

# Onboard Sensors Reveal New Insights into Animal Decision-Making

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## Keywords

animal behavior, behavioral ecology, long-term monitoring, field manipulations

## Abstract

The continuous process of decision-making in animals is crucial for their survival. For example, when deciding when, where, and with whom to forage, they need to consider their internal state, previous experience, and social information in addition to external factors such as food distribution and weather conditions. Studying animal decision-making in the wild is a complicated task due to the complexity of the process, which requires continuous monitoring of the examined individual and its environment. Here, we review the most advanced methods to examine decision-making from an individual point of view, namely tracking technologies to monitor the movement of an individual, the sensory information available to it, the presence and behavior of other animals around it, and its surrounding environment. We provide examples for studying decision-making during competition, examining the ontogeny of decision-making, and describing the importance of long-term monitoring and field manipulation for understanding decision processes throughout different life stages.

## 1. INTRODUCTION

Animals constantly make decisions across different temporal and spatial scales (Prat & Yovel 2020). Migratory species, for instance, must choose their navigation destination twice a year, and once they arrive at their destination, they must decide daily where to forage, whether to exploit familiar patches they relied on last year or to explore new ones, and if they decide to explore, they often have to determine whether to do so alone or by joining a group (van de Kerk et al. 2021). Sometimes, animal decisions need to be updated on the move. For example, an animal that fails to find food must change its strategy momentarily. To make effective decisions, animals must integrate and consider various sources of information, including current incoming sensory input, social cues, and previously acquired knowledge, and they are also affected by genetic and developmental factors (e.g., food preferences) and environmental conditions such as the food distribution (Levin et al. 2006) or weather conditions. This decision-making process involves weighing different factors and accounting for various trade-offs to optimize survival and fitness (Prat & Yovel 2020).

Animals make decisions as individuals (even when they are operating within a group), and thus, since the decisions of other individuals may affect an individual's decisions, it is preferable to study a group of individuals. However, despite the enormous advances in sensing and tracking technology in recent decades, studying individual animal behavior poses significant challenges, especially when doing so in the wild, where decision complexity is high. First, monitoring the same individual over extended periods while also tracking the resources available to it is extremely difficult. Second, monitoring the infinite number of environmental factors potentially affecting decision-making is impossible. Third, monitoring a substantial portion of a population on the individual level is challenging, resulting in a limited sample size and inadequate knowledge about social interactions and population dynamics. Finally, manipulating an individual in its natural environment to observe its response is seldom possible. These limitations severely constrain our ability to study how animals make decisions in the real world.

As a result of these limitations, decision-making has been traditionally studied indoors, where the animal is presented with a single (or a handful) of varying cues while keeping everything else constant (Budaev et al. 2019). In the few cases in which animal decision-making is studied outdoors, the animal is usually observed for short periods of time around the time of decision, but the history and/or future of this animal are unknown. In this article, we review the state-of-the-art advancements in animal tracking and sensing technology, highlighting how they could be used to study individual decision-making under natural conditions.

## 2. MINIATURE ONBOARD MULTI-SENSORS FOR STUDYING BEHAVIOR

Before discussing the actual questions that can be addressed with modern tracking technology, we present a brief overview of the available individual monitoring technology. With the miniaturization of electronics, global positioning system (GPS) or other position-tracking technology is now only one of many types of sensors that can be mounted on animals in the wild. Many additional sensors that provide complementary valuable information, allowing us to document the decision-making process, are now available, some of which include: (a) detailed movement sensors such as accelerometers and magnetometers (Nathan et al. 2022), (b) physiological sensors such as heart-rate (Sapir et al. 2011) and temperature sensors, (c) microphones, (d) social sensors [i.e., proximity sensors (Ripperger & Carter 2021)] that document the presence of nearby conspecifics, and (e) environmental sensors such as illumination or ambient temperature sensors.

Accelerometers and magnetometers have been shown to be useful for identifying the animal's behavioral modes (Nathan et al. 2012) (e.g., foraging, commuting, or resting). Such information can be important for understanding the animal's state when making a decision: Has it been resting

until now, or has it just finished foraging? Accelerometers have even been used to assess prey ingestion rates (Lok et al. 2023) and energy expenditure (Elliott et al. 2013) in birds and to detect infection in wild boars (Morelle et al. 2023). These sensors can also indicate the maneuverability capacity of an individual, which could be relevant when deciding whether to engage in a fight or to attack prey.

Physiological sensors can be used to monitor heart rates, muscle activity, or body temperature (Luo et al. 2021) and can provide valuable information about the animal's internal state, revealing its degree of fatigue and stress, all of which might affect its decisions. Physiological sensors can also be used to assess the energetic costs of an animal's decision (Halsey et al. 2011).

Microphones enable audio recordings, offering a method for monitoring interactions between conspecifics (Cvikel et al. 2015, Egert-Berg et al. 2018, Sørensen et al. 2018) and heterospecifics (Lewanzik et al. 2019), in addition to monitoring foraging success based on chewing sounds (Krivoruchko et al. 2024, Stidsholt et al. 2023). In the case of echolocating bats, audio recordings can also provide insights into the momentary sensorimotor decisions of the individual (Greif & Yovel 2019).

Proximity sensors allow the presence of conspecifics to be tracked and their distance to be estimated. GPS is mostly not accurate enough to infer social ties in groups with proximate individuals, and therefore, proximity sensors are often used as complementary sensors to report the presence of conspecifics in the animal's vicinity, as this can be a critical factor when making decisions for many animals, such as when monitoring mother-pup interactions (Ripperger et al. 2019). Unfortunately, most laboratory studies on decision-making isolate the focal animal, thus ignoring this very important factor (Gold & Shadlen 2007).

Ambient sensors can be used to monitor the environment in which the animal is operating, measuring, for instance, illumination or temperature (Chudnovsky et al. 2023), which may affect an animal's decisions. Below, we discuss the importance of completing the story by monitoring the environment with external sensors to provide additional information about the population and the environment and because, unfortunately, not everything can be measured from the animal's point of view.

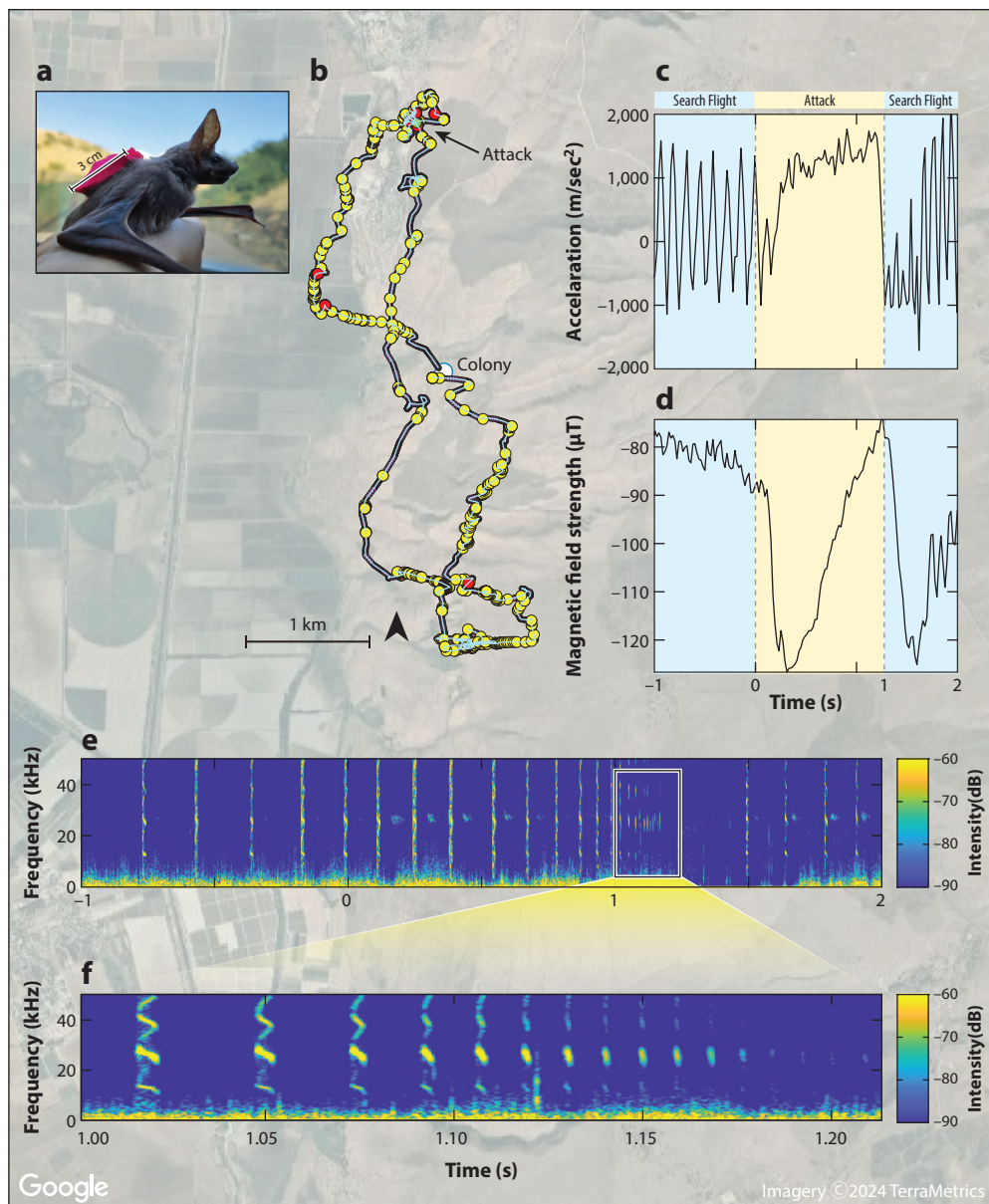
Next, we demonstrate how individual decision-making can now be studied outdoors at different levels using the abovementioned technologies while taking into account many of the covariates and relevant factors affecting it.

### 3. EXAMINING DECISION-MAKING FROM THE INDIVIDUAL'S POINT OF VIEW

Although movement alone can sometimes allow the study of decision-making (Strandburg-Peshkin et al. 2015), monitoring individuals' movements while collecting additional information, as described in the previous section, provides a unique opportunity to comprehensively examine various considerations in the decision-making process from the individual's point of view. In this part, we showcase a few fundamental questions related to decision-making that can be addressed using this methodology.

#### 3.1. Sensorimotor Decisions: How Sensory Input Facilitates Navigation

A major question in navigation is how sensory information is integrated and translated into movement. How do some migratory birds find their route when navigating halfway around the globe, often flying with little sensory information? In order to study this, in addition to tracking the animal, one must know what information is available to it. In the case of echolocating bats, analyzing the echoes received by the bat, which can be recorded using onboard microphones, can reveal how bats negotiate obstacles as they move (**Figure 1**). Video recordings onboard larger animals, as used



**Figure 1**

Greater mouse-tailed bats' foraging behavior was monitored using onboard sensors. (a) A greater mouse-tailed bat (*Rhinopoma microphyllum*) with a tracking device attached to its back. Photo provided by Lee Harten. (b) The flight trajectory of one individual during one night (light blue line). Attacks on prey were recognized based on their echolocation (i.e., interpulse intervals < 0.01 s) and are represented in the figure by yellow circles. Successful attacks were identified based on the chewing sounds that followed the attack and are represented here by red circles. The bat's (c) z-axis acceleration, (d) z-axis magnetic field strength, and (e) echolocation are presented for one unsuccessful attack. The location of this attack is indicated by an arrow on the map. The acceleration reveals how the bat stops flapping during the attack, and the change in magnetic field strength reveals a turn. (f) A close-up view of the echolocation during the final part of the attack.

to study foraging in New Caledonian crows, Adélie penguins, and Northern goshawks (Kane et al. 2015, Rutz et al. 2007, Watanabe & Takahashi 2013), can similarly be used to analyze and model navigation (Yoda 2019). An alternative approach is to use the trajectory of the animal to record or model the information available to it as it navigates through the environment (Menzel et al. 2019) (**Figure 2a**). Once recorded, sensory information can be fed into various models in an attempt to explain navigation (Baddeley et al. 2012, Goldshtein et al. 2022a, Guilford et al. 2004, Müller et al. 2018). In one such study, we flew a drone along the ~20 km route used by a fruit bat to record the visual information available to this animal during its daily commute. Using this information, we trained an artificial neural network, which allowed us to suggest how bats use visual information to navigate over dozens of kilometers (Goldshtein et al. 2022a). A similar approach was used to examine ant navigation (Baddeley et al. 2012).

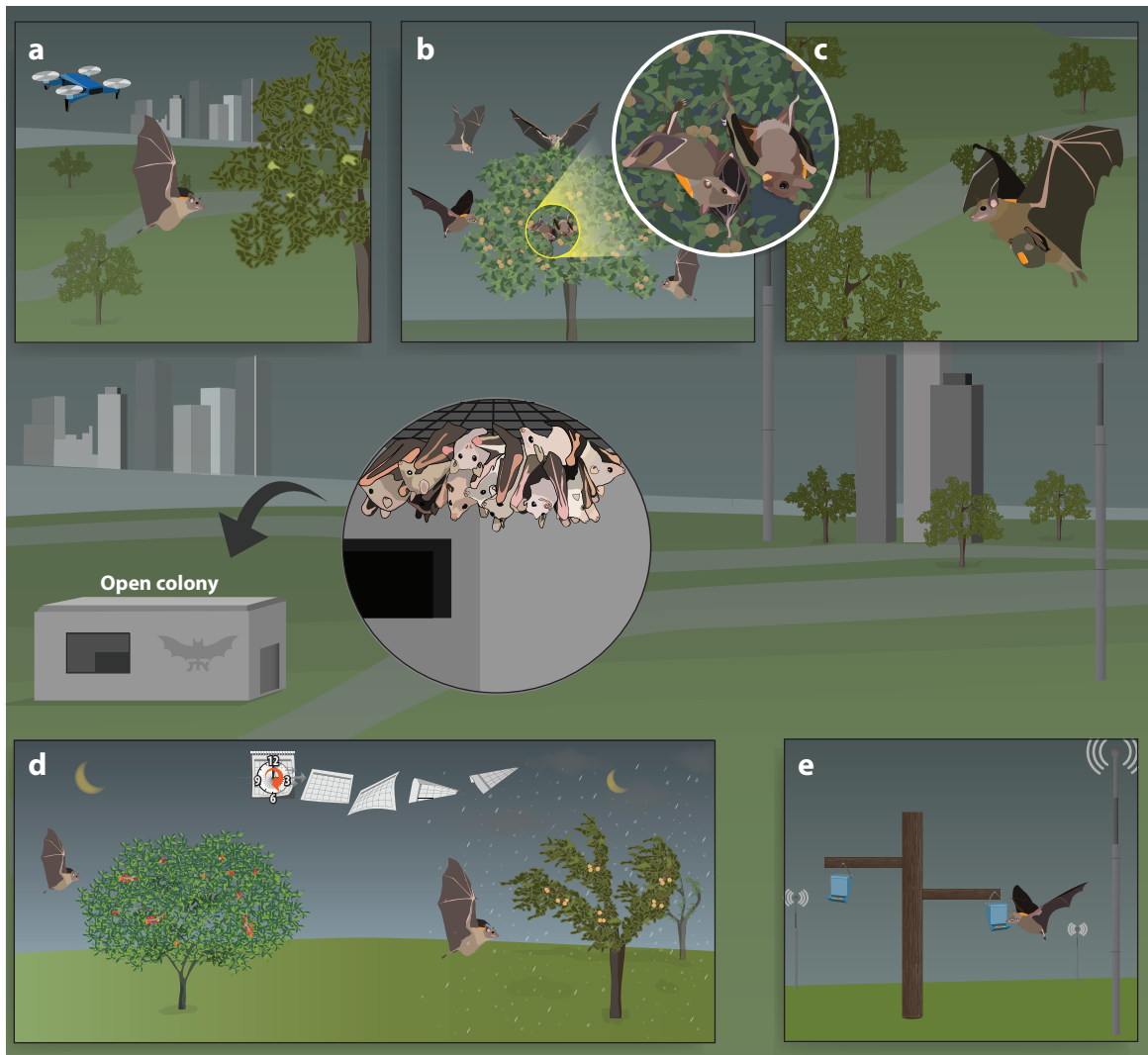
Insects are mostly too small to be tagged with active sensors (but see Fisher et al. 2021, Liégeois et al. 2016, Menz et al. 2022). However, harmonic radar transponders provide an alternative for tracking free-flying insects in the wild (Cant et al. 2005, Lihoreau et al. 2012, O'Neal et al. 2004, Woodgate et al. 2016). This approach enabled tracking of honey bees as they navigated hundreds of meters back to their colony after translocation experiments. Using their movement trajectories alongside models of their expected visual input allowed their decision-making during movement to be studied and revealed their navigational strategies (Menzel et al. 2005, 2019).

Measuring environmental conditions, such as wind velocity, can be crucial for understanding animals' decision-making. For example, monitoring migration departure time in addition to the local wind regime measured by local weather stations revealed how dunlins (*Calidris alpina*) time their departure according to the prevalent wind regime (Grönroos et al. 2012). However, understanding decision-making during commute or navigation requires high-resolution temporal and spatial environmental measurements that are usually impossible to obtain directly but can be estimated using detailed atmospheric models (Safi et al. 2013). For example, a detailed atmospheric model was used to show how straw-colored fruit bats (*Eidolon helvum*) compensate for wind drift (Sapir et al. 2014) and how European free-tailed bats (*Tadarida teniotis*) use uplifts to climb up to 1,600 m above the ground during their long daily commute flights (O'Mara et al. 2021). Such insights are crucial for understanding why volant animals fly at specific trajectories and the related energetic cost.

### 3.2. Sociality and Decision-Making Under Competition

Many animals must make foraging decisions while dealing with competition. Behavioral ecology has developed several models that suggest how they might do so (Dukas & Edelstein-Keshet 1998, Makin & Kotler 2019, Robinson et al. 2022). Recent advances in tracking technology allowed us to GPS tag the lesser long-nosed bat (*Leptonycteris yerbabuena*), a small nectarivorous bat, that forages in cacti fields while competing with conspecifics for energy-rich nectar. The challenge that these bats face is common to many other nectarivorous foragers (Garber 1988, Gilbert 1975, Gill 1988, Janson et al. 1981, Kadmon & Shmida 1992, Lihoreau et al. 2012, Stiles 1971), i.e., the food sources are fixed in place but ephemeral in time. In the specific case of the lesser long-nosed bats, the cacti, whose locations can be memorized by the bats, provide nectar over several weeks, with each cactus opening a different number of flowers every evening and thus offering a changing amount of nectar over consecutive nights. Moreover, these flowers are depleted and replenished during the night so that food is ephemeral both within and between nights. The bats must thus map the resources available to them on any given night and then maximize the exploitation of this resource while minimizing competition. Tracking the bats using miniature GPS devices showed that they start by exploring the field early in the evening to map and probably memorize a set of profitable cacti. We showed that bat behavior can be explained by assuming that they use a reinforcement





**Figure 2**

Studying decision-making in wild fruit bats. (a) Remote sensing can complement onboard tagging for studying decision-making. Drone imaging can be used to monitor food availability or to collect sensory input from the animal's point of view. (b) Tracking multiple individuals simultaneously (*orange tags*) allows the study of social aspects of decision-making, such as intraspecific competition and social communication. (c) Tracking mothers and pups simultaneously allows us to unravel the ontogeny of decision-making. (d) Long-term monitoring is crucial for understanding how early and ongoing life experiences affect the decision-making process. This includes questions on topics such as how foraging decision-making changes according to seasonal changes in food availability. In the background, an open colony provides a roosting place for the bats and allows them to forage freely in their natural environment, while also allowing us to routinely replace their tracking devices to overcome the difficulty of conducting long-term tracking of these small animals. (e) Real-time tracking systems now allow field manipulations, such as timed changes in the availability of food sources. These manipulations are critically needed to fully understand animals' decision-making mechanisms.

learning strategy to update the value of each cactus they visit. Explicitly, when a cactus provides more nectar than average, its value increases. Using this approach, each bat gradually converges on a set of cacti that they visit more often, a strategy that allows them to efficiently divide the resources (Goldshtein et al. 2020).

In this study, we combined onboard tracking with remote sensing: We used drone imaging to reconstruct the bats' foraging sites and to map the number of flowers that were open on each of the cacti in the fields where the bats foraged. This information was essential for interpreting the behavior of the bats.

Various remote-sensing methods, including satellite red–green–blue, hyperspectral imaging, light detection and ranging (Hermans et al. 2023), and synthetic aperture radar, provide information on available resources and can be used to map different properties of the 3D environment. Some of these active sensors can also be implemented on unmanned aerial vehicles (UAVs), such as drones, to provide higher resolution over smaller areas (Tuia et al. 2022). In addition to documenting resources, remote sensing can be used to monitor the entire population within which the individual is behaving and moving (Hodgson et al. 2018, Lyons et al. 2019, Wu et al. 2023). Recent advances in machine learning algorithms provide an opportunity to use drone-based videos to reconstruct the movement trajectories of all individuals in the scene, in some cases, together with their body posture (Graving et al. 2019, Koger et al. 2023). While the use of UAVs to record animal behavior is limited in time and space and should be done cautiously to avoid reaction to the UAV (Mo & Bonatakis 2021), it can provide unprecedented datasets to examine collective decision-making in the natural environment.

Examining the movement of animals in relation to their habitat's landscape is crucial for understanding movement decisions, particularly in terrestrial species. In another example, researchers tracked the movement of Olive baboon troops (*Papio anubis*) and created a 3D reconstruction of their habitat using drone imaging to examine how social ties interact with the local landscape to shape their collective. The study found that the baboons' movement decisions are primarily influenced by the previous trajectories of conspecifics and further demonstrated how the landscape's structure plays an important role in shaping the emergent social structures within the baboon group (Strandburg-Peshkin et al. 2017).

### 3.3. The Ontogeny of Decision-Making: Vertical Transfer of Knowledge

Another major question in decision-making is, How do juveniles obtain the information necessary to facilitate decisions, or more generally, how do they acquire knowledge about the world? Vertical information transformation from parents to offspring is one way to acquire knowledge, but this is very hard to study in the wild because both the parent and offspring must be monitored simultaneously over time.

By mounting GPS devices on both mothers and pups, we revealed that mother fruit bats place their pups on drop-off trees positioned approximately 0.5–1 km away from their colony before heading off to forage at farther foraging grounds each night. This behavior probably allows the pups to learn to navigate from the cave to one specific key location (the drop-off tree), from which the pups can start exploring the world independently, while the mother also assists them in returning to the cave at the end of the night. Indeed, when the pups are approximately 10 weeks old, they start emerging from the cave on their own, and when doing so, they first return to the same drop-off trees where they were left by their mothers. Using accelerometers, in addition to GPS, allowed us to confirm that when transferring the pups to the drop-off trees, the pups are always carried by the mothers and never fly behind them. This revealed that pups can learn navigating even without active self-experience (Goldshtein et al. 2022b).

This study also provided new insights into bats' abilities to reason. In one case, we observed a mother who returned to the cave at approximately 2 a.m., discovered that her already-independent pup was absent, and flew out again, heading directly to the drop-off tree, where she found the pup and brought it back to the cave (Goldshtein et al. 2022b). This behavior suggests a remarkable

ability to use deduction in her decision process. Although anecdotal, such observations provide valuable insights into the animals' cognition, and they are nearly impossible to obtain unless studying the system from the individual's point of view, as onboard tracking allows.

The Caspian tern (*Hydroprogne caspia*) is a migratory species that migrates in small family groups or alone and is therefore especially suited to disentangling vertical and horizontal information transfer about the migratory route. Researchers used a similar method of tracking parents and young to examine how young terns learn to migrate. They found that young birds usually spend their first migration journey with their father. Moreover, during the following navigation season, they use the same flight path and stopover locations as were used by their fathers, indicating vertical paternal, rather than maternal, information transfer (Byholm et al. 2022). Furthermore, information transfer is also essential for the success of the migration journey in some bird species that do not migrate in family groups, such as white storks (*Ciconia ciconia*), in which young birds cannot navigate by themselves and must follow experienced adults to accomplish the journey (Chernetsov et al. 2004).

## 4. LONG-TERM MONITORING

Long-term monitoring of animals over months and years is crucial for understanding how early and ongoing life experiences shape behavior and decision-making, how aging affects the decision process, and how animals incorporate information over multiple years when making foraging or migration decisions. Many behavioral patterns, such as where to lay one's eggs or where to migrate to, are probably shaped over the life of an individual, and many habits, such as which water hole or which trees to visit, are probably maintained and updated over the years. Long-term monitoring can also reveal insights into animal cognition, allowing us to address questions such as whether animals track time and whether they return to the same food sources at the same locations every year at the same time—an ability referred to as episodic-like memory (Harten et al. 2024).

### 4.1. Challenges and Solutions of Long-Term Tracking

Studying these questions requires long-term monitoring of individual animals. However, our ability to monitor the same individuals over long periods is limited, especially for relatively small-sized animals. The weight limits of the onboard sensors that are essential for monitoring the same individual over years dramatically restrict the size of the battery we can use. This, in turn, limits the data sampling rate and the life span of the tracking devices, constituting a major challenge for field biologists interested in the long-term monitoring of small animals. Using solar panels to recharge the battery is one approach used to overcome battery limitations with diurnal animals, but it cannot be applied to nocturnal animals. Nowadays, solar-powered GPS devices that transfer localization information via satellites or cellular networks are commonly used for tracking large diurnal animals over long periods without the need to recapture the tagged animals to download the collected data or replace batteries (Berthold et al. 2002).

Another approach to overcome the weight limitation is by using miniature sensors that provide relatively inaccurate data. One example is lightweight (0.3–3.3 g) light-level geolocators. These tags typically measure blue light intensity and, by following sunrise and sunset timing, provide an estimated location with a substantial error of ~200–300 km. Such devices are commonly used in researching the long-distance migration of small birds (Halpin et al. 2021, Phillips et al. 2004). The method requires tag retrieval and could be used to provide insight into migration-related decisions, such as choosing the timing and route of migration. Deciding when to migrate is critical for migratory animals, who must trade off the need to accumulate reserves before taking off on the long journey with the need to leave early in order to find and take over a good habitat at the



destination (van de Kerk et al. 2021). Additional sensors can be added to this device to monitor long-term acceleration, ambient pressure, temperature, etc., allowing researchers to identify different behavioral states, such as when a bird is standing, eating, and actively or passively flying (Nathan et al. 2012), as well as its flight height and body or environmental temperature (Sjöberg et al. 2021). Such an approach was employed to demonstrate the outstanding phenomenon of the Alpine swifts, which continuously fly for 200 days during migration, foraging, and resting (Liechti et al. 2013).

A major challenge of long-term tracking is logging the large datasets that are generated by the tracking device, such as those generated from monitoring acceleration at 50 Hz over a long period. One option to address this is to strategically plan the recording schedule to align with specific research questions, recording during predetermined parts of the day or activating the recording based on other less energy-demanding sensors crossing a threshold, e.g., initiating audio recordings only when movement is detected based on acceleration. Another solution that is usually employed for real-time tracking devices, where the data are uploaded via satellite or the internet of things (IoT) network (see Section 4.2), relies on calculating a proxy for the desired sensor instead of transmitting the raw recordings. For example, calculating the periodic sum of acceleration (e.g., overall dynamic body acceleration or vectorial dynamic body acceleration) as a proxy for activity level. This approach dramatically reduces storage space and transmission energy costs (Wild et al. 2023, Wilson et al. 2020), but note that this method should be carefully calibrated to estimate the accuracy of the measured behavior.

## 4.2. Studying Decision-Making in the Wild Using Long-Term Tracking

Here, we describe a few attempts to study individual decision-making over long time periods.

Long-term tracking was used to follow a white stork (*C. ciconia*) from when it was 3 years old in 1994 until it died in 2006, using satellite-based localization devices (Berthold et al. 2004, Kays et al. 2015). The researchers recaptured the stork multiple times over the years, retagging it again and again with improved tracking technology and better batteries that provided greater temporal resolution for extended periods. Eventually, the device was replaced with a solar panel-based GPS satellite device (Chernetsov et al. 2004). This technology allowed researchers to track the migration behavior of several populations of white storks over several years, revealing how individual experience (Flack et al. 2016) and external factors such as weather conditions (Berthold et al. 2002) and food availability (Chernetsov et al. 2004) shape migration decision-making in storks.

Long-term monitoring of a population can reveal variability in individuals' decision-making. Tracking 139 savanna elephants (*Loxodonta africana*), which are known for their large-scale movement, allowed interindividual variability in migratory behavior to be examined. Tracking the elephants over a period of 1 to 4 years revealed that they exhibit facultative migration behavior; 18% of the individuals migrated but not necessarily on a yearly basis. The timing of wet season migration corresponded with rainfalls and subsequent green waves; however, the timing of the dry season migration varied idiosyncratically. Such variation in animal behavior provides a great opportunity to examine individuals' decision-making processes, revealing what drives some individuals to migrate and what shapes such variation in a population.

Another impressive attempt to monitor a large population utilized short-term movement tracking of 600 wandering albatrosses (*Diomedea exulans*). Here, researchers gathered over 25 years of data and used long-term annual monitoring of an entire population, which has been ongoing since 1966. This comprehensive monitoring offered an opportunity to explore how internal states such as age and reproductive status affect foraging decision-making in the wild. For instance, it was

found that young juveniles foraged in tropical and subtropical warmer waters with calm winds near the northern border of their distribution range, while older individuals foraged in cold Antarctic waters. Complementing the tracking data, stable isotope analysis allowed the identification of the different food sources the albatrosses rely on (Weimerskirch et al. 2014).

Long-term monitoring can also assist our understanding of how an individual's experience affects decision-making. Orchan et al. (2016) examined whether stone curlews (*Burbinus oediacnemus*) use the map and compass strategy during true navigation, i.e., navigation from an unfamiliar location, and the role of previous experience when solving the same navigation task. First, they tracked a few individuals using high-resolution GPS devices for over a year and showed that their home range spans over 3 km from their nest. Then, they translocated the birds to unfamiliar remote locations, located 30–100 km from their nest, and examined their flight trajectories during their journey back to their nest. A few weeks to months later, after the birds returned home, they retranslocated the same individuals to the same remote locations. They found that translocated birds first conducted a relatively long tortuous wandering phase and then switched to a short return phase, in accordance with the map and compass theory. They further showed that during the second translocation experiment, experienced birds conducted the same two-phase movement pattern; however, this time, the wandering phase was shorter and spread over a smaller area, and the return phase was conducted over a shorter or straighter flight path. These results suggest that the wandering phase facilitates a learning process and that previous experience eases the navigation decision-making process (Orchan et al. 2016).

Long-term monitoring also contributes to our understanding of animal decision-making in light of global anthropogenic changes. Such changes usually occur over long timescales and require long periods of monitoring before and after the change in order to understand how animals respond to environmental changes. This approach was adopted, for example, to investigate the behavioral changes of lesser black-backed gulls (*Larus fuscus*) in response to landfill removals. Using long-term GPS tracking before and after landfill removal, researchers demonstrated how the gulls switched to a new habitat and the extra movement effort they invested (Langley et al. 2021).

### 4.3. Using an In-House Wild Bat Colony to Overcome Long-Term Tracking Challenges

An innovative approach we have taken to overcome some of the limitations related to battery size is to establish an in-house colony of wild Egyptian fruit bats. These bats naturally roost in man-made structures in urban environments, allowing us to convert one of our lab rooms into a dark, cave-like environment that is open to the outside and enables the bats to roost and fly out for foraging. We took advantage of the bats' philopatric nature, which indeed motivated many of the bats to adopt the open colony as their roost, living within it for years. This daily access to the same individual bats allowed us to use small logging tags and replace them every few days to continuously monitor the same individuals over long time periods (Figure 2).

We used this setup to continuously monitor young bats over many months from birth to adulthood. With full knowledge of their movement history, we were able to demonstrate that the bats use novel shortcuts through unfamiliar paths when navigating, suggesting that they possess a cognitive map-like representation of their environment. We also demonstrated immense behavioral and movement-related interindividuality, which translated into interindividual differences in exploration and, accordingly, in mapping and navigation capacities (Harten et al. 2020). The setup also allowed us to examine bat behavior under controlled laboratory conditions and compare it to the foraging strategies and decision-making of the same individuals (Harten et al. 2021) and demonstrate the bat's ability to track temporal patterns in its environment (by tracking the bat's choice of various fruit trees, we will be able to examine whether they track tree phenology) (Harten

et al. 2024). Future work should focus on several key aspects of decision-making, including: (a) manipulating bats' experience and observing the effect on their decision strategies (there are many ways to affect an individual's experience, such as exposing it to a more or less enriched environment before releasing it), and (b) monitoring changes in decision strategies over time (some of the bats have been roosting in the open colony for more than 5 years now, so by examining their foraging yearly we can document age-related changes in decision-making).

## 5. FIELD MANIPULATION

In order to fully test and validate hypotheses on animal decision-making, it is often necessary to go beyond simple observations and include manipulations of the tracked individual and/or the environment. Doing so in the wild with freely behaving animals is challenging but becoming more and more feasible thanks to modern technology.

### 5.1. Manipulating the Animal Before Tracking

Because it is not easy to manipulate an animal that is freely moving outdoors and whose location is hard to predict a priori, a common way to examine the decisions of animals under a specific manipulation is to manipulate them before releasing them and then record their behavior and movement in response to the treatment.

In one such example, Aplin et al. (2015) trained Great tits (*Parus major*) that were brought into the lab to open a feeding device by pushing a small wooden door. They created two groups of birds with different preferences—to push the door from right to left or vice versa. The birds were then released back to the wild and allowed to voluntarily visit similar feeders that were placed in various locations in the forest. The tits maintained their directional (i.e., right or left) door opening preference in the wild, and new birds that were not part of the captive experiment but observed the birds adopted the same culture of preferred pushing direction as the birds they observed. This study nicely demonstrated the importance of cultural transmission in decision-making under fully natural conditions. In this study, the authors did not continuously track the animals and examined them only at the feeding sites, but new miniature technology available today would enable tracking of the birds to reveal more of their interactions and how they affect decision-making (Aplin et al. 2015).

Manipulating the animal before release is common in navigation studies, especially those aiming to examine which sensory modality facilitates navigation. In homing experiments, animals are translocated away from home and released, often after some sensory manipulation. For instance, the magnetic field experienced by the animal is rotated (Holland et al. 2006) or olfaction is deprived (Pollonara et al. 2015) to examine magnetic or olfactory-based navigation. The animal's journey back home is then tracked to unravel how the available sensory information affects their navigation strategy. Notably, rotation of the magnetic field and other manipulations of different sensory modalities can also be done when studying long-distance migration (Cochran et al. 2004).

### 5.2. Manipulating the Animal's Food Source While Tracking Decision-Making in the Wild

Even if the full movement of the animal is difficult to predict, often some of its foraging locations can be manipulated based on prior observation. For example, Nachev et al. (2017) examined the coevolution between flowers and their bat pollinators. They manipulated the foraging behavior of free-flying Commisaris's long-tongued bats (*Glossophaga commissarisi*) using electronically controlled nectar feeders that dynamically evolved in real time, according to the foraging decisions of the bats—i.e., the electronic flowers in the experiment offered different sugar concentrations, and the flowers that were visited more often by the bats were more frequently represented in the next

generation. Thus, bats' decisions had an effect on the evolution of sugar concentration, demonstrating how decision-making in a complex environment might be important on an evolutionary scale.

### 5.3. Real-Time Monitoring

Several new technologies now allow nearly real-time tracking of animals on a large scale, thus facilitating real-time manipulations to examine dynamic decision-making.

Reverse GPS systems [such as advanced tracking and localization of animals in real-life systems (ATLAS) (Nathan et al. 2022, Toledo et al. 2020)] require the establishment of an array of antennae but then allow animals to be tagged with lightweight and long-lasting tags that provide the location of the animal in real time. Another relatively recent approach for monitoring large-scale movement for extended periods utilizes a low-powered network, such as the Sigfox IoT network, which is deployed worldwide to track animals in real time. This technology currently provides localization accuracy of ~10 km (but it can be improved dramatically according to the number of available antennae), it does not require tag retrieval, and it is not limited to tracking diurnal animals. Here as well, external sensors can be added to the tags (Wild et al. 2023). It should be noted that, due to their limited bandwidth, these systems can mostly provide online location and periodic sum of acceleration data, while any additional information needs to be stored and downloaded either by retrieving the device or by coming near it.

Combining these tracking methods with automatic feeders that allow the available foraging resources to be manipulated based on the detection of specific individuals can be used to close the loop and examine specific foraging decision-making models with carefully planned and precise manipulations. In addition to manipulating the resource, a few other manipulations that can be performed include (a) eliciting playback of conspecific or heterospecific vocalizations to examine the effects of intra- and interspecifics' presence on decision-making; (b) manipulating a distinguished environmental feature or a set of landmarks that are located near the feeders, such as a light source, to understand which sensory modalities animals use to locate and navigate to this food source; and (c) examining the animal's response to a controlled interference such as human and predator presence, noise, and even artificial weather events to examine their decision-making in an unpredictable environment.

Real-time tracking has additional advantages, such as assisting in the protection of endangered species when abnormal activity is reported or when the animal enters a hazardous area such as a wind turbine farm (a strategy known as geofencing). Such an approach was demonstrated during efforts to protect Griffon vultures (*Gyps fulvus*) (Acácio et al. 2023).

## 6. MAJOR CHALLENGES AND FUTURE DIRECTIONS

Some of the main challenges that have to be overcome to further improve our ability to advance the field include the following:

1. Smaller, high-resolution loggers need to be developed. Despite the advances described above, most animals, including many vertebrates and nearly all arthropods, cannot be tracked using onboard sensors today due to weight limitations. In many cases, even if the animal is large enough to be tracked, data collection must be sparse due to battery limitations. In such cases, novel data processing and AI algorithms might help narrow the data gap. Additional tag improvements include remote download of large datasets, real-time tracking, onboard power charging, and additional sensors. Hand in hand with the development of tags, the impact of the tags needs to be further examined to assess their safety for the animals carrying them. These efforts should include safer methods to mount the tags temporarily.

2. Individual cognition and personality need to be connected to behavior in the wild. Most studies on animal behavior in the wild describe animal behavior according to its average and mostly ignore the variability (except for reporting the variance). Yet, ample evidence has been accumulated showing that individuals behave consistently differently and exhibit individual levels of cognition. Indeed, the rare examples where individual cognition was assessed revealed novel insight into the drivers of behavior (Heathcote et al. 2023).
3. Methods are required to track large groups and large parts of populations. Sociality is clearly a main factor in decision-making. Tracking large groups (Roeleke et al. 2022) or, when possible, most of the individuals in a population of wild animals would thus likely shed new light on their behavior. Long-term tracking of social ties has already proven insightful in predicting social decisions (Roeleke et al. 2022). Yet, currently, most studies of individual tagging focus on very small parts of the population. Among others, one serious bottleneck currently limiting such studies is the high cost of many of the tracking devices. One solution would be using remote sensing (e.g., radar) to track the population while mounting tags on a subset of it.
4. Tracking multiple species in the community would provide valuable information. Currently, nearly all tracking studies focus on a single species, but animals never operate in a vacuum. One interesting direction would be tracking both individual predators or parasites and individual potential prey. In most cases, this would require the application of different tags for the two taxa.
5. Remote-sensing and mapping data need to be updated. This review clearly demonstrates the essentiality of external data for the interpretation of animal decisions based on their movement. Some examples include accurate 3D mapping as well as mapping of various climate, pollution, and vegetation parameters and their current states. Obtaining access to maps with such high spatial–temporal resolution can dramatically advance the field.

## 7. DISCUSSION AND SUMMARY

In this review, we summarize the importance of studying individual decision-making using novel miniature sensors and advancements in this field. However, sophisticated technology is not enough. Many of the sensors mentioned above generate immense amounts of data that are logged on local storage, and even the best sensor is worth nothing if the data cannot be retrieved. Since we are still far from developing devices weighing less than 1 g that can store high-resolution data and allow satellite-based remote download, we must complement the onboard sensing approach by choosing a good model animal. Such a model should exhibit the behavior of interest while also allowing data collection and retrieval. It should be big enough to carry the relevant payload and be accessible to allow downloading of the data. Data retrieval can be done by recapturing the animal, collecting the device after it falls off the animal in the roost, or using some sort of low-energy remote download (e.g., Bluetooth). Tracking breeding individuals that maintain roost fidelity can simplify data collection, but it must be done with caution to avoid disrupting the animals' breeding behavior.

Egyptian fruit bats, which we mostly focus on in our research, offer several advantages: (a) They are small but large enough (~150 g) to carry a payload of several grams; (b) they show high philopatry, returning to their home roost where they can be recaptured to download the data; and (c) they exhibit interesting spatiotemporal behaviors and advanced cognitive capabilities, for example, memorizing the locations of dozens of fruit trees whose quality changes over time.

Understanding animal decision-making is also crucial for their conservation. Multiple decisions, such as which areas should be protected and how to regulate anthropogenic development, depend on animals' reactions to possible changes in land use. Without a better understanding



of how animals respond to changes, it will remain difficult to advise policymakers and other stakeholders involved in the preservation of the animals' habitat.

In conclusion, by taking advantage of our technological era and combining data from multiple sources, we can gain a more comprehensive understanding of the complex processes underlying animal behavior and decision-making in the wild. This understanding is also crucial for conservation efforts in light of the rapid ongoing global changes.

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