Challenges and solutions for studying collective animal behavior in the wild

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Summary

Mobile animal groups provide some of the most compelling examples of self-organization in the natural world. While field observations of songbird flocks wheeling in the sky or anchovy schools fleeing from predators have inspired considerable interest in the mechanics of collective motion, the challenge of simultaneously monitoring multiple animals in the field has historically limited our capacity to study collective behavior of wild animal groups with precision. However, recent technological advancements now present exciting opportunities to overcome many of these limitations. Here we review existing methods used to collect data on the movements and interactions of multiple animals in a natural setting. We then survey emerging technologies that are poised to revolutionize the study of collective animal behavior by extending the spatial and temporal scales of inquiry, increasing data volume and quality, and expediting the post-processing of raw data.

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Introduction

Group living is common in animals and directly influences important biological processes such as resource acquisition, predator avoidance and social learning [1]. In addition to the biological and ecological significance of collective behavior, the spectacle of coordinated animal groups navigating the environment (e.g. flocking birds, marching locusts, schooling fish) continues to drive an intense interest in understanding the mechanics behind these impressive displays. The past several decades have marked a revolution in scientific understanding of the causes and consequences of collective behavior. This is due, in large part, to a feedback between high-precision measurements of the behaviors of animal groups, and mathematical and computational models that seek to re-create these behaviors. In 1987, Reynolds [2] took an unlikely but germinal step in this direction when he showed, via computer simulations, that complex collective motion resembling the flocking, herding and schooling behaviors of animals could result from simple, local rules of interaction among individuals. In the following decades, researchers extended these early models to describe larger groups of individuals with more sophisticated and biologically justifiable interaction rules [3–5]. Simultaneously, advancements in videography and computer vision have made it possible to empirically test some of these models in the lab [6–9]. This feedback between mathematical and computational models and high-resolution data from laboratory experiments has defined an era of hypothesis-driven research and facilitated the development of a mechanistic understanding of collective decision-making in animal groups.

Extending this theoretical-empirical feedback to include group-living species in their natural environments is a critical step toward understanding how the dynamics of collective behavior relate to broader ecological and evolutionary questions. Recent advances in field-deployable tracking technologies (e.g. stationary imaging techniques, bio-loggers, and remote sensing; figure 1) present new opportunities for conducting field-based studies of collective behavior at ecologically meaningful spatiotemporal scales. By studying social interactions in wild animal groups, researchers are starting to identify the social and ecological mechanisms that drive collective behaviors in a broader range of animal species, to quantitatively describe interaction rules at the individual level that drive movement decisions at the group level, and to empirically assess the ecological significance of collective movement in the wild [10–12]. In addition, we are poised to explore collective processes that cannot be studied in the lab, such as long distance collective migration, predator-prey interactions in large, group-living species, and information transfer across the landscape.

This prospectus aims to provide an overview of existing and emerging technologies used to collect data on movements, behavior and interactions within animal groups in the field and highlights the challenges and opportunities presented by each. We have omitted a discussion of the extensive literature on collective behavior of wild social insects, as well as the literature on human groups, primarily because the techniques used in these systems often differ substantially from techniques used to study other social animals. Our aim is to survey current and state of the art technologies used to study social animals in the wild, as well as a look towards the kinds of studies these technologies will make possible in the future.

Stationary field imaging techniques

High-resolution stationary imaging has been one of the most widely used methods for studying the collective behavior of wild animals. Modern imaging methods include three-dimensional videography, high-speed single-camera and multi-camera videography, thermal infrared imaging, and imaging sonar. All of these methods are capable of recording high-resolution data on both animals and environmental features within the camera field of view, facilitating the study of social and ecological interactions on a fine spatial scale. In addition, many stationary cameras have the advantage of being compatible with a large, external power supply. This can extend the duration and frequency of data collection, making stationary cameras appropriate for a wide range of taxa, habitats and movement modes (i.e. from disparate individuals to large, cohesive groups). However, the inherent limitation of imaging from a fixed location may reduce the utility of stationary cameras in complex environments or areas of low animal density. In this section, we provide a selective review of some of these technologies and address challenges that arise when using stationary cameras to study collective behavior of animals in the field.

Imaging large groups

Stationary cameras have provided important opportunities to make precise measurements of collective behavior in the wild. For example, Cavagna *et al. [13]* used carefully calibrated cameras placed atop a building to record individual positions and movements of starlings (*Sturnus vulgaris*) in large flocks. Similarly, Ginelli *et al. [14]* used digital cameras placed atop a tower to record the behaviors of large groups of domestic sheep (*Ovis aries*) in outdoor enclosures, and Theriault *et al. [15]* reconstructed flight paths of groups of wild Brazilian free-tailed bats (*Tadarida brasiliensis*) and cliff swallows (*Petrochelidon pyrrhonota*) flying through volumes of up to 7,000 m^3. In all of these studies, researchers chose imaging equipment and configurations to strike a balance between achieving a wide field of view and maintaining sufficient resolution to allow tracking of individual movements. When it is not possible to film animals from a distance, or high-resolution images are required, multiple synchronized cameras may be used to increase the total field of view (e.g. an array of downward looking cameras in shallow water [16]; figure 2).

When designing a camera setup, it is important to consider the speeds and spatial scale of the movements of the study animal, in addition to the method by which data will be analyzed. Many studies of collective behavior make inferences by studying covariance among positions, speed, or accelerations of tracked animals. This type of analysis requires tracks that are long enough to encompass the behavioral sequences of interest, but also replicated enough to detect correlations in the presence of noise. Using stationary cameras positioned far from the group of interest might make it possible to observe animals for longer periods of time before they leave the camera frame, but this typically comes at the cost of lower resolution, which can lead to increased tracking noise, tracking errors and lower quality tracks. Therefore, it is worth performing power analyses on simulated data in advance of data collection to determine what kind of track resolution, track lengths and replication will be needed to detect phenomena of interest. In some cases, the best strategy may be to dispense with tracking individuals altogether, and instead to

focus on studying the detailed behaviors of individuals when they are present at a particular site using fixed-location cameras (e.g. [16]) or other means (e.g. PIT tag readers sensu [17]).

Tracking animal positions from field imagery

More often than not, image-based analyses of collective behavior involve tracking animal positions from one image to the next. This has become a highly streamlined task in laboratory studies (but see Hong *et al.* [18] and Berman *et al.* [19] for more challenging extensions), where behavioral arenas can be configured to minimize occlusions (i.e. instances where one animal passes between another individual and the camera), and to facilitate the use of inexpensive recording equipment and off-the-shelf tracking software (see Dell *et al. [20]* for a review).

Tracking animals in field images with complex backgrounds and objects in the foreground is far more challenging. Moreover, the need to simultaneously track many individuals that may frequently occlude one another makes studying collective behavior using field imagery particularly difficult. However, in some field settings, one or more of these complications can be avoided. For example, Attanasi *et al.* [21] achieved high-precision three-dimensional reconstructions of individual fly (the midge, *Cladotanytarsus atridorsum*) trajectories by filming swarms in front of a suspended dark cloth background. In many cases, however, modifying the background will be either impossible or undesirable, and occlusions are almost inevitable when many animals interact in the same place at the same time. Alternatively, there are several technologies that have made it possible to extract high-precision tracks from field imagery, even when conditions are far from optimal. The most common of these are three dimensional imaging and specialized filtering, detection and tracking algorithms.

Three-dimensional information can help resolve ambiguities introduced when an individual passes in front of an object with similar color and texture. For example, in a laboratory study, Hong *et al.* [18] used 3D cameras to record pairs of laboratory mice interacting in an experimental chamber. The authors were able to use the camera's depth sensor to separate mice with low-contrast coat colors from the background and to resolve occlusion events in which mice passed over one another. 3D cameras remove some of the need for careful calibrations and multi-camera reconstructions; however, commercially available 3D cameras currently have relatively narrow working range. Depending on the camera model, depth information is generally only reliable for objects that are located within a few meters of the camera lens [18], although stereo camera systems with larger apertures have been developed for tracking animals at longer ranges [18][22]. Moreover, the most common 3D technologies measure the depth of each pixel in an image by projecting an infrared beam and measuring the return time of that signal, limiting these tools to environments where emissions in the infrared range are not strongly attenuated. This limits the utility of 3D cameras in aquatic environments, although researchers have recently developed technologies that can improve the performance of 3D cameras for underwater use [23].

Heterogeneous, dynamic lighting is another challenge commonly encountered in field imagery,

particularly in shallow water systems, where refraction of sunlight through surface waves results in rapidly changing illumination patterns on the substrate, known as "sunflicker" [24]. Sunflicker makes object tracking challenging because features that are useful for detecting an individual in one image may yield poor performance in the next if local light conditions change. Dynamic lighting also renders background subtraction – a standard technique in which a background image is subtracted from recorded images to retain only moving objects – far less useful.

When it is not possible to avoid sunflicker altogether, it may still be possible to correct for dynamic lighting through video post-processing. Modern methods for correcting local dynamic light patterns in video were adapted from algorithms originally developed to produce smooth transitions between images in photo mosaics such as those created by cell phone apps [24]. De-flickering techniques apply similar methods to smooth the severe local gradients in pixel intensity produced when nearby regions of an image are illuminated to different degrees by sunflicker. Though these techniques have been applied to underwater imagery with promising results [24],[25], in our experience, they can require significant tuning. More recent methods for automatically tuning de-flickering filters may dramatically reduce the need for manual tuning, making it more feasible to correct lighting in long sequences of images from field video [26].

Finally, cameras that record spectral bands outside of the visible range (e.g. thermal or acoustic imaging systems such as acoustic sonar) can be useful as either primary or secondary imaging devices. For example, Wu *et al.* [27] used thermal imaging cameras to reconstruct large groups of free-ranging bats in nocturnal footage. Benoit-Bird and Gilly [28] used split-beam sonar to track movements of individual jumbo squid (*Dosidicus gigas*) in the Gulf of California, which allowed them to measure the trajectory, velocity, tortuosity, and depth of multiple individuals at once. Other studies have used sonar to observe synchronous diving and foraging behavior of cetaceans [29],[30], and collective hunting and evasion in fish shoals [12,31]. Thermal and sonar imaging techniques are particularly exciting because they extend the range of environmental conditions where collective behavior can be studied to include low-light environments previously hidden from traditional videography techniques. However, both spatial and temporal resolution are currently limited for these methods.

Postural tracking and fine-scale behaviors

Technological developments will undoubtedly continue to improve the usefulness of visual imagery for studying collective behavior. Among the most exciting of these is the development of algorithms that automatically extract more detailed information about individuals than body or head centroid locations. These include segmentation schemes, which may be able to provide postural information about individuals. For example, fully convolutional networks - relatively new tools from deep learning - appear to be well suited to semantic segmentation of complex images in which objects of interest can have variable size and shape, and be partially occluded [32]. Algorithms that explicitly model body orientation, structure and limb orientation using multi-camera reconstructions [33] or 3D cameras [18],[34] also appear promising. These and

similar methods will allow researchers to access information about individuals that is not contained in the time series of positions typically collected from tracked field imagery. Access to features like body posture and gait could fundamentally deepen what we can learn from visual imagery. For example, in dense schools or swarms, postural tracking can allow one to reconstruct the visual information available to each individual within the group (see laboratory studies by Strandburg-Peshkin *et al.* [9] and Rosenthal *et al. [35]*). Information about body posture, limb motion, and morphology may make it possible to apply new quantitative methods for characterizing behavioral states of individuals [18],[19],[36], [37] and to better understand how social interactions might influence these states [38].

Remote sensing

While stationary cameras have facilitated some of the earliest field-based studies of collective animal behavior, remote imaging platforms now offer a promising opportunity to extend these investigations to organisms moving across increasingly large spatial scales ([39]; figure 3). In addition, the flexibility of remote operation makes it possible to track specific animals or entire groups of interest while executing experimental manipulations under natural conditions. Together, these capabilities afford an opportunity to expand the scope of theoretical and empirical insights to be gained from studying collective motion to a broad range of natural systems.

Unmanned aerial vehicles (UAVs)

UAVs currently provide the most affordable and flexible imaging platforms for obtaining an aerial perspective in the field. In addition to greatly expanding the simultaneous field of view afforded by stationary cameras, UAVs provide the ability to adjust camera positioning on the fly and at distances up to several kilometers from the operator. This capability facilitates truly non-invasive filming of collective animal behavior (but see guidelines below) and when combined with bio-loggers (e.g. [10]; figure 4) or computer vision techniques (e.g. [20],[39,40]; figure 5 and ESM 1, 2), can be used to track the fine scale movements (e.g. individual positions, trajectories and turning angles) of entire groups over large distances and time scales. For example, Torney *et al. [39]* used UAV videography and computer vision to measure individual trajectories and quantify information transfer across large groups of migrating caribou.

In addition, a growing commercial market is continually increasing the utility and affordability of UAVs by offering a wide range of airframe designs, payload capacities, and technical configurations to suit the needs and budget of most academic research programs [41][42]. Alternatively, a thriving DIY community offers limitless opportunities for researchers needing bespoke solutions at low cost. Given this range of equipment configurations and capabilities, specific recommendations will depend on the question of interest, focal species, budget and logistical constraints of the field site, and there are several technical and political considerations to be made before establishing any UAV-based research program for wildlife (see Anderson and Gaston [41] for a more thorough treatment of these topics).

The inability to film animals through dense canopy, turbid water, or to resolve smaller species (less than about 30 kg) at appropriate altitude is currently the largest limitation of UAVs for studies of collective animal behavior. However, thermal infrared and increasingly compact, high-resolution cameras are rapidly expanding future possibilities for filming under these conditions. Limited battery life presents an additional challenge, though significant gains stand to be made from utilizing alternative airframes. For example, fixed-wing UAVs afford significantly longer flight times than compact, multi-rotor designs (i.e. up to two days for the largest fixed wings vs. <1 hour for most multi-rotor systems [41]). However, a multi-rotor system affords the advantage of hovering in place without the need to circle continuously as required by a fixed-wing aircraft. Regardless of design, all aerial platforms bring a suite of post-processing challenges such as image stabilization, correction for oblique filming angles, changing light and environmental conditions, plus many of the limitations outlined previously for processing footage from field cameras (see "Stationary field imaging techniques" above).

In addition, many low-cost commercial systems can produce stimuli perceived to be threatening by many species (i.e. motor noise [43] or semblance to an aerial predator [44]), though impacts may be reduced by modifying equipment or methodology [45],[46]. Furthermore, there is some evidence that UAVs may cause physiological changes in study animals (i.e. increased heart rate [43]), which may not manifest as behavioral changes, but could confound results if not properly accounted for. Though all of these issues are addressed with increasing efficiency in new versions of hardware and software, there is no replacement for thoughtfully developed "best practices" for UAV use around wildlife [45],[46]. Alternatively, non-motorized platforms (i.e. kites, aerostats and stratospheric balloons [47]) offer some advantages over traditional UAVs, including reduced noise, significantly longer flight times, and increased payloads. Of course, these gains come at the cost of maneuverability, though this may be partially mediated by use of a remote controlled camera gimbal, or increased altitude.

Finally, depending on the study area, UAVs may present a multitude of legal challenges, which will generally require advance permitting and licensing at a minimum, and partial to total restriction of flights at a maximum. Thus, it is essential work with local stakeholders and law enforcement agencies during the early phases of project planning to clarify procedures and ensure compliance prior to beginning work.

Satellites

While UAVs offer unparalleled affordability, flexibility, and resolution for imaging animal groups from an aerial perspective, there have been notable advances in satellite remote sensing technology that will facilitate truly "landscape scale" studies of collective behavior in the very near future [48]. Commercial satellite companies maintain the largest collection of archived images with the resolution appropriate for identifying individual animals (30 cm [49] to 50 cm [49,50]), but the random and disparate temporal distribution of coverage generally limits the use of archived images for studies of collective movement. While there is some promise for using

new, commissioned images to capture time series of large animal groups moving across the landscape, this will require future increases in satellite availability for civilian use coupled with a significant decrease in cost.

Alternatively, the advent of "CubeSats" (i.e. miniaturized satellite constellations) has recently disrupted the traditional market for high resolution satellite imagery by providing low-cost access to high-resolution still imagery (80 cm - 5 m) and video (1m, up to 90 seconds at 30 fps) collected at daily or near-daily intervals (e.g. [51],[52],[53]). Obtaining such high resolution, high frequency satellite imagery presents a first opportunity to study entire herds of large animals (e.g. migratory wildebeest, caribou, livestock) moving across hundreds of square kilometers without disturbance from observers on the ground. In addition, this truly multi-scale perspective will afford researchers the opportunity to better understand how social and environmental processes interact across environmentally relevant spatial scales and facilitate the study of collective behavior in more natural systems than ever before (figure 3).

Bio-loggers

Animal mounted sensors (or bio-loggers) present another promising and complementary approach to imagery-based studies of collective behavior. Such on-board sensors - including GPS, accelerometers, magnetometers, pressure sensors, and acoustic recorders, among others - are opening up new directions in a range of biological disciplines, as they allow data to be collected continuously and directly at the location of the study animal, irrespective of changes in accessibility or visibility of the animal, and without need for re-identifying the same individual repeatedly. For studying collective behavior in particular, on-board sensors allow animal position, movement and behavior to be monitored with increasing resolution and across a range of habitats and contexts [54,55]. In addition, many tags now include multiple types of sensors integrated with one another, making it possible to test how the movements, vocalizations, behaviors, and social interactions of freely-moving animals influence one another [56].

However, the utility of bio-loggers is limited by the need to affix sensors to each monitored animal, a process that usually requires capture (for collars, backpacks, or glue attachment) or close range physical interaction (for suction cup or dart attachments). Additionally, the need for animals to carry devices imposes strong weight and size restrictions, thereby limiting the sensor payload and battery size, and resulting in tradeoffs between sensor sampling rate, duty cycling, and battery life. Retrieving data can also present challenges. In some cases, it may be possible to download data remotely from tags, while in others, tags must be retrieved (either through recapturing animals or by having a remote drop-off system) to offload data. Another complication that is especially relevant to studies of collective behavior is the need to deploy many devices simultaneously. If instrumentation happens over an extended period of time, tags need a pre-programmed start time to maximize simultaneous recording time. Additionally, the

internal clocks of independent tags will drift over time, and thus tags that do not include a GPS sensor will need a system for intermittently synchronizing tags. Lastly, on-board sensors are typically expensive, so deploying many tags may become cost-prohibitive for some research projects. Despite these challenges, continued advances in technology have reduced the size and cost of on-board sensors while also increasing their spatial and temporal resolution. Due to these advances, their use in behavioral biology is rapidly growing, and they are becoming an increasingly powerful tool for studying collective animal behavior. We explore these advances and associated challenges in greater detail below.

Monitoring location

Modern GPS tags are capable of monitoring animal locations at sub-second rates, and with spatial resolution that can achieve sub-meter precision. These advances mean that data can now be collected at the temporal and spatial scales necessary for studying fine-scale social interactions within groups [54]. Several recent studies have deployed GPS tags on all or most individuals within animal groups to study collective movement dynamics, including work on pigeons (*Columba livia domestica*) [57], baboons (*Papio anubis*) [58], domestic sheep [59], African wild dogs (*Lycaon pictus*) [59,60] and domestic dogs (*Canis lupus familiaris*) [61] (see figure 4 for an example with baboons).

Collecting movement data via GPS tags has a number of advantages. First and foremost, it is possible to monitor animals in areas where visual observation is impossible. Moreover, animals can be tracked over multiple spatial scales (from local interactions within groups to long-range collective migrations[62]) and with an adjustable temporal rate. Such high-density data can allow for estimating individual interaction rules and leadership [63], differences in relative position within a group that are related to individual differences or personality traits [64,65], or tracking fine-scale interactions with the local environment [10,62]. GPS sensors require a relatively large amount of power, but recent low-power GPS tags now allow for multi-week continuous (1 Hz position updates) tracking of medium-sized animals such as baboons [58]. However, this increased spatial or temporal resolution may not be high enough to resolve fine-scale movements and social interactions for some systems and contexts. Therefore, these methods are most appropriate for groups that are dispersed over at least tens of meters, or for addressing interactions that take place over such distances. In contrast to overhead imaging, there are no limits to maximum separation distance so it is more feasible to study social dynamics of fluid groups on the move. For smaller animals or more compact group interactions, high-resolution imaging from either stationary cameras or UAVs are likely better approaches to differentiating interactions.

For marine animals or other systems where a significant component of movement takes place vertically, cheap and power-efficient pressure sensors can monitor the depth of a tagged animal. Tags with pressure sensors generally store and transmit summary data or store raw depth measurements. This information can provide data on dive and foraging behavior, and can be merged with ARGOS positions to provide detailed data on foraging ecology of deep-diving

animals [66]. Although it is possible to use pressure sensors to quantify dive initiation and other characteristics of leadership, so far this technology has only been used to a limited extent for studies of collective behavior [67]. This is due in part to problems with separating lack of coordination from lack of horizontal cohesion, and in part due to inevitable clock drift between independently sampling tags. Novel approaches to solve these two issues are therefore needed, such as synchronization pulses or incorporation of GPS or fast-lock GPS technology with accurate timing information.

Detecting presence, proximity, and social networks

Even when precise positions are not known, information on the presence or proximity of animals to one another, or to fixed geographical locations, can still provide a useful quantification of social structure and interactions. Such methods can be particularly important for species whose size, environment, or behavior make continuous monitoring impractical or impossible, or for processes that span longer time scales such as social learning. A range of active and passive transponder systems have been used to obtain such data so far, and are thought to be increasingly important to future work [68].

Passive integrated transponder (PIT) tags are extremely small, lightweight and inexpensive devices that carry a unique barcode and are typically implanted internally in animals. PIT tags do not require an internal power source so they can usually remain with an animal for its entire lifetime and are well suited to automated setups. While PIT tag systems do not monitor position continuously, they are well suited to systems in which animals spend time at specific locations such as nests and foraging patches, or to monitor their movements through specific movement corridors such as rivers (e.g. during migration). Arrays of transponder readers can also give more detailed information on animal positions and movement directions [69], and co-occurrences at specific locations can be used to infer social structure [70]. A limitation of PIT tags is that their detection range is very short, typically on the order of a few meters or less. In the context of collective behavior, PIT tags have been used to monitor decision-making, social network structure, and information transfer in populations of wild birds [17,71,72], bats (*Myotis bechsteinii*) [73] and house mice (*Mus musculus*) [74], among others.

Active transponder tags, including VHF radio beacons or acoustic transponders that contain their own power source for signal generation, can provide a longer-range alternative, though these also require deployed receiving stations. Several lakes have recently been instrumented with relatively dense arrays of acoustic receivers to track active transponders implanted in multiple species of fish, allowing for a detailed perspective into interactions both within and between species in an ecosystem [68,75].

Proximity sensors are active transponder tags that can themselves receive information from other transponders and store information on time and ID of encountered tags [76]. Tags can either be tuned to record signals above a certain threshold or to record signals and signal strength, where the latter can be used to infer encounter distance [77]. These tags have been used to automatically

map association patterns and investigate social learning in free-ranging New Caledonian crows (*Corvus moneduloides*) [78] and to investigate social dynamics of zebras (*Equus quagga*) [79] and sharks (*Carcharhinus galapagensis*) [80],[81].

Estimating body orientation, activity, and behavior

A full understanding of how animal groups coordinate movement will require information, not just on where animals are, but on the sensory information they are taking in and the behaviors that they are engaging in. Recent laboratory studies of animal groups have begun to incorporate sensory information, such as the visual field of each individual in a school of fish [9],[35],[82], to build more predictive and biologically-motivated models of collective motion [83]. Onboard inertial sensors such as accelerometers, magnetometers, and gyroscopes provide an opportunity to obtain detailed behavioral information for animal groups in the wild, even when they cannot be directly observed by humans, and may also provide the means for tracking body orientation and gaze direction of animals within moving groups. Both accelerometers and magnetometers are commonly used in bio-logging tags since they are compact, cheap, and power efficient [84],[85]. Gyroscopes have some advantages when measuring energetics and body posture, but have seen only limited use in bio-logging tags due to their higher power consumption, drift and complex data processing [86].

Tri-axial accelerometers measure both static acceleration (caused by the gravitational field of the Earth) and dynamic acceleration (caused by acceleration of the animal and thereby the sensor itself) along three dimensions. Depending on sensor placement, dynamic acceleration can be related to the movement of the animal itself, and various proxies for energy expenditure or activity level using tri-axial accelerometers have been developed as a result (ODBA [87]; veDBA [88]; MSA [89]). Accelerometers may also be used to estimate body orientation, often quantified as the pitch, roll and heading of an animal. To measure all three axes of body orientation, an accelerometer and magnetometer are needed, and magnetic heading must be corrected for the magnetic inclination and declination at the study site. Magnetometers are seldom used by themselves because they cannot fully specify the orientation of the tag due to rotational ambiguity around the magnetic field vector. However, with triaxial accelerometers and magnetometers, time series of body orientation can be used to quantify the gait of an animal over time [90]. Packages combining accelerometers and magnetometers with gyroscopes provide a more robust quantification of both energetics and gait [86,91]. See Martín López *et al.* [86] for a comparison between these approaches.

Since accelerometers and magnetometers are more power efficient, they can generally be sampled much faster (typically tens to thousands of times per second) than GPS tracking systems, which are constrained by battery power. Thus, there is increasing potential for using time series analysis to estimate movement influence and social interactions between simultaneously tagged animals at higher temporal resolution using inertial sensors than is possible using GPS sensors. Inertial sensors also offer the possibility of identifying specific behaviors (e.g. foraging events or prey capture success [92,93]) and behavioral states [94–96]). To

do this, a ground-truthed dataset consisting of time-synchronized behavioral observations is typically collected during a subset of sensor recordings. Based on this training dataset, machine learning techniques can then be used to develop an automatic behavioral classifier, allowing behaviors to be identified in the absence of direct observation [92].

Improving positional data using inertial sensors

Integrating data from sensors with different spatial or temporal resolutions can help improve tracking accuracy. For example, by merging high sample rate inertial data from accelerometers, magnetometers, and/or gyroscopes with low sample rate, larger error position data from GPS tags, it is possible determine the orientation of an animal, then combine this information with estimates of speed and integrate across velocity vectors to reconstruct movement tracks [97]. Such "dead-reckoning" methods (reviewed in [98]) can help establish movement tracks without directly measuring positions [99] and can also be combined with GPS, ARGOS or acoustic localization position data to improve the temporal resolution of movement tracks [100,101]. Dead reckoning methods are also critical for species that live in areas where GPS reception is poor, such as marine environments and densely forested areas. However, it is important to note that errors in the inferred positions of animals will accumulate over the length of a track and rapidly limit the accuracy of dead-reckoned position estimates, whereas estimated orientation will keep the same accuracy throughout. Thus, it is better to base studies of movement influence between animals on orientation estimates rather than dead-reckoned tracks.

Interactions beyond proximity

Collective behaviors are mediated by a variety of passive and active information flows between individuals in a group. Behaviors other than movement, such as vocalizations and gestures, are key to the coordination of movement in many species (primates [102],[103]; meerkats (*Suricata suricatta*) [104]; birds [105]; elephants (*Loxodonta africana*) [106]; dolphins (*Tursiops truncatus*) [107]). Animal mounted cameras, sound recorders or accelerometers provide a number of options for measuring interactions between individuals in the field, and linking these to individual-level movement decisions recorded simultaneously by GPS or other sensors.

Perhaps the most intuitive option is the use of still or video imaging from the perspective of the study animal itself [108],[109]. Animal-borne video can be used to identify or validate behaviors, especially as recorded by other lower cost sensors (e.g. accelerometers), and has been used extensively to understand foraging ecology of many species, it also has great potential for contributing to our understanding of collective behavior. Cameras can map encounters or social interactions with conspecifics that occur out of sight of observers [110–112]. While technology is continuously improving, video cameras consume more power than many other sensors, analysis is often labor intensive, and it may be difficult to get a field of view that can capture all interactions of interest.

The last 15 years have seen an increase in animal-borne sound recorders, especially for research on cetaceans [113–115], but also on terrestrial mammals [116], birds and bats (e.g. [56], [117]).

Since acoustic communication is a fundamental means of information transfer in many systems, acoustic recorders that can pick up these signals from tagged animals open a wide range of possibilities for understanding collective behaviors, from active mediation of group cohesion [118] to negotiation of consensus decisions.

While manual processing of acoustic data can be time-consuming, automated detection and discrimination algorithms can speed up analysis dramatically [117,119]. One potential advantage over camera tags is that a single acoustic sensor can record sounds from the tagged animal, incoming sounds from other nearby conspecifics, and sounds from other sources in the environment [56]. However, for many species, it can be a significant challenge to correctly discriminate vocalizations of the tagged individual from nearby conspecifics, and accurate differentiation of tagged animal vocalizations can be difficult to demonstrate without a ground-truthed dataset. Stereo tags may help since one can use time differences between channels to estimate a bearing to an incoming sound [120], thereby more easily identifying sounds from the tagged animal [121,122]. Additionally, high sample rate accelerometers may be able to pick up on body vibrations associated with sound production in both marine [123] and terrestrial [124] systems.

While bio-loggers that monitor the orientation and movement of animals are only beginning to be employed in studies of collective animal behavior [94],[125], their use offers great promise for achieving a deeper understanding of the mechanics governing collective motion. Such data will also provide valuable information about the context in which group coordination occurs, and will allow individual behaviors- not just locations- to be incorporated into models of collective movement. At the same time, the ability to collect such detailed data opens up a new set of challenges, as integrating multiple streams of raw sensor data to obtain biologically relevant information is a difficult analytical and computational task, though software to facilitate this process is gradually becoming available [126]. Furthermore, since instrumentation of animals is both costly and time intensive, future studies that combine animal bio-logging methods with other tools such as visual tracking of group members from overhead cameras, may facilitate studies of collective behavior while building on the strengths of each method.

Discussion

Deeper knowledge of the ecology and evolution of collective behavior is important for the advancement of both basic scientific understanding and for the conservation of fundamental ecosystem processes that occur in communities around the world [1],[127–129]. The technologies discussed above offer new, and in many cases, more efficient tools for studying the dynamics of these processes in the wild. Each of these approaches come with their own advantages and caveats, and thus the choice of study approach will depend heavily on the problem, especially the spatiotemporal scale at which data is needed.

In general, both stationary and remotely sensed imagery afford the advantage of simultaneously capturing high resolution data on environmental features and animal movement, but differ in the range of spatiotemporal scales that can be captured. For example, fixed cameras provide high definition (and in some cases, 3D) imaging at a local scale that is constrained by the field of view of the (often immobile) camera, and thus are most suitable for monitoring movement interactions of small, less mobile animals, or for monitoring interactions in specific areas (e.g. fish moving around a reef, birds foraging in a tree). For larger, group living or highly mobile animals, UAVs offer a promising alternative. The choice of airframe design will depend on the scale of inquiry, with larger aggregations or longer time periods necessitating fixed-wing UAVs that fly higher and cannot hover, but that reach extended flight times of hours to days compared to the 10's of minutes of commercial multi-copters. For landscape scale questions, high resolution satellite imaging is becoming an increasingly accessible option that may allow for tracking mass movements of larger animals over time scales of weeks to months, albeit at low temporal scales that do not allow tracking of individual animals without the coordinated use of bio-loggers or stationary cameras.

In contrast to field imaging techniques, bio-logging tags offer the ability to track unique individuals over time scales of weeks to years, which can be a significant advantage when studying highly mobile [57][10] or highly fluid social groups. In addition, bio-loggers afford the advantage of incorporating environmental sensors such as cameras or microphones that can record social interactions in situ and allow researchers to test mechanistic hypotheses for the collective decision-making processes observed in a broad range of taxa. Finally, it may be advantageous to think about bridging these approaches, for example by combining fine-scale habitat mapping from UAV with high-resolution individual-level tracking of animals [10]; figure 4).

While we have emphasized the new research opportunities these methods will facilitate, the methods themselves should not be viewed as a panacea, or as a replacement for more traditional techniques of field biology. As Hebblewhite and Hayden [130] point out, higher resolution datasets do not necessarily lead to increased understanding of animal ecology. Additionally, one should critically evaluate the true costs of data collection (i.e. handling wildlife to apply sensors, or processing and analyzing large amounts of data) before adopting any new techniques for research. It is also important to note that there is no replacement for the deep intuition and novel questions born from directly observing animal behavior in the field. Thus, these new technologies should be viewed as complementary approaches to more traditional field methods and encourage deeper understanding of classic ecological theories through cross-discipline collaborations.

Moving forward, there are a number of promising avenues for extending collective behavior research in both theoretical and applied directions through experimental, field-based enquiry. Much of what we currently know about collective animal behavior, both in the laboratory and in the wild, comes from observational studies rather than experimental manipulations. With the aid

of mathematical and computational models, these studies have shed considerable light on the interaction rules that generate phenomena such as coordinated motion (e.g. [6],[8],[11],[131,132]) and collective predator evasion (e.g. [12],[35]). However, it is becoming increasingly clear that hypotheses about the causes and consequences of collective behavior should be tested further through manipulative experiments in a natural setting. Several field studies (e.g. [16],[133]) have already begun to move in this direction, and recent technological advancements will enable researchers to build on these early efforts by combining the power of modern animal tracking technology with traditional methods for studying behavior in the field. For example, acoustic playbacks (e.g. [133–135]), food manipulation (e.g. [72],[136]), and predator threat stimuli [16] can be used in combination with any of the imaging or bio-logging technologies discussed above to experimentally test hypotheses about how information is transmitted among individuals and how that information affects collective dynamics across natural landscapes.

In addition to these new applications, the technologies reviewed here hold tremendous potential to extend the study of collective behavior to contexts where it has seldom been studied in the past. Questions about what selects for and maintains collective migration, how collective foraging might influence nutrient dynamics and ecosystem processes, how individuals balance information they gather directly from the environment with information gleaned by watching neighbors, and how the demography and persistence of species might depend on social interactions have long fascinated biologists. The technological revolution that is currently taking place in the study of collective behavior is bringing answers to these questions more rapidly than ever been before, and should continue to strengthen the relationship between theoretical models, empirical observations and manipulative experiments in the years to come.

Additional Information

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4001157.

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Authors' Contributions

LFH, AMH, ASP, and FHJ wrote the manuscript.

Competing Interests

We have no competing interests.

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Figure captions

Figure 1. Technology is changing our view of collective behavior, offering a variety of different perspectives on animal movement and interactions. High-resolution satellite imaging, fixed-wing or multicopter photography allows imaging groups of animals as they move across the landscape or migrate great distances. Stationary or semi-stationary imaging techniques allow for high-definition tracking of large groups, potentially in three dimensions, using standard cameras, imaging sonar, or infrared cameras. Biologging tags that sample location, behavior, activity, or interactions with conspecifics provide a continuous stream of data from tagged individuals, even in otherwise inaccessible locations or when moving across large distances.

Figure 2. Still frame from a video sequence showing movement tracks of individual fish filmed from a stationary camera array in shallow water [16].

Figure 3. Remotely sensed imagery affords a unique opportunity to empirically study the ecology of collective motion in large animal systems. For example, satellite (A,B) and aerial (C) imagery of ungulate herds reveals aggregation patterns that are structurally similar to those previously described for smaller taxa in a laboratory setting: (A) Vacuole (fish), (B) Cruise (insects), (C) Wave front (slime mold). Remote sensing now enables hypotheses regarding the form and function of these repeated patterns to be experimentally tested under natural conditions and for a wider range of taxa than ever before. Images were reproduced with the following permissions: (A) Wildebeest: Google Earth, © 2017 Digital Globe; (A) Fish: iStock.com/Connah/Cropped from original; (B) Insects: "A column of Matabele ants streaming towards a termite mound" by Piotr Naskrecki © 2013/Cropped from original; © Slime mold: "Physarum polycephalum (Physaridae)" by Norbert Hülsmann, used under CC BY-NC-SA-2.0 (https://creativecommons.org/licenses/by-nc-sa/2.0/)/ Cropped and rotated from original.

Figure 4. Combining bio-logging with UAV imagery enables investigation of how the environment shapes collective movement in wild animal groups. Colored lines show trajectories for the majority of baboons within a single troop (obtained using GPS collars), and background image shows 3-dimensional point cloud rendering of their habitat (obtained from UAV imagery) . White lines show scale (each line extends 50 m). Data from [10,58].

Figure 5. Still frame from a UAV video sequence demonstrating ability to automatically track unique individuals and species (e.g. zebra in red versus wildebeest in blue) across video frames (sensu [39,137]. Still frame was reproduced with permission from Colin J. Torney [39].

Figures

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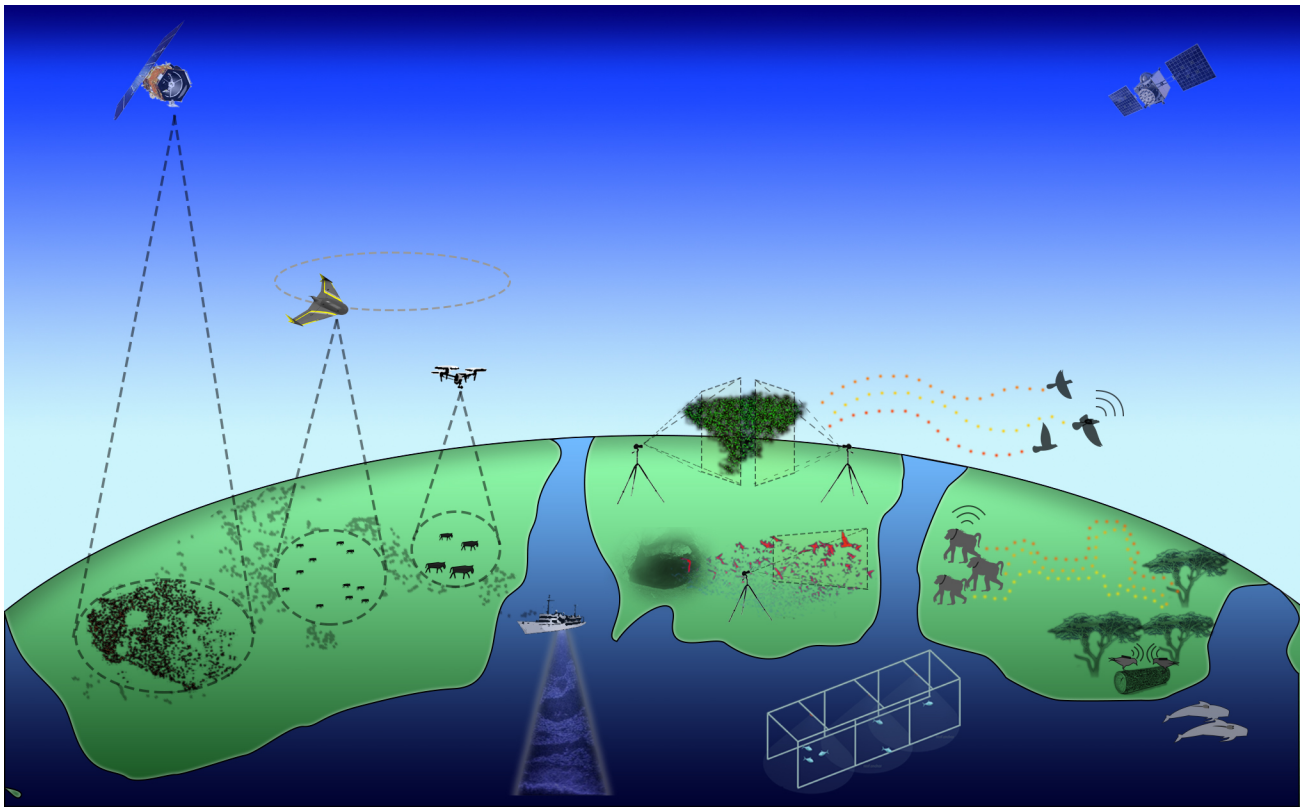

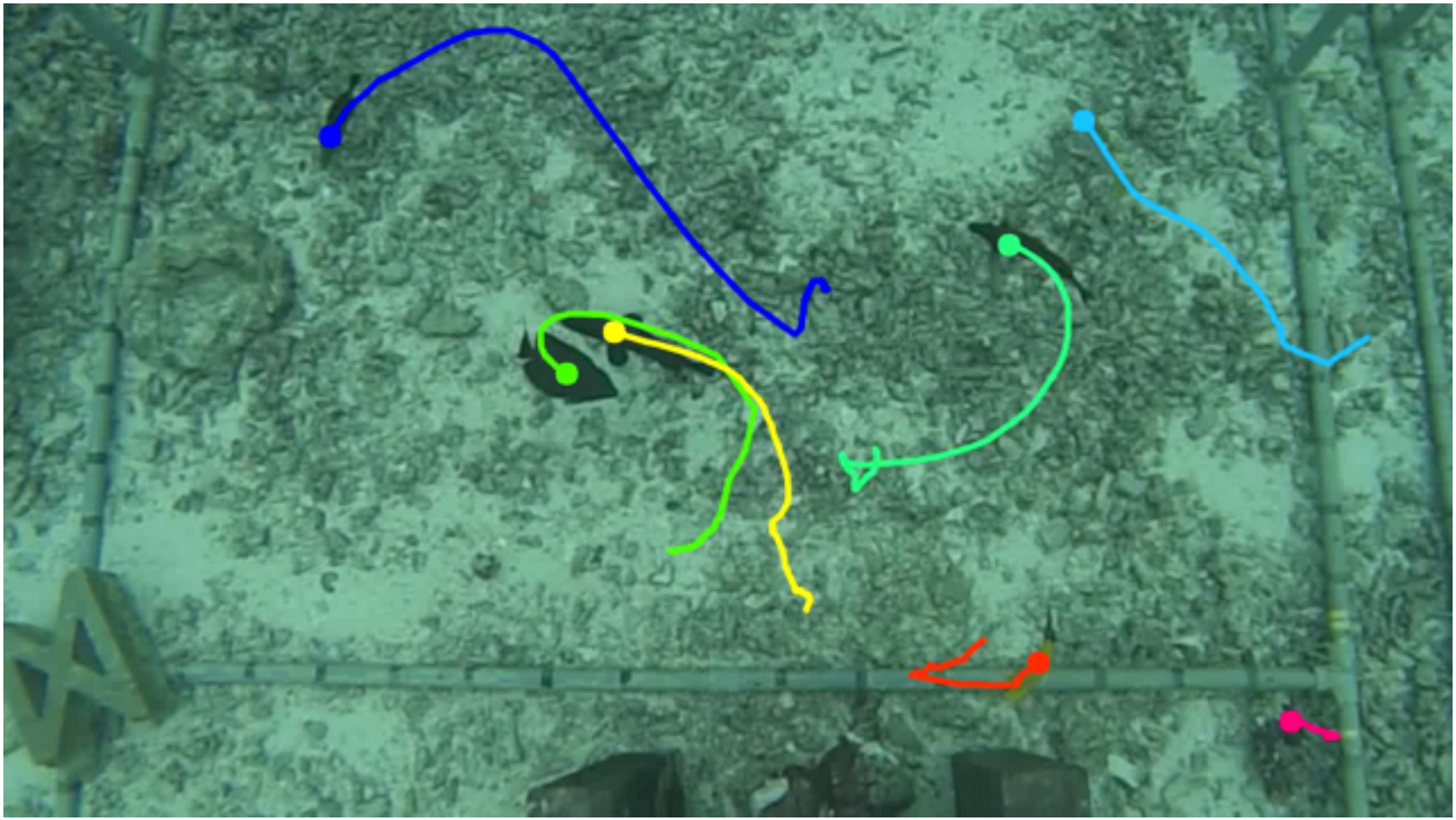

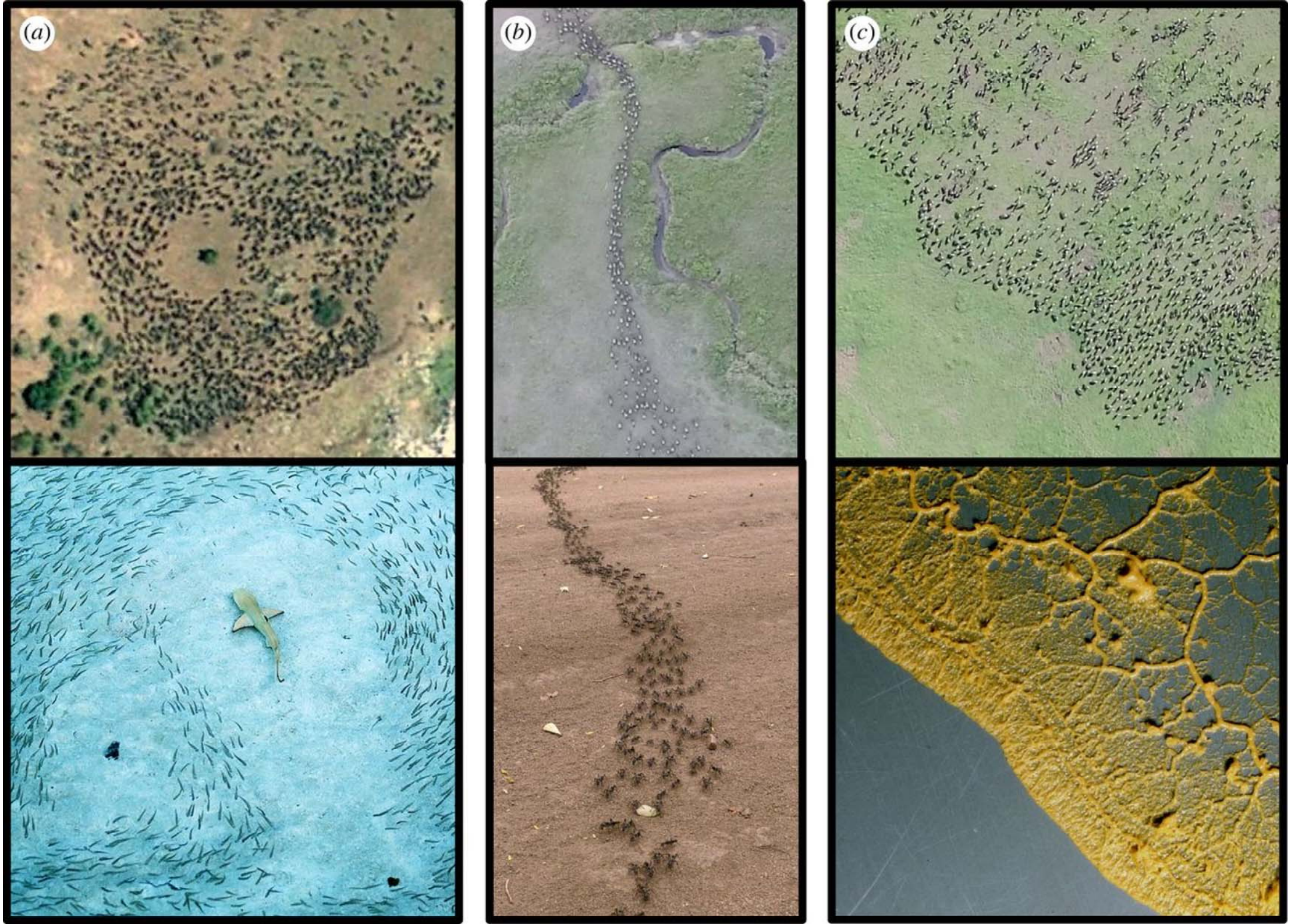
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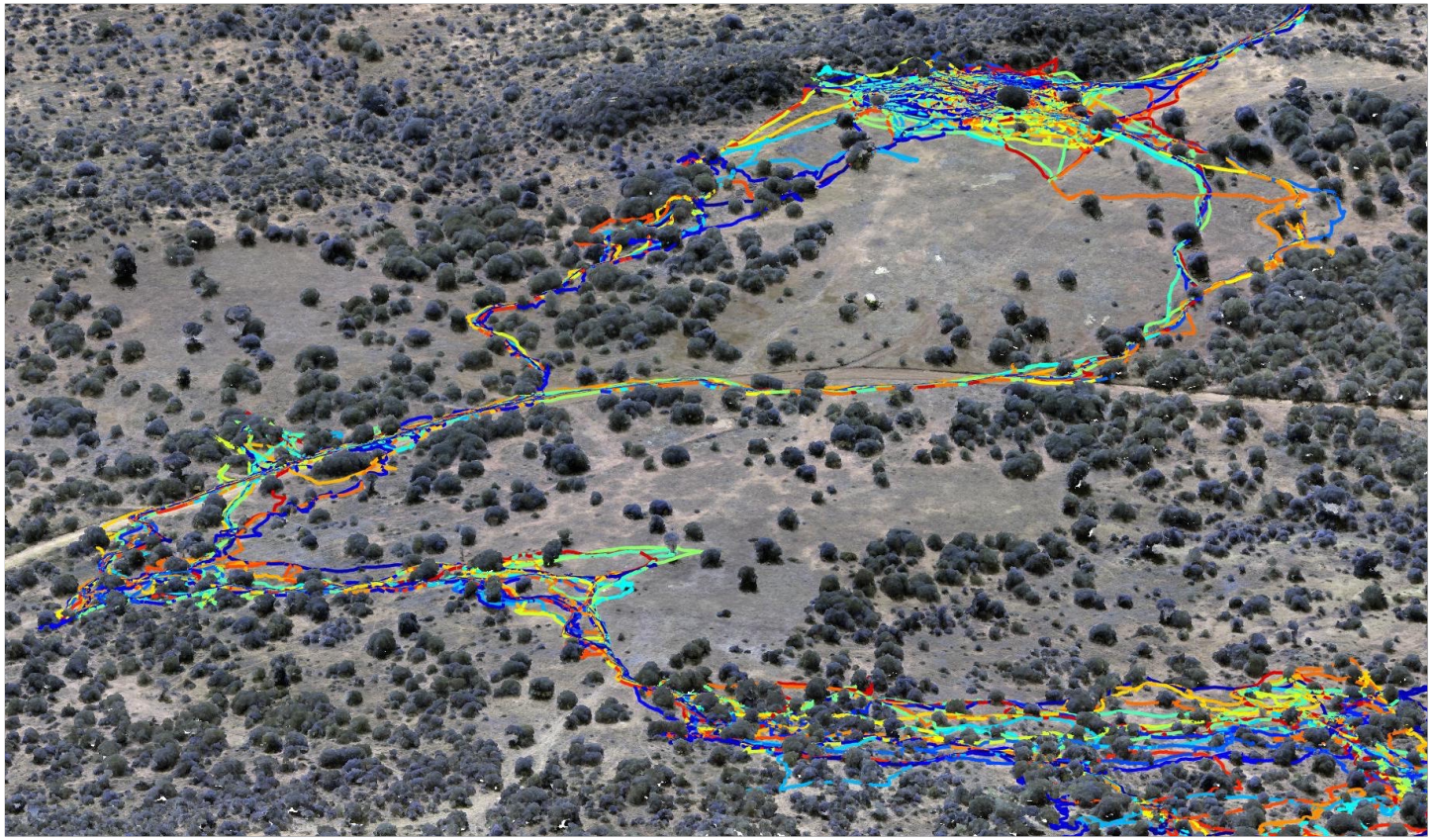

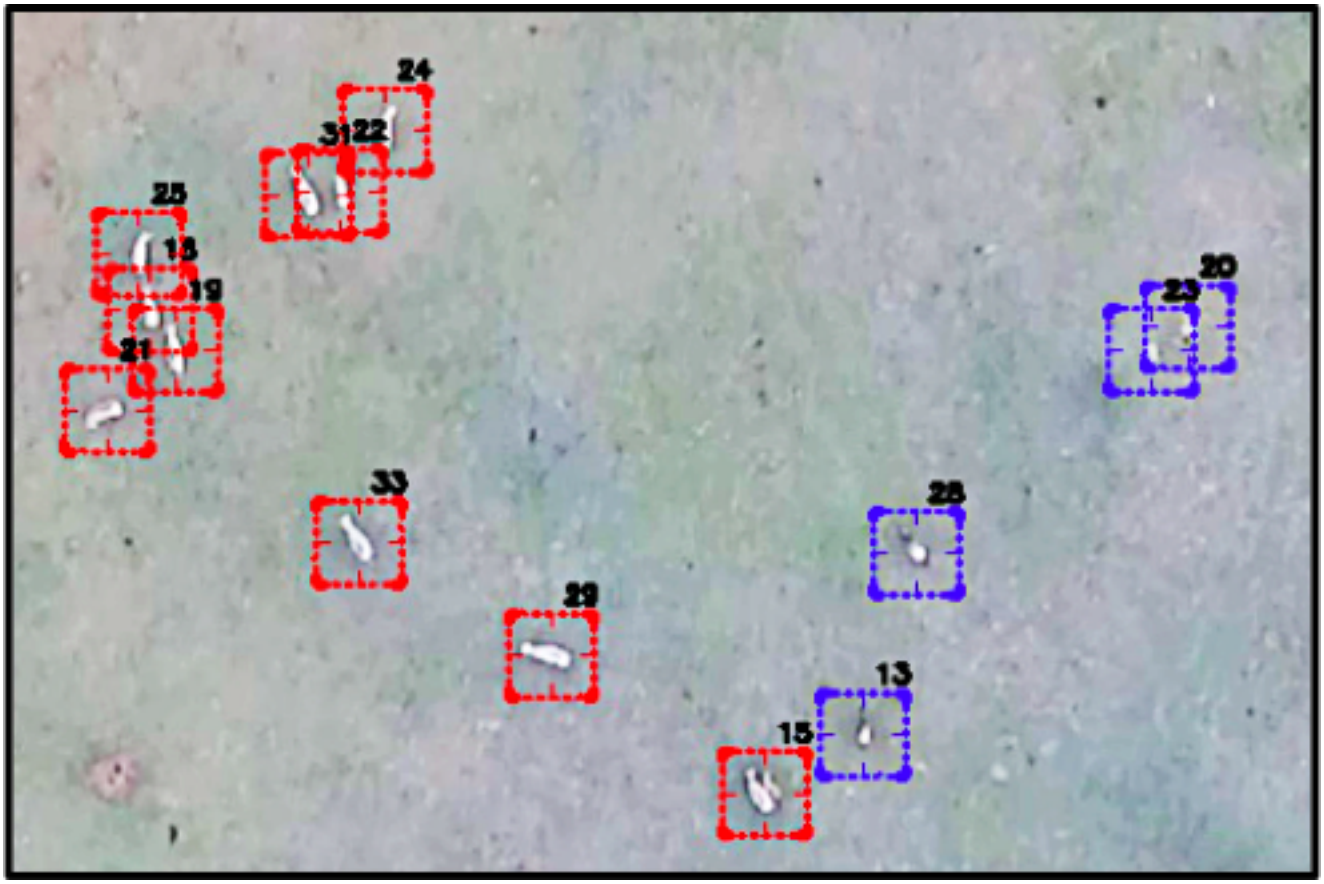
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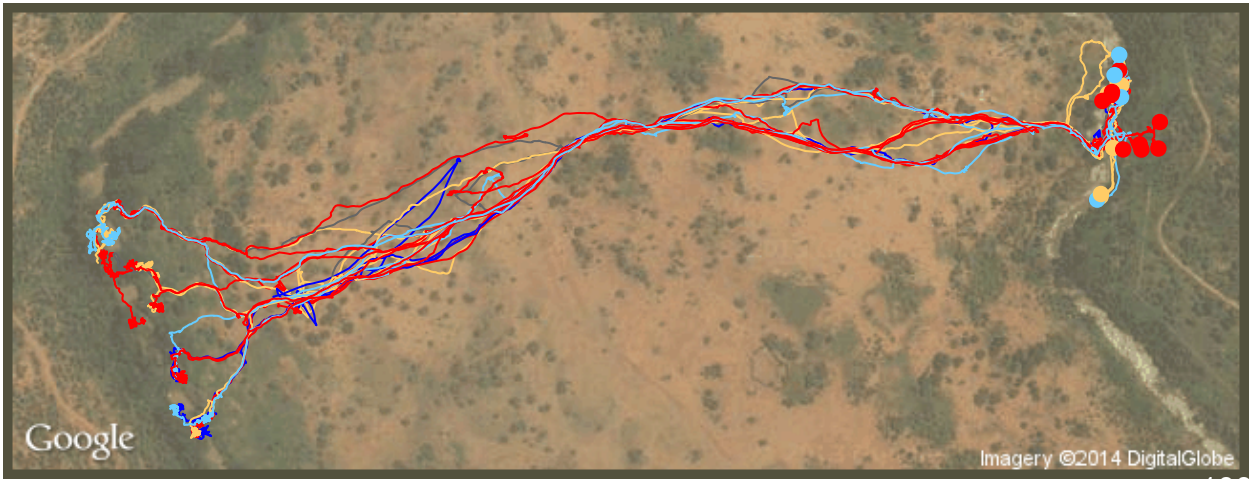
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