cave.

Current Biology
Article

ꝏ CellPress
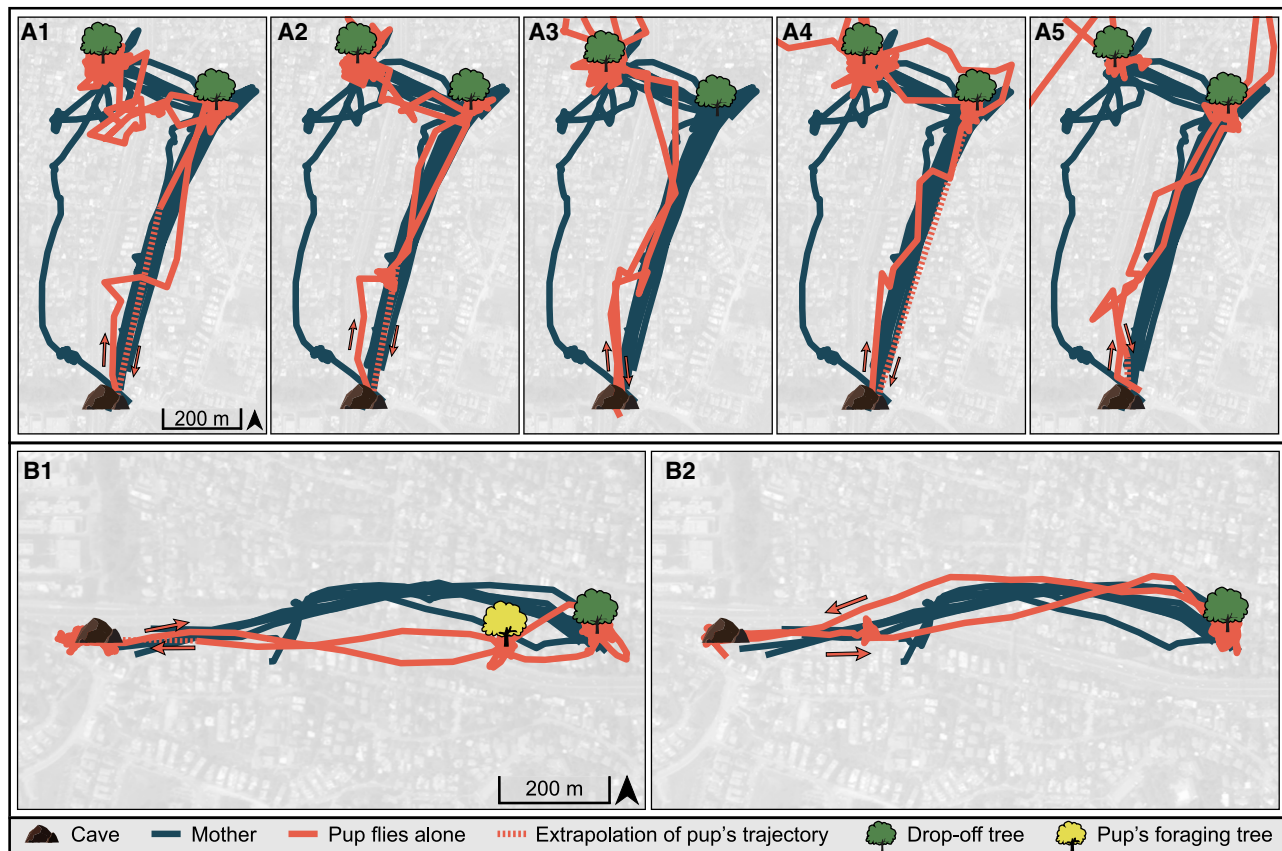
Figure 5. Independent pups use similar paths to the ones they were carried along

Flight path of pups that flew alone to drop-off sites in the "independent navigation" and the "exploration" stages (solid orange) and of the same pups when they were carried to the drop-off tree by their mothers in drop-off stage (blue). Extrapolation of pup's trajectory between the last GPS point and cave is depicted by an orange dotted line.

(A) A pup's first five consecutive independent nights (A1–A5).

(B) Another pup's first two consecutive independent nights (B1 and B2). Note that on day one (B1), the pup first flies to a drop-off tree (green) and, only on the way back, stops and explores a new tree (yellow).

See also Figure S3.

where pups did not do so approaching sunrise. In nearly all of these cases, when no-drop-off pups failed to return home on time, they stayed on trees in close proximity to the colony during daytime, returning to it on the next night after sunset. Notably, as the no-drop-off pups grew and explored further, this behavior

disappeared. The comparison between the two groups of bats should be taken with a grain of salt, as they were raised in two different colonies, which probably differ in additional factors other than experiencing the drop-off behavior. However, we note that the two colonies share many similarities. They are

(C) The transition between the drop-off and independent navigation stage. (C1) The mother carried the pup and dropped it off. (C2) On the next night, the pup was left in the cave and failed to emerge. (C3) On the third night, the mother retreated back to the "drop-off" stage, after which, (C4) on the fourth night, the pup once again was left in the cave and flew to a tree ~30 m from the cave, a movement that does not require navigation. Hanging at the entrance of the cave or on a tree a few meters away is typical for both adults and juvenile bats. (C5) On the fifth night, the pup emerged from the cave independently and spent 2 h on the same tree next to the cave. Then, it flew independently and navigated alone to the tree where it was dropped off by its mother on previous nights, about 850 m from the cave. Note that the pup passed dozens of fruit trees on the way, but it navigated straight to the tree where it was dropped off before by its mother (green) and, only on the way back to the cave, did it explore a new tree (yellow). The pup does not follow the exact route that its mother took, but it flies along the same highway that was visible when she carried it, and it knows when to leave the highway and turn toward the tree, suggesting that it uses a strategy potentially learned while it was passively carried by its mother. (C6) A zoom in on the flight trajectory of the pup on the fifth night is shown. Note that, on nights when the pup was left alone in the cave, the mother returned to the cave in the middle of the night from a remote drop-off tree (C2 and C5), which is something she did not do on other nights (C1, C3, and C4) and which is not typical for this species. Note that X scale and Y scale are different (see bars) to ease reading of the behavior.

(D) Mothers seem to correct pups' behavior during first independent foraging bouts. (D1) The pup exited independently to a previous drop-off site, while the mother flew directly to her foraging site and then returned to the cave. (D2) Two hours before sunrise, the pup failed to return to the cave on time, and the mother returned to the drop-off site, picked up the pup, and brought it back to the cave. Pick-up time (2 h before sunrise) was in close proximity to the mother's typical time of return in the drop-off stage (on average 1 h and 40 min before sunrise).

See also Figure S4 and Tables S2 and S3.
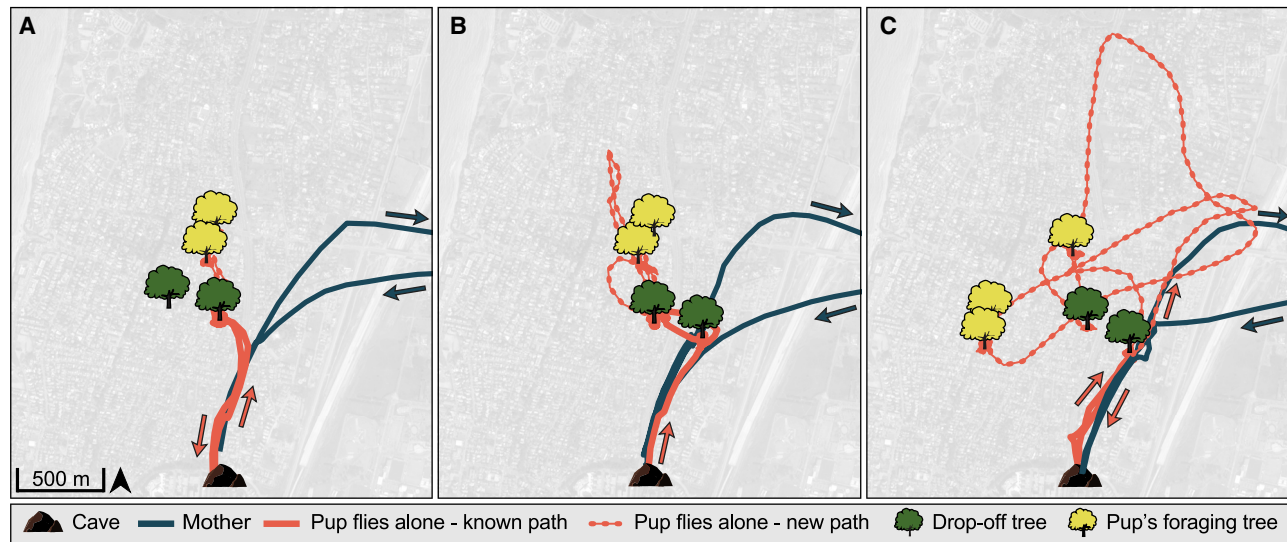
Figure 6. Exploration stage
Independently exploring pups gradually increase both the distance traveled and the number of new foraging sites across days (A–C present the first three exploration nights) while consistently returning to drop-off sites during the night. The pup's tracks along known paths (used by its mother, blue lines) are depicted by orange solid lines, while new paths are depicted by orange dotted lines, drop-off trees are depicted in green, and new trees in yellow.

both situated in the city, near the same highway, and in vicinity to patches of similar fruit trees.

Taken together, our results show that mothers accompany pups on their journey from dependency to independence. Thanks to the mothers' behavior, the pups are exposed to situations allowing them to learn to navigate to specific trees, flying along the similar paths used by the mothers while transporting them, and to learn to return home on time (Figures 4 and 5). Caro and Hauser[4] argued that a behavior is considered active teaching if teachers modify their behavior in the presence of a naive observer at some personal cost or at least without any self-benefit. A teacher's behavior must set an example for the naive observers who learn as a result.[4] Our results suggest that mothers modify their behavior during the pups' relevant developmental stage at some personal cost. We cannot prove the mothers' intentions, but parts of their behaviors suggest intentionality. For example, after leaving the pups in the cave for the first time, mothers returned from a far foraging site to the cave or drop-off site, which is a behavior they did not exhibit during the previous developmental stages (compare the behavior of the mother in Figures 4C1, 4C3, and 4C4 to 4C2 and 4C5). Specifically, bat mothers' behavior resembles Caro and Hauser's definition of "opportunity teaching," where "the teacher puts the pupil in a situation conducive to acquiring a new skill or knowledge."[4] Yet, to be careful, we refer to our findings as a behavior that facilitates learning (rather than as a teaching behavior).

We suggest four non-exclusive functions that the drop-off behavior provides pups, ruling-out food presentation as drop-off trees in this study mostly did not provide fruit that is edible for fruit bats.

Home base. In the "exploration" stage, the pups expanded their movement beyond the drop-off sites. While doing so, the pups returned to the drop-off sites multiple times within and between nights, in line with drop-off sites acting as home bases for navigation (Figure 6). In rodents, it has been hypothesized that a home base may facilitate navigation by anchoring environmental cues to self-movement cues and thus allow to reset navigation and reduce the accumulation of errors between trips.[68]

Familiarity. In addition to assisting with navigation,[69–73] a familiar location can act to decrease neophobia in newly volant pups.[74,75]

Homing. As discussed above, returning home on time is crucial for survival. Drop-off sites may provide a known location from which pups could return home along a familiar route.

Safety. Drop-off sites can be thought of as secondary roosts and can reduce exposure to predators, not allowing them to learn the location of the young and vulnerable pups that are scattered across multiple trees.[69–73] Supporting this, drop-off trees were evergreen trees or deciduous trees in their green season, thus providing coverage from predator detection (94% of the identified drop-off sites were evergreen trees; the remaining 6% were deciduous trees in their green season). Adult Egyptian fruit bats often use non-edible dense trees as perching locations where they eat recently collected fruit and rest—probably to reduce competition and increase safety.[76,77] This may be especially important for young pups with low flight efficiency.[69]

Notably, the distance of the late drop-off sites (up to 1.5 km of the roost) seems advantageous for several reasons: it is not too far for such young navigators, allowing the pups to reach them independently on their first navigation flight. The distance is also not too close to the roost, spreading the pups rather than having them all compete in proximity to the cave.

To our surprise, pups appear to have learned to navigate while passively being carried upside down by mothers. Although most research supports the advantages of active learning,[78,79] a few previous studies suggest that active navigation learning might not necessarily require self-motion.[80] Furthermore, evidence

Current Biology
Article

CellPress

shows that different aspects of navigation are better learned actively and others passively.[78,79,81] What sensory modality guides pups' learning? Fruit bats are visual navigators,[60,77,82,83] and evidence suggests that non-volant pups keep their eyes open while being carried at least part of the time (Figures S4C and S4D). Additionally, exploratory flights by pups around drop-off trees in late phases of the drop-off stage (Figure 3) can potentially contribute to pup's visual mapping of the area and to their first independent navigation to the site.[84] We thus hypothesize that pups use vision to collect information about the route to the drop-off trees. Interestingly, the three-dimensional spatial representation in the fruit bat brain has been shown to be invariant of pitch, allowing a continuous spatial representation even when the animal is upside down.[85]

To summarize, using high-resolution GPS tracking, we suggest how mothers actively facilitate the process of young fruit bats learning how to forage and navigate independently. We suggest that pups learn how to navigate to specific drop-off sites while repeatedly being transported upside down by mothers. The drop-off sites most likely provide pups with a combination of non-exclusive benefits, including a home base for navigation and safety. To our knowledge, this is the first example of bat mothers actively facilitating the acquisition of pups' navigation skills.[78,79,86–88]

STAR★METHODS

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

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact
  - Materials availability
  - Data and code availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
  - Animal **capturing, training and housing**
  - Age estimation
  - Estimating the duration of stage 1
  - Telemetry and GPS
  - Controlling for GPS weight
  - Movement and drop-off trees analysis
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.11.010.

AUTHOR CONTRIBUTIONS

A.G., L.H., and Y.Y. designed the experiments and wrote the manuscript; A.G. and L.H. conducted the experiment and carried the analysis. Y.Y. supervised the study.

REFERENCES

1. Clutton-Brock, T.H. (1991). The Evolution of Parental Care (Princeton University).

2. Sibly, R.M. (1999). Evolutionary biology of skill and information transfer. In Mammalian Social Learning: Comparative and Ecological Perspectives, H.O. Box, and K.R. Gibson, eds. (Cambridge University), pp. 57–71.

3. Raihani, N.J., and Ridley, A.R. (2008). Experimental evidence for teaching in wild pied babblers. Anim. Behav. 75, 3–11.

4. Caro, T.M., and Hauser, M.D. (1992). Is there teaching in nonhuman animals? Q. Rev. Biol. 67, 151–174.

5. Thornton, A. (2008). Social learning about novel foods in young meerkats. Anim. Behav. 76, 1411–1421.

6. Seyfarth, R.M., and Cheney, D.L. (1986). Vocal development in vervet monkeys. Anim. Behav. 34, 1640–1658.

7. Roush, R.S., and Snowdon, C.T. (2001). Food transfer and development of feeding behavior and food-associated vocalizations in cotton-top tamarins. Ethology 107, 415–429.

8. Nicol, C.J., and Pope, S.J. (1996). The maternal feeding display of domestic hens is sensitive to perceived chick error. Anim. Behav. 52, 767–774.

9. Vitikainen, E.I.K., Thompson, F.J., Marshall, H.H., and Cant, M.A. (2019). Live long and prosper: durable benefits of early-life care in banded mongooses. Philos. Trans. R. Soc. B 374, 20180114.

10. Olsson, O., Brown, J.S., and Helf, K.L. (2008). A guide to central place effects in foraging. Theor. Popul. Biol. 74, 22–33.

11. Daniel, S., Korine, C., and Pinshow, B. (2008). Central-place foraging in nursing, arthropod-gleaning bats. Can. J. Zool. 86, 623–626.

12. Lewis, S.E. (1995). Roost fidelity of bats: a review. J. Mammal. 76, 481–496.

13. Noser, R., and Byrne, R.W. (2014). Change point analysis of travel routes reveals novel insights into foraging strategies and cognitive maps of wild baboons. Am. J. Primatol. 76, 399–409.

14. Milton, K. (1981). Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. Am. Anthropol. 83, 534–548.

15. Mendes, N., and Call, J. (2014). Chimpanzees form long-term memories for food locations after limited exposure. Am. J. Primatol. 76, 485–495.

16. Berthold, P., and Helbig, A.J. (1992). The genetics of bird migration: stimulus, timing, and direction. Ibis 134, 35–40.

17. Mouritsen, H., Derbyshire, R., Stalleicken, J., Mouritsen, O.Ø., Frost, B.J., and Norris, D.R. (2013). An experimental displacement and over 50 years of tag-recoveries show that monarch butterflies are not true navigators. Proc. Natl. Acad. Sci. USA 110, 7348–7353.

18. Scott, R., Marsh, R., and Hays, G.C. (2014). Ontogeny of long distance migration. Ecology 95, 2840–2850.

19. Lonsdorf, E.V. (2006). What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? Anim. Cogn. 9, 36–46.

20. Gardner, A., and Smiseth, P.T. (2011). Evolution of parental care driven by mutual reinforcement of parental food provisioning and sibling competition. Proc. Biol. Sci. *278*, 196–203.

21. Hoppitt, W.J.E., Brown, G.R., Kendal, R., Rendell, L., Thornton, A., Webster, M.M., and Laland, K.N. (2008). Lessons from animal teaching. Trends Ecol. Evol. *23*, 486–493.

22. Jaeggi, A.V., Dunkel, L.P., Van Noordwijk, M.A., Wich, S.A., Sura, A.A.L., and Van Schaik, C.P. (2010). Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. Am. J. Primatol. *72*, 62–71.

23. Bray, J., Emery Thompson, M., Muller, M.N., Wrangham, R.W., and Machanda, Z.P. (2018). The development of feeding behavior in wild chimpanzees (*Pan troglodytes schweinfurthii*). Am. J. Phys. Anthropol. *165*, 34–46.

24. Verderane, M.P., and Izar, P. (2019). Maternal care styles in primates: considering a New World species. Psicol. USP *30*, e190055.

25. Weinrich, M. (1998). Early experience in habitat choice by humpback whales (*Megaptera novaeangliae*). J. Mammal. *79*, 163–170.

26. Box, H.O., and Gibson, K.R. (2000). Mammalian Social Learning: Comparative and Ecological Perspectives (Cambridge University).

27. Lee, P.C., and Moss, C.J. (1999). The social context for learning and behavioural development among wild African elephants. In Mammalian Social Learning: Comparative and Ecological Perspectives, H.O. Box, and K.R. Gibson, eds. (Cambridge University), pp. 102–125.

28. Kitchener, A.C. (1999). Watch with mother: a review of social learning in the Felidae. In Mammalian Social Learning: Comparative and Ecological Perspectives, H.O. Box, and K.R. Gibson, eds. (Cambridge University), pp. 236–258.

29. Burgin, C.J., Colella, J.P., Kahn, P.L., and Upham, N.S. (2018). How many species of mammals are there? J. Mammal. *99*, 1–14.

30. Kerth, G., Ebert, C., and Schmidtke, C. (2006). Group decision making in fission-fusion societies: evidence from two-field experiments in Bechstein's bats. Proc. Biol. Sci. *273*, 2785–2790.

31. Harten, L., Matalon, Y., Galli, N., Navon, H., Dor, R., and Yovel, Y. (2018). Persistent producer-scrounger relationships in bats. Sci. Adv. *4*, e1603293.

32. Willis, C.K.R., and Brigham, R.M. (2004). Roost switching, roost sharing and social cohesion: forest-dwelling big brown bats, *Eptesicus fuscus*, conform to the fission–fusion model. Anim. Behav. *68*, 495–505.

33. Kerth, G. (2008). Causes and consequences of sociality in bats. BioSci. *58*, 737–746.

34. Wilkinson, G.S. (1986). Social grooming in the common vampire bat, *Desmodus rotundus*. Anim. Behav. *34*, 1880–1889.

35. Dechmann, D.K.N., Heucke, S.L., Giuggioli, L., Safi, K., Voigt, C.C., and Wikelski, M. (2009). Experimental evidence for group hunting via eavesdropping in echolocating bats. Proc. Biol. Sci. *276*, 2721–2728.

36. Safi, K., and Kerth, G. (2007). Comparative analyses suggest that information transfer promoted sociality in male bats in the temperate zone. Am. Nat. *170*, 465–472.

37. Wilkinson, G.S., and Wenrick Boughman, J. (1998). Social calls coordinate foraging in greater spear-nosed bats. Anim. Behav. *55*, 337–350.

38. Ripperger, S.P., Carter, G.G., Duda, N., Koelpin, A., Cassens, B., Kapitza, R., Josic, D., Berrío-Martínez, J., Page, R.A., and Mayer, F. (2019). Vampire bats that cooperate in the lab maintain their social networks in the wild. Curr. Biol. *29*, 4139–4144.e4.

39. Rose, A., Wöhl, S., Bechler, J., Tschapka, M., and Knörnschild, M. (2019). Maternal mouth-to-mouth feeding behaviour in flower-visiting bats, but no experimental evidence for transmitted dietary preferences. Behav. Processes *165*, 29–35.

40. Vaughan, T.A., and Vaughan, R.P. (1987). Parental behavior in the African yellow-winged bat (*Lavia frons*). J. Mammal. *68*, 217–223.

41. Kunz, T.H., and Hood, W.R. (2000). Parental care and postnatal growth in the chiroptera. In Reproductive Biology of Bats, E.G. Crichton, and P.H. Krutzsch, eds. (Academic), pp. 415–468.

42. Kohles, J.E., Page, R.A., Dechmann, D.K.N., and O'Mara, M.T. (2018). Rapid behavioral changes during early development in Peters' tent-making bat (*Uroderma bilobatum*). PLoS ONE *13*, e0205351.

43. de Fanis, E., and Jones, G. (1995). Post-natal growth, mother-infant interactions and development of vocalizations in the vespertilionid bat *Plecotus auritus*. J. Zool. *235*, 85–97.

44. McLEAN, J.A., and Speakman, J.R. (1997). Non-nutritional maternal support in the brown long-eared bat. Anim. Behav. *54*, 1193–1204.

45. Ripperger, S., Günther, L., Wieser, H., Duda, N., Hierold, M., Cassens, B., Kapitza, R., Koelpin, A., and Mayer, F. (2019). Proximity sensors on common noctule bats reveal evidence that mothers guide juveniles to roosts but not food. Biol. Lett. *15*, 20180884.

46. Geipel, I., Kalko, E.K.V., Wallmeyer, K., and Knörnschild, M. (2013). Postweaning maternal food provisioning in a bat with a complex hunting strategy. Anim. Behav. *85*, 1435–1441.

47. Bunkley, J.P., and Barber, J.R. (2014). An observation of apparent teaching behavior in the pallid bat, Antrozous pallidus. West. North Am. Nat. *74*, 249–252.

48. Hernández-Mijangos, L.A., Horváth, A., and Canales, R.P. (2009). Observations on female bats transporting non-volant juveniles during flight. Chiropt. Neotrop. *15*, 472–476.

49. Radhamani, T.R., Marimuthu, G., and Chandrashekaran, M.K. (1990). Relationship between infant size and carrying of infants by hipposiderid mother bats. Curr. Sci. *59*, 602–603.

50. Marimuthu, G. (1988). Mother–young relations in an insectivorous bat, *Hipposideros speoris*. Curr. Sci. *57*, 983–987.

51. Schnitzler, H.-U., Moss, C.F., and Denzinger, A. (2003). From spatial orientation to food acquisition in echolocating bats. Trends Ecol. Evol. *18*, 386–394.

52. Rossiter, S.J., Jones, G., Ransome, R.D., and Barratt, E.M. (2002). Relatedness structure and kin-biased foraging in the greater horseshoe bat (*Rhinolophus ferrumequinum*). Behav. Ecol. Sociobiol. *51*, 510–518.

53. Fenton, M.B. (1969). The carrying of young by females of three species of bats. Can. J. Zool. *47*, 158–159.

54. Reckardt, K., and Kerth, G. (2007). Roost selection and roost switching of female Bechstein's bats (*Myotis bechsteinii*) as a strategy of parasite avoidance. Oecologia *154*, 581–588.

55. Hayssen, V., and Kunz, T.H. (1996). Allometry of litter mass in bats: maternal size, wing morphology, and phylogeny. J. Mammal. *77*, 476–490.

56. Hughes, P., and Rayner, J.M.V. (1993). The flight of pipistrelle bats *Pipistrellus pipistrellus* during pregnancy and lactation. J. Zool. *230*, 541–555.

57. Nelson, M.E. (1998). Development of migratory behavior in northern white-tailed deer. Can. J. Zool. *76*, 426–432.

58. Radford, A.N., and Ridley, A.R. (2006). Recruitment calling: a novel form of extended parental care in an altricial species. Curr. Biol. *16*, 1700–1704.

59. Lewis, S.E. (1992). Behavior of Peter's tent-making bat, *Uroderma bilobatum*, at maternity roosts in Costa Rica. J. Mammal. *73*, 541–546.

60. Kwiecinski, G.G., and Griffiths, T.A. (1999). *Rousettus egyptiacus*. Mamm. Species, 1–9.

61. Kulzer, E. (1966). Die geburt bei Flughunden der gattung *Rousettus* gray (Megachiroptera). Zeitschrift ftir Saugertierkd. *31*, 226–233.

62. Hall, E.R. (1968). The Bats of West Africa by D.R. Rosevear. J. Mammal. *49*, 350–351.

63. Norberg, U.M. (1987). Wing form and flight mode in bats. In Recent Advances in the Study of Bats, B.M. Fenton, P.A. Racey, and J.M.V. Rayner, eds. (Cambridge University), pp. 335–427.

64. Hughes, P.M., and Rayner, J.M.V. (1991). Addition of artificial loads to Long-eared bats *Plecotus auratus* (Chiroptera: Vespertilionidae): Handicapping flight performance. J. Exp. Biol. *161*, 285–298.

Current Biology
Article

65. Egert-Berg, K., Hurme, E.R., Greif, S., Goldstein, A., Harten, L., Herrera M, L.G., Flores-Martínez, J.J., Valdés, A.T., Johnston, D.S., Eitan, O., et al. (2018). Resource ephemerality drives social foraging in bats. Curr. Biol. *28*, 3667–3673.e5.

66. Speakman, J.R. (1991). Why do insectivorous bats in Britain not fly in daylight more frequently? Funct. Ecol. *5*, 518–524.

67. Harten, L., Katz, A., Goldstein, A., Handel, M., and Yovel, Y. (2020). The ontogeny of a mammalian cognitive map in the real world. Science *369*, 194–197.

68. Eilam, D., and Golani, I. (1989). Home base behavior of rats (*Rattus norvegicus*) exploring a novel environment. Behav. Brain Res. *34*, 199–211.

69. Oliveira-Santos, L.G.R., Forester, J.D., Piovezan, U., Tomas, W.M., and Fernandez, F.A.S. (2016). Incorporating animal spatial memory in step selection functions. J. Anim. Ecol. *85*, 516–524.

70. Stamps, J. (1995). Motor learning and the value of familiar space. Am. Nat. *146*, 41–58.

71. Henry, M., and Stoner, K.E. (2011). Relationship between spatial working memory performance and diet specialization in two sympatric nectar bats. PLoS ONE *6*, e23773.

72. Ambrose, H.W. (1972). Effect of habitat familiarity and toe-clipping on rate of owl predation in *Microtus pennsylvanicus*. J. Mammal. *53*, 909–912.

73. Brunyé, T.T., Wood, M.D., Houck, L.A., and Taylor, H.A. (2017). The path more travelled: Time pressure increases reliance on familiar route-based strategies during navigation. Q J Exp Psychol (Hove) *70*, 1439–1452.

74. Tsoar, A., Nathan, R., Bartan, Y., Vyssotski, A., Dell'Omo, G., and Ulanovsky, N. (2011). Large-scale navigational map in a mammal. Proc. Natl. Acad. Sci. USA *108*, E718–E724.

75. Korine, C., Izhaki, I., and Arad, Z. (1999). Is the Egyptian fruit-bat *Rousettus aegyptiacus* a pest in Israel? An analysis of the bat's diet and implications for its conservation. Biol. Conserv. *88*, 301–306.

76. Morrison, D.W. (1980). Efficiency of food utilization by fruit bats. Oecologia *45*, 270–273.

77. Izhaki, I., Korine, C., and Arad, Z. (1995). The effect of bat (*Rousettus aegyptiacus*) dispersal on seed germination in eastern Mediterranean habitats. Oecologia *101*, 335–342.

78. James, K.H., Humphrey, G.K., Vilis, T., Corrie, B., Baddour, R., and Goodale, M.A. (2002). "Active" and "passive" learning of three-dimensional object structure within an immersive virtual reality environment. Behav. Res. Methods Instrum. Comput. *34*, 383–390.

79. Chrastil, E.R., and Warren, W.H. (2012). Active and passive contributions to spatial learning. Psychon. Bull. Rev. *19*, 1–23.

80. Gaunet, F., Vidal, M., Kemeny, A., and Berthoz, A. (2001). Active, passive and snapshot exploration in a virtual environment: influence on scene memory, reorientation and path memory. Brain Res. Cogn. Brain Res. *11*, 409–420.

81. Appleyard, D. (1970). Styles and methods of structuring a city. Environ. Behav. *2*, 100–117.

82. Danilovich, S., Krishnan, A., Lee, W.J., Borrisov, I., Eitan, O., Kosa, G., Moss, C.F., and Yovel, Y. (2015). Bats regulate biosonar based on the availability of visual information. Curr. Biol. *25*, R1124–R1125.

83. Danilovich, S., and Yovel, Y. (2019). Integrating vision and echolocation for navigation and perception in bats. Sci. Adv. *5*, eaaw6503.

84. Jones, G. (2000). The ontogeny of behaviour in bats: a functional perspective. In Ontogeny, Functional Ecology and Evolution of Bats, R.A. Adams, and S.C. Pedersen, eds. (Cambridge University), pp. 362–392.

85. Hughes, P.M., Rayner, J.M.V., and Jones, G. (1995). Ontogeny of 'true' flight and other aspects of growth in the bat *Pipistrellus pipistrellus*. J. Zool. *236*, 291–318.

86. Reyes-Alcubilla, C., Ruiz, M.A., and Ortega-Escobar, J. (2009). Homing in the wolf spider *Lycosa tarantula* (Araneae, Lycosidae): the role of active locomotion and visual landmarks. Naturwissenschaften *96*, 485–494.

87. Wehner, R., Gallizzi, K., Frei, C., and Vesely, M. (2002). Calibration processes in desert ant navigation: vector courses and systematic search. J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol. *188*, 683–693.

88. Seitz, A.R., and Watanabe, T. (2003). Psychophysics: is subliminal learning really passive? Nature *422*, 36.

89. Richardson, B.L., Wuillemin, D.B., and MacKintosh, G.J. (1981). Can passive touch be better than active touch? A comparison of active and passive tactile maze learning. Br. J. Psychol. *72*, 353–362.

90. Pinter-Wollman, N., Hobson, E.A., Smith, J.E., Edelman, A.J., Shizuka, D., de Silva, S., Waters, J.S., Prager, S.D., Sasaki, T., Wittemyer, G., et al. (2014). The dynamics of animal social networks: analytical, conceptual, and theoretical advances. Behav. Ecol. *25*, 242–255.

91. Watanabe, T., Náñez, J.E., and Sasaki, Y. (2001). Perceptual learning without perception. Nature *413*, 844–848.

92. Finkelstein, A., Derdikman, D., Rubin, A., Foerster, J.N., Las, L., and Ulanovsky, N. (2015). Three-dimensional head-direction coding in the bat brain. Nature *517*, 159–164.

93. Cvikel, N., Egert Berg, K., Levin, E., Hurme, E., Borissov, I., Boonman, A., Amichai, E., and Yovel, Y. (2015). Bats aggregate to improve prey search but might be impaired when their density becomes too high. Curr. Biol. *25*, 206–211.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
All data and code	This paper	https://doi.org/10.17632/gpcg9m5758.1
Experimental models: Organisms/strains		
Rousettus aegyptiacus	Caves in central Israel (Herzelia and Tel Aviv)	Taxonomy ID: 9407
Software and algorithms		
MATLAB R2018a	MathWorks	https://www.mathworks.com/downloads/;
Other		
GPS - Robin	lucid Inc. Israel	N/A
GPS - Vesper	Asd Inc. Israel	N/A
VHF radio transmitters - LB-2X	Holohil Systems Ltd	N/A
VHF radio transmitters - PicoPip Ag379	Biotrack Ltd	N/A
Three-element yagi antenna	Titley Scientific Ltd	N/A
Magmount VHF antenna	Biotrack Ltd	N/A
Telemetry receiver - R1000	Communication specialists Inc.	N/A
Data logging telemetry receiver – DataSika	Biotrack Ltd	N/A
RFID system	Read bee Ltd	N/A
RFID system	Trovan, Ltd	N/A

RESOURCE AVAILABILITY

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

Materials availability
This study did not generate new unique reagents.

Data and code availability
All original data and code have been deposited at Mendeley and is publicly available as of the date of publication. The DOI is listed in the key resources table. Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

All experiments were performed with permission from the Tel Aviv University Institutional Animal Care and Use Committee (permits number L-15-058 and L-12-031). All experiments have been conducted in The Zoological Research Garden at Tel Aviv University and in Tel-Aviv and Herzeliya.

METHOD DETAILS

Animal capturing, training and housing
Mother-pup pairs of Egyptian Fruit-bat (*Rousettus aegyptiacus*) were captured together in a cave in Herzliya, Israel, before pups became volant, and were brought to the Zoological garden at Tel-Aviv University. At this stage the pup still suckles and travels while latched to its mother's nipple, thus it is easy to capture mothers and pups as pairs. Bats were held in social groups (between 15-30 mother-pup pairs) for up to 10 days, in an indoor flight room (2.5 X 2 X 2.5 m³) with a naturally fluctuating day/night light cycle and a regulated temperature of 27°C.

In the lab, each pups' flight ability was assessed and categorized into five flight development stages from non-volant to volant (A–E as described in Table S4). Using measurements from all pups brought to the lab during this study, we fine-tuned the calibration

Current Biology
Article

🔓 **CellPress**

between forearm and flight ability. This allowed us to accurately choose pups in the appropriate developmental stage for the experiment, i.e., just before reaching independent flight to assure that they never foraged or navigated independently (Table S4; n = 76; Figure S5A). Pups were assessed at least three times over 7 days. Assessments included: forearm length measurement, body mass, flight ability category, and general health. Weight was gradually added to the pups' backs with every assessment, in order to prepare them to fly with a total of ~5 g, the weight of our GPS device. Weight was mounted to pups' back using a combination of a ball chain necklace, found to be safe for use in bats[80] and polymorph plastic beads (Blrtronics, Material District), gently glued to their back (Perma-Type Surgical Cement, AC). The combination of the necklace and plastic weight glued to their back assured the weight was more widely distributed, easing their flight training.

Between April 2015 and May 2019 a total of 115 mother-pup pairs were brought to the lab for assessment. 71 Mother pup pairs were then released back into the wild with radio-tags, GPS or GPS with on-board acceleration sensor (50Hz), 39 of which yielded usable tracking data. An additional 13 pairs were released with only radio-tags to control for weight (0.3 g versus ~5.5 g, Table S5).

Age estimation
Each pup's age was approximated using a polynomial equation fitted to empirical data of pups born in the lab between 2012-2019 and thus the real age (days) and forearm length (mm) was approximated (Equation 1: $f(x) = 121.2 \exp(-0.002x) + (-86.22)\exp(-0.016x)$ n = 38, Figures S5B–S5D).

Estimating the duration of stage 1
Due to the small size of the pups in the 'constantly attached' stage (1-3 weeks), they could not be assessed via GPS tracking. To validate previous observations that fully dependent non-volant new born pups are constantly attached to their mothers for the first few weeks of life[60–62], we used data from both our captive and in-house open colonies[89].

The captive colony consisted of ~25 adults and their respective young. The foraging behavior of mothers with young pups was monitored for a minimum of three times a week[31], including constant monitoring of whether pups were latched on mothers or hanging alone in the colony. The first time any given non-volant pup was seen hanging alone marked the end of 'constantly attached' stage for that pair. This occurred between 1 and 3 weeks of age, 14 ± 5 (n = 7) days on average.

The in-house open colony is composed of fruit-bats (N = 30-50 individuals) that roost in Tel-Aviv University and fly out to forage in the wild[79,81]. They behave like bats in the nearby wild colonies, flying similar distances, visiting nearby colonies and occasionally switching roosts[90,91]. Video surveillance in combination with an automated RFID system in the entrance of the colony (Read bee Ltd., Trovan, Ltd.), allowed us to monitor all mother-pup pairs entering and exiting the colony. We could then detect the first time a mother appeared without her pup. The duration of the 'constantly attached' stage was estimated using the time lag between the first day a mother was observed with her newly-born pup and the first day she was observed alone. Estimations of the stage duration were similar to the captive colony (1-3 weeks, Table S1).

Telemetry and GPS
After seven days of captive training, mother-pup pairs were released back into their natural roost fitted with a miniature GPS device (Robin, Lucid Ltd or Vesper, ASD Inc) and VHF radio transmitters (LB-2X 0.3 g, Holohil Systems Ltd or PicoPip Ag379, Biotrack). The GPS sample rate ranged between a sample every 15-120 s for mothers (43.5 ± 38 s) and a sample every 20-120 s for pups (53 ± 39 s). The tag was coated with Parafilm (Heathrow Scientific) and duct tape then glued to the bats' back using medical cement glue (Perma-Type Surgical Cement, AC). The mean weight mounted on a bat including GPS, telemetry and coating was 5.6 ± 0.65 g for pups and 7.2 ± 0.68 g for mothers, which constitute 5.4% ± 1.3 and 11.6% ± 3.4 of the mothers and pups' body mass upon release respectively.

In the 3-10 nights after pairs were released back into the cave, we conducted radio tracking for the first 1-4 hours following emergence. Radio-tracking pairs aimed both to (1) increase our sample size by identifying the pups' developmental stage, given expected GPS device failure and loss and (2) increase the chances of finding devices at individually preferred foraging sites after they fall off the bats. We noted information allowing identification of the pups' behavioral stage including: whether pairs exited together, moved together, if and when they separated, what tree the pup was left on, and whether the pup was visited by its mother.

Three to four observers participated in telemetry tracking, each equipped with an R1000 mobile receiver (Communication Specialist, USA) and a three-element yagi antenna (Titley Scientific, Australia). Cross-bearings of foraging bats were taken as often as possible, from three strategic locations: (1) The cave entrance: allowing to distinguish if pairs exited simultaneously. (2) A ten-story building situated 200 m south-east of the cave, allowing to easily asses: direction of flight, whether pairs flew in synchrony (i.e., together), and events where mothers and their pups separated. (3) A mobile observer with a vehicle (Magmount VHF antenna, Biotrack Ltd) - allowing to locate pups left on trees within up to ~two km radius from the cave, using cross-bearings.

A pup was noted as in the 'drop-off' stage if mother and pup were (1) observed leaving the cave simultaneously, (2) heard separating and (3) the pup was located on a tree alone. A pup was noted in the beginning of the 'independent navigation' stage if the mother was heard exiting and the pup signal continued to be heard from the cave. A pup was noted as an independent navigator if it was heard exiting separately from its mother and later heard at a previously located drop-off site. The 'constantly attached and 'exploration' stages were not validated based on telemetry data as they are hard to asses accurately.

Controlling for GPS weight

The extra weight loaded on the bats was similar to that found to allow proper behavior in several previous studies[92]. In order to further validate that the bats could forage with this extra weight we performed several controls: (1) Captive training for pups before release (see STAR Methods above). With each increment of weight added to pups, we assured that their flight ability did not deteriorate, and we further monitored pups progress in the following days. (2) Pup behavior after releasing them back into the wild revealed no correlation between GPS weight and pups' flight abilities during independent navigation and exploration stages (GLM with GPS weight set as a fixed factor and pair index set as a random effect: time spent outside the cave $R^2 = 0.96$, $p = 0.67$, $n = 14$ nights of 7 pairs; commute duration $R^2 = 0.20$, $p = 0.95$, $n = 13$ nights of 6 pairs; path length $R^2 = 0.03$, $p = 0.85$, $n = 13$ nights of 6 pairs). (3) Light telemetry tags ($< 1\%$ of the bats' body mass) were mounted on mother and pup pairs, to compare the 'drop-off' stage behavior to that of bats with heavier GPS tags ($n = 3$ pairs, 2 nights each). We found that in this light-weight condition mothers dropped-off pups at sites on average 1.2 km from their roost – this is within the range of the experimental condition drop-off sites (Figure S1). (4) In order to verify that drop-off behavior occurred in naive mother-pup pairs, we carried out observations on 5 trees over 3 nights in order to identify whether non-volant pups were left alone on trees by mothers (i.e., dropped-off). 17 non-volant pups were found, volancy was assessed by shining bright lights at trees. All volant individuals then dispersed – leaving only non-volant-pups (Figures S2E and S2F). (5) To assure that pups were not left in the cave at the beginning of the 'independent navigation' stage due to extra weight, we sampled and validated that non-manipulated pups of the appropriate size for this stage (i.e., forearm > 73 mm, Table S1) were left alone in the cave by mothers, across five days over one month ($n = 29$ pups). (6) The behavior of mothers with young pups ($n = 4$ pairs, average 2.2 nights each) in our in-house wild colony suggested that the drop-off behavior (in the 'drop-off' stage) was not an artifact of extra weight. These mothers often exited the colony with their non-volant pups latched and then returned to the colony in the middle of the night without them (finally returning to the colony with the pups at the end of night). Tagging these pups with telemetry tags ($n = 2$) allowed us to find the pups outdoors, validating pups were stationary at drop-off sites while mothers foraged. In one pair, we were able to compare and validate that the mother dropped-off and picked up her pup between nights with varying weight loaded (0%–10% of body mass). (7) Notably, a pup with up to 13.2% extra weight managed to independently fly to drop-off sites and navigate beyond them, covering an accumulative flight distances of 12 km during the third night of exploration stage (see Figure 6).

Movement and drop-off trees analysis

Flight speed

Flight speed was estimated based on the derivative of the GPS positioning, and data points with speed beyond 3 SDs from the average flight speed during commute flight ($\sim$5 m/s) were removed.

Foraging versus commute

GPS trajectories were divided into "Commute" and "Foraging" segments based on the mean of the standard deviation of x and y coordinates. This procedure was carried out for each GPS point over the entire trajectory in windows of four GPS points. Commute segments were defined as having values above 50, and all remaining GPS points were defined as foraging. Segments where bats flew above 40 m above ground were classified as commute regardless of their index (for estimating flight altitude see Cvikel et al.[93]).

Foraging and drop-off trees

Stationary GPS data is characterized by large error which can be mitigated when averaging the positions (When the animal is moving, the positions become much more accurate (< 10 m error) as we have quantified before[93]). We detect that the animal is perching when we see the distribution of points around it, and thus the locations of the foraging sites were defined as the average position of each foraging segment. To validate this point, we performed a control experiment where we placed four stationary GPS tags on the tree at the entrance of the cave. The results show that: the accurate position of the GPS can be estimated by averaging the locations (Figure S6).

All trees visited by mothers and pups ($n = 908$ trees) were identified based on the GPS or radio-tracking data, as described above, and physically surveyed. Each tree was then categorized into species and further classified as either deciduous or evergreen and as food-trees or non-food trees. "Food trees" were defined as trees currently containing food items (fruit or leaves) known to be eaten by bats. 94% of the drop-off trees were identified at the species level, 71% of the identified trees were not edible or non-fruiting trees. 29% of the identified trees were edible and included *Ficus microcarpa* and *Eucalyptus* trees.

Mothers visit at drop-off sites

Visits at drop-off sites were defined as events where the mother was in proximity of less than 50 m from the drop-off tree (The average minimum distance was 13.1 ± 6.4 m, $n = 13$ pairs). Visit duration and interval between visits were calculated.

Pups flight speeds at different stages

Pups' flight speed was calculated as average flight speed for each flight segment (e.g., flight from cave to foraging site considered as one segment). Pups flew much slower when flying independently than when flying with their mothers, suggesting that they were carried by them during the drop-off stage (2.9 ± 0.3 m/s versus 5.7 ± 0.08 m/s; GLM with developmental stage set as a fixed factor and pair index set as a random effect $R^2 = 0.64$, $p < 0.001$, $n = 2$ pairs and 19 flight segments on average for each pup, Figures 2A and S2A–S2D). Quantifying pups' flight ability in a 10 m long corridor in captivity supported these findings: flight speed of pups at late drop-off stage (Forearm: 73.5 ± 3.0mm, $n = 8$ pups) was 2.2 ± 0.4 m/s and their flight bouts were short and unstable. Pups flight at this stage is highly unstable and jittery, allowing them to fly shortly between a tree branches and close by trees.

Current Biology
Article

 CellPress

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analysis was conducted using MATLAB R2018a with a significance level of 0.05. Prior to each statistical analysis we assured that the data met the assumptions of the statistical approach. We used a generalized linear mixed-effects models to account for the effect of multiple measurements per individual: we set the examined parameter as a fixed factor such as flight mode (alone/with mother), developmental stage, etc., and the mother-pup pair index as a random effect (Each analysis is presented in the text with detailed information regarding the examined parameters and sample size). We used the Wilcoxon rank sum test to examine the difference in flight distance between the cave and the first tree visited by drop-off and no-drop-off pups because the data were not distributed normally (See Figure S3D).