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Tracking technologies: advances driving new insights into monarch migration

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Understanding the rules of how monarch butterflies complete their annual North American migration will be clarified by studying them within a movement ecology framework. Insect movement ecology is growing at a rapid pace due to the development of novel monitoring systems that allow ever-smaller animals to be tracked at higher spatiotemporal resolution for longer periods of time. New innovations in tracking hardware and associated software, including miniaturization, energy autonomy, data management, and wireless communication, are reducing the size and increasing the capability of next-generation tracking technologies, bringing the goal of tracking monarchs over their entire migration closer within reach. These tools are beginning to be leveraged to provide insight into different aspects of monarch biology and ecology, and to contribute to a growing capacity to understand insect movement ecology more broadly and its impact on human life.

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Introduction

Many questions remain open about how monarch butterflies make their annual North American migration, such as how they navigate to precise locations, what specific conditions trigger migratory phenotypes, or how they utilize certain landscape features along their trip. Bottom-up approaches have been used to identify monarchs' general orienting strategy, the cues relevant for orientation, and the neurological basis of orienting (reviewed in [1]). Studying monarchs in their natural settings gives us critical insights into the environmental, climatic, and landscape variables that control migration dynamics and strategy. The goal of this brief review is to present an overview of the methods that have been used for investigating monarch movements, as well as to introduce new developments that promise to give us unprecedented access to different aspects of this iconic journey.

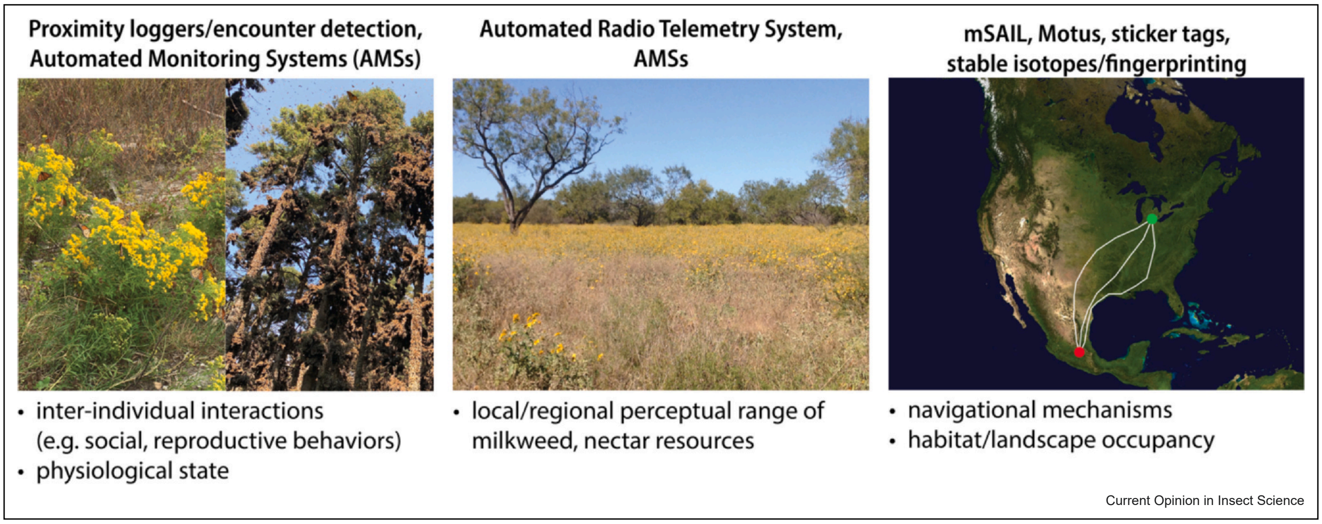
Bottom-up approaches to understanding monarch migration

Classical techniques for studying monarch migratory behavior, including disappearance bearing [2], flight mills (e.g. [3,4]), and the Mouritsen-Frost (MF) flight simulator [5], are being updated to uncover additional insights into migration and orientation mechanisms. Successful demonstration of a noninvasive tethering technique [6] and indoor operation [7] expands the utility of the MF simulator, enabling longitudinal behavioral assessment and year-round testing. New approaches are augmenting the study of monarchs in controlled environments. Tracking monarchs in large arenas or pressure chambers [8–10] or in virtual reality environments [11] will facilitate new research on monarch flight kinematics and potentially uncover additional unique migratory behavioral traits. As well, these methods will prove useful for evaluating novel tracking technologies as they are increasingly applied to monarchs. Neuroanatomical mapping of the monarch brain [12,13] has opened the door to electrophysiological recording from behaving monarchs in light-emitting diode (LED) arenas [14,15]. Methods to conduct wireless neural activity recordings in freely behaving insects are being developed [16–18]. Pairing these methods with new ways to dissect molecular and genetic function in monarchs [19] will reveal the neural, genetic, and environmental basis of migration and navigation.

Monitoring monarchs on local/regional landscapes

While miniaturization of radio-based tracking devices has enabled their widespread use on different insect species for over thirty years (reviewed in [20]), they have only been applied to monarchs relatively recently (in 2012 by Martin Wikelski and Chip Taylor, National Geographic Resource Library). Very high frequency radio telemetry (RT) has proven promising for understanding monarch movements on local landscape scales. RT transmitters/transponders use active radio transmission, forcing trade-offs between weight, power, and signal range (batteries

Figure 1



Different tracking technologies and their potential use in understanding monarch behavior and migration across local (left), regional (middle), or continental (right) scales.

required to power units and increase signal range lead to increased tag weight). They tend to have moderate signal range (< 1 km), requiring tagged individuals to be followed with receiver antennae carried by hand, mounted on small planes (e.g. [21]), or even carried on unmanned aerial vehicles [22–24]. RT tags have been used to track monarch breeding season resource use [25], estimate local flight paths [26], and estimate host plant and nectar resource perceptual range [27]. Fisher and Bradbury [28] implemented an automated radio telemetry system (ARTS), an array of stationary, directional antennas, to localize individual monarchs carrying LB-2X transmitters at relatively high temporal resolution (per min).

New approaches are being developed that will expand our ability to study monarchs on local or regional landscape scales (Figure 1). Proximity loggers/encounter detection (e.g. Encounternet [32] or Broadly Applicable Tracking System or BATS [30]) presents exciting opportunities for studying social networks and even physiological state, which may further research on monarch mate preference [29] or open new research on the role of sociality in monarch migration, which is relatively little explored. Proximity tags or 'mobile nodes' have very recently been sufficiently miniaturized for use on insects, including monarchs (BluMorpho tag, Cellular Tracking Technologies). As RT tags become smaller, reverse global positioning system (GPS) methods (e.g. Advanced Tracking and Localisation of Animals in real-life Systems or ATLAS [31]) show promise for tracking multiple individuals at high temporal resolution ($\sim sec^{-1}$) on regional (10–100 s km^2) scales for long periods of time (many months). Regional-scale tracking can be combined with agent-based models to determine monarch movement algorithms (as in [33]). These methods will allow us to understand how local location-based decisions are made (e.g. navigating between milkweed patches in spring and summer or choosing specific roosting sites during fall migration) or how interindividual interactions may shape monarch ecology.

Automated monitoring systems (AMSs) are increasingly being used to study real-time dynamics of local ecological communities (reviewed in [34]). A major benefit of AMSs is that they do not require individual tagging, which not only eliminates the miniaturization problem, but also substantially increases the number of individuals that can be analyzed at a reduced cost. AMSs use images, radar, lidar, or acoustic signals to detect individual insects and infer certain characteristics about them such as size, behavior, and so on [35,36]. Computer vision approaches are especially attractive, as they have the potential to gather information on species' identities, abundance, behaviors, and interactions [37]. The identification problem for these methods, which often requires labor-intensive manual annotation, is still quite challenging, limiting their resolution. Algorithms enabling active learning or even fully automated video-object segmentation and tracking in natural settings are currently being developed (reviewed in [38]). AMSs are necessarily spatially restricted, however, and thus are most useful for monitoring specific locations of predetermined interest.

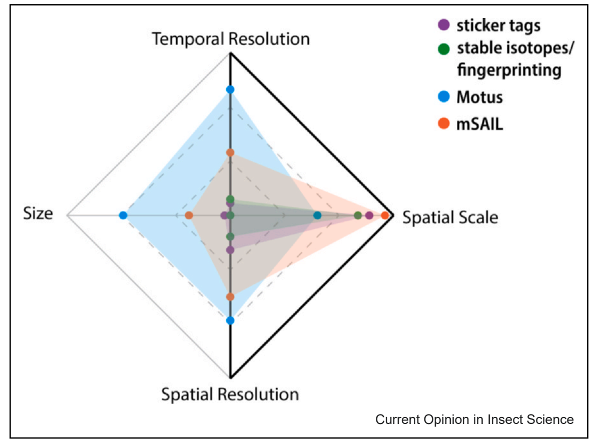
Altogether, these methods will provide increasingly accurate estimates of monarch movement ecology and habitat use, such as perceptual range, step length, and local directionality. These measurements are required to inform agent-based population simulation models that will prove invaluable for conservation practice [39].

Monitoring monarchs at continental scale

Tracking migration paths of individual monarch butterflies has been of interest to monarch biologists for over half a century [40]. Citizen scientist-aided sticker tagging efforts have led to important, sometimes surprising [41], insights into monarch paths (e.g. [42]) and dynamics. Taylor et al. [43] combined over a decade of monarch tagging data with environmental data to predict determinants of migratory flight dynamics. Chemical identification methods have also provided invaluable information on monarch biology and migration patterns. Cardenolide fingerprinting uses thin-layer chromatography to profile milkweed-derived cardenolides that are stored in adult bodies. These profiles can be used to determine natal origins of monarchs (e.g. [44]), or, because different milkweed species show different phenologies across their range, to infer monarch movement patterns across their life cycle (e.g. [45–47]). Correlations between stable isotope (δD and $\delta^{13}C$) ratios in milkweed and adult wings reveal the natal origin of monarchs [48]. This method has been used to demonstrate broad panmixia across the Mexican overwintering sites [49] and to track multigenerational recolonization patterns [50]. The utility of chemical methods is being extended to understand monarch movement ecology, such as using isotopic tracing to study nectaring patterns during migration [51] or combining fingerprinting and stable isotope analysis with genomic sequencing to infer possible alternative migration routes [52]. While these tools provide unique advantages — these signatures are permanent, which enables analysis of historical samples, and they allow for direct assessment of ecological parameters, for example, feeding behavior — they lack spatial and temporal resolution to understand finer-scale continental movements. Methods are being developed to address this gap, such as next-generation radar, which aims to detect group-level monarch abundance, orientation, and velocity [53], but at the cost of individual-level information.

The two primary challenges for automated insect tracking — tag miniaturization and accurate, efficient global-scale positioning — present trade-offs that make a comprehensive solution difficult to achieve (Figure 2). High-resolution, precise positioning requires collecting and transmitting large amounts of data. Data storage, processing, and transmission require physical space and power, which necessarily make tags larger. The smallest insect tags are passive radio transponders, such as harmonic radar or radio frequency ID (RFID) tags, which can reach as low as 5 mg in weight (~1% the size of a typical 0.5-g migratory monarch). These tags do not have data storage capacity, however, and must be in close proximity (~1 m for RFID and ~0.5 km for harmonic radar) of a local receiver in order to determine location. Given that monarchs have a nearly

Figure 2



Qualitative evaluation of methods to track individual monarch butterflies at continental scale (based on four indicated axes: spatial scale, spatial resolution, size, and temporal resolution). Distance along axes are approximations by the author. The optimal tracker would occupy the area (triangle) within the black border (i.e. maximal temporal resolution, spatial resolution, and spatial scale, and minimized size).

continental-scale distribution, determining location via these methods would require an impractical receiver network. GPS, on the other hand, the most precise onboard localization method, provides automatic position triangulation via satellite-based data storage and wireless communication (e.g. International Cooperation for Animal Research Using Space or ICARUS, https://www.icarus.mpg.de/en). GPS has unacceptably high-power demand, however, making units too big to be implemented on insects: the smallest commercially available GPS-based units are still 1–5 g (200–1000% monarch bodyweight). Ultimately, viable solutions for monarch migration trackers will achieve small size through 1) efficient power consumption and management and 2) efficient data collection, storage, and processing (Table 1). Energy savings that allow miniaturization have been achieved through novel circuit design, such as low-power digital CMOS design in [54]. Monarch trackers will also require sufficient energy harvesting since an individual monarch's migration will occur over several weeks. This has been achieved using solar energy harvesting (e.g. [55]), however, alternative sources may also be explored, such as piezoelectric transducers to generate energy from insect flight [56].

Geolocators, which use environmental conditions to estimate geographical locations, are useful positioning systems because the associated data collection is relatively low power since it does not require active data transmission or wireless communication (unlike GPS). As such, geolocators have been used for global-scale positioning for over three decades and have become increasingly common as they become smaller (reviewed in [57]). Light-level geolocators, the most commonly

Table 1

Comparison of sub-gram-scale tracking devices and systems.

Tracking system/transmitter	Coverage	Size (g)	Tracking lifetime (d)	Spatial resolution (km)	Proximity logging	References
mSAIL	Global	0.062	^60+	20–100	No	54, 58, 68
Lotek NanoPin (*Motus*)	~ Global (land)	0.13	7–29	*RD (~10 s)	No	64
Automated Telemetry Systems T15	Regional/local	0.15	7	*RD	No	-
Holohil LB-2X (*ARTS*)	Regional/local	0.27	12	*RD (0.01)	No	25, 28
ATLAS	Regional/local	1	10	0.005	No	31
BATS	Regional/local	1	8	0.004	Yes	30
Encounternet	Local	0.8	~1	RD*(0.002)	Yes	29

Specific transmitters are indicated in standard font and tracking systems (combination of transmitter and associated receiver network) are indicated in italics. Only the smallest reported sizes of the specific devices/systems are given. Many of these devices are available in multiple sizes and therefore have alternate specifications (e.g. increased tracking lifetime or increased receiver range). I note that one additional transmitter was released during press of this article (Cellular Tracking Technologies BluMorpho tag) that is not included in this table. ^Unpublished data from author and colleagues indicate continuous mSAIL operation for two months. *RD = receiver-dependent. These transmitters rely on a distributed network of receiver stations for localizing individuals rather than automatically triangulating position. Therefore, spatial resolution of locations is determined by the density of receiver stations and the signal reception range. A multitude of factors impact signal reception range, including antenna type and orientation, geography, electromagnetic disturbance, and so on.

used type, suffer challenges with accurate localizing at equinoxes, when day length is the same across the globe. As well, light-level data tend to be noisy due to weather, habitat, and behavior. New computational calibration methods are being developed to aid data analysis [58], including deep learning-based methods (e.g. [59,84]). Multimodal geolocators overcome the limitations of light data by combining different environmental sensing capabilities, for example, merging light intensity with sea surface temperature [60], air pressure [61], acceleration [62], or air temperature [59,84], to localize signals more accurately. Newer solutions such as Pressure, Accelerometer, Magnetometer (PAM) sensors simultaneously measure barometric pressure, acceleration, and local magnetic fields (reviewed in [58]). Despite their demonstrated promise in vertebrate systems, PAM loggers are still too large to be implemented on insects. Geolocator data still must be transmitted back to the researcher, however, requiring power-intensive wireless communication or tag recapture. Increasing complexity and volume of multidimensional datasets necessitates new solutions for efficient data acquisition, storage, and processing to keep units sufficiently small (reviewed in [63]). Internet of Things approaches are being implemented to overcome data-imposed challenges such as restricted battery life, memory space, and remote download capacity [64].

Despite these challenges, monarch-automated tracking efforts are now underway. Knight et al. [65] made an important advance by leveraging the Motus Wildlife Tracking System [66] to passively track monarchs tagged with the Lotek NTQB-1 VHF RT tags for up to hundreds of kilometers. Motus has been used to attempt to clarify the migratory capacity of captive-reared monarchs [67,68]. Although a viable solution for investigating local-scale dynamics, Motus transmitters are still likely prohibitively large (~200 mg, 40% monarch bodyweight) for efficiently studying the full migratory path. Although the transmitter signal range can be relatively large (15 km), a prohibitively expansive receiver station network would be required to encompass monarchs' entire migratory range. Lee et al. [55] combine innovations in energy autonomy, power management, data management, and wireless communication to develop a 62-mg (12% monarch bodyweight) RT multimodal geolocator called 'mSAIL'. mSAIL records and stores light and air temperature onboard, and data are downloaded from tagged individuals via a custom gateway at the overwintering sites. mSAIL has been tested on individual monarchs at known locations for a short period of time, but not yet across the entire migration. These technologies make important steps forward yet leave room for improvement by continued efforts to miniaturize tags and increase localization precision.

Toward a more complete understanding of monarch migration and the impact of insect movements

Given the rapid pace of tracking technology advancement, we are moving closer to ever more detailed accounts of monarchs' daily lives, as well as to the first tracks of individuals across their entire migration. This new data will not only be of tremendous scientific value, helping to uncover the rules of animal navigation and collective migration, but also of special conservation interest, revealing new rules for how monarchs use different landscapes for their migration. Moreover, tracking methods can contribute to our understanding of how and why monarchs choose specific overwintering sites, and the environmental factors that impact site choice, which could be of critical importance to local communities with cultural and economic ties to these butterflies.

A next major challenge will be to integrate these data with synergistic datasets, such as physiological recording (e.g.

[70], reviewed in [71]) or more detailed descriptions of behavior. For example, PAM sensors augment the repertoire of behaviors that can be studied, from migratory flight patterns [72] and group dynamics [61], to breeding behavior [73], or social activities [74]. We should also combine tracking developments with a uniquely rich resource available to monarch biologists: the deeply enthusiastic and committed community of students, learners, and citizen scientists who are fascinated with this butterfly. Citizen scientists can provide a valuable source of images, videos, samples (e.g. [75]), and even testing ([59], proposed by Parlin et al. [6]) across the monarch's migratory range. Additional efforts should be made to make data — and insights derived from those data — more publicly accessible and interpretable. The ICARUS Movebank project (www.movebank.org), which facilitates easy and quick use of ICARUS tracking data by wildlife managers, is a primary example. Interdisciplinary and multiperspective collaborations will be paramount for achieving this comprehensive understanding of monarch migration.

To be sure, insect tracking technologies are being applied far beyond the study of monarch migration. Automated monitoring of pollinator communities will lead to increasingly specific models of pollination interactions [76] and assessments of threats to pollinator population health (e.g. neonicotinoid impacts on bumblebee nest behaviors [77]). Mosquito behaviors are subject to highly innovative local- [78] and landscape-scale [36] tracking analyses to better monitor and control pathogen spread. Integrating collective and individual behaviors into models of insect gene drive spread will be important for evaluating their potential ecological impacts and long-term effectiveness as disease and pest controls [79]. Miniaturized geolocators (e.g. millimeter-scale Small Animal Integrated Logger or mSAIL), which have the dual ability to measure location as well as microclimate condition experienced by individuals, may enable more precise forecasting of insect distributions and dispersal dynamics under changing climate scenarios or anthropogenic pressures [80]. Indeed, because insect movements have profound impacts on some of the most pressing global challenges, such as sustainable food production systems [81], human vector-borne disease spread [82,83], and the biodiversity crisis [84], attention to and investment in this field will continue to grow [78,80].

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

None.

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