Egyptian Fruit Bats: The Efficient Foragers

David Shohami, Sivan Toledo and Ran Nathan tell the story of their recent research into the use of cognitive maps in Egyptian fruit bats (Toledo et al., 2020).

As the sun sets, hundreds of Egyptian fruit bats begin to stretch their wings, inch towards their cave opening and make short warm-up flights in anticipation for nightfall. Then, when the time comes, one after the other they leave their cave and fly out into the night. Their goal: trees bearing ripe fleshy fruit. They must consume up to 250% their own ~150 gram body mass of this relatively uncommon resource each night, to meet their high energetic demands for flapping flight and thermoregulation, and to offset some of its low nutritional values (Korine et al. 1996). They return home to their colony every morning rather than spend the day on trees within their foraging home range. An efficient strategy for locating these fruit trees is, therefore, highly beneficial. And what they do is indeed very efficient – but we will get back to that.

There are several navigational strategies that animals employ to find food or other resources. One is simply to search randomly, perhaps with some additional simple rules such as directional or angular tendency. Then, once the resource is located, the animal could go straight back home using path integration ("dead reckoning") – an internal mechanism for recording self-motion from which the direction home is calculated. Desert ants use this strategy (Wehner 2003). For fruit bats, random search is not efficient; while fruit trees are spatially patchy, once found their location never changes and they continue to bear fruit for days or weeks. A goal-directed navigation strategy, then, would do better. The easiest is probably beaconing, the ability to sense (by seeing, smelling etc.) a target from the animal's current location and then to move towards it. For targets beyond detection range, piloting ("route / landmark following") can be used: following a series of landmarks from which only the next one is detectable, until the target is reached – essentially, a series of beaconing steps. Homing pigeons use this strategy (Guilford & Biro 2014). The number of targets that can be reached is limited by the capacity of remembering the many landmarks that are associated with them. Furthermore, the route followed is highly unlikely to be straight, so more time and energy is spent reaching the target than would have been by a straight direct movement (Biro et al. 2004).

A much more flexible, yet cognitively demanding, navigation strategy is having the ability for relational self-positioning anywhere within the animal's home range. This form of navigation uses spatial memory not just as a series of landmarks or specific targets, but as a frame of reference for the locations of objects or places relative to one another (Wiener et al.

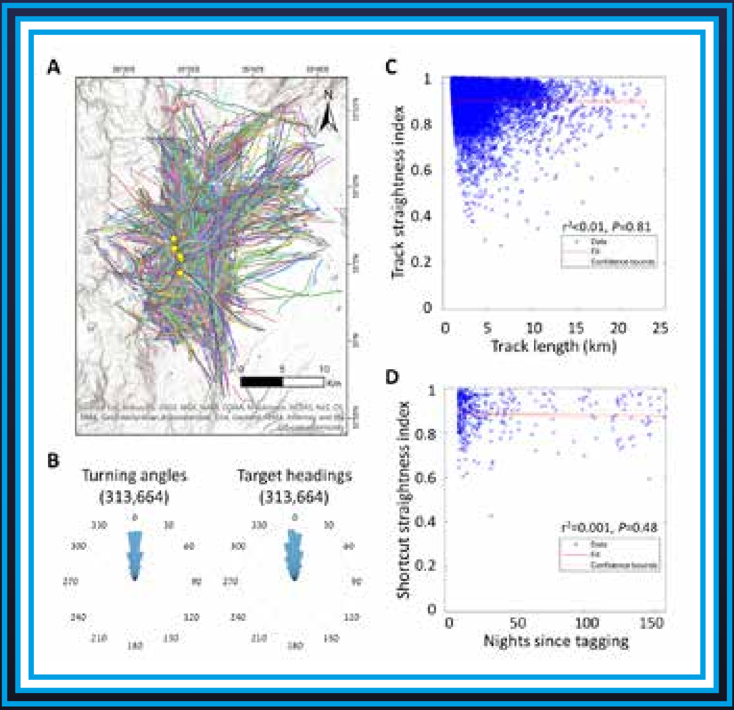

Figure 1.A) 9218 fight tracks of 172 Egyptian fruit bats, collected over 3449 cumulative nights in the Hula Valley, Israel in 0.125 to 1 Hz sampling rate with the ATLAS system. Yellow pentagons mark the 5 known bat caves in the study area. B) Distribution of turning angles (left) and headings to target (right) of all in-flight bat localizations. C) Straightness (efficiency) index of all flight tracks as a function of track length. D) Straightness index of shortcuts as a function of time of occurrence (nights after tagging) of the shortcut.

2011). The memorized relational positions of self, target and landscape features, from which one can compute a direction, constitute an internal "cognitive map", which allows reaching previously-visited targets beyond detection range in a most efficient (usually straight) manner. This ability is best exemplified by shortcutting – taking a novel route between any two previously-visited locations.

Do animals possess a cognitive map of their environment, or is this ability restricted only to humans? This fundamental scientific question has intrigued biologists for more than 70 years. Originating with Tolman (1948) and thoroughly developed by O'Keefe & Nadel (1978), the cognitive map concept has garnered much neurobiological support that led, more generally, to increased understanding of how spatial representation and spatial cognition are performed by the brain (Moser et al. 2008). But there was still no convincing evidence for possession and utilization of a cognitive map outside the lab, in free-ranging wild animals. We set out to resolve this scientific question.

Our quest began more than a decade ago, starting with simple radio tags and hand-held receivers. These allowed us to discover that Egyptian fruit bats visit the same fruit trees for days or even weeks, and that these favourite trees are often far away from their caves. But we could not accurately know which paths they took to get there and back. When GPS-logger tags became small enough to be attached to these bats, we found that they reach these trees directly from their caves in straight flights. But what was then cutting-edge technology was still very limited (and very expensive): the tags operated for only one full night or a few partial nights, so we could not tell how pervasive these flights are and how the bats find and switch favourite trees. We also had to find the GPS devices after they had fallen off the bat to retrieve the data they stored… not an easy task when dealing with free-ranging, flying animals. We desperately needed technology that could show us detailed bat flights paths. Many of them.

The shortcomings of light-weight GPS / GNSS trackers hampered not only our quest to demonstrate a cognitive map in Egyptian fruit bats, but also many other investigations involving small birds, other bats and nocturnal animals. To address these shortcomings, we developed ATLAS, a regional time-of-arrival transmitter localization system that can localize miniature radio tags that transmit wideband pings (Toledo et al. 2016, Weller-Weiser et al. 2016). This "reverse-GPS" system can track dozens of tags simultaneously in a region spanning tens of kilometres. The smallest ATLAS tag weighing 1 gram can ping every 8 seconds for 29-35 days; a tag weighing 3.5 grams can ping every second for 17 days. The system relies on terrestrial receivers, so it does not have global coverage like GPS / GNSS tracking tags. In 2014, we set up the first ATLAS system in the Hula Valley in northern Israel, where it covers roughly 88,200 ha, or 35×25 km.

During four years of study, we tagged and followed 172 Egyptian fruit bats caught either at their cave entrance or on fruit trees (Toledo et al. 2020). Bats were tracked on average for 47 nights (maximum 219) for tags attached by a custom-made collar, or for 13 nights (maximum 38) for tags attached by glue to the bats' back. In total, we recorded 3449 full nights of bat foraging movements, yielding ~18 million localizations in 0.125 to 1 Hz sampling rate, a dataset of unprecedented magnitude for such a small animal. We also surveyed meticulously an area of 19,000 ha comprising the core of bat foraging in the study area, and every individual fruit tree that can potentially be eaten by Egyptian fruit bats – wild or ornamental – was mapped and identified. Thus, we had a pretty good idea of what kind of resource landscape the Hula Valley bats are foraging in: 14,314 fruit trees of 33 species, plus ~18,000 orchard trees.

We found that the somewhat anecdotal early observations of straight flight paths and favourite tree fidelity were, in fact, extremely ubiquitous for this species (Figure 1A). Analysis of the >9,000 individual movement tracks made by the tagged bats revealed a typical pattern of straight goal-directed flights to specific fruit trees. The tracks were on average 4.5 km long (maximum 23 km, though about 10% of tracks were even longer and went out of ATLAS range), and very straight: mean track straightness was 0.9, with 1 being a completely straight line. Regardless of track length or of what the target and origin were (tree, cave, or very long out-of-range tracks), thorough analyses of turning angles and target headings along the tracks all told the same story: as soon as a bat leaves its cave or a tree, it already knows where it wants to go and the location of its target relative to its current position (Figure 1B, 1C). We found almost no cases where random foraging seemed to take place, even for our longest-tracked bat which we followed for more than 7 months. Visiting on average 4 trees per night, the bats remain loyal to these trees for weeks, and when they do switch to a new favourite tree, they fly straight towards it. It is very unlikely that simpler modes of navigation, such as beaconing and piloting, generate these fantastic straight goal-directed flight tracks.

If you navigate using a map (including a cognitive one, not just paper maps or maps on a screen), you can make novel shortcuts. You can go straight from A to B even if you never went from A to B or from B to A before. Do Egyptian fruit bats make shortcuts? They certainly do. We found many cases where bats seemed to make shortcuts, flying for the first time between two locations they had previously stopped in (caves or trees) but previously reached from other locations (Figure 2). These shortcuts were, again, very straight, and indistinguishable from any other track in all our analyses regardless of how many nights had passed since tagging when a shortcut was made (Figure 1D).

Are these shortcuts novel? We only know what the bats did since we tagged them, so these so-called shortcuts cannot, in the strict sense, be considered novel because we cannot be certain that a shortcut is indeed the first incidence of this track in the life of this bat. But, with an average shortcut occurrence of 37 nights after tagging and an astonishing maximum of 158 nights, we can certainly say that the bats show superb map-like

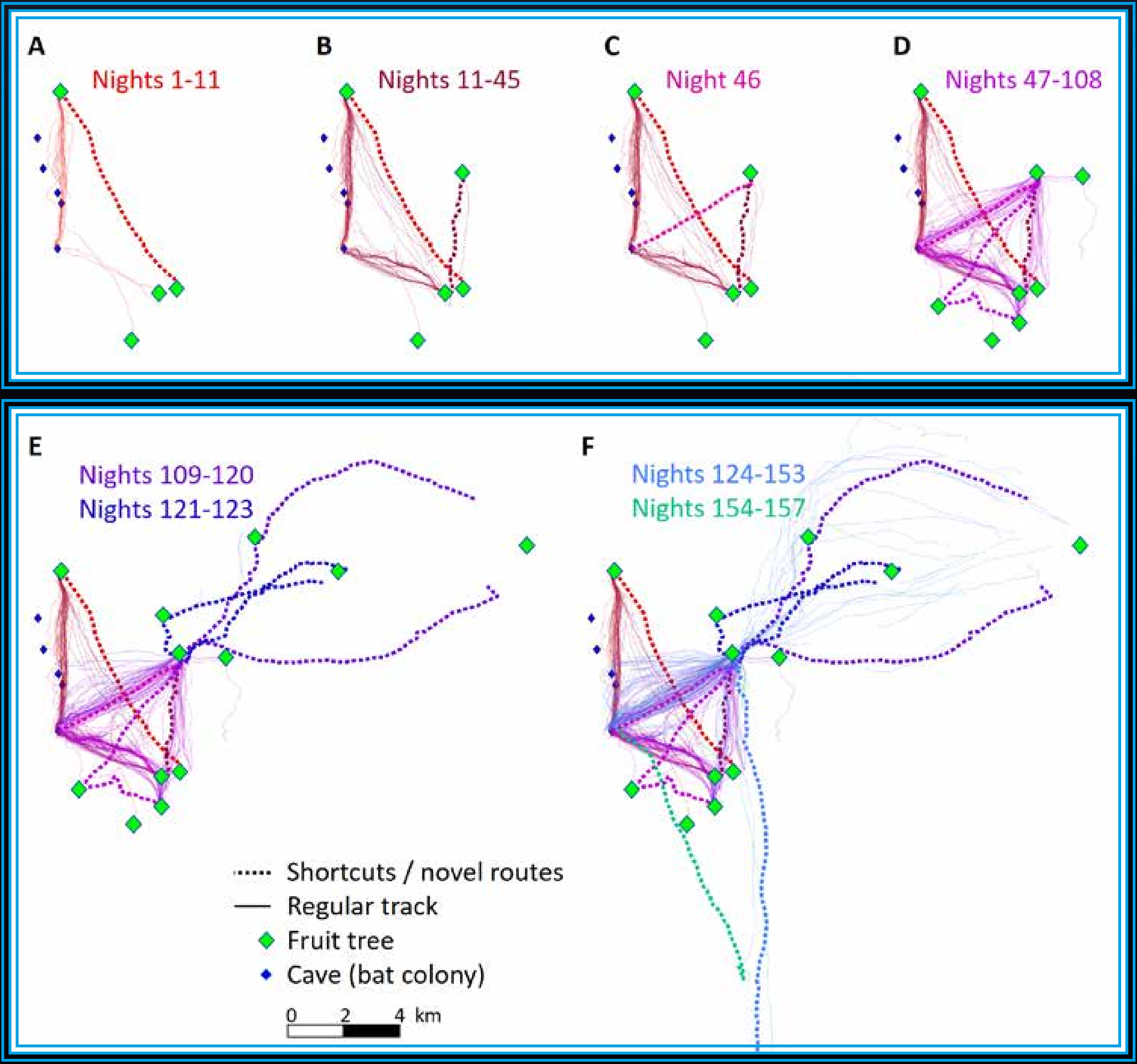

Figure 2. 157 full nights of one bat. Thin complete lines are regular tracks, thick dotted lines are shortcuts. Each panel shows, in a different colour, the additional flight tracks made by the bat in the nights from the previous panel up to the night in which a new shortcut was made. Thus, each colour group of nights and tracks ends with a shortcut. Blue diamonds mark the 5 known bat caves in the study area. Green diamonds mark fruit trees this bat visited during the tracking period. Lines not ending in a cave or tree went out of ATLAS range.

spatial knowledge and memory with no decay in navigation performance for at least 5 months. Interestingly, juvenile (3-8 months old) bats performed similarly to adults, suggesting that this map-like navigation ability is acquired already after the very first flight bouts of newly-volant pups.

Another group of scientists, working concurrently with us and independently, showed that Egyptian fruit bats do make strictly novel shortcuts. They used snapshot-GPS loggers to track 22 bats that roost in a lab (these bats roam free, but they are used to being handled by humans, so the loggers can be retrieved and recharged). This allowed them to track bats from their first flight outside and to thus demonstrate strictly novel shortcuts (Harten et al 2020).

Egyptian fruit bats are long-lived (25 years or more) and so are the fruit trees they feed on. The resource landscape they encounter throughout their long lives is patchy but stable and mostly temporally predictable. And so, it seems that these bats build a detailed "mental map" of memorized spatial features of the landscape and their positions relative to one another. This reasoning accords the "ecological intelligence" hypothesis explaining the high cognitive skills of frugivorous primates (Milton 1981) and birds. When coupled with excellent long-term memory of the locations of many different individual fruit trees, this map enables direct navigation to these trees and back home from any location in their ~1000 km2 home range. With cognitive map-based navigation, the bats do not need to randomly search for fruit trees every night – a costly, impractical, and unnecessary effort with a stationary and stable food resource. Rather, they can take the shortest, most efficient routes to a small number of trees (and back to their colony) for many nights in a row, until resources are depleted.

It seems that each bat remains loyal for years to favourite places that it memorizes, returning to them every season. Just like we do.

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Egyptian Fruit Bats: The Efficient Foragers

SUBMARINE NAVIGATION – THE STORY CONTINUES


PAGE 10

INTRODUCING THE RESILIENCE SERIES


PAGE 20

THE RIN FELLOWSHIPS AND AWARDS 2020


PAGE 14

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SEPT / OCT 2020

We're back at our offices – fully COVID-secure of course – @ 1 Kensington Gore, starting on Tuesdays and Thursdays only. Our doors remain virtually wide open at all times, but now physically open too. Long may it last!

Reflecting on the past five months of remote and virtual working, I am immensely grateful for all the can-do attitudes and positive energy that have allowed the Institute to do so much. We have built a video content library of impressive depth and breadth via multiple webinars; many special interest groups and branches have continued to be active; two full rounds of Committee and Council meetings have been completed, with strong focus on delivering the Institute's vision and the strategy; and we have conducted a virtual Annual General Meeting, including announcements of awards and Fellowships. Thank you to the RIN HQ team and many volunteers who have made this possible.

As of early August, more individual members have paid membership subscription renewals than was the case at this time last year. We have extended a helping hand to some members who are in temporary financial distress due to impact of the Pandemic; we have also been so fortunate to have a number of members able to add a voluntary donation when paying subscriptions, effectively directly supporting their peers. One corporate member has been lost due to the fall-out from the Pandemic; though we have been able to move most corporate members onto our new more flexible RIN Corporate Partner offer and are in discussion with a range of organisations who are considering becoming new RIN Corporate Partners.

Looking forward, I am not about to predict the next phases of the pandemic (!). I can, though, say with certainty that energy levels at the Institute are high and that we are planning much more in the way of webinars, including more debate-style interactive forums where possible, and more in the way of publications and other content. Our aim remains to bring diverse disciplines together to build insights and knowledge towards a more navigable world and we don't intend to let a global pandemic stand in our way!

Thank you, as ever, for your continued and active support of the Institute.

Best wishes,

John Pottle, Director RIN

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The cover image:
An Egyptian fruit bat.
Credit: Emmanuel Lourie

IN THIS ISSUE

FEATURES

REGULARS