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Moving beyond the individual: large-scale observational and experimental approaches
to understand collective motion in wild ungulates

A dissertation submitted in partial satisfaction

of the requirements for the degree

Doctor of Philosophy in Ecology, Evolution & Marine Biology

by

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Moving beyond the individual: large-scale observational and experimental approaches
to understand collective motion in wild ungulates

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by

Lacey Hughey

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ABSTRACT

Moving beyond the individual: large-scale observational and experimental approaches
to understand collective motion in wild ungulates

by

Lacey Hughey

Animal aggregations are common in nature and directly influence important biological processes such as resource acquisition, predator avoidance, and reproduction. Yet our ability to study the behavior of animal groups with precision has been limited by the challenge and expense of tracking multiple individuals at once. As a result, the majority of knowledge about collective behaviors – particularly in large, or far-ranging species – has been derived from detailed observations of relatively few individuals (i.e. field observations or marked individuals), or theoretical simulations lacking validation in the field. While these approaches have formed the foundation of animal behavior research, they frequently suffer from an inability to generalize individual-level observations to population-level processes.

Recent advancements in high-resolution remote sensing now present exciting opportunities to overcome many of these limitations by obtaining a comprehensive view of individual behaviors and the full socio-environmental context in which they are embedded. By adapting high-resolution remote sensing technologies to study large groups of animals in the wild, I aim to examine the role of environmental and social forces in driving behavioral

shifts in ungulate herds across multiple scales of space and biological organization (i.e. individuals to populations).

To accomplish this, I first establish the historical context for these new techniques by conducting a literature review of modern and historic methods for studying collective animal behavior in the field. This review outlines the strengths and limitations of such methodologies while identifying opportunities for advancement afforded by recent and upcoming technological innovations. I then demonstrate the utility of this technology by developing a new method to study the distribution and behavior of tens of thousands of animals (white-bearded wildebeest; *Connochaetes taurinus*) identified in high-resolution (≤ 50 cm) satellite imagery. This non-invasive method is directly scalable from individuals to populations and reliably predicts three behavioral states (82% accuracy overall) from a single metric of group structure (i.e. coordinated orientation). Such an advancement represents a step-change in our ability to study social processes under natural conditions and forecasted advancements in both resolution and automated image processing are likely to expand applications for this technique in the near future.

Finally, I combine these new remote sensing techniques with traditional animal tracking methods (e.g. GPS telemetry and transect surveys) to evaluate the factors that drive habitat selection by a reintroduced, free-ranging ungulate (tule elk; *Cervus canadensis nannodes*) in a cattle-dominated ecosystem in northern California. These analyses confirmed that reintroduced elk largely avoided areas managed for and used by cattle across all seasons. Further, the use of remotely sensed data revealed that this pattern likely resulted from differential habitat preferences rather than outright avoidance behavior. As a result, the potential for conflict between cattle and reintroduced elk is expected to be minimal in this ecosystem, and managers may continue to rely on manipulation of resources (e.g. providing

artificial water sources) to limit interactions between the two species. By presenting this updated approach to the study of animal behavior, I aim to demonstrate the value of remotely sensed data for providing both basic and applied insights into the behavioral ecology of large animal systems.

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Chapter I. Challenges and solutions for studying collective animal behavior in the wild

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Abstract

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.

Introduction

Group living is common in animals and directly influences important biological processes such as resource acquisition, predator avoidance and social learning (Parrish et al. 2002). 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 recreate these behaviors. In 1987, Reynolds 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 (Reynolds 1987). In the following decades, researchers extended these early models to describe larger groups of individuals with more sophisticated and biologically justifiable interaction rules (Axelsen et al. 2001; Couzin & Krause 2003; Gordon 2014). Simultaneously, advancements in videography and computer vision have made it possible to empirically test some of these models in the lab (Katz et al. 2011; Buhl et al. 2006; Herbert-Read et al. 2011; Strandburg-Peshkin et al. 2013). 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 1.1) 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 describe interaction rules quantitatively at the individual level that drive movement decisions at the group level, and to assess empirically the ecological significance of collective movement in the wild (Ballerini et al. 2008; Handegard et al. 2012; Strandburg-Peshkin et al. 2017). 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 some of the earliest opportunities to study collective behavior in the wild. For example, Cavagna et al. 2008 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. 2015 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. 2014 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 m³. 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 (Gil & Hein 2017); figure 1.2).

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. Gil & Hein 2017) or other means (e.g. PIT tag readers *sensu* Aplin et al. 2014).

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 Berman et al. 2014 and Hong et al. 2015 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. 2014 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. 2014 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. 2015 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 (Hong et al. 2015), although stereo camera systems with larger apertures have been developed for tracking animals at longer ranges (Hong et al. 2015; Macfarlane et al. 2015). 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 (Anwer et al. 2017).

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" (Gracias et al. 2008). 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 (Gracias et al. 2008). 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 (Gracias et al. 2008; Shihavuddin et al. 2012), 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 (Trabes & Jordan 2015).

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, Zheng Wu et al. 2009 used thermal imaging cameras to reconstruct large groups of free-ranging bats in nocturnal footage. Benoit-Bird and Gilly 2012 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 (Benoit-Bird & Au 2003; Godø et al. 2016), and collective hunting and evasion in fish shoals (Handegard et al. 2012; Rieucou et al. 2015). 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 is currently limited for these studies.

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 (Shelhamer et al. 2017). Algorithms that explicitly model body orientation, structure, and limb orientation using multi-camera reconstructions (Cheng et al. 2016) or 3D cameras (Hong et al. 2015; Barnard et al. 2016) 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. 2013 and Rosenthal et al. 2015). Information about body posture, limb motion, and morphology may make it possible to apply new quantitative methods for characterizing behavioral states of

individuals (Stephens et al. 2008; Berman et al. 2014; Hong et al. 2015; Berman et al. 2016) and to understand better how social interactions might influence these states.

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 (figure 1.3). 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. Strandburg-Peshkin et al. 2017; figure 1.4) or computer vision techniques (e.g. Dell et al. 2014; Weinstein 2018; figure 1.5), 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.

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 (Anderson & Gaston 2013; Lowman & Voirin 2016). 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. But in general, there are several technical and political considerations to be made before establishing any UAV-based research program for wildlife (see Anderson & Gaston 2013 for a more thorough treatment of these topics).

For example, 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 or “quad-copter” designs (i.e. up to two days for the largest fixed wings vs. <1 hour for most multi-rotor systems; Anderson & Gaston 2013). 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 (Ditmer et al. 2015) or semblance to an aerial predator (Korczak-Abshire et al. 2016), though impacts may be reduced by modifying equipment or methodology (Hodgson & Koh 2016; Mulero-Pázmány et al. 2017). Furthermore, there is some evidence that UAVs may cause physiological changes in study animals (i.e. increased heart rate; Ditmer et al. 2015), 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 (Hodgson & Koh 2016; Mulero-Pázmány et al. 2017). Alternatively, non-motorized platforms (i.e. kites and aerostats) 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.

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. Commercial satellite companies maintain the largest collection of archived images with the resolution appropriate for identifying individual animals (30 cm to 50 cm (Anonymous 2017a; Anonymous 2017b), 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. Urthecast Team 2017; Earth-i Team 2017; Planet Team 2017). 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 1.3).

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 (Kays et al. 2015; Fehlmann & King 2016). 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 (Cvikel et al. 2015).

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 (Kays et al. 2015). 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*; Nagy et al. 2010), baboons (*Papio anubis*; Strandburg-Peshkin et al. 2015), domestic sheep (King et al. 2012), African wild dogs (*Lycaon pictus*; Hubel et al. 2016; King et al. 2012), and domestic dogs (*Canis lupus familiaris*; Ákos et al. 2014) (see figure 1.4 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) and with an adjustable temporal rate. 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 (Strandburg-Peshkin et al. 2015). 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 (Robinson et al. 2012). 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 (Akamatsu et al. 2013). 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 (Krause et al. 2013).

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 (Lucas et al. 1999), and co-occurrences at specific locations can be used to infer social structure (Psorakis et al. 2015). 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 (Aplin et al. 2014; Farine et al. 2014; Aplin et al. 2015), bats (*Myotis bechsteinii*; Kerth et al. 2006) and house mice (*Mus musculus*; König et al. 2015), 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 (Arlinghaus et al. 2009; Krause et al. 2013).

Proximity sensors are active transponder tags that can themselves receive information from other transponders and store information on time and ID of encountered tags (Ji et al. 2005). 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 (Rutz et al. 2015). These tags have been used to automatically map association patterns and investigate social learning in free-ranging New Caledonian crows (*Corvus moneduloides*; Rutz et al. 2012) and to investigate social dynamics of zebras (*Equus quagga*; Zhang et al. 2015) and sharks (*Carcharhinus galapagensis*; Holland et al. 2009; Guttridge et al. 2010).

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 in which they are engaging. 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 (Strandburg-Peshkin et al. 2013; Harpaz R 2014; Rosenthal et al. 2015), to build more predictive and biologically-motivated models of collective motion (Collignon et al. 2016). 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 (Ropert-Coudert & Wilson 2005; Brown et al. 2013). 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 (Martín López 2016).

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 (Wilson et al. 2006; Qasem et al. 2012; Simon et al. 2012). 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 (Martín López et al. 2015). Packages combining accelerometers and magnetometers with gyroscopes provide a more robust quantification of both energetics and gait (Martín López et al. 2016; Ware et al. 2016). See Martín López et al. 2016 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; Williams et al. 2014; Ydesen et al. 2014) and behavioral states (Wilson et al. 2008; Nathan et al. 2012; Fehlmann et al. 2017). 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 (Williams et al. 2014).

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 (Wilson & Wilson 1988). Such “dead-reckoning” methods (reviewed in Bidder et al. 2015) can help establish movement tracks without directly measuring positions (Ware et al. 2006) and can also be combined with GPS, ARGOS, or acoustic localization position data to improve the temporal resolution of movement tracks (Schmidt et al. 2010; Wensveen et al. 2015). 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, Fischer & Zinner 2011, King & Sueur 2011; meerkats (*Suricata suricatta*), Gall & Manser 2017; birds, Radford 2004; elephants (*Loxodonta africana*); Leighty et al. 2008; dolphins (*Tursiops truncatus*), Lusseau & Conradt 2009). 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 (Marshall 1998; Marshall 2007;). 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 (Yoda et al. 2011; Rosen et al. 2015; Troscianko & Rutz 2015). 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 (Burgess 2000; Johnson & Tyack 2003; Akamatsu et al. 2005), but also on terrestrial mammals (Lynch et al. 2013), birds and bats (e.g. Cvikel et al. 2015; Stowell et al. 2017). 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 (Gall et al. 2017) 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 (Dugan et al. 2010; Stowell et al. 2017). 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 (Cvikel et al. 2015). 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 (Johnson et al. 2009), thereby more easily identifying sounds from the tagged animal (Jensen et al. 2011; Pérez et al. 2016). Additionally, high sample rate accelerometers may be able to pick up on body vibrations associated with sound production in both marine (Goldbogen et al. 2014) and terrestrial (Anisimov et al. 2014) systems.

While bio-loggers that monitor the orientation and movement of animals are only

beginning to be employed in studies of collective animal behavior (Fehlmann et al. 2017; Isbell et al. 2017), 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, because 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 (Walker et al. 2015). 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 (Parrish et al. 2002; Guttal & Couzin 2010; Mueller et al. 2013; Berdahl et al. 2014). 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 (Nagy et al. 2010; Strandburg-Peshkin et al. 2017) 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 (Strandburg-Peshkin et al. 2017; figure 1.4).

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 Haydon (2010) 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. Vicsek et al. 1995; Ballerini et al. 2008; Lukeman et al. 2010; Herbert-Read et al. 2011; Katz et al. 2011) and collective predator evasion (e.g. Handegard et al. 2012; Rosenthal et al. 2015). 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. Templeton & Greene 2007; Gil & Hein 2017) 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. Templeton & Greene 2007; Bousquet et al. 2010; Dechmann et al. 2010), food manipulation (e.g. Aplin et al. 2015; Firth et al. 2016), and predator threat stimuli (Gil & Hein 2017) 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.

Figures

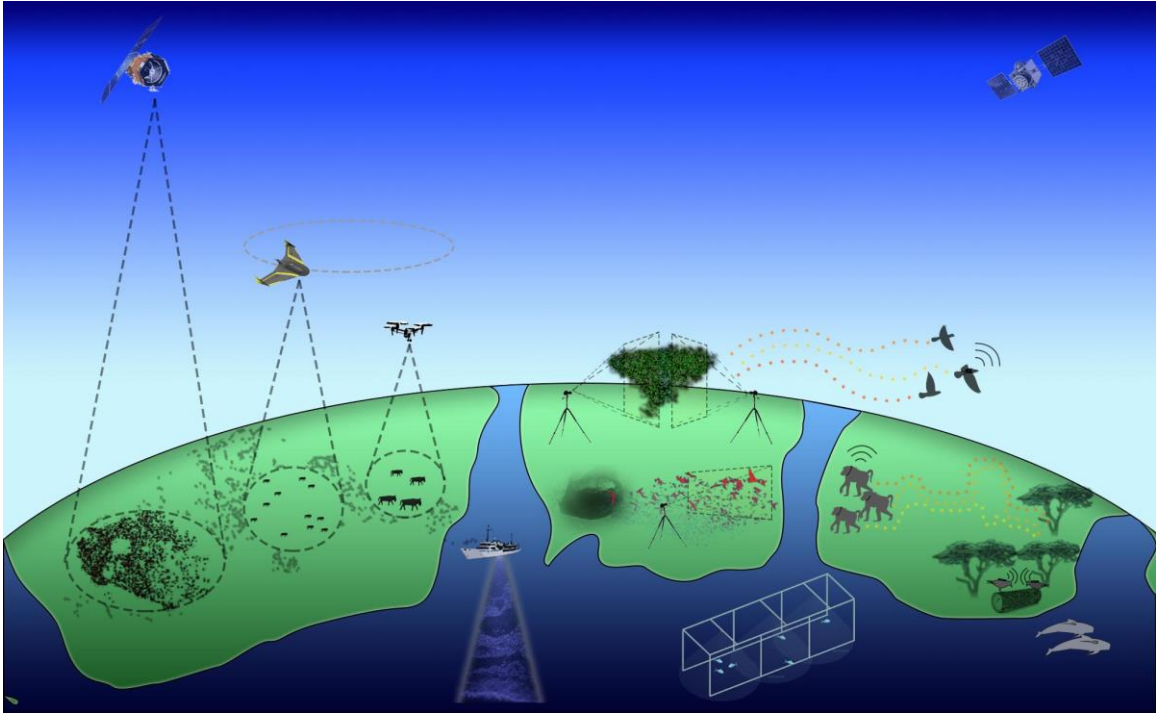


Figure 1.1. Technology is changing our view of collective behavior, offering a variety of different perspectives on animal movement and interactions. High-resolution satellite imaging, and fixed-wing or multicopter photography allows imaging groups of animals as they move across the landscape or migrate 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 or, and with both sonar and imaging sonar or infrared camera options that can be applied if visibility is low. Biologging tags that sample location, behavior, activity, or interactions with conspecifics instead provide a continuous stream of data from highly dense perspective on behaviors of tagged individuals, even in otherwise inaccessible locations or when moving across large distances.

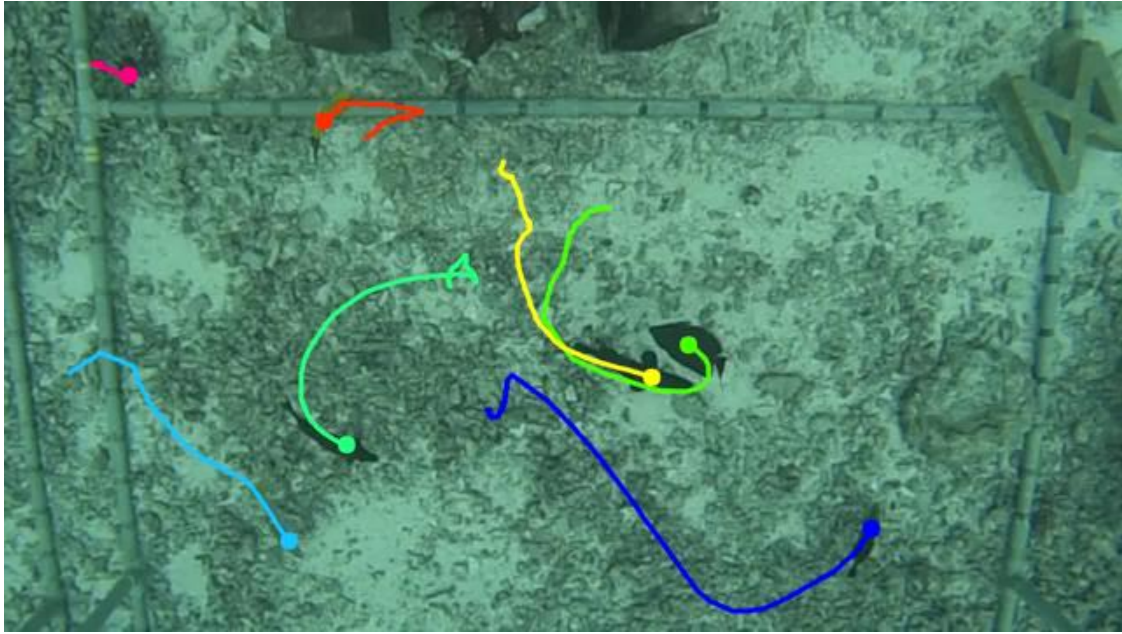


Figure 1.2. Still frame from a video sequence showing movement tracks of individual fish filmed from a stationary camera array in shallow water (Gil and Hein 2017).

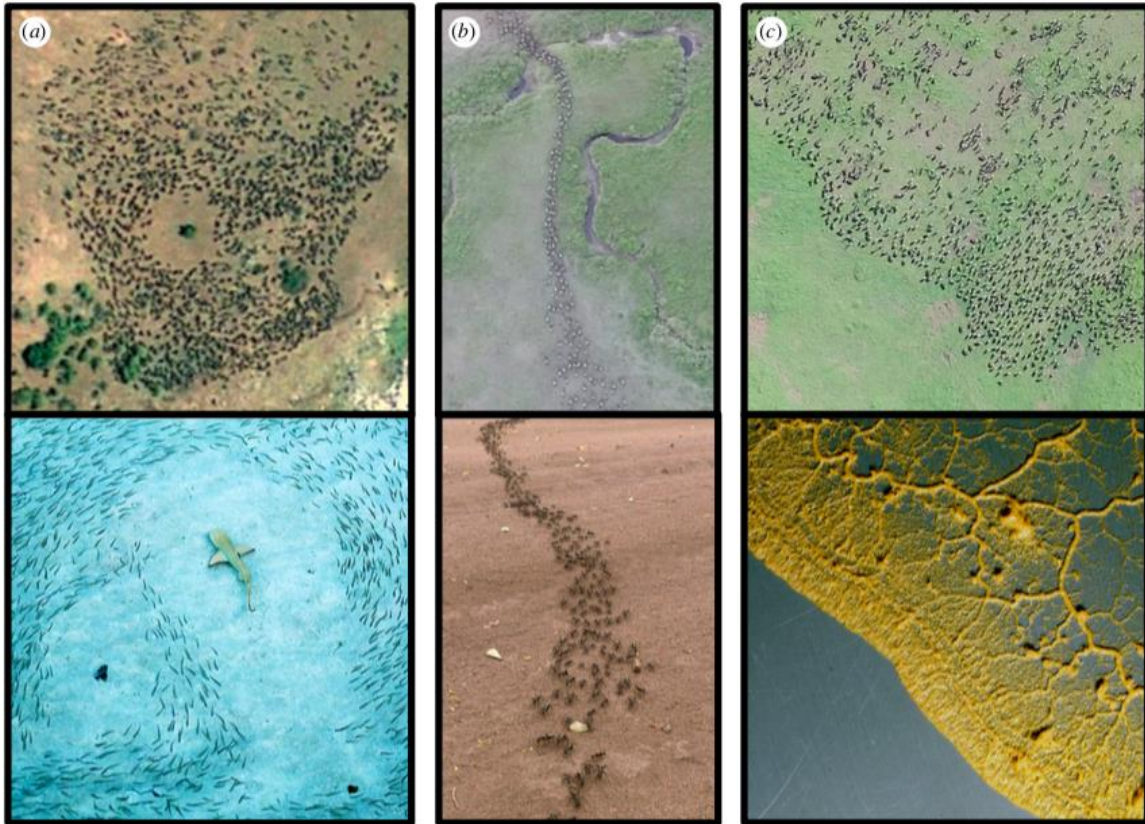


Figure 1.3. Remotely sensed imagery affords a unique opportunity to empirically study the ecology of collective motion in large animal systems. For example, satellite (a,b) and aerial (c) imagery of ungulate herds reveals aggregation patterns that are structurally similar to those previously described 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; (c) 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.

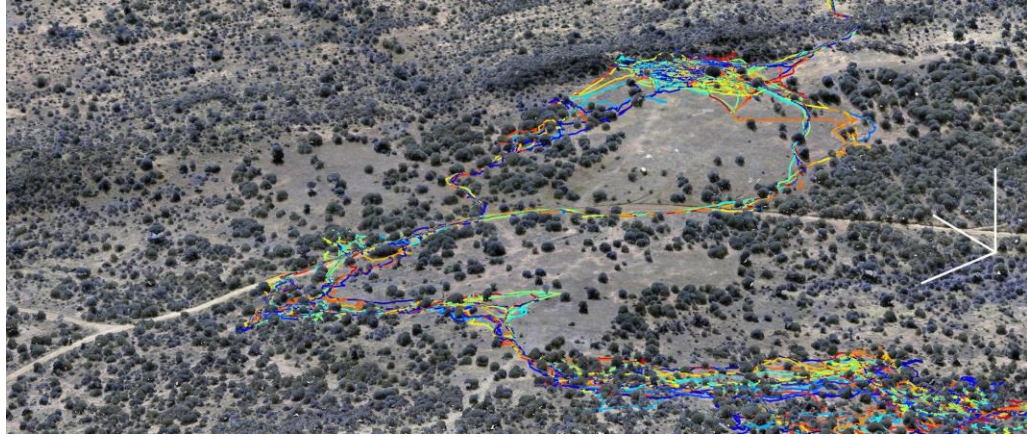


Figure 1.4. Combining bio-logging with UAV imagery enables investigation of how the environment shapes collective movement in wild animal groups over larger spatiotemporal scales than is possible with field imaging techniques alone. Colored lines show trajectories for the majority of baboons within a 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 Strandburg-Peshkin et al. 2015 & 2017.

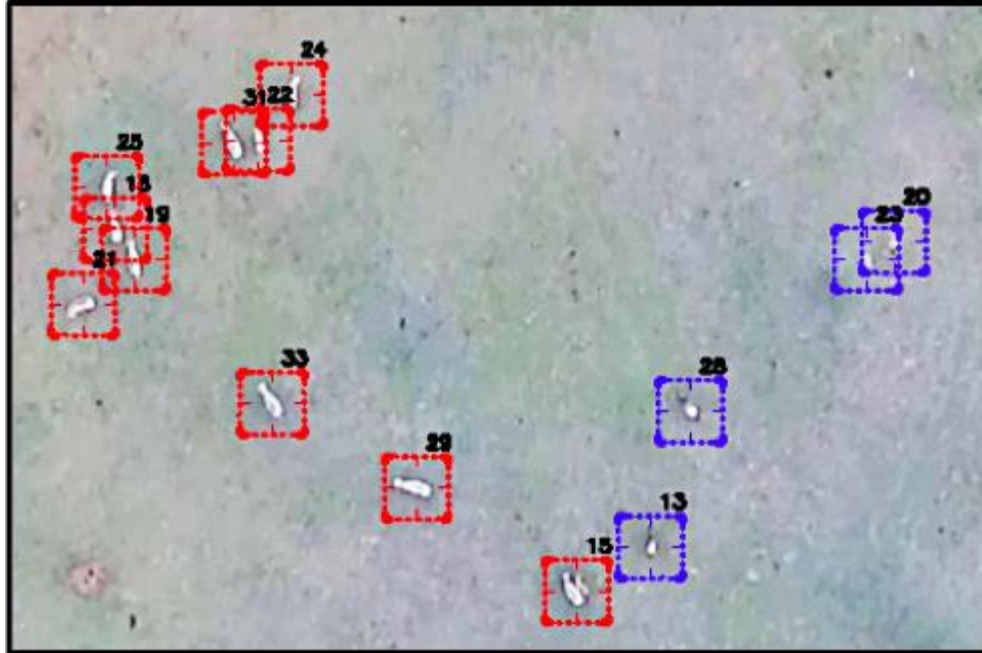


Figure 1.5. Still frame from a UAV video sequence demonstrating ability to automatically track unique individuals and species (e.g. zebra in red versus wildebeest in blue) across video frames (*sensu* Torney et al. 2016). Still frame video was reproduced with permission from Colin J. Torney.

References

- Akamatsu, T. et al., 2013. Acoustic time synchronization among tags on porpoises to observe their social relationships. *The Journal of the Acoustical Society of America*, 134(5), pp.4006–4006. Available at: <http://dx.doi.org/10.1121/1.4830613>.
- Akamatsu, T. et al., 2005. New stereo acoustic data logger for free-ranging dolphins and porpoises. *Marine Technology Society Journal*, 39(2), pp.3–9. Available at: <http://dx.doi.org/10.4031/002533205787443980>.
- Ákos, Z. et al., 2014. Leadership and path characteristics during walks are linked to dominance order and individual traits in dogs. *PLoS Computational Biology*, 10(1), p.e1003446. Available at: <http://dx.doi.org/10.1371/journal.pcbi.1003446>.
- Anderson, K. & Gaston, K.J., 2013. Lightweight unmanned aerial vehicles will revolutionize spatial ecology. *Frontiers in Ecology and the Environment*, 11(3), pp.138–146. Available at: <http://dx.doi.org/10.1890/120150>.
- Anisimov, V.N. et al., 2014. Reconstruction of vocal interactions in a group of small songbirds. *Nature Methods*, 11(11), pp.1135–1137. Available at: <http://dx.doi.org/10.1038/nmeth.3114>.
- Anonymous, 2017a. About us. *Our constellation - Digital Globe*. Available at: <https://www.digitalglobe.com/about/our-constellation> [Accessed July 1, 2017].
- Anonymous, 2017b. Pléiades satellite imagery: The very-high-resolution constellation. *Pleiades Satellite Imagery: Airbus Defense and Space*. Available at: <http://www.intelligence-airbusds.com/pleiades/> [Accessed 1 July, 2017].
- Anwer, A. et al., 2017. Underwater 3D scanning using Kinect v2 time of flight camera. In *Thirteenth International Conference on Quality Control by Artificial Vision 2017*. Available at: <http://dx.doi.org/10.1117/12.2266834>.
- Aplin, L.M. et al., 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518(7540), pp.538–541. Available at: <http://dx.doi.org/10.1038/nature13998>.
- Aplin, L.M. et al., 2014. Individual-level personality influences social foraging and collective behavior in wild birds. *Proceedings. Biological Sciences / The Royal Society*, 281(1789), p.20141016. Available at: <http://dx.doi.org/10.1098/rspb.2014.1016>.
- Arlinghaus, R. et al., 2009. Physiological and behavioral consequences of catch-and-release angling on northern pike (*Esox lucius* L.). *Fisheries Research*, 97(3), pp.223–233. Available at: <http://dx.doi.org/10.1016/j.fishres.2009.02.005>.
- Attanasi, A. et al., 2014. Collective behavior without collective order in wild swarms of

- midges. *PLoS Computational Biology*, 10(7), p.e1003697. Available at: <http://dx.doi.org/10.1371/journal.pcbi.1003697>.
- Axelsen, B.E. et al., 2001. Pretty patterns but a simple strategy: predator-prey interactions between juvenile herring and Atlantic puffins observed with multibeam sonar. *Canadian Journal of Zoology*, 79(9), pp.1586–1596. Available at: <http://dx.doi.org/10.1139/cjz-79-9-1586>.
- Ballerini, M. et al., 2008. Interaction ruling animal collective behavior depends on topological rather than metric distance: evidence from a field study. *Proceedings of the National Academy of Sciences of the United States of America*, 105(4), pp.1232–1237. Available at: <http://dx.doi.org/10.1073/pnas.0711437105>.
- Barnard, S. et al., 2016. Quick, accurate, smart: 3D computer vision technology helps assessing confined animals' behavior. *PLoS One*, 11(7), p.e0158748. Available at: <http://dx.doi.org/10.1371/journal.pone.0158748>.
- Benoit-Bird, K. & Au, W., 2003. Hawaiian spinner dolphins aggregate midwater food resources through cooperative foraging. *The Journal of the Acoustical Society of America*, 114(4), pp.2300–2300. Available at: <http://dx.doi.org/10.1121/1.4780872>.
- Benoit-Bird, K.J. & Gilly, W.F., 2012. Coordinated nocturnal behavior of foraging jumbo squid *Dosidicus gigas*. *Marine Ecology Progress Series*, 455, pp.211–228. Available at: <http://dx.doi.org/10.3354/meps09664>.
- Berdahl, A. et al., 2014. A collective navigation hypothesis for homeward migration in anadromous salmonids. *Fish and Fisheries*, 17(2), pp.525–542. Available at: <http://dx.doi.org/10.1111/faf.12084>.
- Berman, G.J. et al., 2014. Mapping the stereotyped behavior of freely moving fruit flies. *Journal of the Royal Society, Interface / the Royal Society*, 11(99). Available at: <http://dx.doi.org/10.1098/rsif.2014.0672>.
- Berman, G.J., Bialek, W. & Shaevitz, J.W., 2016. Predictability and hierarchy in *Drosophila* behavior. *Proceedings of the National Academy of Sciences of the United States of America*, 113(42), pp.11943–11948. Available at: <http://dx.doi.org/10.1073/pnas.1607601113>.
- Bidder, O.R. et al., 2015. Step by step: reconstruction of terrestrial animal movement paths by dead-reckoning. *Movement Ecology*, 3(1), p.23. Available at: <http://dx.doi.org/10.1186/s40462-015-0055-4>.
- Bousquet, C.A.H., Sumpter, D.J.T. & Manser, M.B., 2010. Moving calls: a vocal mechanism underlying quorum decisions in cohesive groups. *Proceedings of the Royal Society B: Biological Sciences*, 278(1711), pp.1482–1488. Available at: <http://dx.doi.org/10.1098/rspb.2010.1739>.
- Brown, D.D. et al., 2013. Observing the unwatchable through acceleration logging of animal

- behavior. *Animal Biotelemetry*, 1(1), p.20. Available at:
<http://animalbiotelemetry.biomedcentral.com/articles/10.1186/2050-3385-1-20>.
- Buhl, J. et al., 2006. From disorder to order in marching locusts. *Science*, 312(5778), pp.1402–1406. Available at: <http://dx.doi.org/10.1126/science.1125142>.
- Burgess, W.C., 2000. The bioacoustic probe: A general-purpose acoustic recording tag. *The Journal of the Acoustical Society of America*, 108(5), pp.2583–2583. Available at:
<http://dx.doi.org/10.1121/1.4743598>.
- Cavagna, A. et al., 2008. The STARFLAG handbook on collective animal behavior: 1. Empirical methods. *Animal Behavior*, 76(1), pp.217–236. Available at:
<http://dx.doi.org/10.1016/j.anbehav.2008.02.002>.
- Cheng, X.E., Wang, S.H. & Chen, Y.Q., 2016. Estimating orientation in tracking individuals of flying swarms. In *2016 IEEE International Conference on Acoustics, Speech and Signal Processing (ICASSP)*. Available at:
<http://dx.doi.org/10.1109/icassp.2016.7471926>.
- Collignon, B., Séguret, A. & Halloy, J., 2016. A stochastic vision-based model inspired by zebrafish collective behavior in heterogeneous environments. *Royal Society Open Science*, 3(1), p.150473. Available at: <http://dx.doi.org/10.1098/rsos.150473>.
- Couzin, I.D. & Krause, J., 2003. Self-organization and collective behavior in vertebrates. *Advances in the Study of Behavior*. pp. 1–75. Available at:
[http://dx.doi.org/10.1016/s0065-3454\(03\)01001-5](http://dx.doi.org/10.1016/s0065-3454(03)01001-5).
- Cvikel, N. et al., 2015. Bats aggregate to improve prey search but might be impaired when their density becomes too high. *Current Biology: CB*, 25(2), pp.206–211. Available at:
<http://dx.doi.org/10.1016/j.cub.2014.11.010>.
- Dechmann, D.K.N. et al., 2010. *Experimental evidence for group hunting via eavesdropping in echolocating bats*, Available at:
https://books.google.com/books/about/Experimental_Evidence_for_Group_Hunting.html?hl=&id=KqHInQAACAAJ.
- Dell, A.I. et al., 2014. Automated image-based tracking and its application in ecology. *Trends in Ecology & Evolution*, 29(7), pp.417–428. Available at:
<http://dx.doi.org/10.1016/j.tree.2014.05.004>.
- Ditmer, M.A. et al., 2015. Bears show a physiological but limited behavioral response to unmanned aerial vehicles. *Current Biology: CB*, 25(17), pp.2278–2283. Available at:
<http://dx.doi.org/10.1016/j.cub.2015.07.024>.
- Dugan, P.J. et al., 2010. North Atlantic Right Whale acoustic signal processing: Part I. comparison of machine learning recognition algorithms. In *2010 IEEE Long Island Systems, Applications and Technology Conference*. Available at:
<http://dx.doi.org/10.1109/lisat.2010.5478268>.

- Earth-i Team, 2017. The DMC3 Constellation. *earthi.space*. Available at: <http://earthi.space/dmc3/> [Accessed June 1, 2017].
- Farine, D.R. et al., 2014. Collective decision making and social interaction rules in mixed-species flocks of songbirds. *Animal Behavior*, 95(100), pp.173–182. Available at: <http://dx.doi.org/10.1016/j.anbehav.2014.07.008>.
- Fehlmann, G. et al., 2017. Identification of behaviors from accelerometer data in a wild social primate. *Animal Biotelemetry*, 5(1). Available at: <http://dx.doi.org/10.1186/s40317-017-0121-3>.
- Fehlmann, G. & King, A.J., 2016. Bio-logging. *Current Biology: CB*, 26(18), pp.R830–1. Available at: <http://dx.doi.org/10.1016/j.cub.2016.05.033>.
- Firth, J.A., Sheldon, B.C. & Farine, D.R., 2016. Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. *Biology Letters*, 12(6). Available at: <http://dx.doi.org/10.1098/rsbl.2016.0144>.
- Fischer, J. & Zinner, D., 2011. Communication and cognition in primate group movement. *International Journal of Primatology*, 32(6), pp.1279–1295. Available at: <http://dx.doi.org/10.1007/s10764-011-9542-7>.
- Gall, G.E.C. et al., 2017. As dusk falls: collective decisions about the return to sleeping sites in meerkats. *Animal Behavior*, 132, pp.91–99. Available at: <http://dx.doi.org/10.1016/j.anbehav.2017.08.001>.
- Gall, G.E.C. & Manser, M.B., 2017. Group cohesion in foraging meerkats: follow the moving “vocal hot spot.” *Royal Society Open Science*, 4(4), p.170004. Available at: <http://dx.doi.org/10.1098/rsos.170004>.
- Gil, M.A. & Hein, A.M., 2017. Social interactions among grazing reef fish drive material flux in a coral reef ecosystem. *Proceedings of the National Academy of Sciences*, 114(18), pp.4703–4708. Available at: <http://dx.doi.org/10.1073/pnas.1615652114>.
- Ginelli, F. et al., 2015. Intermittent collective dynamics emerge from conflicting imperatives in sheep herds. *Proceedings of the National Academy of Sciences of the United States of America*, 112(41), pp.12729–12734. Available at: <http://dx.doi.org/10.1073/pnas.1503749112>.
- Godø, O.R. et al., 2013. Synchronous behavior of cetaceans observed with active acoustics. *Deep-sea research. Part II, Topical Studies in Oceanography*, 98, pp.445–451. Available at: <http://dx.doi.org/10.1016/j.dsr2.2013.06.013>.
- Goldbogen, J.A. et al., 2014. Using accelerometers to determine the calling behavior of tagged baleen whales. *The Journal of Experimental Biology*, 217(Pt 14), pp.2449–2455. Available at: <http://dx.doi.org/10.1242/jeb.103259>.

- Gordon, D.M., 2014. The Ecology of Collective Behavior. *PLoS Biology*, 12(3), p.e1001805. Available at: <http://dx.doi.org/10.1371/journal.pbio.1001805>.
- Gracias, N. et al., 2008. A motion compensated filtering approach to remove sunlight flicker in shallow water images. In *OCEANS 2008*. Available at: <http://dx.doi.org/10.1109/oceans.2008.5152111>.
- Guttal, V. & Couzin, I.D., 2010. Social interactions, information use, and the evolution of collective migration. *Proceedings of the National Academy of Sciences of the United States of America*, 107(37), pp.16172–16177. Available at: <http://dx.doi.org/10.1073/pnas.1006874107>.
- Guttridge, T.L. et al., 2010. Novel acoustic technology for studying free-ranging shark social behavior by recording individuals' interactions. *PloS One*, 5(2), p.e9324. Available at: <http://dx.doi.org/10.1371/journal.pone.0009324>.
- Handegard, N.O. et al., 2012. The dynamics of coordinated group hunting and collective information transfer among schooling prey. *Current Biology: CB*, 22(13), pp.1213–1217. Available at: <http://dx.doi.org/10.1016/j.cub.2012.04.050>.
- Harpaz R, S.E., 2014. Receptive-field like models accurately predict individual zebrafish behavior in a group. *Journal of Molecular Neuroscience: MN*, 53, p.S61.
- Hebblewhite, M. & Haydon, D.T., 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 365(1550), pp.2303–2312. Available at: <http://dx.doi.org/10.1098/rstb.2010.0087>.
- Herbert-Read, J.E. et al., 2011. Inferring the rules of interaction of shoaling fish. *Proceedings of the National Academy of Sciences of the United States of America*, 108(46), pp.18726–18731. Available at: <http://dx.doi.org/10.1073/pnas.1109355108>.
- Hodgson, J.C. & Koh, L.P., 2016. Best practice for minimising unmanned aerial vehicle disturbance to wildlife in biological field research. *Current Biology: CB*, 26(10), pp.R404–5. Available at: <http://dx.doi.org/10.1016/j.cub.2016.04.001>.
- Holland, K.N., Meyer, C.G. & Dagorn, L.C., 2009. Inter-animal telemetry: results from first deployment of acoustic “business card” tags. *Endangered Species Research*, 10, pp.287–293. Available at: <http://dx.doi.org/10.3354/esr00226>.
- Hong, W. et al., 2015. Automated measurement of mouse social behaviors using depth sensing, video tracking, and machine learning. *Proceedings of the National Academy of Sciences of the United States of America*, 112(38), pp.E5351–60. Available at: <http://dx.doi.org/10.1073/pnas.1515982112>.
- Hubel, T.Y. et al., 2016. Additive opportunistic capture explains group hunting benefits in African wild dogs. *Nature Communications*, 7, p.11033. Available at: <http://dx.doi.org/10.1038/ncomms11033>.

- Isbell, L.A. et al., 2017. GPS-identified, low-level nocturnal activity of vervets (*Chlorocebus pygerythrus*) and olive baboons (*Papio anubis*) in Laikipia, Kenya. *American Journal of Physical Anthropology*. Available at: <http://dx.doi.org/10.1002/ajpa.23259>.
- Jensen, F.H. et al., 2011. Calling under pressure: short-finned pilot whales make social calls during deep foraging dives. *Proceedings. Biological Sciences / The Royal Society*, 278(1721), pp.3017–3025. Available at: <http://dx.doi.org/10.1098/rspb.2010.2604>.
- Ji, W., White, P.C.L. & Clout, M.N., 2005. Contact rates between possums revealed by proximity data loggers. *The Journal of Applied Ecology*, 42(3), pp.595–604. Available at: <http://dx.doi.org/10.1111/j.1365-2664.2005.01026.x>.
- Johnson, M.P. & Tyack, P.L., 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering*, 28(1), pp.3–12. Available at: <http://dx.doi.org/10.1109/joe.2002.808212>.
- Johnson, M., de Soto, N.A. & Madsen, P.T., 2009. Studying the behavior and sensory ecology of marine mammals using acoustic recording tags: a review. *Marine Ecology Progress Series*, 395, pp.55–73. Available at: <http://dx.doi.org/10.3354/meps08255>.
- Katz, Y. et al., 2011. Inferring the structure and dynamics of interactions in schooling fish. *Proceedings of the National Academy of Sciences*, 108(46), pp.18720–18725. Available at: <http://dx.doi.org/10.1073/pnas.1107583108>.
- Kays, R. et al., 2015. Ecology. Terrestrial animal tracking as an eye on life and planet. *Science*, 348(6240), p.aaa2478. Available at: <http://dx.doi.org/10.1126/science.aaa2478>.
- Kerth, G., Ebert, C. & Schmidtke, C., 2006. Group decision making in fission-fusion societies: evidence from two-field experiments in Bechstein's bats. *Proceedings of the Royal Society B: Biological Sciences*, 273(1602), pp.2785–2790. Available at: <http://dx.doi.org/10.1098/rspb.2006.3647>.
- King, A.J. et al., 2012. Selfish-herd behavior of sheep under threat. *Current Biology: CB*, 22(14), pp.R561–2. Available at: <http://dx.doi.org/10.1016/j.cub.2012.05.008>.
- King, A.J. & Sueur, C., 2011. Where next? Group coordination and collective decision making by primates. *International Journal of Primatology*, 32(6), pp.1245–1267. Available at: <http://link.springer.com/10.1007/s10764-011-9526-7>.
- König, B. et al., 2015. A system for automatic recording of social behavior in a free-living wild house mouse population. *Animal Biotelemetry*, 3(1), p.541. Available at: <http://www.animalbiotelemetry.com/content/3/1/39>.
- Korczak-Abshire M, Kidawa A, Zmarz A, Storvold R, Karlsen SR, Rodzewicz M, Chwedorzewska K, Znój A, 2016. Preliminary study on nesting Adélie penguins disturbance by unmanned aerial vehicles. *CCAMLR Science*, 23, pp.1–6.

- Krause, J. et al., 2013. Reality mining of animal social systems. *Trends in Ecology & Evolution*, 28(9), pp.541–551. Available at: <http://dx.doi.org/10.1016/j.tree.2013.06.002>.
- Leighty, K.A. et al., 2008. Rumble vocalizations mediate interpartner distance in African elephants, *Loxodonta africana*. *Animal Behavior*, 76(5), pp.1601–1608. Available at: <http://dx.doi.org/10.1016/j.anbehav.2008.06.022>.
- Lowman, M. & Voirin, B., 2016. Drones - our eyes on the environment. *Frontiers in Ecology and the Environment*, 14(5), pp.231–231. Available at: <http://dx.doi.org/10.1002/fee.1290>.
- Lucas, M.C. et al., 1999. Use of a flat-bed passive integrated transponder antenna array to study the migration and behavior of lowland river fishes at a fish pass. *Fisheries Research*, 44(2), pp.183–191. Available at: [http://dx.doi.org/10.1016/s0165-7836\(99\)00061-2](http://dx.doi.org/10.1016/s0165-7836(99)00061-2).
- Lukeman, R., Li, Y.-X. & Edelstein-Keshet, L., 2010. Inferring individual rules from collective behavior. *Proceedings of the National Academy of Sciences of the United States of America*, 107(28), pp.12576–12580. Available at: <http://dx.doi.org/10.1073/pnas.1001763107>.
- Lusseau, D. & Conradt, L., 2009. The emergence of unshared consensus decisions in bottlenose dolphins. *Behavioral Ecology and Sociobiology*, 63(7), pp.1067–1077. Available at: <http://link.springer.com/10.1007/s00265-009-0740-7>.
- Lynch, E. et al., 2013. The use of on-animal acoustical recording devices for studying animal behavior. *Ecology and Evolution*, 3(7), pp.2030–2037. Available at: <http://dx.doi.org/10.1002/ece3.608>.
- Macfarlane, N.B.W. et al., 2015. A 3D stereo camera system for precisely positioning animals in space and time. *Behavioral Ecology and Sociobiology*, 69(4), pp.685–693. Available at: <http://dx.doi.org/10.1007/s00265-015-1890-4>.
- Marshall, G., 2007. Advances in animal-borne imaging. *Marine Technology Society Journal*, 41(4), pp.4–5. Available at: <http://dx.doi.org/10.4031/002533207787441926>.
- Marshall, G.J., 1998. Crittercam: An animal-borne imaging and data logging system. *Marine Technology Society Journal*, 32(1), p.11.
- Martín López, L.M. et al., 2015. Gait switches in deep-diving beaked whales: biomechanical strategies for long-duration dives. *The Journal of Experimental Biology*, 218(Pt 9), pp.1325–1338. Available at: <http://dx.doi.org/10.1242/jeb.106013>.
- Martín López, L.M. et al., 2016. Tracking the kinematics of caudal-oscillatory swimming: a comparison of two on-animal sensing methods. *The Journal of Experimental Biology*, 219(Pt 14), pp.2103–2109. Available at: <http://dx.doi.org/10.1242/jeb.136242>.

- Mueller, T. et al., 2013. Social learning of migratory performance. *Science*, 341(6149), pp.999–1002. Available at: <http://dx.doi.org/10.1126/science.1237139>.
- Mulero-Pázmány, M. et al., 2017. Unmanned aircraft systems as a new source of disturbance for wildlife: A systematic review. *PloS One*, 12(6), p.e0178448. Available at: <http://dx.doi.org/10.1371/journal.pone.0178448>.
- Nagy, M. et al., 2010. Hierarchical group dynamics in pigeon flocks. *Nature*, 464(7290), pp.890–893. Available at: <http://dx.doi.org/10.1038/nature08891>.
- Nathan, R. et al., 2012. Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *The Journal of Experimental Biology*, 215(Pt 6), pp.986–996. Available at: <http://dx.doi.org/10.1242/jeb.058602>.
- Parrish, J.K., Viscido, S.V. & Grünbaum, D., 2002. Self-organized fish schools: an examination of emergent properties. *The Biological Bulletin*, 202(3), pp.296–305. Available at: <http://dx.doi.org/10.2307/1543482>.
- Pérez, J.M. et al., 2016. Different modes of acoustic communication in deep-diving short-finned pilot whales (*Globicephala macrorhynchus*). *Marine Mammal Science*, 33(1), pp.59–79. Available at: <http://dx.doi.org/10.1111/mms.12344>.
- Planet Team, 2017. Planet application program interface: In space for life on earth. *planet.com*. Available at: <https://api.planet.com> [Accessed June 1, 2017].
- Psorakis I, Voelkl B, Garroway CJ, Radersma R, Aplin LM, Crates RA, Culina A, Farine DR, Firth JA, Hinde CA, Kidd LR, 2015. Inferring social structure from temporal data. *Behavioral Ecology and Sociobiology*, 69(5), pp.857–866. Available at: <http://link.springer.com/10.1007/s00265-015-1906-0>.
- Qasem, L. et al., 2012. Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PloS One*, 7(2), p.e31187. Available at: <http://dx.doi.org/10.1371/journal.pone.0031187>.
- Radford, A.N., 2004. Vocal coordination of group movement by green woodhoopoes (*Phoeniculus purpureus*). *Ethology: formerly Zeitschrift fur Tierpsychologie*, 110(1), pp.11–20. Available at: <http://doi.wiley.com/10.1046/j.1439-0310.2003.00943.x>.
- Reynolds, C.W., 1987. Flocks, herds and schools: A distributed behavioral model. In *Proceedings of the 14th Annual Conference on Computer Graphics and Interactive Techniques - SIGGRAPH '87*. Available at: <http://dx.doi.org/10.1145/37401.37406>.
- Rieucou, G., Sivle, L.D. & Handegard, N.O., 2015. Herring perform stronger collective evasive reactions when previously exposed to killer whales calls. *Behavioral Ecology: official journal of the International Society for Behavioral Ecology*, 27(2), pp.538–544. Available at: <http://dx.doi.org/10.1093/beheco/arv186>.

- Robinson, P.W. et al., 2012. Foraging behavior and success of a mesopelagic predator in the northeast Pacific Ocean: insights from a data-rich species, the northern elephant seal. *PloS One*, 7(5), p.e36728. Available at: <http://dx.doi.org/10.1371/journal.pone.0036728>.
- Ropert-Coudert, Y. & Wilson, R.P., 2005. Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment*, 3(8), p.437. Available at: <http://dx.doi.org/10.2307/3868660>.
- Rosen, H. et al., 2015. Chromogenic behaviors of the Humboldt squid (*Dosidicus gigas*) studied in situ with an animal-borne video package. *The Journal of Experimental Biology*, 218(Pt 2), pp.265–275. Available at: <http://dx.doi.org/10.1242/jeb.114157>.
- Rosenthal, S.B. et al., 2015. Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion. *Proceedings of the National Academy of Sciences of the United States of America*, 112(15), pp.4690–4695. Available at: <http://dx.doi.org/10.1073/pnas.1420068112>.
- Rutz, C. et al., 2012. Automated mapping of social networks in wild birds. *Current Biology: CB*, 22(17), pp.R669–71. Available at: <http://dx.doi.org/10.1016/j.cub.2012.06.037>.
- Rutz, C. et al., 2015. Calibrating animal-borne proximity loggers. *Methods in Ecology and Evolution / British Ecological Society*, 6(6), pp.656–667. Available at: <http://dx.doi.org/10.1111/2041-210X.12370>.
- Schmidt, V. et al., 2010. Underwater tracking of humpback whales (*Megaptera Novaeangliae*) with high-Frequency pingers and acoustic recording tags. *IEEE Journal of Oceanic Engineering*, 35(4), pp.821–836. Available at: <http://dx.doi.org/10.1109/joe.2010.2068610>.
- Shelhamer, E., Long, J. & Darrell, T., 2017. Fully convolutional networks for semantic segmentation. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 39(4), pp.640–651. Available at: <http://dx.doi.org/10.1109/TPAMI.2016.2572683>.
- Shihavuddin, A. S. M., Nuno Gracias, and Rafael Garcia, 2012. Online Sunflicker Removal using Dynamic Texture Prediction. In *Proceedings of the International Conference on Computer Vision Theory and Applications*. pp. 161–167. Available at: <http://dx.doi.org/10.5220/0003811901610167>.
- Simon, M., Johnson, M. & Madsen, P.T., 2012. Keeping momentum with a mouthful of water: behavior and kinematics of humpback whale lunge feeding. *The Journal of Experimental Biology*, 215(Pt 21), pp.3786–3798. Available at: <http://dx.doi.org/10.1242/jeb.071092>.
- Stephens, G.J. et al., 2008. Dimensionality and dynamics in the behavior of *C. elegans*. *PLoS Computational Biology*, 4(4), p.e1000028. Available at: <http://dx.doi.org/10.1371/journal.pcbi.1000028>.

- Stowell, D., Benetos, E. & Gill, L.F., 2017. On-Bird Sound Recordings: Automatic Acoustic Recognition of Activities and Contexts. *IEEE/ACM Transactions on Audio, Speech, and Language Processing*, 25(6), pp.1193–1206. Available at: <http://dx.doi.org/10.1109/taslp.2017.2690565>.
- Strandburg-Peshkin, A. et al., 2015. GROUP DECISIONS. Shared decision-making drives collective movement in wild baboons. *Science*, 348(6241), pp.1358–1361. Available at: <http://dx.doi.org/10.1126/science.aaa5099>.
- Strandburg-Peshkin, A. et al., 2017. Habitat and social factors shape individual decisions and emergent group structure during baboon collective movement. *eLife*, 6. Available at: <http://dx.doi.org/10.7554/eLife.19505>.
- Strandburg-Peshkin, A. et al., 2013. Visual sensory networks and effective information transfer in animal groups. *Current Biology: CB*, 23(17), pp.R709–11. Available at: <http://dx.doi.org/10.1016/j.cub.2013.07.059>.
- Templeton, C.N. & Greene, E., 2007. Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *Proceedings of the National Academy of Sciences of the United States of America*, 104(13), pp.5479–5482. Available at: <http://dx.doi.org/10.1073/pnas.0605183104>.
- Theriault, D.H. et al., 2014. A protocol and calibration method for accurate multi-camera field videography. *The Journal of Experimental Biology*, 217(Pt 11), pp.1843–1848. Available at: <http://dx.doi.org/10.1242/jeb.100529>.
- Torney, C.J. et al., 2016. Assessing Rotation-Invariant Feature Classification for Automated Wildebeest Population Counts. *PloS One*, 11(5), p.e0156342. Available at: <http://dx.doi.org/10.1371/journal.pone.0156342>.
- Torney, C.J. et al., 2018. Inferring the rules of social interaction in migrating caribou. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 373(1746). Available at: <http://dx.doi.org/10.1098/rstb.2017.0385>.
- Trabes, E. & Jordan, M.A., 2015. Self-tuning of a sunlight-deflickering filter for moving scenes underwater. In *2015 XVI Workshop on Information Processing and Control (RPIC)*. Available at: <http://dx.doi.org/10.1109/rpic.2015.7497107>.
- Troscianko, J. & Rutz, C., 2015. Activity profiles and hook-tool use of New Caledonian crows recorded by bird-borne video cameras. *Biology Letters*, 11(12), p.20150777. Available at: <http://dx.doi.org/10.1098/rsbl.2015.0777>.
- Urthecast Team, 2017. The UrtheDaily constellation. *Urthecast.com*. Available at: <https://www.urthecast.com/urthedaily/> [Accessed June 1, 2017].
- Vicsek, T. et al., 1995. Novel type of phase transition in a system of self-driven particles. *Physical Review Letters*, 75(6), pp.1226–1229. Available at: <http://dx.doi.org/10.1103/PhysRevLett.75.1226>.

- Walker, J.S. et al., 2015. Prying into the intimate secrets of animal lives; software beyond hardware for comprehensive annotation in “Daily Diary” tags. *Movement Ecology*, 3(1), p.29. Available at: <http://dx.doi.org/10.1186/s40462-015-0056-3>.
- Ware, C. et al., 2016. Averaged propulsive body acceleration (APBA) can be calculated from biologging tags that incorporate gyroscopes and accelerometers to estimate swimming speed, hydrodynamic drag and energy expenditure for Steller sea lions. *PloS One*, 11(6), p.e0157326. Available at: <http://dx.doi.org/10.1371/journal.pone.0157326>.
- Ware, C. et al., 2006. Visualizing the underwater behavior of humpback whales. *IEEE Computer Graphics and Applications*, 26(4), pp.14–18. Available at: <https://www.ncbi.nlm.nih.gov/pubmed/16863093>.
- Weinstein, B.G., 2018. A computer vision for ecology. *The Journal of Animal Ecology*, 87(3), p. 533-545. Available at: <https://doi.org/10.1111/1365-2656.12780>.
- Wensveen, P.J., Thomas, L. & Miller, P.J.O., 2015. A path reconstruction method integrating dead-reckoning and position fixes applied to humpback whales. *Movement Ecology*, 3(1), p.31. Available at: <http://dx.doi.org/10.1186/s40462-015-0061-6>.
- Williams, T.M. et al., 2014. Mammalian energetics. Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. *Science*, 346(6205), pp.81–85. Available at: <http://dx.doi.org/10.1126/science.1254885>.
- Wilson, R.P. et al., 2006. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *The Journal of Animal Ecology*, 75(5), pp.1081–1090. Available at: <http://dx.doi.org/10.1111/j.1365-2656.2006.01127.x>.
- Wilson, R.P., Shepard, E. & Liebsch, N., 2008. Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research*, 4, pp.123–137. Available at: <http://dx.doi.org/10.3354/esr00064>.
- Wilson, R.P. & Wilson, M.-P., 1988. *Dead reckoning: a new technique for determining penguin movements at sea*, Available at: https://books.google.com/books/about/Dead_reckoning.html?hl=&id=YzmAtwAACA AJ.
- Ydesen, K.S. et al., 2014. What a jerk: prey engulfment revealed by high-rate, super-cranial accelerometry on a harbour seal (*Phoca vitulina*). *The Journal of Experimental Biology*, 217(Pt 13), pp.2239–2243. Available at: <http://dx.doi.org/10.1242/jeb.100016>.
- Yoda, K. et al., 2011. Social interactions of juvenile brown boobies at sea as observed with animal-borne video cameras. *PloS One*, 6(5), p.e19602. Available at: <http://dx.doi.org/10.1371/journal.pone.0019602>.
- Zhang P, Sadler CM, Liu T, Fischhoff I, Martonosi M, Lyons SA, Rubenstein DI, 2005. Habitat monitoring with ZebraNet: design and experiences. In wireless sensor

networks: A systems perspective, pp.235–257.

Zheng Wu et al., 2009. Tracking a large number of objects from multiple views. In *2009 IEEE 12th International Conference on Computer Vision*. Available at: <http://dx.doi.org/10.1109/iccv.2009.5459274>.

Chapter II: Remotely sensing animal behavior

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Abstract

The ability to generalize observations from individuals to populations has been a perennial challenge for researchers working in a number of ecosystems, particularly since individual decisions do not necessarily scale to the emergent properties of large groups. Such challenges are especially pertinent to the study of animal behavior, where individual responses may drive social processes at higher levels of biological organization (i.e. individual behaviors may impact a group's ability to avoid predators, access forage, find mates, etc.). Yet our ability to study such processes in the wild has been hindered by the

technical limitations of conventional tools for animal observation. Recent advances in satellite remote sensing now provide a powerful opportunity to capture non-invasive, multi-scale information on the behavioral dynamics of animal groups in the wild. Here, we introduce a new method for remotely studying the distribution and behavior of tens of thousands of animals (white-bearded wildebeest; *Connochaetes taurinus*) identified in high-resolution (≤ 50 cm) satellite imagery. To develop this method, we: 1) identified and ground-truthed group-level attributes of herd structure that were associated with common behavioral states of individuals, 2) used these observations to develop an automated classifier that reliably predicted three behavioral states (82% accuracy overall) from a single metric of group structure (i.e. coordinated orientation), and finally 3) applied the classifier to categorize the distribution of these same behavioral states in a high-resolution satellite image of nearly 50,000 wildebeest spread across a 25 km² study area. The algorithm resulted in classifications for 62% ($n = 30,711$) of the wildebeest identified in the satellite image and, of these, the majority (77%; $n = 23,667$) were classified with high confidence (i.e. $\geq 75\%$). This non-invasive method for mapping the behavior of animal groups presents a novel opportunity to study the social and environmental drivers of animal behavior across multiple scales of space and biological organization (i.e. individuals to populations). Forecasted reductions in cost and increases in the resolution of satellite imagery, coupled with advances in machine learning techniques for automated image analysis, are likely to expand applications for this technique in the near future.

Introduction

The challenge of making population-level inferences from observations of a few well-studied individuals has been a major limitation to our capacity to study many social species (Calabrese et al. 2018; Hughey et al. 2018; Torney et al. 2018; Westley et al. 2018). These shortcomings are largely attributed to the difficulty of collecting behavioral data on multiple individuals with adequate precision, especially in large animal systems. For example, GPS collars afford long-term, high-resolution insights into the behaviors of single animals. But the challenge and expense of applying tags to multiple individuals limits our ability to obtain insights on the diversity of social processes thought to play an important role in most movement decisions (but see Nagy et al. 2010; King et al. 2012; Cvikel et al. 2015; Strandburg-Peshkin et al. 2015; Hubel et al. 2016; Strandburg-Peshkin et al. 2017 for notable exceptions). Similarly, field observations and camera traps can provide detailed behavioral snapshots of tens to hundreds of animals at once, but these studies are inherently limited in spatial and temporal scope. Finally, laboratory and theoretical investigations have produced numerous and valuable insights into cross-scale patterns of animal behavior in a range of systems (Gueron & Levin 1993; Buhl et al. 2006; Herbert-Read et al. 2011; Katz et al. 2011), but those focused on large animal models are frequently lacking validation in the field (Hughey et al. 2018).

Recent advances in high-resolution satellite technology now present a powerful opportunity to extend the current suite of animal observation tools by providing a high-resolution, aerial perspective of animal groups across tens to hundreds of kilometers. This is made possible by a growing archive of high-resolution imagery (i.e. 30-50 cm) and the ability to commission new images on-demand for almost any location on earth (Hughey et al. 2018). Likewise, the burgeoning nanosatellite industry (i.e. miniaturized satellites

weighing 1-10 kg) is making low-cost, sub-daily images at 2.5 m resolution a reality for scientists and practitioners alike. Alongside the rapid development of these constellations of imaging satellites, advances in machine learning and automated image processing present promising avenues for high-efficiency detection of large animals in this imagery (Torney et al. 2016; Xue et al. 2017).

Although animal identification from satellite imagery is a nascent concept, researchers have demonstrated the potential value of this technique by using it to enumerate more than 20 vertebrate species in a variety of habitats, including African savannas, arctic tundra, and the open ocean (Febbo et al. 2017; Fretwell et al. 2017; LaRue et al. 2017; Hollings et al. 2018). These studies have formed the foundation of satellite-based animal observation, and the next logical step is to push this technology beyond the enumeration of species and towards the acquisition of broader ecological insights. Specifically, when combined with the knowledge that individual behaviors can result in unique and predictable patterns of herd structure, high-resolution satellites present a novel opportunity to obtain a deeper understanding of the behavioral and ecological processes that promote the persistence of social species.

In this study, we focus on the migration of white-bearded wildebeest (*Connochaetes taurinus*; hereafter “wildebeest”) across the Serengeti-Mara ecosystem of Kenya and Tanzania to test a satellite-based approach to the study of animal behavior. The mass movement of 1.3 million wildebeest is an inherently social process that drives the ecological functioning of the entire Serengeti-Mara ecosystem (Sinclair et al. 2015). By collectively grazing and redistributing more than 4,500 tons of grass per day, wildebeest influence everything from nutrient cycles and trophic interactions to vegetation communities and fire regimes (Milner-Gulland et al. 2011; Subalusky et al. 2017). However, research into this

phenomenon has historically been focused on identifying environmental drivers of individual movements (Wilmshurst et al. 1999; Boone et al. 2006; Hopcraft et al. 2014; Sinclair et al. 2015), despite a growing body of literature suggesting that social processes are also likely to play an important role in determining the success of this highly gregarious species (Sinclair & Norton-Griffiths 1984; Holdo et al. 2009; Berdahl et al. 2016; Torney et al. 2018). The objective of this analysis is to develop and test novel techniques using satellite remote sensing to accurately classify the behavioral states of large groups of social animals at once. This forms the foundation for efficiently and non-invasively extracting information about collective behavior from wild free-living animals.

To develop a method for remotely classifying and studying the behavior of wildebeest, we first recorded the behavior and spatial structure (i.e. geometric properties of the group) of wildebeest groups identified in the field. Using this ground-truthed data, we then trained an automated classifier (i.e. random forest model) to identify three behavioral states (e.g. encamped, mobile feeding, and transit; figure 2.1) that could be reliably predicted by the structural attributes of the group (e.g. orientation, nearest neighbor distance, and relative positioning; figure 2.2). Next, we applied this same classifier to a manually annotated, high-resolution satellite image covering 25 km² and containing nearly 50,000 individual wildebeest (figure 2.3 & figure 2.4). We then describe how large-scale, spatially explicit maps of behavior such as these may be used to conduct cross-scale investigations of social and environmental drivers of animal behavior and offer recommendations for further development of this method.

Methods

Study area

Field data collection took place between March and May of 2015, 2017, and 2018 in the medium and short grass plains of Serengeti National Park in northern Tanzania.

Serengeti National Park is a federally protected conservation area and no hunting or off-road driving is permitted within the park. The boundaries of the protected area were historically defined by the movements of approximately 1.3 million wildebeest that travel more than 2,600 km on their annual migration between a dry season refuge in southern Kenya and calving grounds on the shortgrass plains of Serengeti. The seasonal rains and rich volcanic soils of this area produce nutritious grasses and the open, flat landscape provides little cover for predators during the critical parturition period (Sinclair & Norton-Griffiths 1984).

Ground-based measures of behavior and herd structure

We relied on ground observations to identify common behavioral states and the associated spatial structure that defines these states in wildebeest herds. Wildebeest groups ($n = 315$; at least 400 m was maintained between observations of each group) were opportunistically located while driving on main roads and tracks across the short-grass plains of Serengeti National Park. When a group was located, a single observer (same observer was used throughout) randomly selected 10-15 focal animals and assigned each to one of the following behavioral categories after 10 seconds of observation at 50 to 100 m from the herd: 1) *encamped* (i.e. bedded or stationary > 10 seconds, or feeding followed by ≤ 2 steps forward), 2) *mobile feeding* (i.e. feeding followed by > 2 steps forward), 3) *transit* (i.e. uninterrupted forward motion > 10 seconds), and 4) *other* (i.e. chasing, sparring; dropped

from analysis; Appendix 2.A). We then recorded the following metrics of herd structure for each focal animal: 1) *orientation* (i.e. direction of body axis visually estimated from compass bearing, plus orientation for each of its three nearest neighbors); 2) *distance* to each of its three nearest neighbors (visually estimated in units of wildebeest body-lengths); and 3) *position* (i.e. visually estimated angle of the focal animal's location relative to the location of each of its three nearest neighbors; figure 2.2). Values were then averaged across the focal animal and its three nearest neighbors for each observation and metric, resulting in a single value per metric (i.e. orientation, distance, and position) per focal animal ($n = 4,055$). These mean values were obtained as follows:

To calculate mean *orientation* for each focal animal, we first transformed unidirectional bearings to bi-directional bearings (i.e. $90^\circ = 270^\circ$; (Davis 2011) so that results would be transferable to satellite images where direction of travel may not be discernable at the given resolution. We then measured the circular dispersion (i.e. uniformity) of all four orientations (i.e. focal animal plus three nearest neighbors; 'circ.disp' function in the 'CircStats' package in R (Agostinelli & Lund 2005). This resulted in a measure of coordinated orientation ranging from 0 to 1, where a measure of 0 indicates uniform dispersion (or low coordination of orientation) and a measure of 1 indicates concentration in one direction (or high coordination of orientation; figure 2.2). We then calculated mean *distance* for each focal animal by averaging across each group of four animals (i.e. focal animal plus three nearest neighbors; 'spatstat' package in R (Baddeley et al. 2014) and multiplying by this value by 2 (to convert from wildebeest body lengths to meters). Finally, we obtained a mean *position* for each focal animal by first transforming unidirectional angles to bi-directional angles so that, for example, neighbors positioned

immediately to the right of the focal animal received the same score as neighbors positioned immediately to the left of the focal animal (i.e. $90^\circ = 270^\circ$). We then averaged these values across all three neighbors to obtain the average *position* for each focal animal. Relative position and orientation of the focal animal's three nearest neighbors was not recorded for individual-level observations in 2015 ($n = 3,256$). As a result, values for orientation of individuals were inferred from group-level averages for each behavioral state and relative positions were estimated from observations in the 2017/2018 datasets with matching herd characteristics ($n = 799$; details in Appendix 2.B).

Classifying behavioral state with random forest algorithms

We employed random forest classification models (i.e. decision tree classifiers that fit various subsamples of the dataset and use averaging to improve predictive accuracy and control over-fitting) to assign one of three behavioral states (e.g. encamped, mobile feeding, transit) to focal animals based upon the three structural metrics described above (e.g. orientation, distance, and position). In our application of this method, we withheld 25% ($n = 200$) of the 2017/2018 dataset in order to test the predictive power of the resultant algorithm with a novel dataset. Then we used the remaining data ($n = 3,855$) to train 500 decision trees with all three metrics of herd structure (e.g. orientation, distance, and position) as explanatory variables and three categories of behavior (e.g. encamped, mobile feeding, and transit) as the response variable ('randomForest' package, 'randomForest' function in R; (Liaw et al. 2002)).

We then used the resulting algorithm to make categorical predictions of known behaviors in the testing dataset using the ‘predict’ function in R (R Core Team 2018). Results from this external validation procedure were then compared to results from a second validation procedure employed by the ‘randomForest’ package, in which 33% of the cases are withheld from a bootstrapped sample of the original data and then the withheld samples are used to test algorithm performance each time a tree is constructed. Finally, we employed a backwards stepwise selection routine in which each main effect (i.e. all three metrics of herd structure) and two-way interaction was dropped from the model, one at a time until the model offering the best predictive performance was identified. This procedure indicated that behavioral state was best predicted by the single metric of *orientation* (table 2.1). As a result, *position* and *distance* were excluded from the final algorithm.

Satellite image annotation and processing

A single contiguous satellite image encompassing an area of 25 km² at 50 cm resolution (GeoEye acquired on August 10, 2009; Google 2009) was analyzed using an open-source, cloud-based computer program (BisQue; Kvilekval et al. 2010) designed for processing large images with associated spatial information. Trained analysts then used a purpose-designed plug-in to manually annotate the axis of orientation and/or geographic location of each potential wildebeest using three levels of certainty: 1) *wildebeest with known orientation* (annotated as a line along the central body axis without respect to head vs. tail), 2) *wildebeest with unknown orientation* (annotated as a point), and 3) *possible wildebeest* (annotated as a point; ultimately dropped from following analysis). Wildebeest were distinguished from inanimate or permanent objects using the following criteria: 1)

proximity to other objects similar in size (i.e. approximately 2 pixels long), oblong shape, and black color (figure 2.3) and 2) visual comparison with images of the same area collected on different dates (i.e. mobile objects should not be present in images taken on another date). The only other species visible at 50 cm resolution that may occur in the study area and in large enough numbers to be mistaken for wildebeest include zebra and domestic cattle. However, cattle are restricted from the Serengeti National Park study area and a preliminary analysis of ground-truthed satellite images indicated that both cattle and zebra can be reliably distinguished from wildebeest by their contrasting size and color (figure 2.3).

We classified the behavioral state for all animals annotated in the satellite image by first measuring the degree of coordinated *orientation* between each animal and its three nearest neighbors (using the same methods as described above in the processing of the ground-based measurements). To do this, we first calculated the bearing for annotations with a known orientation by turning the endpoints of each line into a pair of nodes using the ‘line2df’ function in the ‘stplanr’ package in R (Lovelace et al. 2015). We then calculated the bearing in circular degrees using the ‘bearing’ function in the ‘geosphere’ package in R (Hijmans 2016) and employed an angle doubling procedure to convert unidirectional bearings to bi-directional bearings (i.e. $90^\circ = 270^\circ$; Davis 2011). This step facilitated calculation of circular dispersion in cases where the direction of travel was unknown due to an inability to distinguish head from tail in most satellite images. To facilitate transformation from degrees to radians (using the ‘rad’ function in the ‘CircStats’ package in R; Lund & Agostinelli 2007) and account for the circular nature of the dataset, we designated all bearings as circular data using ‘as.circular’ function in the ‘circular’ package in R (Pewsey et al. 2013). Then we calculated the circular dispersion for all points with at least two nearest

neighbors having known orientations by using the ‘circ.disp’ function in the ‘CircStats’ package in R (Agostinelli & Lund 2005); procedures for calculating position and distance from satellite images are described in Appendix 2.C & Appendix 2.D).

Behavioral classification in satellite image

To classify behavioral states for animals identified in a high-resolution satellite image, we used the random forest classifier developed with the ground observation data to make categorical predictions of behavior (e.g. encamped, mobile feeding, or transit) from the *orientation* calculated above. Again, while multiple parameters of herd structure (e.g. orientation, distance, and position) were tested for predictive accuracy when developing the random forest model, we relied solely on orientation data given the predictive success of this one measure as observed from the ground truthing procedure (table 2.1). We then mapped predicted behavioral states for all animals with defined orientations in the satellite image ($n = 30,711$; figure 2.4).

Results

Algorithm performance- ground observations

Both unidirectional (i.e. orientation defined by direction of travel) and bidirectional (i.e. direction of travel is unknown within a plane of 180°) datasets had comparably low error rates across all three behavioral states (2.4% and 2.9% average error respectively with internal validation; 7.6% and 8.7% average error respectively with external validation). Between categories, *transit* had the lowest error rate overall (< 1% for both unidirectional

and bidirectional datasets) and *mobile feeding* had the highest (4.8% unidirectional, 5.7% bidirectional; table 2.2 & table 2.3). Classifications for both *mobile feeding* and *encamped* were most commonly confused with *transit*.

Algorithm performance- satellite image classification

When applied to the annotated satellite image, the random forest algorithm was able to classify behavior for 62% ($n = 30,711$) of the wildebeest identified in the satellite image. Of the animals classified, 77% of these ($n = 23,667$) were classified with high probability (i.e. $\geq 75\%$) and 2% ($n = 717$) were classified with low probability (i.e. $< 50\%$) in any class, meaning that behavioral states were assigned with little confusion between classes. No class occurred significantly more than another in either high or low confidence subsets. Finally, the *encamped* state was the most common behavioral classification in the satellite image (54%, $n = 16,489$), followed by *transit* (31%, $n = 9,404$), and *mobile feeding* (16%, $n = 4,818$).

Discussion

Our study of the Serengeti-Mara wildebeest population presents a novel approach to conducting animal behavior research that is both non-invasive and directly scaleable from individuals to populations. Although further development of relevant technologies (especially machine learning) is needed to deploy this method at-scale, the perspective afforded by remotely sensed images stands to advance fundamental understanding of animal behavior by facilitating cross-scale research on the social and ecological mechanisms that drive behavioral decisions in animal groups. For example, by confirming that a small number of attributes (e.g. coordinated orientation) can be used to effectively predict complex

behaviors, we have created an opportunity to test whether basic rules of interaction at the individual level persist across space and higher levels of biological organization (i.e. individuals to populations). Such insights are critical for understanding how patterns of occupancy and distribution might depend on social interactions and how these dependencies might change with predicted shifts in environmental conditions.

Broader ecological applications

By creating a spatially explicit time series of individual behaviors across the landscape, we can quantitatively evaluate patterns of behavior in response to any number of environmental features, including the relative distribution of other animals and their associated behavioral states. This approach presents a step-change in our ability to measure the social context of behavioral transitions with precision and stands to improve the realism of predictive models resulting from these investigations. Further, the representation of animal behavior as both a social and a spatial process presents a powerful opportunity to investigate the interplay between proximity to features of interest and behavioral outcomes at multiple scales of enquiry.

In the case of the Serengeti-Mara ecosystem, such methods may be used to better understand the non-lethal impacts of anthropogenic infrastructure on animal movement. In this system, roads are expected to negatively impact the persistence of the wildebeest population through direct mortality and impediment of migratory movements (Dobson et al. 2010; Holdo et al. 2011). However, the non-lethal impacts of roads and associated infrastructure has been shown to extend well beyond the immediate structural footprint (Loarie et al. 2009; Northrup et al. 2015; D'Amico et al. 2016; Prokopenko et al. 2017), so it is important to determine the degree to which this proposed development may cause

deviations in behavior associated with increased energetic costs or mortality risk. Although individual-level tracking data presents a useful starting point for answering such questions, it is unlikely to capture sufficient variability in individual behavioral response for a population this size. Further, it cannot afford insights into the complex relationships between group size, individual behavior, and proximity to roads that are necessary to properly contextualize observed patterns. In such cases, high-resolution satellites present a promising alternative that is both non-invasive and able to measure behavioral changes for tens of thousands of animals across large distances.

In practice, this method also presents promising opportunities to augment conventional approaches to monitoring zoonotic disease transmission between wild and domestic species (e.g. biological sampling or tagging animals with GPS or VHF sensors (Boadella et al. 2011)). Through increased behavioral monitoring, managers may be able to rapidly identify areas of concern (i.e. areas of overlap or shared feeding sites between wild and domestic species) and increase ground-based monitoring or mitigation efforts in these areas. Further research into the relationship between behavior and rates of disease transmission may reveal additional applications, such as predictive modeling of transmission rates or assessing the risk of behavioral interactions between wild and domestic species. Such advances are increasingly important as rangelands expand globally and generate additional points of contact between wild and domestic species (Gortázar et al. 2007; Perry et al. 2013).

Challenges, opportunities, and future directions

While there is clearly enormous potential for such advances to enrich the fields of animal behavior and wildlife management, the adoption of high-resolution satellite imaging

has been hindered to date by substantial financial and technological (i.e. spatial and temporal resolution) constraints. For example, at the time of publication, an archived, 25 km², 4 band (e.g. Red, Green, Blue, Near Infrared) image collected at 30 cm resolution costs thousands of dollars, with commissioned images quickly reaching tens of thousands. Further, although 30 cm resolution is a consequential improvement on the previous limit of 45-50 cm, this level of detail has only been publically available since 2014 and from two satellites (WorldView 3 & 4), making it less tenable for research requiring historic data or high temporal resolution sampling. However, imagery at 50 cm resolution has been available since 2009 and a growing number of constellations (e.g. WorldView, GeoEye, Pleiades, and others) now make sub-daily revisits a possibility.

In addition, a growing number of granting organizations, federal agencies, and commercial satellite providers are facilitating access to high-resolution imagery at low or no cost through public-private partnerships and imagery granting programs. Further, we contend that after sufficient ground-truthing has taken place, remotely sensed data may reduce the need for investment in field-based infrastructure of comparable cost (e.g. vehicles, housing, airfare, etc.), which could render additional savings for established research programs. Finally, the recent introduction of low-orbiting nanosatellites has prompted a renaissance of earth observation research by offering low-cost, high-frequency, high-resolution (70 cm - 5 m) imaging for a wide range of civilian applications (Staeble et al. 2013; Traganos et al. 2017; Cooley et al. 2017; Ghuffar 2018; Hughey et al. 2018; Cooley et al. 2019). Though these resolutions are at the upper limit of being useful for behavioral analyses, anticipated improvements in remote imaging technology combined with rapidly expanding capabilities of automated image processing techniques (Chabot & Francis 2016; Torney et al. 2016; Gray

et al. 2018; Weinstein 2018) stand to rapidly increase the utility of satellite-based techniques for animal behavior research.

However, we caution that even if access to imagery is secured, there are several considerations to be made before establishing a satellite-based research program for animal behavior. First, satellite imaging (in the visible spectrum) is inherently limited to cloud-free days over open, flat landscapes. Though many large, social species occur in this type of environment (i.e. caribou on the tundra, whales in the ocean, livestock on pastures), this caveat brings obvious limitations to the application of satellite imaging in tropical, forested, and mountainous regions of the globe. In addition, 30-50 cm resolution is not always sufficient for determining the orientation or identification of animals with a body size at or below the pixel size. In this study, orientations could not be confidently assigned for 56% ($n = 27,738$) of the nearly 50,000 animals identified, resulting in classifications for a fraction of the original dataset (62%, $n = 30,711$). Though this sample size could potentially be increased by relaxing the requirements for number or proximity of nearest neighbor calculations, this approach is untested and limited resolution is expected to remain problematic for applying this method to smaller species.

Similarly, the extensive spatial coverage that lends this method its power should also be considered a liability for proper validation of behavioral classifications (i.e. it is not possible to simultaneously validate the behaviors of thousands of animals at the instant of image collection). For this reason, we have selected geometric properties of group structure that can be reliably measured both on the ground and in the air (e.g. orientation, position, distance). We have also shown that both unidirectional (i.e. orientation defined by direction of travel) and bidirectional (i.e. orientation defined along antipodal axis of travel) datasets have comparable misclassification rates, which suggests that this method is robust to the

current limitations of satellite image resolution, even for animals at or near the pixel size. Lastly, we used *a priori* information to strengthen our method against spurious classifications by grouping fine-scale behaviors (i.e. feeding, standing, bedded) into higher-level categories (i.e. encamped, transit, etc.). As a result, we note that there may be additional behavioral states that could be identified from alternative grouping strategies, and encourage independent evaluation of alternative groupings when applying this method to a new species.

The final component required to expand these methods beyond a proof of concept depends upon further advances in automated image processing techniques. The method described here requires a team of trained volunteers to manually identify and annotate animals in selected images. Though humans currently outperform computer-vision techniques for identifying animals in satellite images, there is mounting evidence that machine learning can significantly improve the speed and accuracy of manual counts in images of sufficient resolution (Torney et al. 2016; Xue et al. 2017). Still, specific shortcomings remain, including the ability to distinguish objects of interest from shadows, slow processing speed, and generalization of algorithms between multiple datasets.

If such caveats prove too limiting for a particular research program, we also advocate Unmanned Aerial Vehicles (UAVs) as a promising alternative, or addition to satellites. While most commercial UAV systems cannot match the spatial scope (or historic archive) of satellite imaging, they do afford high-resolution imaging of large animal groups and bring advantages in the form of improved flexibility, lower cost, and higher temporal resolution. Techniques for automated processing of aerial images are also more advanced and accessible compared to those for lower-resolution satellite images. Though our classification method has not been tested on aerial images, we expect that the improved resolution and overhead

perspective afforded by this approach would facilitate analysis of both bidirectional and unidirectional data, resulting in improved algorithm performance over that reported for the satellite image used here.

Conclusion

The ability to accurately quantify the spatial and behavioral relationships for tens of thousands of animals across remote landscapes presents a promising first step towards realizing the full potential of remote imaging techniques. By capturing high-resolution data on the social and environmental context in which animals are embedded, researchers may begin to quantitatively assess the relative impacts of each on the behavioral dynamics of social species. In addition, the ability to study these processes for thousands of individuals on the scale of many kilometers presents a unique opportunity to understand how changes in individual behavior scale up to inform the movement of populations and how these relationships may change with a changing environment. Such insights are critical for identifying the behavioral mechanisms that drive individuals across the landscape and ultimately influence the persistence of populations. Projected advancements in remote imaging and machine learning capabilities only increase our confidence that the ability to capture behavioral data from an aerial perspective will become increasingly important to scientists of the digital age.

Tables and figures

Table 2.1. Model selection results to identify the best combination of predictors for wildebeest behavioral state. *Internal validation:* 33% of samples withheld and validated against bootstrapped samples in ‘randomForest’ package (Liaw et al. 2002) in R. *External validation:* 25% of samples withheld from training set and estimation procedure (Appendix 2.B). O: *Orientation*, D: *Distance*, P: *Position*.

Model	% Error internal validation	% Error external validation
O	1.76	17.7
O + D	3.18	17.7
O + D + O*D	3.31	17.7
O + P + D + O*P	4.84	20.2
O + P + D	4.68	21.3
O + P + D + O*P + O*D + P*D	4.9	21.3
O + P + D + O*P + O*D	4.73	21.3
O + P + D + O*D	4.73	21.3
O + P + D + O*P + P*D	4.94	21.3
O + P + D + O*D + P*D	4.68	21.3
O + P	2.55	22.4
O + P + O*P	2.58	22.4
P + D	40.7	51.1
D + P + D*P	40.27	51.1
P	42.43	63.2
D	42.6	66.7

Table 2.2. Results of the internal validation procedure employed by the ‘randomForest’ classifier package (i.e. 33% of samples withheld and validated against bootstrapped samples; Liaw et al. 2002) in R. The top model included “behavioral state” of each wildebeest (e.g. encamped, mobile feeding, transit) as the response variable and a single measure of relative *orientation* as the explanatory variable. Note that alignment values represent unidirectional data (i.e. direction of travel is known).

	Encamped	Mobile feeding	Transit	% Error
Encamped	1967	0	50	2.5
Mobile feeding	0	719	37	4.8
Transit	8	0	1214	0.6

Table 2.3. Results of the internal validation procedure employed by the ‘randomForest’ classifier package (i.e. 33% of samples withheld and validated against bootstrapped samples; Liaw et al. 2002) in R. The top model included “behavioral state” of each wildebeest (e.g. encamped, mobile feeding, transit) as the response variable and a single measure of relative *orientation* as the explanatory variable. Note that alignment values represent bidirectional data (i.e. direction of travel is unknown within a plane of 180°).

	Encamped	Mobile feeding	Transit	% Error
Encamped	1954	8	55	3.1
Mobile feeding	6	713	37	5.7
Transit	9	0	1213	0.7

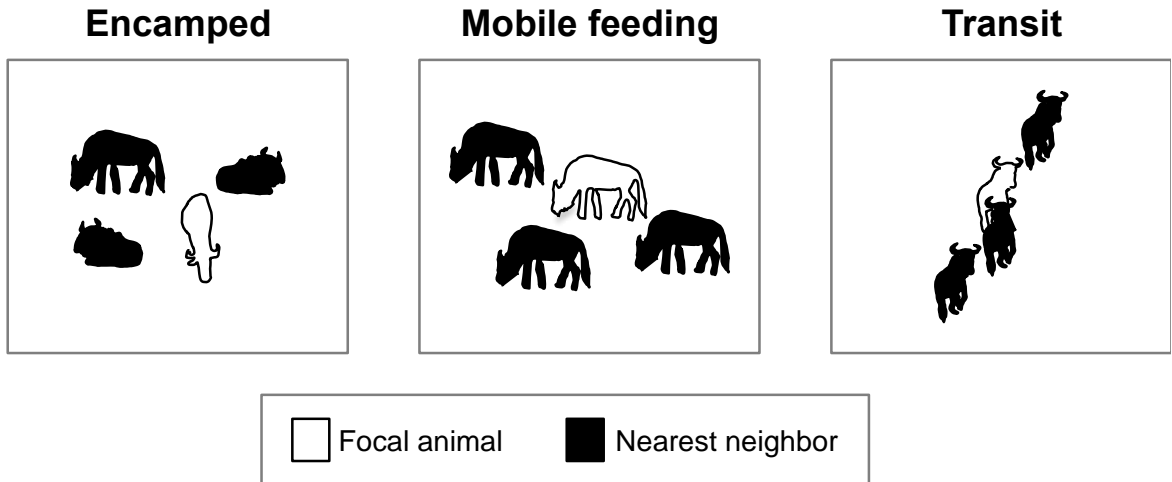


Figure 2.1. Three behavioral states that can be reliably predicted by the structural attributes of a focal animal (white) relative to its three nearest neighbors (black).

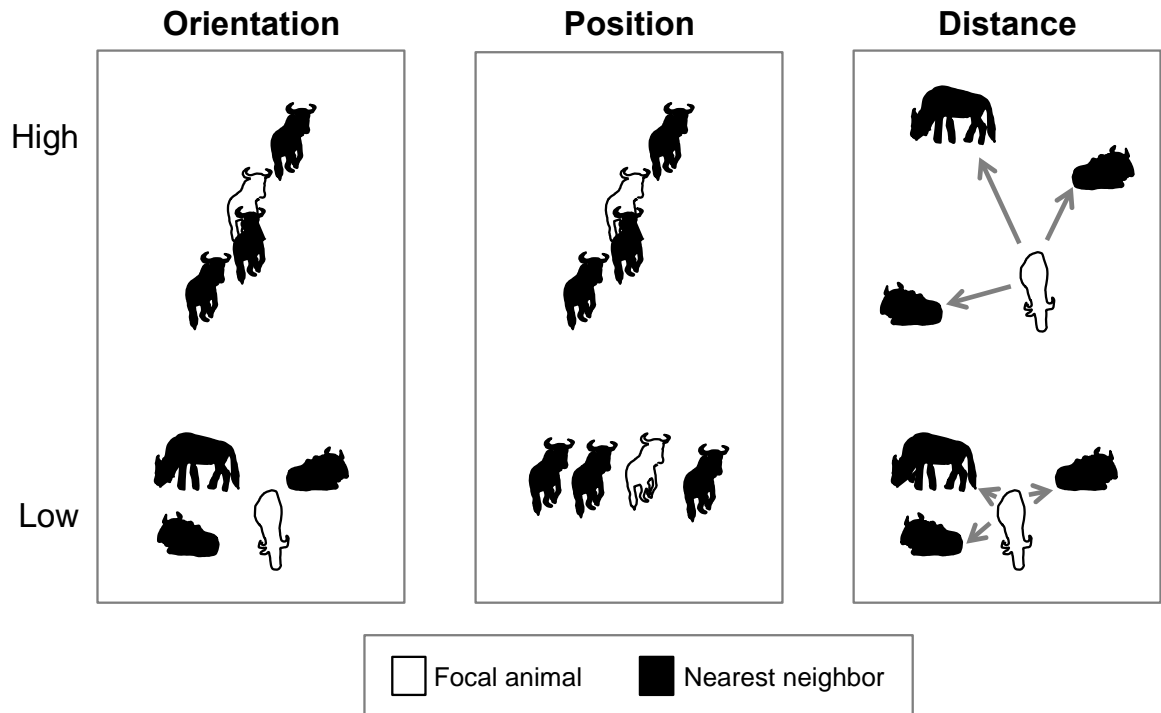


Figure 2.2. Three metrics of herd structure were initially used to predict the behavioral state of a focal animal (white) based on measurements of the following attributes relative to its three nearest neighbors (black): 1) *Orientation* is the degree of circular dispersion exhibited by a focal animal and its three nearest neighbors, 2) *Position* indicates whether a focal individual is aligned head-to-tail or shoulder-to-shoulder with its three nearest neighbors, 3) *Distance* is a measure of the average distance between a focal animal and its three nearest neighbors.

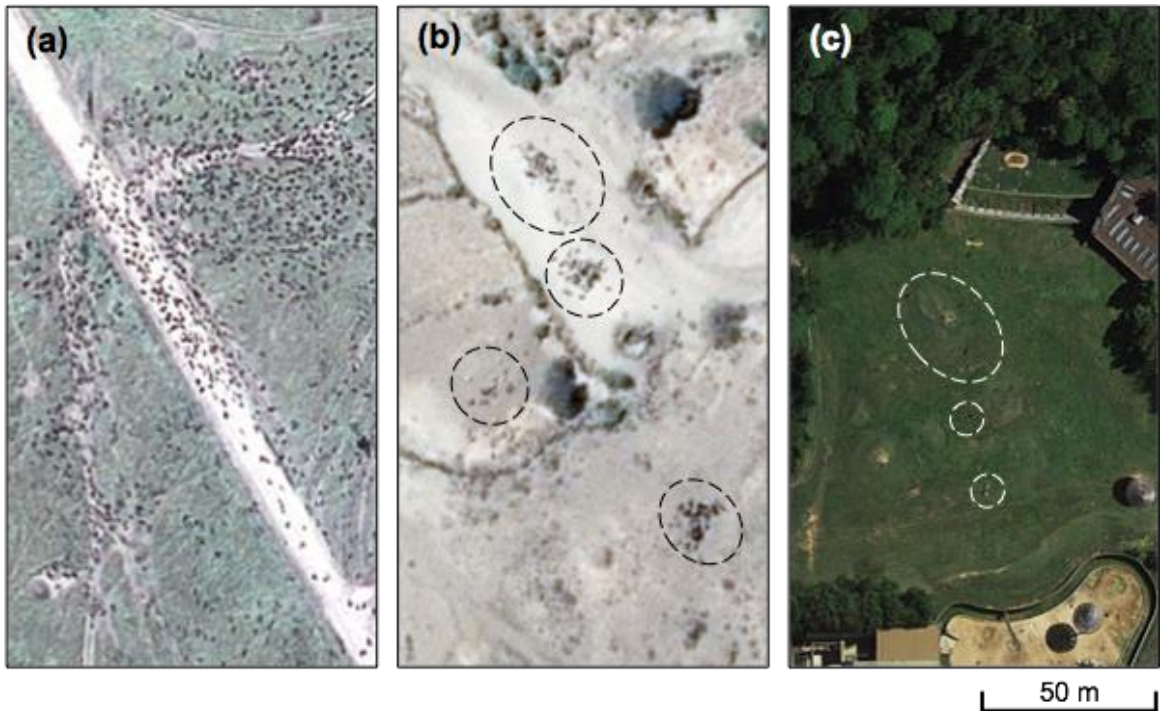


Figure 2.3. Representative example of (a) wildebeest and (b) livestock identified in a high-resolution (50 cm) satellite image (Anon 2009 (a); Anon 2016 (b)). Zebra (c) are shown in a 20 cm resolution aerial image (Anon 2016). Note the distinctive differences in size, patterns of aggregation, and coat color between species.

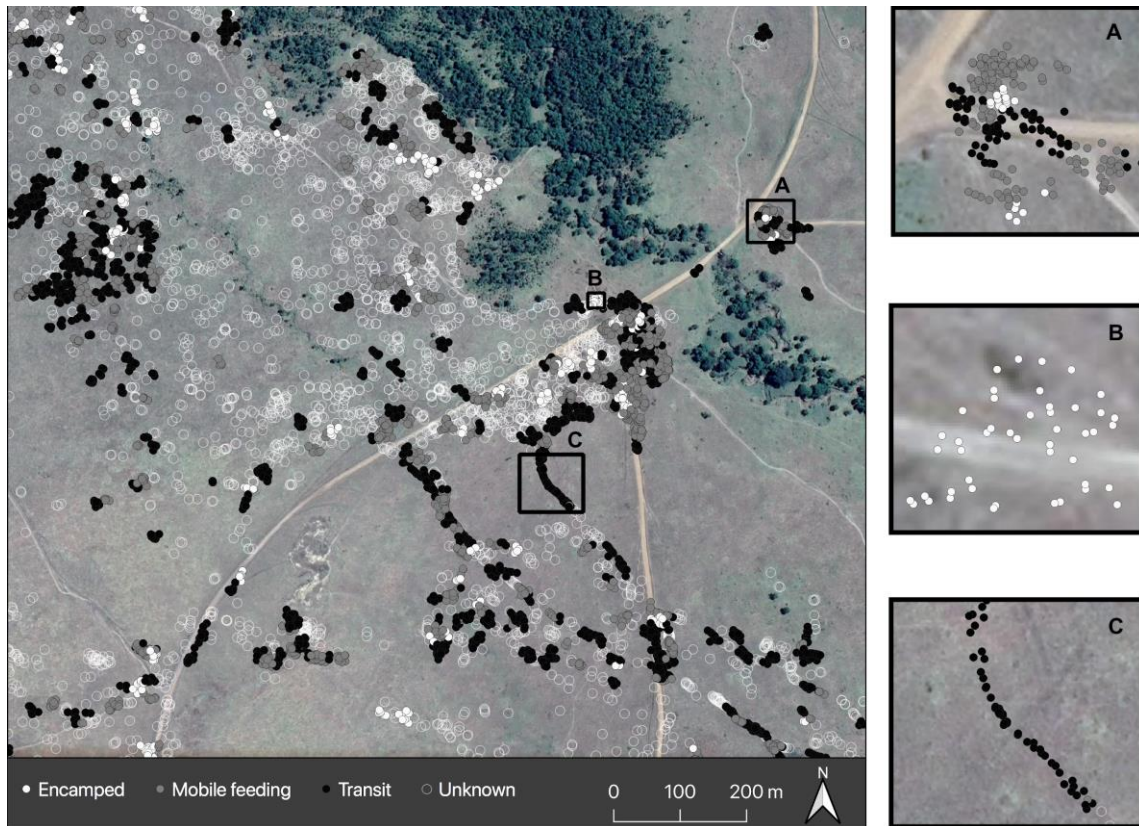


Figure 2.4. A high-resolution (50 cm) satellite image containing more than 30,000 wildebeest and covering 25 km² (image shown is a subset of the full image; (Anon 2009) shows three predicted behavioral states for focal animals based on the degree of coordinated orientation relative to its three nearest neighbors. Inset (A) shows a detailed view of behaviors involved in crossing a road, with leading animals in *transit*, animals in the middle waiting to cross in an *encamped* or intermediate state of *mobile feeding*, and animals behind *transiting* to catch up to the group. Inset (B) shows a representative view of animals in an *encamped* state, and inset (C) is a representative view of animals in *transit*.

References

- Agostinelli, C. & Lund, U., 2005. CircStats: circular statistics. URL <http://cran.r-project.org/src/contrib/Descriptions/circular.html>.
- Baddeley, A., Turner, R. & Rubak, E., 2014. Package Spatstat: spatial point pattern analysis, model-fitting, simulation, tests. Online: <http://cran.r-project.org>.
- Berdahl, A. et al., 2016. Collective behavior as a driver of critical transitions in migratory populations. *Movement Ecology*, 4, p.18. Available at: <http://dx.doi.org/10.1186/s40462-016-0083-8>.
- Boadella, M. et al., 2011. Six recommendations for improving monitoring of diseases shared with wildlife: examples regarding mycobacterial infections in Spain. *European Journal of Wildlife Research*, 57(4), pp.697–706. Available at: <https://doi.org/10.1007/s10344-011-0550-x>.
- Boone, R.B., Thirgood, S.J. & Hopcraft, J.G.C., 2006. Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. *Ecology*, 87(8), pp.1987–1994. Available at: <https://www.ncbi.nlm.nih.gov/pubmed/16937638>.
- Buhl, J. et al., 2006. From disorder to order in marching locusts. *Science*, 312(5778), pp.1402–1406. Available at: <http://dx.doi.org/10.1126/science.1125142>.
- Calabrese, J.M. et al., 2018. Disentangling social interactions and environmental drivers in multi-individual wildlife tracking data. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 373(1746). Available at: <http://dx.doi.org/10.1098/rstb.2017.0007>.
- Chabot, D. & Francis, C.M., 2016. Computer-automated bird detection and counts in high-resolution aerial images: a review. *Journal of Field Ornithology*, 87(4), pp.343–359. Available at: <https://onlinelibrary.wiley.com/doi/abs/10.1111/jofo.12171>.
- Cooley, S.W. et al., 2019. Arctic-Boreal lake dynamics revealed using CubeSat imagery. *Geophysical Research Letters*. Available at: <https://onlinelibrary.wiley.com/doi/abs/10.1029/2018GL081584>.
- Cooley, S.W. et al., 2017. Tracking dynamic northern surface water changes with high-frequency Planet CubeSat imagery. *Remote Sensing*, 9(12), p.1306. Available at: <https://www.mdpi.com/2072-4292/9/12/1306> [Accessed February 18, 2019].
- Cvikel, N. et al., 2015. Bats aggregate to improve prey search but might be impaired when their density becomes too high. *Current Biology: CB*, 25(2), pp.206–211. Available at: <http://dx.doi.org/10.1016/j.cub.2014.11.010>.
- D’Amico, M., Périquet, S. & Román, J., 2016. Road avoidance responses determine the

- impact of heterogeneous road networks at a regional scale. *Journal of Applied Ecology*. Available at: <https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.12572>.
- Davis, J.C., 2011. Statistics and data analysis in geology, 3rd edition, John Wiley & Sons. Available at: <https://market.android.com/details?id=book-uiR0CgAAQBAJ>.
- Dobson, A.P. et al., 2010. Road will ruin Serengeti. *Nature*, 467(7313), pp.272–273. Available at: <http://dx.doi.org/10.1038/467272a>.
- Febbo, E. et al., 2017. Technology and innovation for environmental monitoring on Alaska's North Slope. In *SPE Health, Safety, Security, Environment, & Social Responsibility Conference-North America*. Society of petroleum engineers. Available at: <https://www.onepetro.org/conference-paper/SPE-184471-MS>.
- Fretwell, P.T., Scofield, P. & Phillips, R.A., 2017. Using super-high resolution satellite imagery to census threatened albatrosses. *The Ibis*, 159(3), pp.481–490. Available at: <http://doi.wiley.com/10.1111/ibi.12482>.
- Ghuffar, S., 2018. DEM Generation from Multi Satellite PlanetScope Imagery. *Remote Sensing*, 10(9), p.1462. Available at: <https://www.mdpi.com/2072-4292/10/9/1462> [Accessed February 18, 2019].
- Google, 2009. *Google Earth*, Masai Mara National Reserve, Kenya. Available at: <http://www.earth.google.com> [Accessed April 22, 2019].
- Gortázar, C. et al., 2007. Diseases shared between wildlife and livestock: a European perspective. *European Journal of Wildlife Research*, 53(4), pp.241–256. Available at: <http://dx.doi.org/10.1007/s10344-007-0098-y>.
- Gray, P.C. et al., 2018. A convolutional neural network for detecting sea turtles in drone imagery. *Methods in Ecology and Evolution / British Ecological Society*. Available at: <https://onlinelibrary.wiley.com/doi/abs/10.1111/2041-210X.13132>.
- Gueron, S. & Levin, S.A., 1993. Self-organization of front patterns in large wildebeest herds. *Journal of Theoretical Biology*, 165(4), pp.541–552. Available at: <http://www.sciencedirect.com/science/article/pii/S0022519383712063>.
- Herbert-Read, J.E. et al., 2011. Inferring the rules of interaction of shoaling fish. *Proceedings of the National Academy of Sciences of the United States of America*, 108(46), pp.18726–18731. Available at: <http://dx.doi.org/10.1073/pnas.1109355108>.
- Hijmans, R.J., 2016. geosphere: spherical trigonometry. R package version 1.5-5. See <https://cran.r-project.org/package=geosphere>.
- Holdo, R.M. et al., 2011. Predicted impact of barriers to migration on the Serengeti wildebeest population. *PloS One*, 6(1), p.e16370. Available at: <http://dx.doi.org/10.1371/journal.pone.0016370>.

- Holdo, R.M., Holt, R.D. & Fryxell, J.M., 2009. Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *The American Naturalist*, 173(4), pp.431–445. Available at: <http://dx.doi.org/10.1086/597229>.
- Hollings, T. et al., 2018. How do you find the green sheep? A critical review of the use of remotely sensed imagery to detect and count animals J. McPherson, ed. *Methods in Ecology and Evolution / British Ecological Society*, 9(4), pp.881–892. Available at: <http://doi.wiley.com/10.1111/2041-210X.12973>.
- Hopcraft, J.G.C. et al., 2014. Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecological Monographs*, 84(3), pp.355–372. Available at: <http://doi.wiley.com/10.1890/13-1446.1>.
- Hubel, T.Y. et al., 2016. Additive opportunistic capture explains group hunting benefits in African wild dogs. *Nature Communications*, 7(1). Available at: <http://dx.doi.org/10.1038/ncomms11033>.
- Hughey, L.F. et al., 2018. Challenges and solutions for studying collective animal behavior in the wild. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 373(1746). Available at: <http://dx.doi.org/10.1098/rstb.2017.0005>.
- Katz, Y. et al., 2011. Inferring the structure and dynamics of interactions in schooling fish. *Proceedings of the National Academy of Sciences of the United States of America*, 108(46), pp.18720–18725. Available at: <http://dx.doi.org/10.1073/pnas.1107583108>.
- King, A.J. et al., 2012. Selfish-herd behavior of sheep under threat. *Current Biology: CB*, 22(14), pp.R561–2. Available at: <http://dx.doi.org/10.1016/j.cub.2012.05.008>.
- Kvilekval, K. et al., 2010. Bisque: a platform for bioimage analysis and management. *Bioinformatics*, 26(4), pp.544–552. Available at: <http://dx.doi.org/10.1093/bioinformatics/btp699>.
- LaRue, M.A., Stapleton, S. & Anderson, M., 2017. Feasibility of using high-resolution satellite imagery to assess vertebrate wildlife populations. *Conservation Biology: the journal of the Society for Conservation Biology*, 31(1), pp.213–220. Available at: <http://dx.doi.org/10.1111/cobi.12809>.
- Liaw, A., Wiener, M. & Others, 2002. Classification and regression by randomForest. *R news*, 2(3), pp.18–22. Available at: https://www.researchgate.net/profile/Andy_Liaw/publication/228451484_Classification_and_Regression_by_RandomForest/links/53fb24cc0cf20a45497047ab/Classification-and-Regression-by-RandomForest.pdf.
- Loarie, S.R., Van Aarde, R.J. & Pimm, S.L., 2009. Fences and artificial water affect African savannah elephant movement patterns. *Biological Conservation*, 142(12), pp.3086–3098. Available at: <http://www.sciencedirect.com/science/article/pii/S0006320709003759>.

- Lovelace, R. et al., 2015. Stplanr: Sustainable transport planning. *Comprehensive R archive Network (CRAN)*.
- Lund, U. & Agostinelli, C., 2007. Circstats: circular statistics, from “topics in circular statistics” (2001). *S-plus original by Lund, U. R port by Agostinelli, C. R package version 0. 2-3*.
- Milner-Gulland, E.J., Fryxell, J.M. & Sinclair, A.R.E., 2011. *Animal migration: A synthesis*, Oxford University Press. Available at: <https://market.android.com/details?id=book-q84UDAAAQBAJ>.
- Nagy, M. et al., 2010. Hierarchical group dynamics in pigeon flocks. *Nature*, 464(7290), pp.890–893. Available at: <http://dx.doi.org/10.1038/nature08891>.
- Northrup, J.M., Anderson, C.R., Jr & Wittemyer, G., 2015. Quantifying spatial habitat loss from hydrocarbon development through assessing habitat selection patterns of mule deer. *Global Change Biology*, 21(11), pp.3961–3970. Available at: <http://dx.doi.org/10.1111/gcb.13037>.
- Perry, B.D., Grace, D. & Sones, K., 2013. Current drivers and future directions of global livestock disease dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, 110(52), pp.20871–20877. Available at: <http://dx.doi.org/10.1073/pnas.1012953108>.
- Pewsey, A., Neuhauser, M. & Ruxton, G.D., 2013. *Circular Statistics in R*, OUP Oxford. Available at: <https://market.android.com/details?id=book-qeadAAAQBAJ>.
- Prokopenko, C.M., Boyce, M.S. & Avgar, T., 2017. Characterizing wildlife behavioral responses to roads using integrated step selection analysis A. Tulloch, ed. *The Journal of Applied Ecology*, 54(2), pp.470–479. Available at: <http://doi.wiley.com/10.1111/1365-2664.12768>.
- R Core Team, 2018. R: A Language and Environment for Statistical Computing. Available at: <https://www.R-project.org/>.
- Sinclair, A.R.E. et al., 2015. *Serengeti IV: Sustaining biodiversity in a coupled human-natural system*, University of Chicago Press. Available at: <https://market.android.com/details?id=book-VjPBBwAAQBAJ>.
- Sinclair, A.R.E. & Norton-Griffiths, M., 1984. *Serengeti: dynamics of an ecosystem*, University of Chicago Press. Available at: <https://market.android.com/details?id=book-ffLvZbZYpr0C>.
- Staehle, R. et al., 2013. Interplanetary CubeSats: opening the solar system to a broad community at lower cost. *Journal of Small Satellites*, 2(1), pp.161–186. Available at: <https://www.jossonline.com/wp-content/uploads/2014/12/0201-Interplanetary-CubeSats-Opening-the-Solar-System-to-a-Broad-Community-at-Lower-Cost.pdf>.

- Strandburg-Peshkin, A. et al., 2015. Shared decision-making drives collective movement in wild baboons. *Science*, 348(6241), pp.1358–1361. Available at: <http://dx.doi.org/10.1126/science.aaa5099>.
- Strandburg-Peshkin, A. et al., 2017. Habitat and social factors shape individual decisions and emergent group structure during baboon collective movement. *eLife*, 6. Available at: <http://dx.doi.org/10.7554/eLife.19505>.
- Subalusky, A.L. et al., 2017. Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proceedings of the National Academy of Sciences of the United States of America*, 114(29), pp.7647–7652. Available at: <http://dx.doi.org/10.1073/pnas.1614778114>.
- Torney, C.J. et al., 2016. Assessing rotation-invariant feature classification for automated wildebeest population counts. *PLoS One*, 11(5), p.e0156342. Available at: <http://dx.doi.org/10.1371/journal.pone.0156342>.
- Torney, C.J. et al., 2018. From single steps to mass migration: the problem of scale in the movement ecology of the Serengeti wildebeest. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 373(1746). Available at: <http://dx.doi.org/10.1098/rstb.2017.0012>.
- Traganos, D., Cerra, D. & Reinartz, P., 2017. Cubesat-derived detection of seagrasses using planet imagery following unmixing-based denoising: Is small the next big? *International Archives of the Photogrammetry, Remote Sensing & Spatial Information Sciences*, 42. Available at: https://elib.dlr.de/112901/1/Traganos_isprs-archives-XLII-1-W1-283-2017.pdf.
- Weinstein, B.G., 2018. A computer vision for animal ecology. *The Journal of Animal Ecology*, 87(3), pp.533–545. Available at: <http://dx.doi.org/10.1111/1365-2656.12780>.
- Westley, P.A.H. et al., 2018. Collective movement in ecology: from emerging technologies to conservation and management. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 373(1746). Available at: <http://dx.doi.org/10.1098/rstb.2017.0004>.
- Wilmshurst, J.F. et al., 1999. Spatial distribution of Serengeti wildebeest in relation to resources. *Canadian Journal of Zoology*, 77(8), pp.1223–1232. Available at: <https://doi.org/10.1139/z99-088>.
- Xue, Y., Wang, T. & Skidmore, A.K., 2017. Automatic counting of large mammals from very high resolution panchromatic satellite imagery. *Remote Sensing*, 9(9), p.878. Available at: <https://www.mdpi.com/2072-4292/9/9/878> [Accessed February 25, 2019].

Appendices

Appendix 2.A. Detailed protocol for classifying behavioral state in the field

We located 315 groups of wildebeest in Serengeti National Park according to the methods detailed in the main text. When a group was selected for observation, we recorded a single behavior for each focal animal ($n = 4,055$) according to the definitions below. To improve the predictive power of the final model, these states were then aggregated into the three categories of behavior as shown below:

Encamped:

- Bedded: laying on the ground > 10 seconds
- Standing: remaining stationary > 10 seconds in any posture except feeding or mobile feeding
- Feeding in place: nose to the ground followed by ≤ 2 steps forward

Mobile feeding:

- Feeding while walking forward: nose to the ground followed by > 2 steps forward

Transit:

- Walking: forward motion in a single direction for more than 10 seconds
- Running: forward motion in a single direction for more than 10 seconds (e.g. not chasing or sparring with another animal).

Behaviors other than those described above composed less than 8% of the data ($n = 322$) and were dropped from the analysis.

Appendix 2.B. Estimation procedure for values missing from 2015 dataset.

Due to a change in protocol that occurred in 2017, observations conducted before this date do not contain information on the alignment or position of focal animals relative to their three nearest neighbors (distance was recorded following the same protocol as 2017).

Instead, values for these parameters were estimated as below:

Orientation: For data collected before 2017 ($n = 3,256$), *orientation* was recorded for 10-15 randomly selected individuals across the group, without identification of their nearest neighbors. As a result, we calculated circular variance for each focal animal by first grouping observations by herd and behavior, then using R to calculate the circular variance for each behavior (following methods described in the main text). We then assigned this value to all animals exhibiting the same behavior in the same group.

Position: For data collected before 2017 ($n = 3,256$), *position* was inferred from a categorical description of the group-level geometry. This descriptor consisted of the following categories and was assigned for all observations (2015-2018): 1) *dispersed* (e.g. animals distributed randomly in position and orientation across the focal area), 2) *wave front* (e.g. animals aligned shoulder to shoulder and head to tail with a defined leading edge, followed by gradually decreasing density of trailing individuals), 3) *linear* (e.g. animals aligned head

to tail, moving in a single coordinated direction). Thus, the resulting categories have inherent structural qualities related to the relative position of individuals that we used to infer position for cases where it was missing. To do this, we established the distribution of values for observations where *position* and group-level geometry was defined (n = 799) and replaced missing values with random draws from the appropriate distribution.

Appendix 2.C. Calculating nearest neighbor distance from satellite image

To calculate the average nearest neighbor distance from the satellite annotations, we first identified the midpoint of each *wildebeest with known orientation* using the `gCentroid` function in the `rgeos` package in R (R. Bivand and Rundel 2014). We then combined centroids with point annotations (e.g. *wildebeest with unknown orientation*; all possible *wildebeest* were dropped from further analysis) and converted all points to spatial points data frames using the `SpatialPointsDataFrame` function in the `sp` package in R (R. S. Bivand, Pebesma, and Gómez-Rubio 2013). Then we extracted the ID of each point's three nearest neighbors using the `knearneigh` function in the `spdep` package in R (R. S. Bivand, Pebesma, and Gómez-Rubio 2013). Finally, we calculated the geographic distance between nearest neighbors with the `distGeo` function in the `geosphere` package in R (Hijmans 2016) and standardized all distances to units of “wildebeest body lengths” by dividing all results by 2 meters (average wildebeest length) so as to be directly comparable with the field observations.

Appendix 2.D. Calculating position from satellite image

We calculated the relative position of each point's three nearest neighbors by following the same procedure outlined in "calculating circular variance from satellite images" to calculate the bidirectional bearing between the focal animal and each of its three nearest neighbors.

We then averaged all three values (using the `circ.mean` function in `CircStats`; (Agostinelli and Lund 2005) to arrive at a single estimate for each animal.

Chapter III: Effects of human-altered landscapes on a reintroduced native ungulate: patterns of resource selection at the rangeland-wildland interface

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Abstract

Over the past century, numerous wildlife reintroduction programs have been initiated to restore charismatic, large-bodied ungulates to parts of their former geographic range. Conserving these reintroduced, free-ranging taxa often presents the coupled challenge of achieving sustained population viability while minimizing potential conflicts with domestic cattle and other livestock. Understanding how reintroduced ungulates use cattle-dominated landscapes is critical for assessing the degree to which such conflicts may arise. In a national park in northern California, we used three distinct lines of evidence – long-term visual surveys, short-term GPS telemetry, and high-resolution satellite imagery – to evaluate the factors that drive habitat selection by reintroduced, free-ranging tule elk (*Cervus canadensis nannodes*) and to assess the degree to which grazing by domestic cattle (*Bos taurus*) mediates resource selection by this native ungulate. Our analyses revealed that reintroduced

elk largely avoided areas managed for and used by cattle across all seasons. This pattern likely resulted from differential habitat preferences rather than outright avoidance behavior, given that satellite-derived elk and cattle locations were consistent with a ‘no avoidance’ hypothesis. Furthermore, elk groups occasionally (ca. 4% of observations) entered into close proximity with cattle (≤ 50 m apart), although we did not observe groups of elk and cattle intermixed. Overall, our results suggest that potential for conflict between cattle and reintroduced, free-ranging tule elk is minimal in this human-altered landscape, and that coexistence between domestic and free-ranging ungulates is most likely facilitated via resource partitioning.

Introduction

For centuries, human activities have driven significant changes in the abundance and distribution of wildlife populations throughout the world (Cardillo et al. 2008; Schipper et al. 2008; Dirzo et al. 2014). The compounding impacts of habitat loss, over-exploitation, and climate change have forced population declines and range shifts in species unable to adapt to the rapidly changing environmental conditions that characterize the Anthropocene (Dirzo et al. 2014). In the American west, such declines have been particularly profound and well-documented in large mammals, owing to over-exploitation of these species by early settlers and frequent encounters with modern anthropogenic barriers like roads, fences, and fragmented habitats (Ripple et al. 2019). This loss of megafauna can have pervasive impacts on ecosystem functions, including changes to the physical and trophic structure of communities, shifts in spatial and temporal patterns of nutrient cycles, and in some cases, causing large-scale climatological shifts (Malhi et al. 2016).

In response, a number of reintroduction programs have been initiated over the past century, aiming to restore extirpated large mammals to their historical range or to introduce them to new ranges (Seddon et al. 2007; Armstrong & Seddon 2008; Seddon et al. 2014). Nevertheless, many early reintroduction efforts suffered from a lack of oversight, poor planning, and failure to evaluate reintroductions within their broader ecological context (Johnson & Cushman 2007; Seddon et al. 2007). In many cases, these shortcomings have had unintended negative consequences for human and wildlife populations at recipient sites, including damage to crops and personal property, attacks on humans, zoonotic disease transmission, and opportunity costs for people living near reintroduction sites (Wolf et al. 1996; Dickman 2010; Massei et al. 2010; Fontúrbel & Simonetti 2011). Although such impacts can be minimized via careful selection of reintroduction sites and rigorous post-reintroduction monitoring, pristine reintroduction sites are rare, and human-wildlife conflict remains an important factor to address when planning or implementing reintroduction programs for large mammals.

The potential for detrimental human-wildlife interactions can be particularly acute at the interface between rangelands and wildlands. Where the opportunity exists, some species of wild ungulates readily make seasonal excursions into managed pastures to take advantage of subsidies of water and high-quality forage (Brook & McLachlan 2009; Brook et al. 2013; M. Pruvot et al. 2014). Depending on the ecology of the site, the resulting overlap in habitat use between wild and domestic ungulates may have both positive and negative consequences for ungulates in the system. For example, grazing by wild or domestic species may inhibit the growth of forage types preferred by both groups, or facilitate the growth of low quality or invasive forage (Hobbs et al. 1996; Vavra & Sheehy 1996). Moreover, under certain conditions, increased overlap may also increase the likelihood of resource competition,

negative social interactions, and disease transmission (Hobbs et al. 1996; Stewart et al. 2002; Mathieu Pruvot et al. 2014).

As a result, there is a growing body of literature aimed at quantifying spatio-temporal overlap between wild and domestic ungulates across a range of ecological systems (Brook & McLachlan 2009; Proffitt et al. 2011; Barasona et al. 2014; Russell et al. 2015; Morris et al. 2016; Merkle et al. 2018). Recommendations emerging from these studies have helped managers set priorities for a number of conflict mitigation scenarios, but the unique ecological and political landscape of each site can make it difficult to extend results to new ecosystems. In addition, it can be difficult to obtain accurate information on the density and distribution of livestock due to logistical, financial, and political constraints of working with commercial or private entities. As we demonstrate in this study, the latter shortcoming can be effectively addressed using archived, high-resolution satellite images to document the concurrent locations and densities of livestock and free-roaming ungulates within rangelands.

In this study, we investigate the factors that drive habitat selection by reintroduced, free-ranging tule elk (*Cervus canadensis nannodes*) and assess the degree to which grazing by domestic cattle (*Bos taurus*) mediates resource selection by this native ungulate at the rangeland-wildland interface of Point Reyes National Seashore. Specifically, we integrate satellite-based counts of elk and cattle with long-term surveys and GPS telemetry to ask the following questions: 1) How do reintroduced ungulates select resources seasonally in this human-altered landscape? 2) How does grazing by cattle affect selection of resources by this reintroduced native species? 3) Are there legacy effects (including short-term effects, e.g. exploitation competition) of cattle grazing on movements and habitat selection by reintroduced ungulates? By combining insights from three distinct lines of evidence, our

goal is to provide a more complete understanding of the ecology of this ecosystem than would be possible with any one method alone, and to ultimately yield new insights about the effects of livestock on free-ranging ungulates in a cattle-dominated landscape.

Methods

Study area

Our research was conducted from 2010-2018 at Point Reyes National Seashore in northern California. Point Reyes is a National Park Service unit, established in 1962 and located on a coastal peninsula in Marin County approximately 65 km northwest of San Francisco. The study site encompasses a 30 km² area within the Pastoral Zone of the park (figure 3.1). This zone is a historic cultural and working agricultural landscape composed of fenced dairy cattle ranches that operate under leases or special use permits from the National Park Service. In addition to grazed rangelands (ca. 18 km²), the study site consists of areas that are not grazed by cattle (ca. 6.5 km²), but occur adjacent to active rangelands and are mainly composed of coastal scrub (*Baccharis* spp., *Frangula* spp.) and grasslands that consist of a mixture of annual and perennial grasses (*Deschampsia* spp., *Carex* spp., and *Juncus* spp.). Elevation of this area ranges from sea level to 60 m, mean annual temperatures during the study period ranged from 7° to 16° C, with mean annual precipitation ranging from 1 cm to 45 cm and high winds and dense fog occurring frequently in the summer (June to August).

Study species

Originally extirpated due to hunting and habitat loss, tule elk were absent from the study area (i.e. Drakes Beach and the surrounding landscape; fig. 3.1) for at least 100 years

before a small population (28 individuals) was reintroduced to a neighboring area in 1999 (Carruthers & Millais 1915; Gogan & Barrett 1987; McCullough et al. 1996; Howell et al. 2002). Soon after reintroduction, several of the reintroduced adults dispersed to the current study area and established a population that numbered 93 animals (81 adults) in 2016 (Bernot & Press 2018). This group is known colloquially as the “Drakes Beach Herd” and inhabits a home range of 6 km² within the Pastoral Zone of Point Reyes. Although males and females maintain separate groups outside of the breeding season (July-October), all group members frequently move between grazed rangelands and non-grazed areas, raising concerns about disease transmission (i.e. especially the incurable gastrointestinal “Johne’s Disease,” which was first documented in the Drakes Beach Herd in 2015 (Cook et al. 1997; Foley et al. 1998; Howell et al. 2002; Manning et al. 2003; Crawford et al. 2006; Bernot & Press 2018), and competition for forage (Howell et al. 2002; Johnson & Cushman 2007; Cobb 2010) between elk and livestock. Hunting is prohibited throughout the study area and, although mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*) are present in the park, previous research suggests that predation is not a significant source of mortality for elk in this ecosystem (Thomas & Toweill 2002; Cobb 2010).

Elk activity and habitat characteristics

We used three independent datasets to assess elk activity and resource selection within the study area: (1) long-term visual surveys with nearly complete coverage of the focal population, (2) satellite GPS collars with fine-grained movement data for 8 individuals (3 males and 5 females) within our focal population of 93 individuals, and (3) locations of elk and cattle derived from archived high-resolution (30-50 cm) satellite imagery. For all analyses, we partitioned tule elk activity into four seasons that are differentiated by changes

in behavior and thus selection of resources by elk: winter (November - March), summer (June - July), breeding (July - October), and parturition (April - June).

Visual surveys: All visual surveys were performed between September 2010 and October 2017 by the same observer, who generally conducted elk counts 1 to 2 times per week during crepuscular hours (generally 06:00-10:00 and 17:00-19:00, although 15% of surveys occurred outside of these times) at 76 established survey points. At each survey point, all elk within an approximate 50 m radius were recorded (fig. 3.1). Survey points were originally selected to cover the presumed range of this elk population (100% minimum convex polygon for all historical observation points); a post hoc home range analysis of all GPS telemetry data confirmed this assumption, as the 95% autocorrelated kernel density estimate (AKDE) ('CTMM' package in R ;Calabrese et al. 2016) was fully covered by the 76 visual survey points (figure 3.1). Due to reduced visibility (and therefore lower detectability) on days with heavy fog, we removed all surveys conducted under these conditions (< 4% of the data overall). We randomly rarefied the remaining data to no more than one survey per day (thereby eliminating 18% of surveys), resulting in an average of 138 complete visual surveys per year.

GPS telemetry: Between 2012 and 2018 (see SM1 for detailed deployment schedule), 8 adult elk (3 males and 5 females) from the Drakes Beach herd were captured via chemical immobilization (see SM2 & SM3 for dosage details) and collared according to protocols approved by the National Park Service Institutional Animal Care and Use Committee and consistent with guidelines established by the American Society of Mammalogists for care and use of wild mammals for research (Sikes et al. 2016). Seven of these animals were fitted with Advanced Telemetry Systems GS110E/E2 Iridium GPS collars and one male (ID 24034B) was fitted with a Vectronics GPS collar. All collars collected one point every three

hours, 24 hrs per day (beginning at midnight) and were deployed for 3 to 31 months (16 months on average).

Satellite imagery: We used cloud-based, open-source image analysis software (Kvilekval et al. 2010) to manually digitize the locations of elk and cattle within fenced pastures at fixed points in time on the basis of archived, high-resolution satellite images (i.e. 30 to 50 cm panchromatic images from the WorldView and GeoEye constellations) collected at 10:00 AM or 2:00 PM local time. Trained observers followed a standardized search protocol to classify objects as “cattle” or “elk” (no other livestock or large mammals detectable at this resolution occur in the study area) and the same expert observer manually validated all entries. Counts were conducted for all satellite images that were commercially available ($n = 31$) for the study area at the appropriate resolution, cloud cover ($\leq 10\%$), and dates of interest (2013 to 2018). This resulted in the following distribution of seasonal counts: winter ($n=13$), parturition ($n = 6$), summer ($n = 3$), and breeding ($n = 9$). From these counts, we then calculated mean cattle densities within each pasture by dividing total counts by total pasture area. Temporary pens that held cattle adjacent to ranch compounds were excluded from analyses due to the limited size and extreme variability in densities of cattle in these areas. For analysis of cattle avoidance by elk (see below), only images where elk were observed in cow pastures were used ($n = 28$).

Habitat characteristics: We obtained spatial data on the extent of grazed pastures, vegetation cover (e.g. percent grassland, percent coastal scrub), distance to ponds (m), slope (percent), aspect (radians), and elevation (m) from the Point Reyes GIS database. We then computed slope “northness” (i.e. a proxy for solar radiation) of the terrain as the cosine of aspect and used the Normalized Difference Vegetation Index (NDVI) for each season as an index of seasonal forage availability (computed using Landsat Tier 1 data accessed and

processed via Google Earth Engine; Gorelick et al. 2017). We then masked land cover types that might confound NDVI calculations (i.e. water, beaches, dunes, and riparian vegetation) and rasterized all vector datasets to 10 m resolution ('raster' package in R; Hijmans 2017). Raster cell values were calculated as mean percent cover (e.g. grazed pastures, vegetation), mean feature value (e.g. slope, elevation, aspect), or Euclidean distance to feature of interest (e.g. ponds). A summary of all variables tested is included in table 3.1.

Data analysis

Visual surveys

We subsetted data from visual surveys by season (winter, parturition, summer, breeding) and used the total number of elk observed at each survey site per visit as our primary response variable. In addition, we computed the mean value for all environmental covariates within a 50 m radius buffer around each of the 76 points (i.e. the same distance included around each point during surveys); these values then served as covariates in our count regression models (see below). To aid in model convergence and interpretation of effect sizes, we standardized all quantitative environmental covariates (including satellite-derived cattle densities; see above) by subtracting the mean and dividing by 2X the standard deviation (Gelman 2008).

We used a generalized linear mixed-effects modeling approach (GLMM) to assess the effects of an array of environmental covariates on daily elk counts for each season, alternately assuming (1) Poisson error distribution with a log-link, (2) negative binomial error distribution with a log link, and (3) zero-altered (hurdle) Poisson (ZAP) or negative binomial (ZANB) process model with a logit-link (zero-prediction component) and a log-link (count-regression component) ('glmmTMB' package in R; Magnusson et al. 2016; Zuur et al. 2009). For the ZAP and ZANB models, we used the full set of environmental covariates to model both the zero-prediction and count components (see below). We selected the modeling framework that exhibited lowest AIC and adequate goodness-of-fit. We assessed goodness-of-fit by visually examining scaled (quantile) residuals and performing diagnostic tests (uniformity, overdispersion, zero-inflation, outliers) using the 'DHARMA' package in R (Hartig 2019). In all cases, the ZANB modeling framework was selected as the

appropriate modeling framework (100% of AIC weight and adequate model fit), and therefore only results from these models were interpreted further.

For the seasonal ZANB models (implemented in the ‘glmmTMB’ package in R; Brooks et al. 2017), we included the same set of potentially important covariates and two-way interactions in the zero-prediction component and the count-regression model component (table 3.1). No covariates were highly correlated (i.e. $r < 0.5$; $VIF < 3$; O’Brien 2007), so all were included in the full models for each season. In addition, we modeled “Year” and “Site ID” as random-intercepts for both the zero-prediction and the count-regression components.

For each season, we then employed a two-step information-theoretic approach to model selection of resources, in each case selecting the lowest-AIC model (Burnham & Anderson 2007): (1) we first selected the best-performing cattle stocking rate estimate from among the four candidate estimates (mean, median, mean non-zero, median non-zero), and (2) then we used backward stepwise selection (‘buildmer’ package in R; Voeten 2019) to remove any variables and interaction terms that were uninformative for both the zero-prediction and count-regression submodels.

GPS telemetry

We fitted seasonal Resource Selection Function (RSF) models separately for each individual collared elk using a generalized linear modeling framework (GLM) with a binomial error distribution and a logit-link (logistic regression; ‘glm’ function in R). Models exhibiting complete separation (leading to non-convergence using the ‘glm’ function) were fitted using Firth’s bias-reduced logistic regression (a form of penalized-likelihood regression; Heinze and Ploner 2018). GPS telemetry data for each individual were first partitioned into the four seasons (see “Environmental data”). The ‘used’ points for each

individual were paired with a set of ‘available’ (background) points randomly selected from inside the 100% minimum convex polygon enclosing the known locations (derived from collars and visual surveys) for all individuals in the study population (number of randomly sampled background points for each fitted model was 5X the number of telemetry observations). To account for error in GPS fixes, covariate values (listed in table 3.1) for ‘used’ and ‘available’ locations were computed as the mean value within a 25 m radius of each location. To aid in model convergence and interpretation of effect sizes, we standardized all quantitative environmental covariates (including cattle densities derived from satellite images; see above) by subtracting the mean and dividing by 2X the standard deviation (Gelman 2008). We used a custom bootstrapping algorithm to compute mean resource selection coefficients across all collared individuals and to estimate confidence intervals for these quantities. Specifically, we repeatedly sampled (1000x, with replacement) from among the seasonal used and background points for each individual (maintaining a 5:1 ratio of background to used points), fitted logistic regression models to each individual, and computed mean seasonal selection coefficients across all individuals. Confidence intervals for each mean coefficient value were computed as quantiles from the resulting bootstrap distributions. It should be noted that although these models assumed independence among individuals, the Drakes Beach Herd regularly moves as a single group, so these bootstrapped confidence intervals should be interpreted with caution.

Finally, we used data generated from GPS telemetry to calculate seasonal residence times in grazed vs. non-grazed areas, subdivided by sex and season (including only animals with collars active for the full season of interest). Residence times were calculated as the number and duration of revisits to a polygon based on the number and length of segments of a trajectory passing through the polygon (‘recurse’ package (Bracis et al. 2018) in R).

Satellite imagery

We first examined differences in the spatial distributions of elk and cattle using a multi-response permutation procedure (MRPP; Talbert & Cade 2013) wherein we tested whether mean within-group Euclidean distances (i.e. cattle to cattle or elk to elk, aggregated across all 28 satellite images) were shorter than mean elk-cattle distances (Oehlers et al. 2011; Stewart et al. 2015). We report the average within-group pairwise distance (or delta value), which is a descriptive metric of spatial dispersion, and a p-value from the permutation procedure (fraction of permutation-based delta values that are lower than the observed delta value (Talbert & Cade 2013)).

To test whether observed differences in space-use by elk vs. cattle resulted from behavioral avoidance, we developed a bootstrap procedure to generate a distribution of elk locations under a null model (no cattle avoidance). To do this, we first aggregated all elk locations across all images ($n = 28$) and constructed a kernel-density surface across our study site representing the probability of utilization by elk ('kde2d' function in the 'MASS' package; Venables & Ripley 2002). We then categorized elk into groups within each image (all elk within 50 m of another elk were considered part of the same group). Next, we used this kernel-density surface to generate hypothetical centroids for elk groups within each image (the number of simulated elk groups was held equal to the number observed in each image). For each image, we generated elk locations under the null model by sampling randomly from the observed distribution of location to group-centroid distances, holding the number of elk per group to observed values (directions from the group-centroid were generated randomly). For each bootstrap simulation replicate, we computed three test statistics: (1) the mean distance from each simulated elk location to the nearest observed

cattle location, averaged across all images ($n = 28$) (2) the minimum per-image distance from each simulated elk location to the nearest cattle location, averaged across all images, and (3) the proportion of elk groups occurring within 50 m of one or more cattle groups, averaged across all images. To test for avoidance of cattle by elk, we compared the observed test statistics (e.g. mean distance from elk to nearest cattle location) with the distribution of each statistic generated under the null (no avoidance) model, and we computed a p -value as the proportion of null test statistics suggesting equal or stronger avoidance behavior than the observed statistics. Finally, we used ordinary linear regression to test for a negative relationship between the total number of cattle occupying pasture areas commonly used by elk (cattle located within the 95% kernel density contour defined by all elk locations across all images) and the total number of elk occupying these pasture areas.

Results

Between 2010 and 2017, our visual count surveys resulted in 1,792 observations of elk groups over 589 surveys (average 34 elk per survey, ranging from 10 to 104 individuals). Our GPS telemetry monitoring resulted in 29,014 fixes for 8 individuals from 2012 to 2018 (average 3,627 fixes per individual, ranging from 594 to 6,921). Finally, our satellite image analysis resulted in 1,608 elk locations and 26,943 cattle locations across 31 images. The average number of elk locations recorded per image was 51 (ranging from 0 to 98), and the average number of cattle locations recorded per image was 869 (ranging from 312 to 1,251).

Results from both the visual surveys and GPS telemetry suggest that grazing status (i.e. pasture vs. non-grazed land) had a consistently large, negative effect on probability of resource selection by elk resource (figure 3.5). However, elk tended to occur more often, and

at higher abundances, near sources of water, which in our study area consisted of man-made cattle ponds (figure 3.5). The effect of cattle density on resource selection by elk was somewhat variable by season. For example, during the breeding season, cattle density had a large and negative effect on elk abundance and probability of occurrence (unless the pasture also had high NDVI values, in which case resource selection probability was high; figures 3.5, 3.6, & 3.7). During the summer, cattle density had a weakly positive effect on elk abundance and occupancy (figures 3.5 & 3.6), but this pattern was again reversed for pastures with high NDVI values (figure 3.7). The effect of cattle density on resource selection by elk during the winter season was ambiguous, with negative selection coefficient from GPS telemetry and a positive selection coefficient from visual count records (occurrence sub-model; figure 3.5).

In addition to the patterns of avoidance observed in the resource selection functions, our residency analysis concluded that elk do not generally remain resident on cattle pastures for long periods of time. Instead, GPS locations were consistent with short-term, or transitory use (i.e. < 1 day per year on average) across almost half (46.6%, 7.8 km²) of the pasture area included in the study. Additionally, if elk did remain resident on cattle pastures for extended periods (i.e. more than 3 days per year on average), they tended to occur consistently within small areas of specific pastures (i.e. < 0.1%, 0.01 km² of pasture area included in the study) that were rarely used by cattle (see below).

The satellite imagery provided clear evidence that the spatial distributions of elk and cattle within pasture areas were highly distinct and that cattle were more widely dispersed than elk in our study area (MRPP analysis; $\delta_{\text{cattle}}=2,711$, $\delta_{\text{elk}}=1,203$; $P < 0.0001$; figures 3.2, 3.3, & 3.4). Despite strong evidence for spatial segregation between elk and cattle, we were unable to show behavioral avoidance of cattle by elk on the basis of satellite images; the

observed distances between elk and cattle locations in any given image (average distance from each elk to the nearest cattle was 516 m, ranging from 114 to 1,433 m; minimum elk-cattle distance per image averaged 361 m and ranged from 23 to 1378 m) were generally consistent with a null model in which cattle locations had no effect on elk locations ($p = 0.28$ for mean distances and $p = 0.18$ for minimum distances; figure 3.2). In addition, although specific cattle and elk were observed to come into direct contact very rarely (only 4% of observed elk groups overlapped with one or more cattle group, with overlap defined as any individual elk group member occurring within 50 m of a cattle individual), this result was also consistent with a null no-avoidance model ($p = 0.31$; figure 3.2). Furthermore, we detected a weakly positive relationship between elk use of pastures and the number of cattle occupying pasture areas commonly used by elk ($p = 0.03$, adjusted $R^2 = 0.13$, $n = 28$; figure 3.3), whereas a negative relationship might be expected under a cattle-avoidance hypothesis.

Of the other environmental variables tested, aspect and elevation were consistently important for predicting elk resource selection across all seasons and data types. Specifically, high elevation sites and south-facing slopes were positively associated with the probability of occurrence (although the evidence was slightly less conclusive for the breeding season; figures 3.5 & 3.6). Telemetry data indicated that elk tended to select gentle slopes vs. steeper slopes, but this pattern was not corroborated by data from visual surveys (figure 3.5). Furthermore, the telemetry data suggested a weak interaction between slope and aspect in which shallow, south-facing slopes were preferred – although this interaction was not detected with the visual survey data (figures 3.5 & 3.6).

NDVI was the most seasonally variable feature examined, with avoidance of high NDVI sites during the breeding season, moderate selection for high NDVI sites during parturition and winter, and a more complex selection pattern during summer (i.e. visual

surveys indicated a higher probability of occurrence with increased NDVI, but lower expected counts, figure 3.5). Further, telemetry data indicated that both grassland and scrub sites with high NDVI values were avoided across all seasons, but these terms had little influence on probability of selection from the visual survey data (figure 3.6).

The effects of ponds, grassland, and scrub were consistent in their influence on the probability of habitat selection by elk based on telemetry data (increasing, decreasing, and decreasing probability of selection, respectively). However, those results were only weakly corroborated by the visual survey data, with increased abundance predicted near ponds for breeding and summer seasons only, decreased abundance predicted in scrub habitat during breeding and winter seasons only, and a negative association with grasslands for breeding season only (figure 3.5).

Discussion

In the western United States, cattle grazing is one of the largest drivers of anthropogenic change in an area that hosts the majority of ungulate biodiversity in the nation (Bigelow & Borchers 2017). Although this setting presents unique challenges for the reintroduction of free-ranging ungulates, a comprehensive understanding of potential outcomes will inform expectations and contribute to the continued success of reintroduction projects in this iconic ecosystem. This study aimed to advance understanding of habitat selection and use by reintroduced ungulates in the western United States by employing multiple complementary datastreams to evaluate the suite of habitat selection strategies employed by elk at a rangeland-wildland interface in Point Reyes National Seashore.

Our results indicated that, even when 75% of the available grazing area occurs within cattle pastures, elk exhibited patterns of resource selection that naturally reduced the

potential for negative interactions with cattle (e.g. resource competition, potential disease transmission). Specifically, elk selected for habitat that was either not on grazed pastures, or was at high elevations that were rarely used by cattle. Although similar patterns of avoidance have been documented for many ungulate species in the western US (Loft et al. 1993; Bissonette & Steinkamp 1996; Stewart et al. 2002; Brook et al. 2013), additional research shows that this pattern may also be reversed if supplemental feed or water is accessible to elk – especially during times of nutritional stress (Proffitt et al. 2011; Pruvot et al. 2014). Therefore, we expected to see some plasticity in this avoidance response if the resource landscape were to change in a way that warranted additional overlap between the two species such as seasonal limitation of resources, pasture irrigation, or supplemental feeding of livestock.

In fact, we have some evidence that this switch has already occurred within our study system, specifically when surrounding landscapes are sufficiently dry (i.e. summer), or if NDVI values are sufficiently high to warrant a shift in selection towards specific pastures (i.e. high density pastures during winter and breeding seasons). Surprisingly, this pattern of selection did not hold for high NDVI sites across grassland habitats (regardless of grazing status), which may suggest that elk are responding to some unobserved metric of forage productivity, or that grasslands are dominated by plant species that are relatively unpalatable to elk when mature. In addition, since 75% of the grassland habitat in the study area occurs within cattle pastures, we suspect that avoidance of this resource may be driven by avoidance of associated cattle grazing activities. However, without further investigation of conditions on the ground, it is not possible to sufficiently test this hypothesis.

Despite these notable exceptions, data from archived, high-resolution satellite images provided further evidence that elk largely avoided cattle in this system. We found this by

reconstructing the historic distribution and abundance of both cattle and elk across the study area, and confirming the following: 1) that elk occurred in more compact groups relative to cattle, 2) that cattle rarely used pasture sites frequented by elk, and 3) that there was no evidence of commingling between the two species. Although additional data is needed to confirm that these patterns hold for cattle beyond satellite image collection times (e.g. 10:00 AM and 2:00 PM local time), there is no evidence that elk and cattle commingle under normal circumstances (Dohna et al. 2014), and patterns of distribution observed in this study were consistent with distributions observed in other systems (Dohna et al. 2014; Proffitt et al. 2011).

By facilitating this detailed assessment of the spatial distributions of individuals across the study area, the satellite data also revealed that, despite each species' tendency to avoid the other, individuals from each group can occur in relatively close proximity (nearly 5% of elk groups occurred within 50 m of cattle). This finding suggests that the observed patterns of avoidance were not driven by a behavioral intolerance for proximity to the other, but were instead attributed to contrasting patterns of habitat selection that resulted in decreased temporal overlap. Though several studies have suggested similar mechanisms for avoidance in other elk-cattle ecosystems (Stewart et al. 2002; Coe et al. 2004; Hibert et al. 2010), this is the first study we know of to test this hypothesis with cattle counts derived from archived satellite data.

This novel application of satellite-based animal counts presents a step-change in our ability to study ecological interactions in remote landscapes. By providing a comprehensive snapshot of the entire landscape at multiple points in time, high-resolution satellite images afford the rare benefit of a reproducible record and allow us to retroactively assess animal distributions in areas where access to such information may be limited or impossible.

Although access to such data is inherently limited by cost, processing power, and appropriate environmental conditions (i.e. cloud-free days in open landscapes), anticipated improvements in resolution, imaging frequency, and automated processing are likely to increase the utility of remotely sensed animal counts in the near future.

Moreover, the patterns of proximity revealed by our satellite image analysis raises an important and oft-cited concern about the potential for increased risk of disease transmission in areas of overlap between elk and cattle (Stewart et al. 2002; Manning et al. 2003; Proffitt et al. 2011). In Point Reyes, there is specific concern surrounding the spread of Johne's Disease (*Mycobacterium avium paratuberculosis*, or "MAP"), which is a contagious and usually fatal infection that is spread through contact with contaminated urine or feces and primarily affects the small intestine of wild and domestic ruminants (Chiodini et al. 1984). While there is no public information on infection rates in cattle of Point Reyes, Johne's can persist in the environment for more than a year (Elliott et al. 2015) and has been documented in the Drakes Beach elk herd as recently as 2016, raising concerns over transmission risk between elk and cattle in the study area (Bernot & Press 2018). However, extensive research from other systems suggests that transmission risk cannot be accurately predicted from spatial overlap alone (Knust et al. 2011; Gerritsmann et al. 2014). Rather, there are often complex and site-specific interactions between contact rates, vaccine performance, host susceptibility, and the potential for additional wildlife reservoirs (e.g. badgers, rabbits) which highlight the need for focused investigation into these relationships before drawing conclusions from spatial overlap alone (Stevenson et al. 2009; Knust et al. 2011).

Given that multiple independent datastreams confirm spatial overlap with temporal avoidance in this system, we propose that elk activity in rangelands of Point Reyes may present a risk of disease transmission, but that competition for cattle forage is highly unlikely

under current conditions. We also recommend further investigation into whether cattle grazing activities may be limiting access to forage for elk and whether spatial overlap actually translates into increased transmission risk. In the absence of such data, the observation that elk occur on cattle pastures in highly concentrated and seasonally variable locations suggests that if conflicts do occur, temporally and spatially-targeted management strategies may be both efficient and effective in this ecosystem.

Tables and figures

Table 3.1. Fixed and random effects included in the global model for visual survey and GPS telemetry datasets used to quantify habitat selection for tule elk in the Drakes Beach herd at Point Reyes National Seashore 2010-2018.

Covariate	Definition	Unit	Cell size (m ²)
Cattle stocking rate	Mean (non-zero) density of cattle within cell during season of interest.*	cows/acre	100
Grassland	% of cell covered by grassland (i.e., <i>Deschampsia</i> spp., <i>Carex</i> spp., and <i>Juncus</i> spp.)	% cover	100
Grazing status	% of area within current ranching lease.	% cover	100
Elevation	Height above sea level.	meters	100
NDVI	Median NDVI (Normalized Difference Vegetation Index) during season of interest.	-1 to 1	900
Northness	Relative measure of direction of slope face (cosine(aspect))	-1 to 1	100
Ponds	Distance to nearest pond.	meters	100
Scrub	% of cell covered by scrub (e.g., <i>Baccharis</i> spp., <i>Frangula</i> spp.).	% cover	100
Site ID	Random effect of site ID.	categorical	NA
Slope	% slope of terrain.	degrees	100
Year	Random effect of year.	categorical	NA

*Median density used for winter models in all datasets.



Figure 3.1. Map of study area within Point Reyes National Seashore, CA showing grazed cattle pastures (dark gray), ungrazed areas (white), visual survey route (gray line, representing roads), visual survey locations (circles shaded to indicate mean density of elk, with darker shades corresponding to increased density), and home range of the Drakes Beach elk population (dashed line, representing a 95% autocorrelated kernel density estimate). All data were collected from 2010-2018.

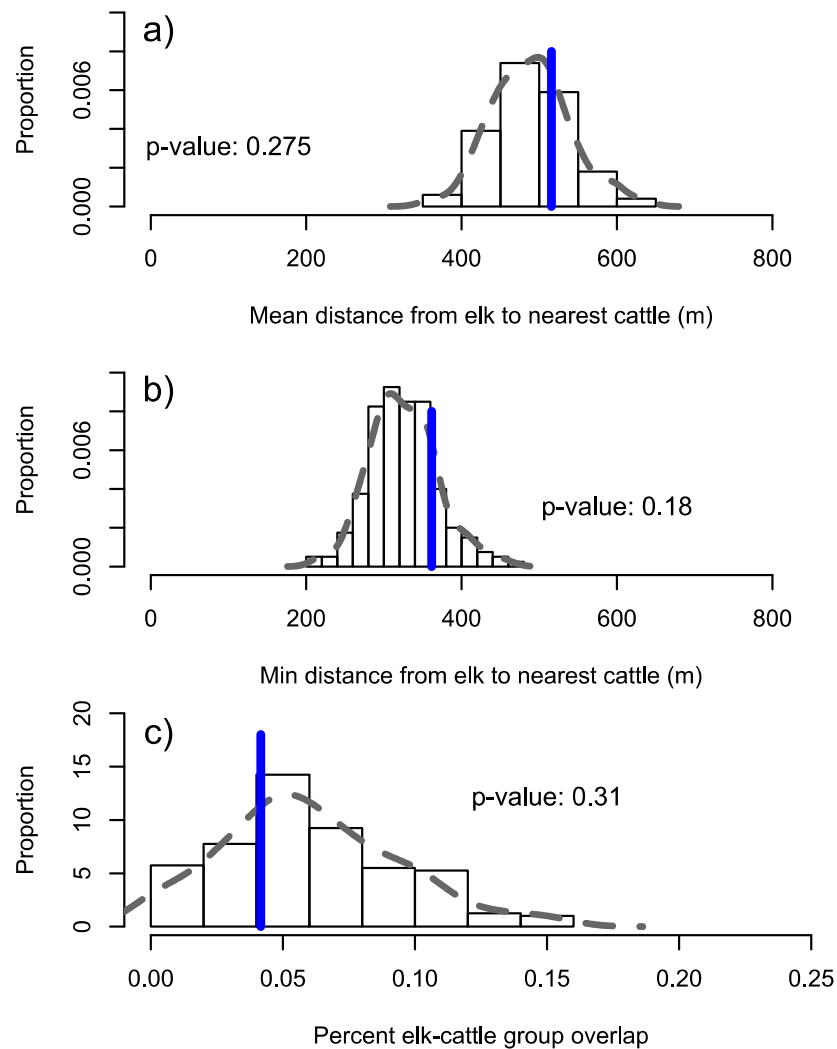


Figure 3.2. Results from semi-parametric bootstrap analyses illustrating observed test statistics relevant to cattle-avoidance by elk (vertical blue lines) and the null distributions of the same test statistics (histograms) under a model whereby elk groups select locations without regard to the location of cattle. Specifically, histograms were generated via random cluster sampling, with cluster centroids sampled from the kernel density distribution of elk points aggregated across all satellite images ($n = 28$). Panel (a) depicts mean distances from each elk location (observed and random) to the nearest cattle location, averaged across images; panel (b) depicts minimum elk-cattle distances averaged across images; Panel (c) depicts the proportion of elk-cattle co-occurrences (defined as the fraction of elk groups for which any members were within 50 m of a cattle location), averaged across all images.

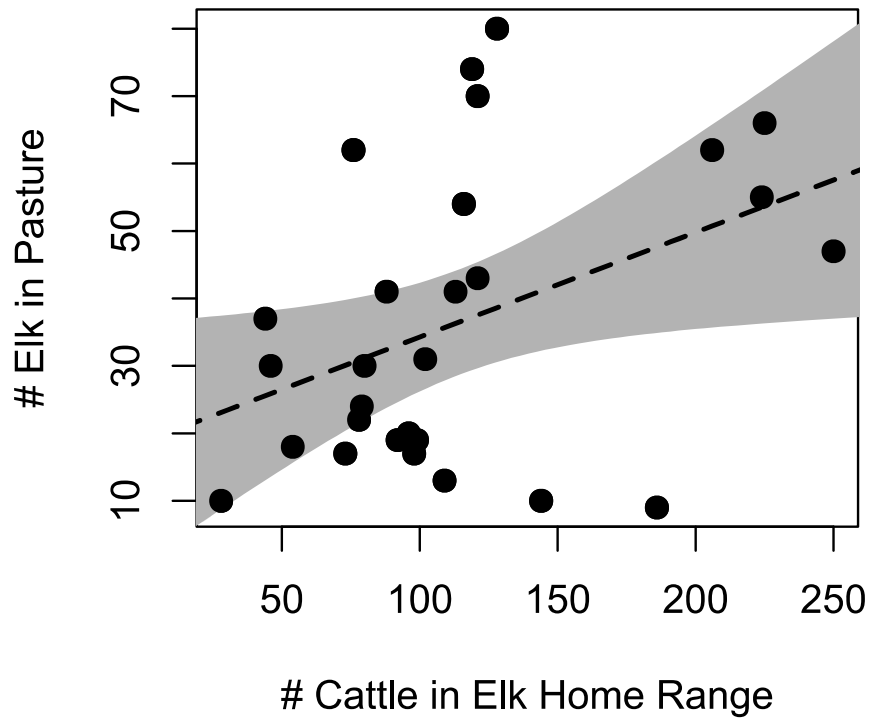


Figure 3.3. Relationship between the total number of elk observed using pasture lands (# Elk in pasture) and the total number of cattle occupying sections of pasture commonly used by elk (# Cattle in Elk Home Range), determined on the basis of annotated satellite imagery ($n = 28$). Specifically, the x-axis represents the number of cattle occupying the 95% kernel density contour defined by all elk points aggregated across all satellite images.

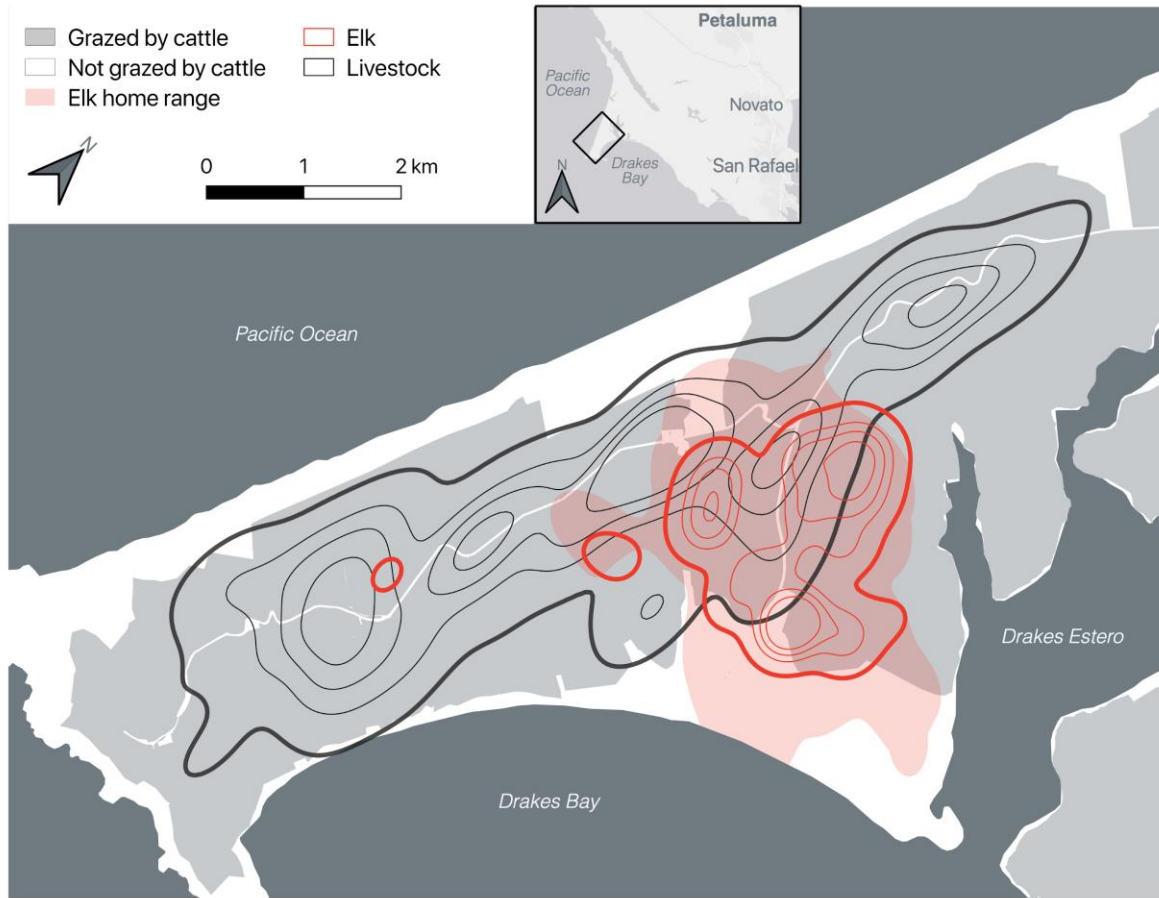


Figure 3.4. Illustration of spatial overlap between elk and cattle within pasture areas at our study site in Point Reyes National Seashore, CA. Figure depicts kernel density contours (isopleths; bolded contours enclose 95% of the kernel density for each species) for elk (red) and cattle (black) defined by all elk and cattle locations across all satellite images ($n = 28$, images collected from 2014-2018). Home range (red shaded polygon) represents a 95% autocorrelated kernel density estimate for all collared elk in the study area ($n = 8$, data collected from 2012-2017).

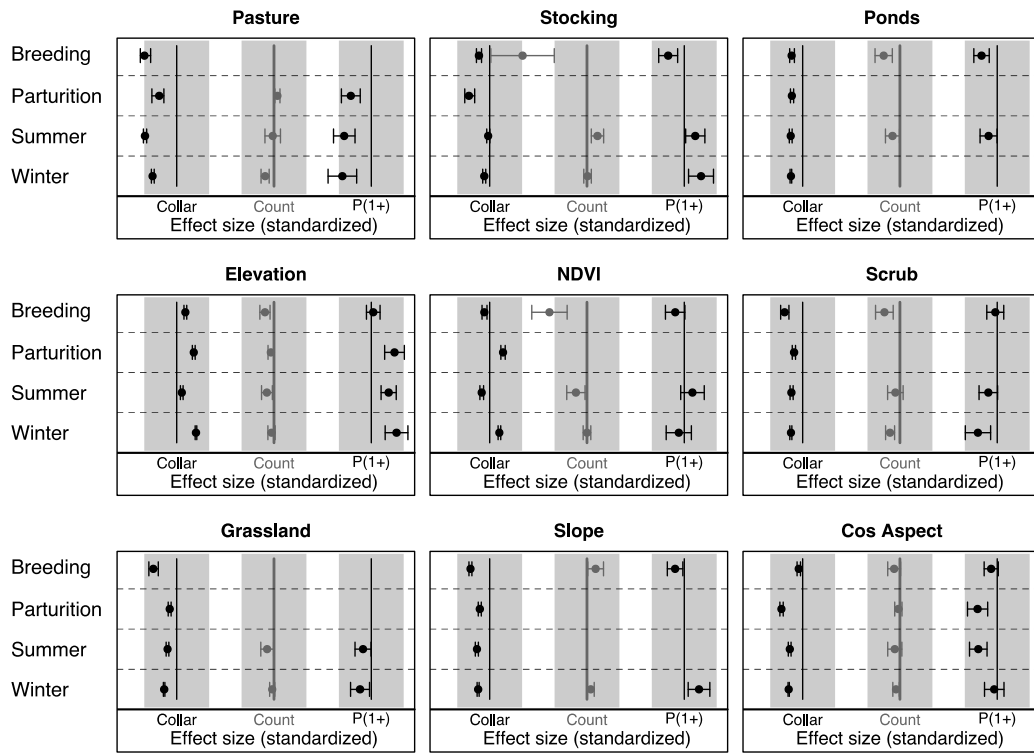


Figure 3.5. Estimated coefficients for tule elk resource selection across multiple seasons and datasets. Vertical lines indicate an effect size of zero, and gray regions represent (standardized) effect sizes between -2 and 2. *Collar*: modeled from GPS collar data collected at Point Reyes National Seashore from November 2012 to March 2018 (see SM1 for details). *Count* and *P(1+)*: Modeled from visual surveys conducted at Point Reyes National Seashore from September 2010 to November 2017. *Count* represents probability that elk abundance will increase as a function of each covariate. *P(1+)* represents probability of elk presence (one or more elk observed) as a function of each covariate.

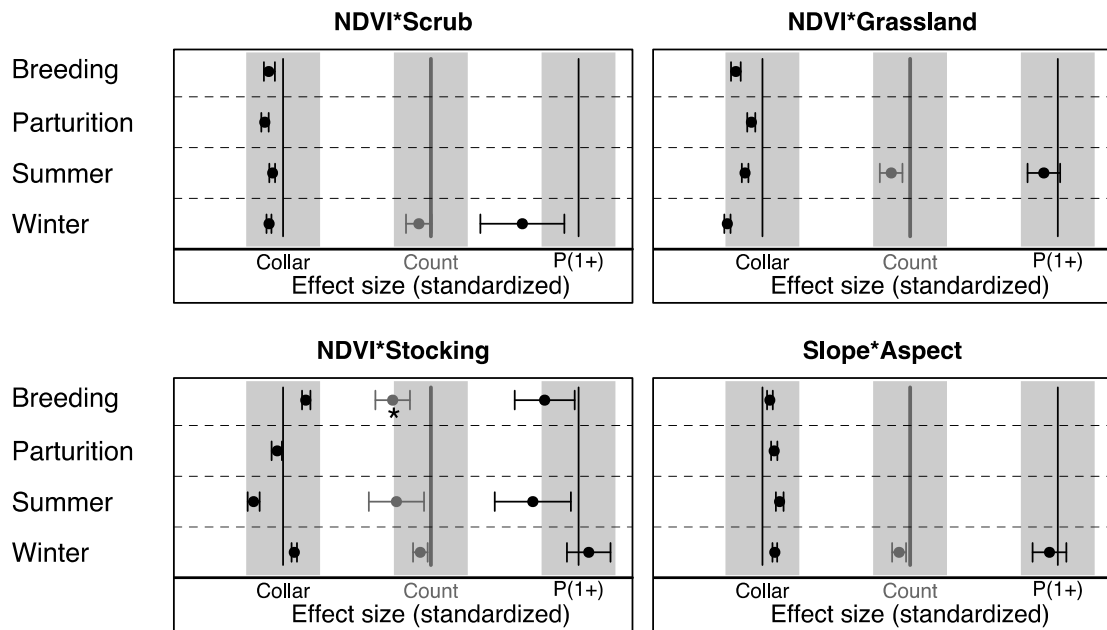


Figure 3.6. Estimated values for interactions between covariates related to patterns of resource selection by tule elk measured across multiple seasons and datasets. Vertical lines indicate an effect size of zero, and gray regions represent (standardized) effect sizes between -2 and 3. *Collar*: modeled from GPS collar data collected at Point Reyes National Seashore from November 2012 to March 2018 (see SM1 for details). *Count* and *P(1+)*: Modeled from visual surveys conducted at Point Reyes National Seashore from September 2010 to November 2017. *Count* represents probability that elk abundance will increase as a function of each covariate. *P(1+)* represents probability of elk presence (one or more elk observed) as a function of each covariate. The asterisk (NDVI x stocking interaction during breeding season) denotes that the effect size for this effect was 5X larger in magnitude that what is depicted here (for visual clarity).

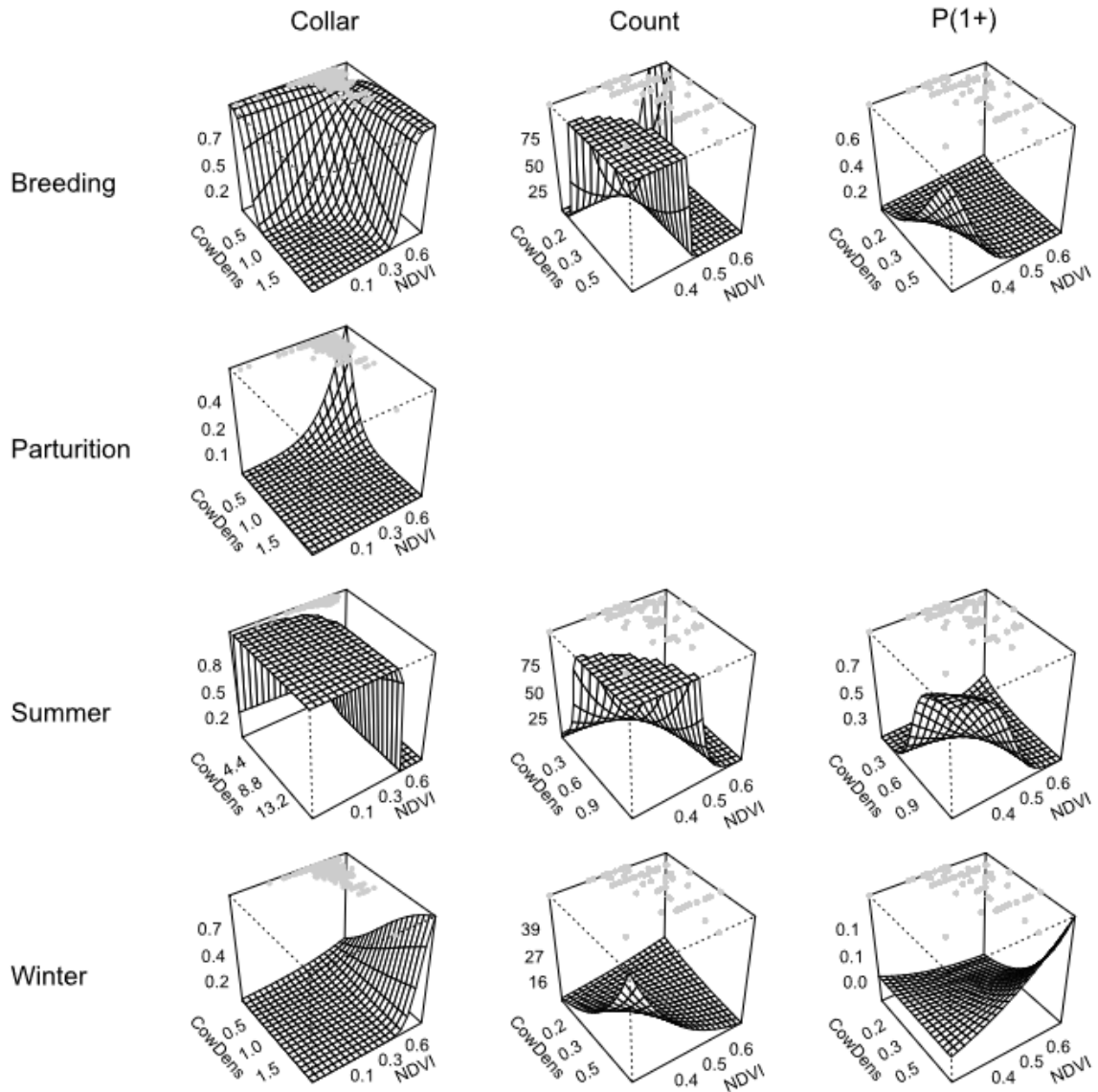


Figure 3.7. Key interactions between variables of interest for estimating patterns of resource selection by tule elk measured across multiple seasons. *Collar*: modeled from GPS collar data collected at Point Reyes National Seashore from November 2012 to March 2018 (see SM1 for details). *Count and P(1+)*: Modeled from visual surveys conducted at Point Reyes National Seashore from September 2010 to November 2017. *Count* represents probability that elk abundance will increase as a function of each covariate. *P(1+)* represents probability of elk presence (one or more elk observed) as a function of each covariate.

References

- Armstrong, D.P. & Seddon, P.J., 2008. Directions in reintroduction biology. *Trends in Ecology & Evolution*, 23(1), p. 20–25. Available at: <http://dx.doi.org/10.1016/j.tree.2007.10.003>.
- Barasona, J.A. et al., 2014. Spatiotemporal interactions between wild boar and cattle: implications for cross-species disease transmission. *Veterinary Research*, 45, p.122. Available at: <http://dx.doi.org/10.1186/s13567-014-0122-7>.
- Bernot, T. & Press, D., 2018. *Tule elk monitoring and management at Point Reyes National Seashore: 2015-2016 Report*, National Park Service.
- Bigelow, D. & Borchers, A., 2017. *Major uses of land in the United States, 2012*, Available at: <https://ageconsearch.umn.edu/record/263079/>.
- Bissonette, J.A. & Steinkamp, M.J., 1996. Bighorn sheep response to ephemeral habitat fragmentation by cattle. *The Great Basin Naturalist*. 56(4), p. 319-325. Available at: <https://www.jstor.org/stable/41712957>.
- Bracis, C., Bildstein K, Mueller T., 2018. Revisitation analysis uncovers spatio-temporal patterns in animal movement data. *Ecography*. 41(11), p. 1801-1811. Available at: <http://dx.doi.org/10.1111/ecog.03618>.
- Brook, R.K. & McLachlan, S.M., 2009. Transdisciplinary habitat models for elk and cattle as a proxy for bovine tuberculosis transmission risk. *Preventive Veterinary Medicine*, 91(2-4), pp.197–208. Available at: <http://dx.doi.org/10.1016/j.prevetmed.2009.05.021>.
- Brook, R.K. et al., 2013. Evaluating use of cattle winter feeding areas by elk and white-tailed deer: implications for managing bovine tuberculosis transmission risk from the ground up. *Preventive Veterinary Medicine*, 108(2-3), pp.137–147. Available at: <http://dx.doi.org/10.1016/j.prevetmed.2012.07.017>.
- Burnham, K.P. & Anderson, D.R., 2007. *Model selection and multimodel inference: A practical information-theoretic approach*, Springer Science & Business Media. Available at: <https://market.android.com/details?id=book-IWUKBwAAQBAJ>.
- Calabrese, J.M., Fleming, C.H. & Gurarie, E., 2016. ctm: an r package for analyzing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution / British Ecological Society*, 7(9), pp.1124–1132. Available at: <http://onlinelibrary.wiley.com/doi/10.1111/2041-210X.12559/full>.
- Cardillo, M. et al., 2008. The predictability of extinction: biological and external correlates of decline in mammals. *Proceedings. Biological Sciences / The Royal Society*, 275(1641), pp.1441–1448. Available at: <http://dx.doi.org/10.1098/rspb.2008.0179>.
- Carruthers, D. & Millais, J.G., 1915. *The gun at home & abroad: The big game of Asia and*

North America, London & Counties Press Association Limited. Available at:
<https://market.android.com/details?id=book-HNvnPQAACAAJ>.

- Chiodini, R.J. et al., 1984. Ruminant paratuberculosis (Johne's disease): The current status and future prospects. *The Cornell Veterinarian*, 74(3), pp.218–262. Available at:
https://www.researchgate.net/profile/Rodrick_Chiodini/publication/16820257_Ruminant_paratuberculosis_Johne's_disease_The_current_status_and_future_prospects/links/566efcea08ae52dd6c12a5e9/Ruminant-paratuberculosis-Johnes-disease-The-current-status-and-future-prospects.pdf.
- Cobb, M.A., 2010. *Spatial ecology and population dynamics of tule elk (Cervus Elaphus Nannodes) at Point Reyes National Seashore, California*, Unpublished dissertation. Available at:
https://books.google.com/books/about/Spatial_Ecology_and_Population_Dynamics.html?hl=&id=9adwAQAACAAJ.
- Coe, P.K. et al., 2004. Spatial and temporal interactions of elk, mule deer, and cattle. *Transactions of the 69th North American Wildlife and Natural Resources Conference: 656-669*. Available at: <https://www.fs.usda.gov/treesearch/pubs/24694>.
- Cook, W.E. et al., 1997. Radiometric culture of Mycobacterium avium paratuberculosis from the feces of tule elk. *Journal of Wildlife Diseases*, 33(3), pp.635–637. Available at: <http://dx.doi.org/10.7589/0090-3558-33.3.635>.
- Crawford, G.C. et al., 2006. Mycobacterium avium subspecies paratuberculosis and Mycobacterium avium subsp. avium infections in a tule elk (Cervus elaphus nannodes) herd. *Journal of Wildlife Diseases*, 42(4), pp.715–723. Available at:
<http://dx.doi.org/10.7589/0090-3558-42.4.715>.
- Dickman, A.J., 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human--wildlife conflict. *Animal Conservation*, 13(5), pp.458–466. Available at:
https://zslpublications.onlinelibrary.wiley.com/doi/abs/10.1111/j.1469-1795.2010.00368.x%4010.1111/%28ISSN%291469-1795.animal_conservation_vi_20th_anniversary_collection.
- Dirzo, R. et al., 2014. Defaunation in the Anthropocene. *Science*, 345(6195), pp.401–406. Available at: <http://dx.doi.org/10.1126/science.1251817>.
- Dohna, H. zu et al., 2014. Wildlife–livestock interactions in a western rangeland setting: Quantifying disease-relevant contacts. *Preventive Veterinary Medicine*, 113(4), pp.447–456. Available at:
<http://www.sciencedirect.com/science/article/pii/S0167587713003863>.
- Elliott, G.N. et al., 2015. Environmental risk factors in the incidence of Johne's disease. *Critical Reviews in Microbiology*, 41(4), pp.488–507. Available at:
<http://dx.doi.org/10.3109/1040841X.2013.867830>.

- Foley, J.E. et al., 1998. *Ehrlichia* spp. in cervids from California. *Journal of Wildlife Diseases*, 34(4), pp.731–737. Available at: <http://dx.doi.org/10.7589/0090-3558-34.4.731>.
- Fontúrbel, F.E. & Simonetti, J.A., 2011. Translocations and human-carnivore conflicts: problem solving or problem creating? *Wildlife Biology*, 17(2), pp.217–224. Available at: <http://www.bioone.org/doi/abs/10.2981/10-091>.
- Gelman, A., 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine*, 27(15), pp.2865–2873. Available at: <http://dx.doi.org/10.1002/sim.3107>.
- Gerritsmann, H. et al., 2014. Multiple strain infections and high genotypic diversity among *Mycobacterium avium* subsp. paratuberculosis field isolates from diseased wild and domestic ruminant species in the eastern Alpine region of Austria. *Infection, Genetics and Evolution*, 21, pp.244–251. Available at: <http://dx.doi.org/10.1016/j.meegid.2013.11.009>.
- Gogan & Barrett, R.H., 1987. Comparative dynamics of introduced tule elk populations. *The Journal of Wildlife Management*, 51(1), pp.20–27. Available at: <http://www.jstor.org/stable/3801622>.
- Hartig, F., 2019. *DHARMA: Residual diagnostics for hierarchical (multi-level / mixed) regression models*, Available at: <http://florianhartig.github.io/DHARMA/>.
- Hibert, F. et al., 2010. Spatial avoidance of invading pastoral cattle by wild ungulates: insights from using point process statistics. *Biodiversity and Conservation*, 19(7), pp.2003–2024. Available at: <https://link.springer.com/article/10.1007/s10531-010-9822-0> [Accessed August 21, 2019].
- Hijmans, R.J., 2017. raster: Geographic data analysis and modeling. Available at: <https://CRAN.R-project.org/package=raster>.
- Hobbs, N.T., Baker, D.L. & Bear, G.D., 1996. Ungulate grazing in sagebrush grassland: effects of resource competition on secondary production. *Ecological Applications*, 6(1). Available at: <http://onlinelibrary.wiley.com/doi/10.2307/2269565/full>.
- Howell, J.A. et al., 2002. Population dynamics of tule elk at Point Reyes National Seashore, California. *The Journal of Wildlife Management*, 66(2), pp.478–490. Available at: <http://www.jstor.org/stable/3803181>.
- Johnson, B.E. & Cushman, J.H., 2007. Influence of a large herbivore reintroduction on plant invasions and community composition in a California grassland. *Conservation Biology: the journal of the Society for Conservation Biology*, 21(2), pp.515–526. Available at: <http://dx.doi.org/10.1111/j.1523-1739.2006.00610.x>.
- Knust, B.M., Wolf, P.C. & Wells, S.J., 2011. Characterization of the risk of deer-cattle interactions in Minnesota by use of an on-farm environmental assessment tool.

- American Journal of Veterinary Research*, 72(7), pp.924–931. Available at: <http://dx.doi.org/10.2460/ajvr.72.7.924>.
- Kvilekval, K. et al., 2010. Bisque: a platform for bioimage analysis and management. *Bioinformatics*, 26(4), pp.544–552. Available at: <http://dx.doi.org/10.1093/bioinformatics/btp699>.
- Loft, E.R., Kie, J.G. & Menke, J.W., 1993. Grazing in the Sierra Nevada: Home range and space use patterns of mule deer as influenced by cattle. *California Fish and Game*, 79(4), p.145. Available at: https://digitalcommons.usu.edu/aspen_bib/2330/ [Accessed July 31, 2019].
- Magnusson, A. et al., 2016. glmmTMB: Generalized linear mixed models using template model builder. *R package version 0. 0, 2*.
- Malhi, Y. et al., 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proceedings of the National Academy of Sciences of the United States of America*, 113(4), pp.838–846. Available at: <http://dx.doi.org/10.1073/pnas.1502540113>.
- Manning, E.J. et al., 2003. Testing for Mycobacterium avium subsp. paratuberculosis infection in asymptomatic free-ranging tule elk from an infected herd. *Journal of Wildlife Diseases*, 39(2), pp.323–328. Available at: <http://dx.doi.org/10.7589/0090-3558-39.2.323>.
- Massei, G. et al., 2010. Can translocations be used to mitigate human–wildlife conflicts? *Wildlife Research*, 37(5), pp.428–439. Available at: <http://www.publish.csiro.au/wr/wr08179> [Accessed March 21, 2019].
- McCullough, D.R., Fischer, J.K. & Ballou, J.D., 1996. From bottleneck to metapopulation: recovery of the tule elk in California. *Metapopulations and Wildlife Conservation*, pp.375–403.
- Merkle, J.A. et al., 2018. Linking spring phenology with mechanistic models of host movement to predict disease transmission risk J. Rohr, ed. *The Journal of Applied Ecology*, 55(2), pp.810–819. Available at: <http://doi.wiley.com/10.1111/1365-2664.13022>.
- Morris, L.R. et al., 2016. Elk resource selection and implications for anthrax management in Montana. *The Journal of Wildlife Management*, 80(2), pp.235–244. Available at: <http://dx.doi.org/10.1002/jwmg.1016>.
- O’Brien, C.M., 2007. Analysing ecological data. *International Statistical Review = Revue Internationale de Statistique*, 75(3), pp.426–427. Available at: http://dx.doi.org/10.1111/j.1751-5823.2007.00030_17.x.
- Oehlers, S.A. et al., 2011. Sex and scale: implications for habitat selection by Alaskan moose *Alces alces gigas*. *Wildlife Biology*, 17(1), pp.67–84. Available at:

<http://www.bioone.org/doi/abs/10.2981/10-039>.

- Proffitt, K.M. et al., 2011. Elk distribution and spatial overlap with livestock during the brucellosis transmission risk period. *The Journal of Applied Ecology*, 48(2), pp.471–478. Available at: <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2664.2010.01928.x>.
- Pruvot, M. et al., 2014. Pathogens at the livestock-wildlife interface in Western Alberta: does transmission route matter? *Veterinary Research*, 45, p.18. Available at: <http://dx.doi.org/10.1186/1297-9716-45-18>.
- Pruvot, M. et al., 2014. What attracts elk onto cattle pasture? Implications for inter-species disease transmission. *Preventive Veterinary Medicine*, 117(2), pp.326–339. Available at: <http://dx.doi.org/10.1016/j.prevetmed.2014.08.010>.
- Ripple, W.J. et al., 2019. Are we eating the world's megafauna to extinction? *Conservation Letters*, p.e12627. Available at: <http://dx.doi.org/10.1111/conl.12627>.
- Russell, R.E. et al., 2015. Identifying priority chronic wasting disease surveillance areas for mule deer in Montana. *The Journal of Wildlife Management*, 79(6), pp.989–997. Available at: <https://onlinelibrary.wiley.com/doi/pdf/10.1002/jwmg.914>.
- Schipper, J. et al., 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science*, 322(5899), pp.225–230. Available at: <http://dx.doi.org/10.1126/science.1165115>.
- Seddon, P.J. et al., 2014. Reversing defaunation: Restoring species in a changing world. *Science*, 345(6195), pp.406–412. Available at: <http://dx.doi.org/10.1126/science.1251818>.
- Seddon, P.J., Armstrong, D.P. & Maloney, R.F., 2007. Developing the science of reintroduction biology. *Conservation Biology: the journal of the Society for Conservation Biology*, 21(2), pp.303–312. Available at: <http://dx.doi.org/10.1111/j.1523-1739.2006.00627.x>.
- Sikes, R.S. & Animal Care and Use Committee of the American Society of Mammalogists, 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97(3), pp.663–688. Available at: <http://dx.doi.org/10.1093/jmammal/gyw078>.
- Stevenson, K. et al., 2009. Occurrence of *Mycobacterium avium* subspecies paratuberculosis across host species and European countries with evidence for transmission between wildlife and domestic ruminants. *BMC Microbiology*, 9(1), p.212. Available at: <http://dx.doi.org/10.1186/1471-2180-9-212>.
- Stewart, K.M. et al., 2015. Sexual segregation in North American elk: the role of density dependence. *Ecology and Evolution*, 5(3), pp.709–721. Available at: <http://dx.doi.org/10.1002/ece3.1397>.

- Stewart, K.M. et al., 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *Journal of Mammalogy*, 83(1), pp.229–244. Available at: <https://academic.oup.com/jmammal/article-abstract/83/1/229/2372874> [Accessed March 26, 2019].
- Talbert, M.K. & Cade, B.S., 2013. USGS Open-file report 2005–1353: User manual for blossom statistical package for R. *U.S. Geological Survey (USGS)*. Available at: <http://pubs.usgs.gov/of/2005/1353> [Accessed June 18, 2019].
- Thomas, J.W. & Toweill, D.E., 2002. *North American elk: ecology and management*, Smithsonian Institution Press, Washington.
- Vavra, M. & Sheehy, D.P., 1996. Improving elk habitat characteristics with livestock grazing. *Rangelands*, pp.182–185. Available at: <https://www.jstor.org/stable/pdf/4001324.pdf>.
- Venables, W.N. & Ripley, B.D., 2002. *Modern applied statistics (Fourth S., editor)* New York.
- Voeten, C.C., 2019. “*buildmer*” package, Wiley Online Library. Available at: <https://cran.r-project.org/web/packages/buildmer/buildmer.pdf>.
- Wolf, C.M. et al., 1996. Avian and mammalian translocations: Update and reanalysis of 1987 Survey Data. *Conservation Biology: the journal of the Society for Conservation Biology*, 10(4), pp.1142–1154. Available at: <http://doi.wiley.com/10.1046/j.1523-1739.1996.10041142.x>.
- Zuur, A. et al., 2009. *Mixed effects models and extensions in ecology with R*, Springer Science & Business Media. Available at: <https://market.android.com/details?id=book-vQUNprFZKHsC>.