# Decision making in foraging bats

Yosef Prat[1,3] and Yossi Yovel[1,2]

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Foraging is a complex and cognitively demanding behavior. Although it is often regarded as a mundane task, foraging requires the continuous weighting and integration of many sources of information with varying levels of credence. Bats are extremely diverse in their ecology and behavior, and thus demonstrate a wide variety of foraging strategies. In this review, we examine the different factors influencing the decision process of bats during foraging. Technological developments of recent years will soon enable real-time tracking of environmental conditions, of the position and quality of food items, the location of conspecifics, and the bat's movement history. Monitoring these variables alongside the continuous movement of the bat will facilitate the testing of different decision-making theories such as the use of reinforcement learning in wild free ranging bats and other animals.

**Addresses**
[1] School of Zoology, Faculty of Life Sciences, Tel Aviv University, 6997801 Tel Aviv, Israel
[2] Sagol School of Neuroscience, Tel Aviv University, 6997801 Tel Aviv, Israel

Corresponding author: Yovel, Yossi (yossiyovel@gmail.com)
[3] Present address: Institute of Biology, University of Neuchâtel, 2000 Neuchâtel, Switzerland.

## Introduction

Bats offer an interesting opportunity for studying foraging decision making. Their immense diversity with ca. 1300 species abundant in different habitats all over the globe [1,2] and their flight-related high energetic demands [3–5] probably drove their many different foraging strategies, and wide diversity of food sources, from nectar and fruits to meat and blood. Their fast mobility allows them to move far and provides ample opportunities for foraging decisions [6•]. Bats exhibit multimodal navigation system [7] relying on vision and acoustics, and perhaps also on magnetic perception [8,9] and olfaction. Bats also demonstrate a variety of social structures [10•]

and social communication systems that enable different means of social information use [11–17]. The diversity of foraging strategies and the range of information acquisition mechanisms posit bats as an appealing mammalian model to the study of foraging decision-making.

With both immediate and long-term effects on the animal's wellbeing, foraging greatly affects the animal's fitness and thus requires adequate decision-making (Figure 1). The most fundamental decision might be when to forage, which depends on internal factors, such as fat reserves, and on external factors, such as the current weather. Other decisions include where to forage and whether to forage alone or to join others. These decisions occur on varying temporal and spatial scales. A migratory species has to decide once a year where to migrate to, while once it has arrived at the foraging site it decides daily (or continuously) whether to exploit familiar patches or to explore new ones.

The decision process must reasonably weigh current sensory input, social information, previously learned information, genetic or developmental predispositions (for example of food preferences) and environmental conditions. While the different sources of information available to a wild animal may be directly or indirectly estimated by researchers, and its performed actions can be measured (e.g. by tracking the animal), the decision process itself is generally unknown (Figure 1, center) and is thus often the focus of laboratory cognitive research.

## Inputs for foraging decision making – sources of information

### Direct sensory information

The immediate source of information for a foraging bat is its sensors. The fact that many bat species heavily rely on acoustics to find and consume food has drawn much attention [18]. Many studies demonstrated species-specific specialization of auditory production and perception to foraging ecology [2]. However, many bats combine complementary sensory modalities, primarily vision, with echolocation when foraging [19,20]. Due to the short sensing range of echolocation (up to dozens of meters for large objects [21]), many bats probably use vision for long distance navigation but also obstacle avoidance. How bats integrate vision with echolocation is still poorly understood. Egyptian fruit-bats (*Rousettus aegyptiacus*) were recently shown to transfer echo-based acoustic information into visual information [22]. Olfactory cues also play a role in food detection and identification in many fruit-eating bats [23,24] and other sensory modalities have not been yet thoroughly explored.

**Figure 1**
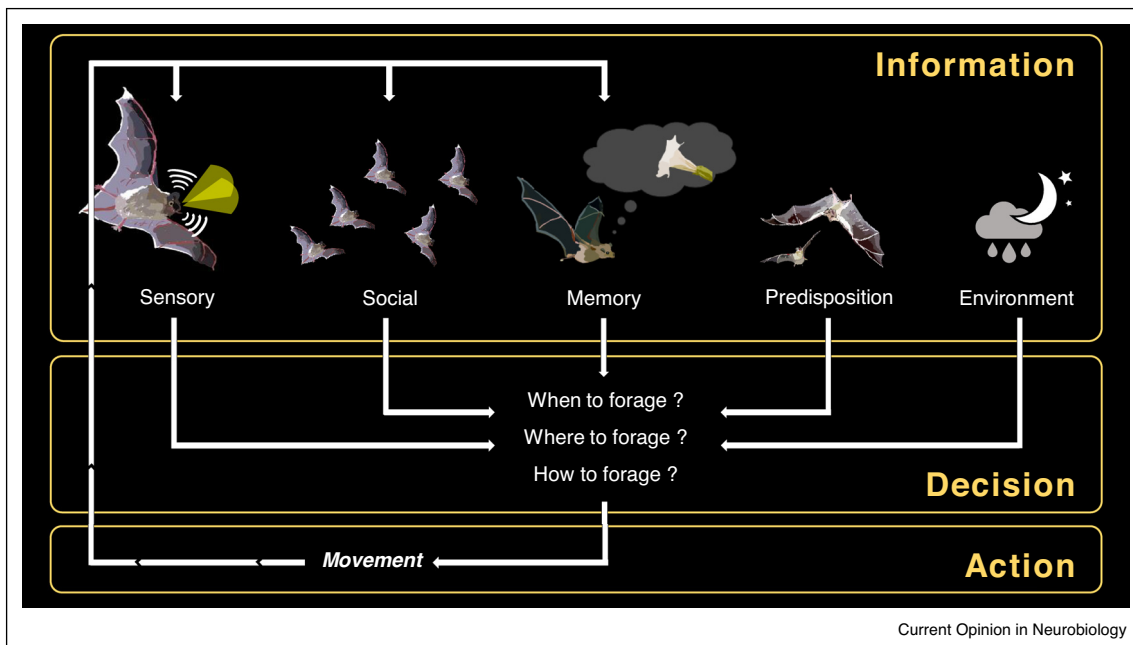
The foraging decision making framework.

Bats continuously integrate information from various sources: sensory cues about the location and quality of the food, social indicators such as the foraging behavior of conspecifics, memory of past foraging events, internal preferences (ontogenetic or genetic) for specific food sources, and current environmental conditions. The integration of this knowledge guides three main decisions: when to forage (now, or wait for better opportunities)? how to forage (i.e. what movement or social strategies to adopt)? and where to forage? These decisions ultimately define the bat's movement patterns. This is a recurring process: movement results in new information which in turn might require adjustment of decisions.

## Social information

Another important source of information comes from the social environment [25,26••]. Many bat species roost in colonies and forage in groups or in proximity to conspecifics. As bats constantly emit echolocation sound-signals to sense their environment and search for prey, public information is continuously broadcast, intentionally or not. For instance, when a bat is attempting to attack prey, it will emit typical series of echolocation signals [26••,27] which would then reveal the detection of the prey to any nearby conspecific [17,28]. Many types of insects (and other prey), can be found in dense, though ephemeral, patches. In this case social foraging is often beneficial for the individual bats, since prey detection becomes the bottleneck of the foraging, and the competition between conspecifics in a patch is relatively small. These situations should thus encourage social foraging [17,28]. An example of this behavior can be seen during the summer in northern Israel, where the greater mouse-tailed bat (*Rhinopoma microphyllum*) feeds almost exclusively on queen carpenter ants [29]. The bats search for the queen swarms across dozens of kilometers per night, and use social information in order to improve their search [30]. Another example is the Mexican fish-eating bat (*Myotis vivesi*), which preys on small fish in open sea (specifically, in the Sea of Cortez) [31]. The challenges

this bat faces, are quite similar to those confronted by *R. microphyllum*, namely, to locate ephemeral, but large, swarms of prey. Interestingly, the two species display similar social foraging strategies [32••].

Furthermore, bats can also acquire echolocation-based information about the presence of prey from hetero-specifics, and they will do so more readily when the hetero-specifics rely on similar prey [33]. Relying on conspecifics for enhancing food detection is not limited to insectivorous bats. The nectarivorous Pallas' long-tongued bat (*Glossophaga soricina*) has been shown to follow conspecifics in order to ease flowers detection [34].

Social interactions can also mediate learning of new food resources as has been shown in Seba's short-tailed bat (*Carollia perspicillata*) [35]. A similar behaviour was recently reported in the tent-making bats (*Uroderma bilobatum*) that adapt their feeding preferences according to social cues [36], but here, the bats were also shown to prefer food that was eaten by an unfamiliar conspecific [37], a strategy that is useful for increasing their fruit repertoire. Another case of food-related social learning was demonstrated in the fringe-lipped bat (*Trachops cirrhosis*) which feeds on anurans and detects prey by eavesdropping on mating calls. In the lab,

this bat could learn to associate palatable food items with novel calls [38], and even with artificial sounds [39], after observing the behavior of another demonstrator bat. Correspondingly, bat roosts and foraging sites probably serve as centres for different sorts of information transfer [14,26••,40,41].

## Memory

Bats generally possess highly accurate spatial memory. In some species individuals migrate thousands of kilometers and return to the same roost year after year [42]. Other bats return night after night to the same fruit tree located dozens of kilometers from their roost [43]. Bats also show excellent spatial memory at scales of centimeters [44–46]. When food location is predictable, and thus does not have to be searched for, spatial memory becomes more important than social cues. In fact, under such circumstances, which are common in fruit-eating bats, the main decision a bat makes might be whether to exploit previously visited fruit-trees or to explore new ones. The Egyptian fruit-bat feeds on a variety of fruit types and probably remembers the accurate position of many fruitful trees [43]. Indeed, Egyptian fruit-bats commute to their foraging sites individually without conspecifics [32••], even though they are constantly involved in social interactions in their roost [15,47], and often also on foraging trees [47]. As fruit trees exhibit annual periodicity and bats return to them yearly, it is intriguing to hypothesize that they possess some sort of an episodic-like memory remembering *what* trees are available at certain times (*when*) and locations (*where*) [7,48,49,50••,51]. Because these bats can live several decades [52], such a cognitive ability could be highly beneficial.

The location of insects can occasionally be predictable as well. For example, when insects appear in high densities at specific sites on a regular basis, such as in the case of Pipistrelle bats that hunt insects under street-lights. Another example is the greater mouse-eared bat (*Myotis myotis*) that gleans ground-dwelling insects such as carabid beetles [53]. Because their prey can be abundant in the same ground-patches over many nights (depending on weather and habitat conditions) *M. myotis* bats repeatedly use a small set of individually preferred foraging sites [32••,53], similarly to fruit bats [32••,43].

Nectarivorous bats may remember the locations of multiple food sources (flowering plants) which offer a limited, but replenishing, resource of nectar. In accordance with their need to remember the locations of multiple sources, these bats have been suggested to have an extremely developed spatial memory [54]. They do, however, face another type of decision: in what order should they visit these sources and how often should they re-visit them [55–57,58••]. Females of the lesser long-nosed bat (*Leptonycteris yerbabuenae*) face a similar challenge. They migrate every spring from central and southern Mexico

to the northern Sonoran Desert, where they aggregate in dense maternity roosts and forage on nectar, and then fruit, offered by columnar cacti [59]. The gravid females commute dozens of kilometers to familiar foraging locations, with high fidelity to foraging-areas between consecutive nights [32••,60]. Interestingly, *L. yerbabuenae* fly long distances towards foraging sites, even though alternative sites are available much closer to their roost, similarly to *R. aegyptiacus* [32••,43]. This behavior is probably related to the high density of the bats in their day roost, imposing high competition which might be resolved by spreading according to resource profitability as predicted by the ideal free distribution theory [61].

## Environment

Environmental conditions directly influence prey availability (e.g. [62]), but they also affect bats' hunting abilities. Atmospheric conditions may interfere with echolocation [63], and indeed bats have been suggested to avoid fog [64]. However, bats do forage in light rain [65] and the major effect of rain on bats' activity has been suggested to be due to the added energetic costs to body temperature maintenance [66]. On the other hand, bats usually do not fly in heavy rain. Playback sounds of heavy rain delayed the emergence of common big-eared bats (*Micronycteris microtis*) and Pallas's mastiff bats (*Molossus molossus*) from their natural roosts [67], demonstrating the use of this information for ad-hoc foraging decision-making. Environmental conditions also influence the bat's own predation risk. It has been suggested that bats reduce their activity when the moonlight is intense due to an increased predation risk (a.k.a. lunar-phobia). However, while true for some species (mainly frugivorous bats in the tropics [68]), other species are not affected by moonlight [68,69].

## Output of foraging decision making – movement and behavior

The output of the decision process, namely the movement, has been historically harder to track, mostly because of the small size of most bat species. However, recent technological developments boosted our ability to follow bats' foraging in the wild. Miniature on-board tracking devices now enable the collection of high-resolution spatiotemporal data (GPS), bio-acoustic recordings, micro-movement behaviors (e.g. with accelerometers), physiological conditions (e.g. electroencephalography (EEG) and heart-rate measurements), and environmental parameters (e.g. wind speed, light conditions, ambient noise) [70,71,72•].

These measurements allow researchers to uncover bats' choices under different conditions. For instance, *M. vivesi* and *R. microphyllum*, which both feed on ephemeral swarming prey (fish and ant queens, respectively), present similar patterns of foraging movement (Figure 2), namely, covering large volumes during social foraging [30,32••]. In contrast, *M. myotis* and *R. aegyptiacus*, which feed on predictable food (carabid beetles and fruit,

**Figure 2**



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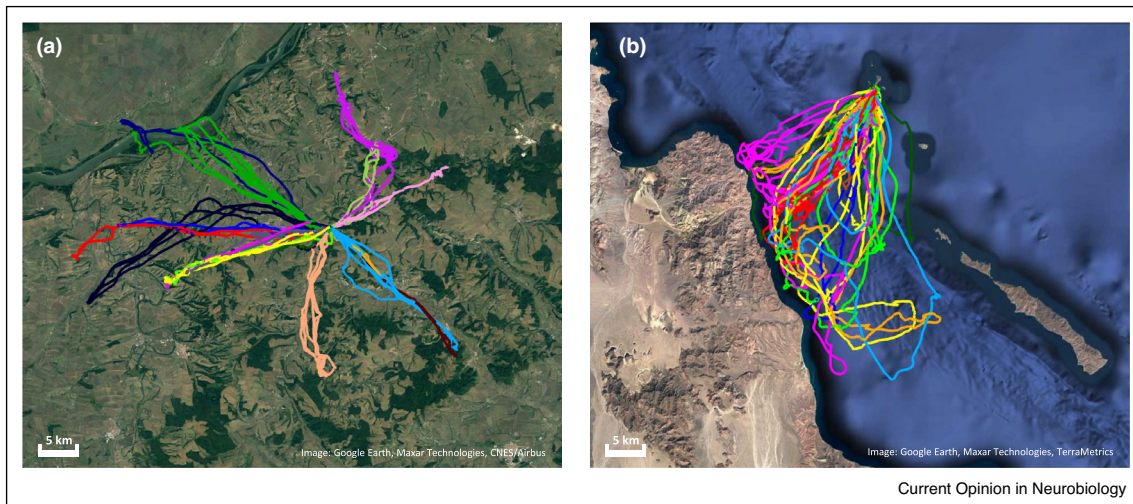
Food predictability determines movement patterns.
**(a)** A bat species feeding on food items with predicted occurrence, *Myotis myotis*, directly commute to their foraging grounds and then return directly to their roost. These bats mostly search for food in a solitary manner and return to the sane sites night after night. **(b)** In contrast, *Myotis vivesi* bats that feed on ephemeral prey, search for food in a more stochastic manner, covering much larger areas during foraging. These bats tend to forage socially. Colors indicate different individuals. Figures reprinted with permission from Ref. [32••].

respectively), demonstrate another type of foraging movement pattern: solitary (or socially independent) long commutes to specific known locations (Figure 2) [32••].

Analysis and modeling of such movement data will shed new light on the decision process itself in the near future. The field of movement ecology is growing rapidly [73] (we will not review it here) and is contributing enhanced analytical procedures to the understanding of foraging decisions.

## Decision making – the endpoint of learning

How an animal makes decisions is a subject of much interest. The process involves weighting information sources, including not only the current context but also historical accounts. Furthermore, rationality, or perfect utility maximization, is rarely observed (e.g. [74,75]). Decision making is tightly dependent upon learning, a process of which we know little about, and which many theories try to explain.

One of the main gaps in our understanding is the ontogeny of foraging decision making. How do young bats learn to forage? In many species of bats, the young forage independently within a few weeks, a period in which they must learn to control flight and echolocation [76]. The neotropical common big-eared bat (*M. microtis*) gleans large insects, such as dragonflies, from vegetation surfaces. In this species, mothers have been shown to provision their weaned young [77], a phenomenon that was rarely documented in bats. Since the large prey requires some expertise in handling it, provisioning of

young bats may facilitate the learning of this task. The presentation of the prey to pups, before they are able to capture it by themselves, can also help them create an acoustic image of this prey [77]. In a lab experiment, lactating *G. soricina* mothers were shown to transfer nectar to their young by regurgitation [78••]. Although such behavior may shape the young bat's food preferences, this kind of learning was not demonstrated. Many bats exhibit very long commutes to foraging sites. Such commutes have been demonstrated in *M. myotis*, *R. aegyptiacus*, *L. yerbabuenae* and others. How pups learn to navigate to the foraging sites and what is the mothers' role (if any) in this procedure is yet to be revealed.

Another gap is our lack of understanding of how momentary data acquisition translates to decisions. Observations of many animal species revealed that the decision-making can be sometimes approximated using simple rules [79,80•]. From the individual's point of view, optimal-foraging theory states that an animal should exploit a given patch as long as staying in it is more beneficial than moving to another average patch (i.e., the marginal value theorem [81]). These simple models indeed capture some of the economic essence of foraging, but their main deficit in describing animals in the wild is their assumption of an agent's complete knowledge. Animals often forage in stochastic environments, where food quality and quantity vary in space and time with some level of uncertainty. To cope with changes in the environment an animal needs to be able to continuously learn and adjust to its surroundings. Moreover, the animal's decision space is usually multidimensional: the quantity of the consumed food is only one factor it

has to evaluate, and many other elements, such as the nutritional value of specific items, also play an important role in foraging decisions. For instance, fruit bats that feed on a great variety of fruits, must choose between fruits of different nutritional values (e.g. protein-rich versus carbohydrate-rich versus fat-rich, etc.). Furthermore, simple decision models usually deal with the average individual, while differences in behavioral traits (i.e. personality) and in individual knowledge might greatly influence foraging decisions [82,83].

It has been postulated that considering foraging as a reinforcement-learning task, a well-established decision making framework, would enhance our understanding of animal foraging [84]. Much of the reinforcement-learning literature has been dedicated to learning and decision-making in various foraging tasks under artificial laboratory conditions, which narrow down the decision space. These studies revealed a wide-range of cognitive and psychological decision making phenomena [85], including the effect of social-learning [86–88] and risk-sensitivity [89]. Nevertheless, laboratory experiments are limited to very specific situations. Until recently, conducting controlled foraging experiments in the wild would have been extremely difficult and bounded with partial data. However, advanced data collection technology now paves the way to test individual foraging models, and specifically reinforcement-learning based decision-making processes, in the wild. We will soon be able to continuously monitor the location of a free-ranging bat, track its foraging decisions, estimate the nutritional benefits and the energetic costs of these decisions, and even evaluate the alternative (unchosen) foraging possibilities. These assessments will be facilitated by increased environmental data collection, for instance, using satellite and drone-based imaging, creating accurate three-dimensional maps. Moreover, the sharp improvement in movement data resolution makes it possible to manipulate resources in the wild. Such manipulation has been conducted, for example, on nectar feeding bats *Glossophaga commissarisi* [90] and with the development of real-time tracking acquisition, we will be able to manipulate individual bats. Moving our focus to the bat's natural environment will enable countless possibilities to pinpoint the evolutionary and ecologically relevant mechanisms that affect bats' decision making. Reinforcement learning paradigms, and other frameworks, that were developed for simple few-choice decisions will have to be adapted to deal with these interesting, but complex real-life situations.

## Conflict of interest statement
Nothing declared.

## Acknowledgements

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