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The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology

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Abstract. Great leaps forward in scientific understanding are often spurred by innovations in technology. The explosion of miniature sensors that are driving the boom in consumer electronics, such as smart phones, gaming platforms, and wearable fitness devices, are now becoming available to ecologists for remotely monitoring the activities of wild animals. While half a century ago researchers were attaching balloons to the backs of seals to measure their movement, today ecologists have access to an arsenal of sensors that can continuously measure most aspects of an animal's state (e.g., location, behavior, caloric expenditure, interactions with other animals) and external environment (e.g., temperature, salinity, depth). This technology is advancing our ability to study animal ecology by allowing researchers to (1) answer questions about the physiology, behavior, and ecology of wild animals in situ that would have previously been limited to tests on model organisms in highly controlled settings, (2) study cryptic or wide-ranging animals that have previously evaded investigation, and (3) develop and test entirely new theories. Here we explore how ecologists are using these tools to answer new questions about the physiological performance, energetics, foraging, migration, habitat selection, and sociality of wild animals, as well as collect data on the environments in which they live.

Key words: accelerometer; animal-borne sensors; behavioral monitoring; bio-logging; biotelemetry; conservation; GPS; physiological monitoring; remotely sensed environmental conditions; tracking.

Introduction

The widespread adoption of consumer mobile electronics such as smart phones and tablets has fueled the development of a multitude of inexpensive miniature sensors such as accelerometers, magnetometers, global positioning systems (GPS), and cameras. These sensors are being packaged into lightweight, animal-borne units that can measure the physiology, behavior, demographics, community interactions, and environment of instrumented subjects in the wild. In the 1960s, biologists attached balloons (Rutz and Hays 2009) and kitchen timers (Kooyman 1965) to marine mammals to investigate basic questions about their movement and diving physiology. Today, and in the near future, electronic sensors have or will have the ability to sense and record nearly all aspects of an animal's locomotion and sensory environment. Tri-axial accelerometers can detect when a fish opens and closes its mouth (Viviant et al. 2014), how many calories a puma is burning as it stalks and attacks prey (Williams et al. 2014), and whether or not a cockroach is infected with fungus (Wilson et al. 2014). Miniature cameras can be used to determine what an animal is eating (Watanabe and Takahashi 2013) or with whom it is interacting. Tri-axial digital compasses, or magnetometers, can be used to dead-reckon exact movement paths (Mitani et al. 2010) or possibly determine the gaze direction of an animal engaged in social interactions with others. And a GPS can be used to pinpoint an animal's location on the planet to within 5-m accuracy. Nearly all biological activity involves change of one kind or another. Increasingly these changes can be sensed remotely.

This technology is revolutionizing our ability to study animal ecology by allowing researchers to (1) answer questions about the physiology, behavior, and ecology of wild animals that would have previously been limited to tests on model organisms in highly controlled settings; (2) study cryptic or wide-ranging animals that have previously evaded investigation; and (3) develop and test

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entirely new theories. Recent reviews have described the different types of sensors (Cooke et al. 2004, 2013, Rutz and Hays 2009), their history (Kooyman 2004), how the sensors are used on different taxa (Cooke et al. 2004) and in different environments (Cooke 2008), their utility in helping to solve conservation problems (Cooke 2008), and ethical considerations in their use (Cooke 2008). Here we examine how these technologies are allowing ecologists to answer new questions about the physiological performance, energetics, foraging, migration, habitat selection, and sociality of wild animals (Table 1) as well as collect data on the environments in which they live. The topic is broad: thousands of papers have been published. As such, we focus our discussion on a wide range of ecological questions that are being answered using these new technologies (e.g., Fig. 1) in particularly innovative ways.

Physiological performance

Understanding the physiological performance of wild animals faced with different environmental challenges is crucial to understanding how these species will adapt to environmental change. It can also lead to insights that inform research on human health as well as the production of new technologies. Over the last several decades, increasingly sophisticated sensor types have enabled remote monitoring of an animal's physiological state in three-dimensional space and time (Ropert-Coudert et al. 2012). These sensors have revealed novel physiological insights for difficult-to-observe species, particularly the diving patterns and capabilities of higher marine vertebrates and teleost fish (for reviews, see Arnold and Dewar 2001, Kooyman 2004, Ponganis 2007, Hart and Hyrenbach 2009, Cooke et al. 2013). Although heart rate, swim speed, and body temperature have been the most commonly studied parameters for oceanic animals (Ponganis 2007), more recently a number of additional measurements have been taken for this group as well as for freshwater (e.g., Cooke et al. 2013), terrestrial (e.g., Rutz and Hays 2009), and avian (e.g., Barron et al. 2010, White et al. 2013) taxa. Measurements as diverse as body and jaw acceleration, diving oxygen utilization, heat flux, biosonar, stomach temperature and pH, and heart rate have all been remotely recorded for many species (see Cooke et al. 2004, Ponganis 2007). These measurements provide windows into the internal states of animals, allowing researchers to collect data on an exciting new array of physiological variables such as metabolic rate, daily energy budget, cardiac and stomach function, heat flux, hunger and satiation cues, hibernation and torpor, oxygen stores, and reproductive state in free-ranging animals (Cooke et al. 2004, Costa and Sinervo 2004, Ponganis 2007).

To interpret these bio-logger-derived physiological data, a "laboratory-to-field" approach is often necessary (Fig. 2). This involves the calibration of certain types of sensors on surrogate species or captive conspecifics in a controlled environment prior to deployment in the wild. For example, Williams et al. (2014) calibrated a combined GPS–accelerometer collar on captive pumas (*Puma concolor*) moving freely in a large enclosure and at various natural speeds on a treadmill (Fig. 2a). Collar accelerometer signatures were matched to the gait-specific energetic costs of locomotion determined via open-flow respirometry during treadmill trials. Once calibrated in this manner, the collars were deployed on free-ranging pumas (Fig. 2c) to investigate the metabolic demands of various activities (Fig. 2e). Data from the collars revealed that the energetic cost of making a kill scaled linearly with prey size. Additionally, total hunting cost decreased with increasing levels of low-activity cryptic behavior, indicating a physiological basis to the evolution of ambush hunting in felids. This laboratory-to-field approach can be used in various other vertebrate species as well. For instance, S. M. Wilson et al. (2013) quantified the relationship between acoustic accelerometers and the oxygen consumption of sockeye salmon swimming under various conditions in swim tunnels. They then deployed these tags on wild sockeye salmon to measure their cost of transport and average swim speeds. This technique can now be used to measure the energetic cost of salmon migration from open ocean to spawning grounds.

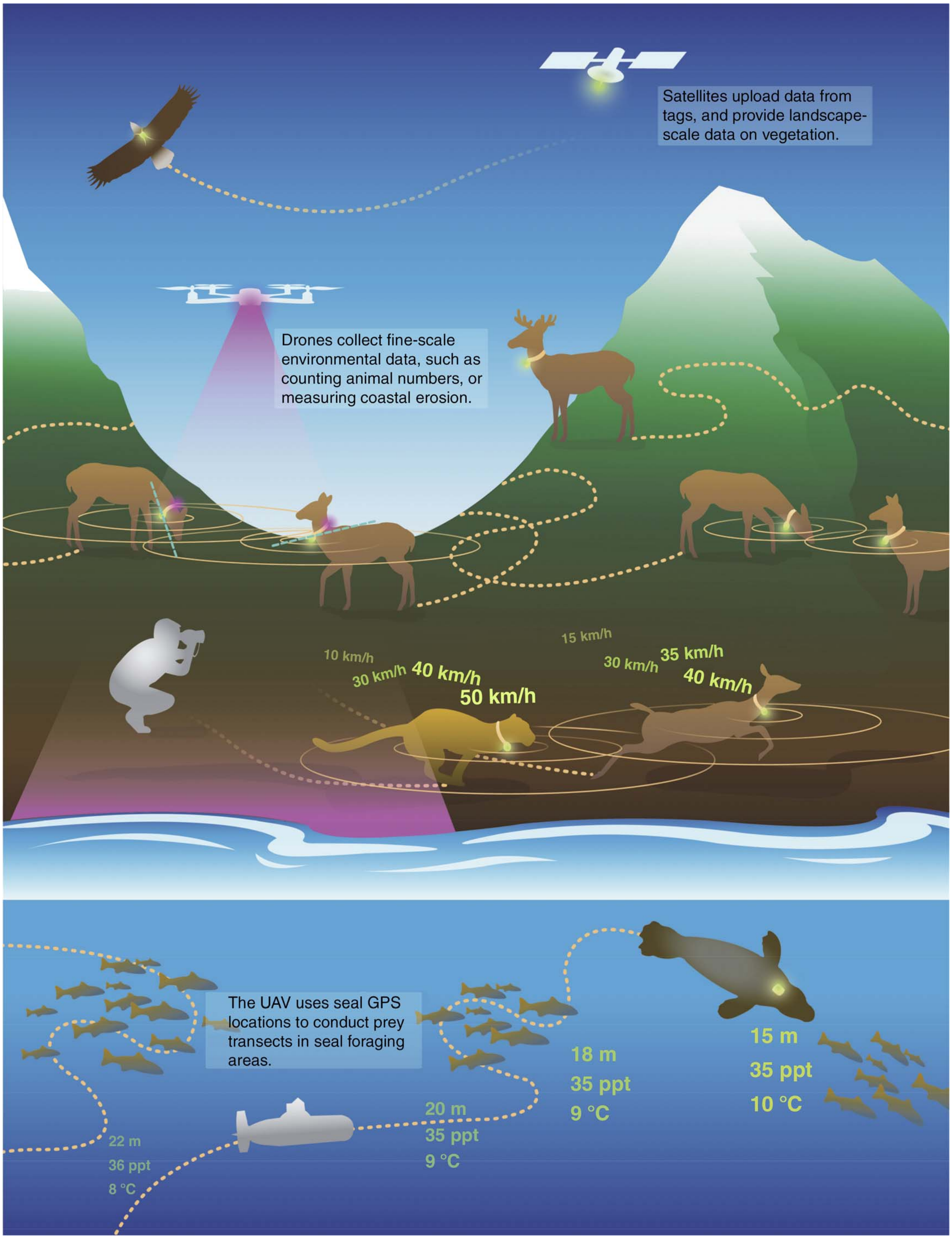
Our ability to measure energy expenditure on a fine spatial and temporal scale has led to increasing interest in how variation in the cost of transport is driven by factors such as vegetation, wind speed, current, incline, snow depth, and various anthropogenic factors. This environmentally driven variation in transport cost is referred to as the "energy landscape" (Shepard et al. 2013), and is dynamic over space and time, lasting from seconds (e.g., an animal responding to a vehicle driving past) to months (e.g., changes in vegetation density with season) to millennia (e.g., the formation of mountains). Because maintaining energetic balance is critical to survival, knowledge of an animal's energetic landscape can elucidate the factors and/or locations in an animal's home range or a species' geographic range that promote or disrupt energetic balance, with important implications for conservation. Mosser et al. (2014), for instance, measured the energetic landscape of woodland caribou by first calibrating the energetic values of different behaviors using a combined accelerometer–GPS collar on captive caribou and then deploying the collars on free-ranging caribou in northern Canada. The study revealed how many calories caribou must expend when moving various distances through differing vegetation densities, snow depths, and temperatures. Woodland caribou have been declining precipitously, and inferences from this study can help to disentangle the mechanistic underpinnings of this decline and inform management and conservation strategies.

Although transport costs drain energy from an animal's metabolic budget, the ability to hunt successfully is critical to replenishing these energy stores. Yet

TABLE 1. A sample of ecological topics and questions currently being addressed by the use of animal-borne sensors.

Topic and question	Animal-borne sensors; paired data sources
Migration	
How plastic are migratory routes and departure dates?	light-level geolocators attached to songbirds (Stanely et al. 2012)
Do migrants jump or surf phenological waves of primary production?	GPS collars on red deer; MODIS satellite-derived phenological data (Bischof et al. 2012)
Is migration an adaptive response to food limitation or predator avoidance?	GPS/VHF collars on migratory and nonmigratory moose populations; measures of nutrition status (mass) and predation risk (White et al. 2014)
Foraging behavior	
How do birds utilize non-food energy sources such as thermals to maximize total energy intake?	GPS, accelerometer, magnetometer, and barometric pressure tag on Andean Condors; use of thermals distinguished by circular vs. straight-line flight (Shepard et al. 2011)
How does kleptoparasitism influence predator energy budgets?	GPS collars on cheetahs; cheetahs followed daily to document kills and scavenging; daily estimate of energy expenditure from doubly labeled water derived from feces (Scantlebury et al. 2014)
Do diving animals forage according to the marginal value theorem?	GPS, two accelerometers (one each on head and back), depth, temperature, and video logger attached to Adélie Penguins; relative motion of two accelerometers used to detect prey capture; video detects prey abundance in patch (Watanabe et al. 2014)
Physiological performance	
How is the energetic cost of movement impacted by different factors in the environment?	GPS, accelerometer collars on caribou; satellite-derived NDVI data as index of forage availability; weather data; paired captive study to calibrate energetic costs of different behaviors (Mosser et al. 2014)
Is ambush predation an adaptation to conserve energy during hunting?	GPS, accelerometer collars on pumas; field-verified kill sites; paired treadmill study to calibrate energetics (Williams et al. 2014)
What strategies do cursorial predators use in the pursuit and capture of prey?	GPS, accelerometer collars on cheetahs; visual observations of chase sequences (A. M. Wilson et al. 2013)
How do endotherms maintain homeostasis in cold environments?	ARGOS satellite tag, time–depth recorder and internal and external temperature loggers on leatherback sea turtles (Casey et al. 2014)
How long can birds remain in flight?	light-level geolocators, accelerometer attached to alpine swifts (Liechti et al. 2013)
Habitat selection	
Is habitat selection a function of resource quality or predation at both small and large spatial scales?	GPS collars on elk; satellite-derived estimates of forage quality and quantity; GPS collars on wolves to measure predation risk (Hebblewhite et al. 2009, Hebblewhite and Merril 2007)
How does anthropogenic disturbance influence habitat selection?	GPS collars on pumas; digitized map of housing locations; field-verified kills, nursery and communication sites (Wilmers et al. 2013)
How dynamic is habitat selection from season to season?	GPS, time–depth recorder and temperature logger on loggerhead sea turtles (Shofield et al. 2009)
Social interaction	
How do contact rates among individuals vary as a function of population density?	proximity collars on elk; count estimates of population density (Cross et al. 2013)
What are the fission–fusion dynamics of social species?	proximity collars on raccoons (Prange et al. 2011)
How do social organization and cooperation stabilize each other in multilevel societies?	GPS collars on Guinea baboons; paired behavioral observations; microsatellite data to determine relatedness (Patzelt et al. 2014)

relatively little is known about the physiological performance of hunting in animals, particularly terrestrial mammals. For instance, cheetahs (*Acinonyx jubatus*) are well known as the fastest land hunter, yet until just recently, quantitative measures of cheetah running mechanics were only made on captive animals chasing a lure, and measures of wild animal speed were only possible through direct observation or with video during daylight hours in open grassland. But how do cheetahs perform in other habitat types? How long do their hunts take? And how do chase speed, turning angles, and other kinematic factors affect hunt success? To answer these questions, A. M. Wilson et al. (2013) deployed combined GPS, accelerometer, and gyroscope collars on wild cheetahs in Botswana, sampling data at up to 300 times a second. This allowed them to measure the velocity, forward and lateral acceleration, and exact travel path of 897 runs of five cheetahs over 17 months. Cheetahs achieved a maximum speed of 25.9 m/s (58 mph), but the mean top speed of 14.9 m/s was usually only sustained for 1–2 s per chase. Maximum speed, the number of turns, or the distance traveled did not influence whether a chase was successful or not, but successful chases were characterized by a rapid deceleration at the end of the chase. Cheetahs were partial to open grassland (48% of kills), but also chased prey through dense vegetation



Satellites upload data from tags, and provide landscape-scale data on vegetation.

Drones collect fine-scale environmental data, such as counting animal numbers, or measuring coastal erosion.

The UAV uses seal GPS locations to conduct prey transects in seal foraging areas.

FIG. 1. A sample of animal-borne sensors and paired environmental data sources for answering ecological questions. From top to bottom: a Bald Eagle is equipped with a GPS–accelerometer–magnetometer backpack. From the GPS and magnetometer, we can dead-reckon its path (dotted yellow line) through space. The yellow light indicates that data are relayed from the tag to the satellite. The accelerometer measures wing beat frequency, which can be used to detect changes in body mass gain from foraging. Satellites can also measure landscape-scale (250-m, 8-day resolution) data on vegetation changes (e.g., MODIS) as well as 1-m scale multispectral imagery on individual plants (e.g., Quickbird). Deer collars can communicate their location to the drone (indicated by purple light), which can sample nearby animal numbers, or measure fine-scale environmental data such as coastal erosion. Deer collars are also equipped with tilt sensors (dashed cyan line) and sound recorders, which measure whether the deer is vigilant or eating, respectively. Additionally, the collars are equipped with proximity sensors (represented by concentric circles), which detect when another animal comes within a threshold distance. The ever-important field ecologist orchestrates data collection and collects

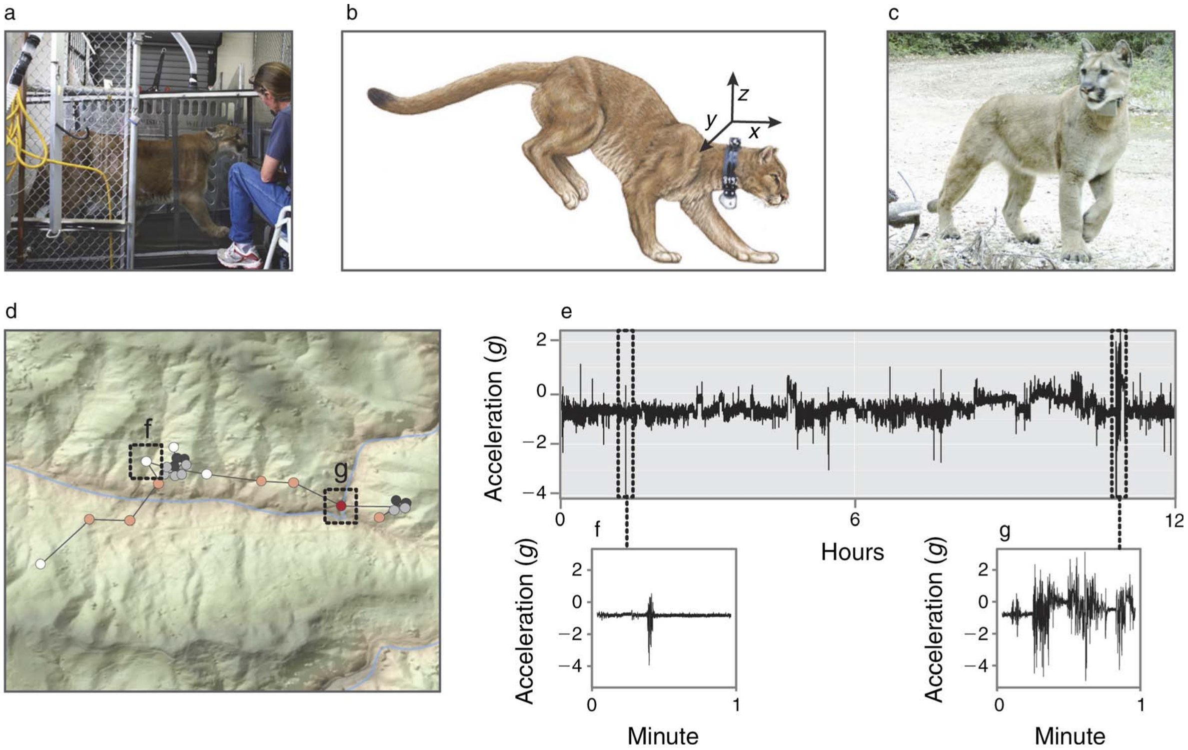


FIG. 2. The "laboratory-to-field" approach used to calibrate a GPS–accelerometer collar to measure the energy expenditure of pumas. (a) The activity-specific metabolic rate of captive pumas is determined by oxygen consumption while moving at a range of speeds on a motorized treadmill. (b) Schematic showing GPS–accelerometer collar axis orientation on an active puma (*x*, surge; *y*, sway; *z*, heave). (c) The collar is then placed on a free-ranging puma in Santa Cruz Mountains, California, USA. (d) The GPS track of the wild puma shows typical movement across landscape. GPS locations are symbolized as a range of low (black) to high (red) activity as determined by an integrated accelerometer with representative low (f) and high (g) activity positions highlighted in square regions. Acceleration (in gravity, *g*) was sampled at 64 Hz and GPS location every 15 minutes. (e) Surge-axis acceleration waveform of the track displayed in panel (d) with a 1-minute sample of acceleration traces for low (f) and high (g) activity displayed below. Behaviors and daily energy expenditure associated with movement can be readily derived from such GPS–accelerometer integration.

(24% of kills). Vegetation cover, however, did not significantly influence kill success. Such detailed performance data on hunting predators will inform numerous questions about the coevolution of predator and prey, as well as the impacts of predators on prey populations. In addition, information on hunting performance in different habitats could be incorporated into habitat selection models, which we will describe, that help managers to prioritize areas critical to conservation.

Maintaining homeostasis is also a prerequisite for animals to survive in their current geographic range or to expand into new ones. Unfortunately, even basic knowledge of how wide-ranging endotherms are able to accomplish this internal equilibrium, particularly in very hot or cold environments, is often lacking. In a novel application of animal-borne sensors, Casey et al. (2014) deployed stomach temperature pills and external platform transmitter terminals (PTT) that combine an ARGOS satellite tag, a time–depth recorder, and an external temperature logger on leatherback sea turtles (*Dermochelys coriacea*). The stomach temperature pills communicated internal temperature data to the PTT, which then transmitted internal and external temperature, location, and time–depth information to the researcher via ARGOS satellite. Using this approach, Casey et al. (2014) were able to document how turtles maintain core body temperatures in high-latitude cold waters of the North Atlantic. They found that leatherbacks are able to maintain body temperatures by increasing their metabolism threefold and by behavioral adjustments of dive depths, whereby they spend more time in relatively warm surface waters. This combination of behavioral and metabolic adjustments is probably

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novel data sets that cannot yet be sensed remotely. The speed, forces, energetics, and success rates of puma attempts to kill deer are recorded on a combined GPS–accelerometer collar. In the ocean, a seal records water depth (m), salinity (parts per thousand, PPT), and temperature (°C). A video camera and accelerometer on its back record its feeding patterns on fish. An underwater autonomous vehicle (UAV) follows the track of the seal and conducts prey transects at seal foraging locations.

why leatherbacks are able to forage over a large range of water temperatures.

These new tools and methods are also allowing scientists to better understand the physiological limits of animals. For instance, researchers have long thought that Alpine Swifts (*Tachymarptis melba*) stay aloft for substantial periods of time while wintering in sub-Saharan Africa, yet only anecdotal evidence was available to support this claim. To formally test this idea, Liechti et al. (2013) outfitted six Alpine Swifts with accelerometers designed to indicate when a bird is prone vs. upright by measuring the orientation of the bird's dorsoventral axis relative to the gravitational vector to six Alpine Swifts. Swifts are prone when flying, and upright when perched, so these loggers can yield a precise measurement of whether or not the bird is flying. The authors found that Alpine Swifts do indeed stay aloft for extended periods of time: over six months. Such a surprising result would have remained unattainable without modern, lightweight bio-logging technologies.

Foraging behavior

Identifying the costs and gains of foraging is crucial to understanding how animals optimize net energy intake so as to maximize fitness (Stephens and Krebs 1986). However, until recently, detailed studies on foraging ecology have only been possible through direct observation. Animal-borne sensors now allow ecologists to measure many variables that were once either impossible to measure or required direct observation. For instance, vigilance rates in ungulates can now be measured using tilt sensors (an accelerometer that measures the orientation of the animals head with respect to gravity), and audio recording devices that can measure when ungulates are chewing or when they are silent to better hear approaching predators (Lynch et al. 2014). Animal-borne sensors can also measure foraging success. For instance, accelerometers placed on the jaws of marine animals can detect when they open and close their mouths to capture prey (Viviant et al. 2014) and on-board video can validate prey capture events (Watanabe and Takahashi 2013). Accelerometers attached to birds can detect wing beat frequency and how it changes with body mass within an individual (Sato et al. 2008); birds beat their wings more quickly as they get heavier after foraging.

The advent of integrated GPS and accelerometer tags also provides a tool to measure energy expenditure at discrete locations throughout an animal's range. This can be further refined by pairing of magnetometers with data on geographic position to reconstruct the precise animal movement paths using an approach referred to as dead reckoning (Wilson et al. 2007), allowing for energy expenditure measurements along the entire path an animal takes. These new devices have given us greater abilities to remotely measure foraging gains as well. Clusters of GPS locations can reveal the kill sites of large terrestrial predators (e.g., Knopff et al. 2009), miniature video loggers can identify prey capture, and accelerometers can be used to identify prey capture in a host of species ranging from fish (Viviant et al. 2014) to penguins (Watanabe et al. 2014) to pumas (Wang et al. 2015).

For all the high-resolution data on animal foraging that we can now collect with bio-loggers, we often lack complementary data of similar resolution on explanatory variables such as prey availability. Remote sensing data on vegetation structure, quality, and biomass can provide a solution for understanding the availability of resources to terrestrial herbivores. For instance, the MODIS satellite provides 250-m resolution data every eight days, allowing for inferences about the effects of vegetation phenology on animals (Bischof et al. 2012), while 1-m resolution LiDAR imagery obtained from planes can characterize fine-scale vegetation structure such as canopy cover or understory biomass (Lone et al. 2014). Pairing autonomous underwater vehicles (AUVs) or unmanned aerial vehicles (UAVs, or drones) with GPS tags is a promising emerging tool for measuring the prey available to both aquatic and terrestrial predators. For instance, Oliver et al. (2012) paired satellite tags on Adélie Penguins (*Pygoscelis adeliae*) with a propeller-driven AUV that used the movement tracks of penguins to sample penguin foraging areas. For terrestrial species that live under canopy, trail cameras placed randomly or on a grid can increasingly sample prey availability as well. New statistical techniques have recently been developed to estimate the density of unmarked animal species captured in photos (Chandler and Royle 2013).

Animal-borne sensing approaches are allowing ecologists to test new questions about foraging behavior. For instance, do birds utilize non-food energy sources such as thermals to maximize total energy intake? Do diving animals forage according to the marginal value theorem? How does kleptoparasitism impact predator foraging efficiency? Using combined barometric pressure (estimates altitude), magnetometer, accelerometer, and GPS tags, Shepard et al. (2011) were able to reconstruct the three-dimensional flight paths of Andean Condors (*Vultur gryphus*) and discovered that their use of thermals was then distinguished by circular vs. straight-line flight. Shepard et al. (2011) found that condor use of thermals was consistent with a strategy to maximize the rate of potential energy gain, but was balanced by a need to depart thermals to acquire food. Although this study illustrates the utility of animal-borne sensors in measuring the energetic costs and gains of animals in flight, a weakness of the study was that it did not measure energy gains from food intake.

Watanabe and Takahashi (2013) solved the problem of remotely sensing food intake by attaching accelerometers capable of continuous sampling for 50 hours to the head and back of Adélie Penguins. These were paired with a video camera capable of sampling for 80 minutes. Video data revealed that penguins move their heads rapidly to catch krill, and that this behavior can be detected by the magnitude of head acceleration relative to body acceleration. Watanabe et al. (2014) then used this dual accelerometer method to test optimal foraging theory with Adélie Penguins. Krill capture rate was found to decrease over time during each dive, but patch quality had opposite effects on dive duration, depending on whether food was distributed in a few large patches or several small ones, as predicted by the marginal value theorem. The benefits of the penguin-borne sensors were twofold: Watanabe et al. (2014) were able to test optimal foraging theory, a feat that would not have been possible previously, as well as to elucidate the multiple scales (within a patch vs. among patches) at which penguins make foraging decisions.

Optimal foraging strategies can be determined by feedbacks between the hunting behavior of predators and the behavior of competitors and scavengers. In this regard, the impacts of large predators on scavengers has received recent attention (e.g., Wilmers et al. 2003), although little work has focused on the impacts of scavengers on the foraging ecology and energy demands of the predators being kleptoparasitized. This concept is nicely illustrated with cheetahs, as they are highly threatened and thought to be negatively impacted by lions and hyenas scavenging their kills. Scantlebury et al. (2014) used GPS collars to locate cheetahs each day in order to visually observe them hunting, feeding, and being kleptoparasitized. They also collected feces and used double-labeled water techniques to measure their daily energetic expenditure. They found that average theft levels of 25% caused cheetahs to hunt 1.1 more hours per day, which increased their daily energetic expenditure by 12%. The authors did not use sensors to estimate energetics (although this is now possible, as described previously), but the study illustrates how animal-borne sensors can be used in a supporting role (e.g., to locate the animals in order to collect samples).

Migration

Migration allows species to follow food resources and escape predation, thus ensuring survival and/or boosting reproductive output (Chapman et al. 2014). The advent of lightweight animal-borne geolocators has been instrumental in identifying the migratory routes and mechanics of many populations of various species (Hedenstrom et al. 2011, Hedenstrom and Lindstrom 2014). Geolocator-derived data have provided critical information to conservation planners aiming to insure spatial connectivity between seasonal ranges. But geolocators are also helping ecologists to answer crucial questions about the biology of migration itself. For instance, how plastic are the migratory routes and departure dates of various species? As climate change shifts both the locations of winter and summer habitat patches, and accelerates the phenology of the underlying food resources, this question becomes increasingly important. We may also ask, do migrants jump or surf phenological waves of primary production? Many systems, such as those with migratory ungulates, are characterized by green waves of primary production as young nutritious forage moves up in elevation or across the landscape in response to receding snows or stochastic rainfall events. Understanding whether species jump or surf these waves will help to predict how species are likely to respond to climate change, which is predicted to reduce the duration and spatial variability of these waves of primary production (Wilmers et al. 2013*a*). Even more fundamentally, it is not well understood why many species migrate at all. Is it a response to food limitation, a way to avoid predation, or some combination of both? Bio-logger data can help to resolve such fundamental ecological questions.

In order to investigate the phenotypic plasticity of migration behavior, Stanley et al. (2012) attached light-level geolocators to a migratory songbird, the Wood Thrush (*Hylocichla mustelina*) and recorded repeated migrations from multiple individuals. The geolocators measure the intensity of blue light, which indicates when it is day and night. Day length and the timing of sunrise yield a coarse approximation of latitude and longitude, respectively. The authors discovered that although the migratory route of individual birds might vary from year to year, their spring departure dates did not. This low plasticity in the timing of spring migration might limit an individual's ability to adjust migration schedules to global warming.

Ecologists have hypothesized that ungulates migrate along a phenological gradient of plant productivity in order maximize energy intake (Forage Maturation Hypothesis; Fryxell et al. 1988, Hebblewhite et al. 2008). To formally test this idea and understand whether migrants jump or surf this gradient, Bischof et al. (2012) placed GPS collars on 167 migratory and 78 resident red deer in Norway and examined their movement in relationship to plant phenological change, measured as the change in weekly NDVI data from MODIS satellite imagery. NDVI values change most rapidly when vegetation is growing quickly and is most nutritious to ungulates (Hebblewhite et al. 2008). The authors discovered that migrants, by following the green wave, had better access to high-quality forage than residents, but that migrants jumped ahead of the green wave, rather than surfing it, thus reducing their maximum potential energy gain. Why they do this, however, is still unclear. Perhaps it is to escape predation or because of constraints such as the need to give birth to calves shortly after arriving on the summer range.

To formally test whether ungulates migrate to escape predation or to gain better access to food, White et al. (2014) placed GPS and VHF collars on 67 moose, roughly half of which were migratory and the other half were nonmigratory. They also measured the accumulation of body fat as an indicator of food access and calf survival as an indicator of predation risk. The authors concluded that predation was the primary driver of migration in this population, because body fat measures did not differ between migratory and nonmigratory individuals, but that calf survival was much lower in nonmigratory animals. These studies have begun to elucidate environmental drivers of migration timing and paths, and will undoubtedly allow for more effective management of migrating species in a changing climate.

Habitat selection

Understanding species preference of one type of habitat over another (habitat selection) is critical to understanding the distribution and abundance of organisms. The advent of GPS collars in the 1990s spurred a large increase in studies on habitat selection. GPS collars are capable of collecting copious spatial location data and thus reflect parts of the landscape that are "used" by animals. These areas can then be compared to randomly generated points that reflect the habitat "available" to animals using resource selection functions (RSFs; Manly et al. 2002). RSFs generate relative probabilities of use indicating which habitats animals prefer, and have been crucial to wildlife managers and conservation practitioners in identifying priority habitats for conservation. Ecologists are often concerned, not only in understanding which habitats species prefer, but also why they prefer those habitats. Once again, this is crucial to understanding how species will adapt to a changing environment. For instance, are individuals selecting a particular habitat type because resources are more abundant there or because there is a lower risk of predation? Does selection vary depending on whether a species is mating, feeding, or engaging in some other behavior? And is selection dynamic and therefore dependent on daily or seasonal changes in environmental conditions such as temperature?

In order to understand the determinants of habitat selection, detailed knowledge of the possible predictor variables influencing animal space use must be measured. Hebblewhite's (2006) study accomplished this by simultaneously collaring wolves with GPS tags and measuring forage availability with MODIS satellite imagery in order to understand the primary determinants of GPS-collared elks' habitat use (i.e., predation risk vs. forage reward). Although forage and predation risk were both important in determining habitat selection, resident elk were found to make fine-scale adjustments in space use that substantially reduced their risk of predation. Similarly, in order to understand how puma behaviors varied in relation to human activity, Wilmers et al. (2013*b*) characterized behavior-specific puma habitat selection with respect to covariates associated with human impact. Specifically, they used GPS collars on pumas to identify kill sites, nursery sites, movement areas, and communication sites (male pumas create "community scrapes" to which they return to every 1–4 weeks to urinate). Each one of these behaviors was measured using a combination of GPS data and field reconnaissance. Each of these spatially referenced behaviors was then predicted using RSF models with various human impact indices (e.g., housing density, road network density) and vegetation cover as covariates. The analysis revealed that pumas are fairly tolerant of people when they are engaged in survival-based behaviors (e.g., feeding and moving), but that they need a wide berth from human development when they are engaged in reproductive behaviors (e.g., communicating and raising small cubs).

Recent research on habitat selection has also begun to make use of coupled tracking sensors whereby the potential environmental drivers of habitat selection (e.g., temperature) can be measured concurrent with GPS locations. For example, Schofield et al. (2009) equipped adult loggerhead turtles (*Caretta caretta*) with GPS and time–temperature–depth recorders to show that individuals actively reposition themselves to take advantage of thermal hotspots at the beginning of the breeding season, but as the sea warms in the summer, temperature selection is no longer evident. Fine-scale selection of warm waters early in the season presumably speeds up egg maturation rates before oviposition, thereby maximizing the number of clutches that can be laid and incubated during the optimal sand conditions of summer.

The ability to derive spatially explicit measures of energetics and behavior directly from animal-borne sensors (as described previously for pumas and cheetahs) will allow ecologists to make even more precise inferences regarding habitat preference and its drivers. Additionally, "smart" collars that use one source of sensor data to inform the collection of other kinds of sensor data can increase sampling resolution to an even finer scale. For instance, collars increase their sampling rate when an animal enters a "GPS fence," a predefined polygon defined by a set of latitude and longitude coordinates. In addition, the sampling of the collar can be can be altered by inputs from the accelerometer (e.g., increase sampling when the animal is moving) (Brown et al. 2012). These data can then be used to identify fine-scaled habitat selection, such as where animals use corridors or cross roads (e.g., LaPoint et al. 2013).

Social interaction

The ability to measure and understand interactions among individuals within a species is critical to understanding the evolutionary basis of social behavior as well as the ecological outcomes of intermingling such as disease transmission. Interactions among individuals can now be remotely sensed through the use of proximity loggers, which use ultra-high-frequency (UHF) transmitters and receivers to record when specific individuals fall within a threshold distance (Prange et al. 2006). GPS collars and tags also can be used to measure social interactions. However, because GPS units have conventionally been configured to download ephemeris data (a time-consuming and power-draining activity that provides location information of each satellite from which the precise location of the animal is derived),

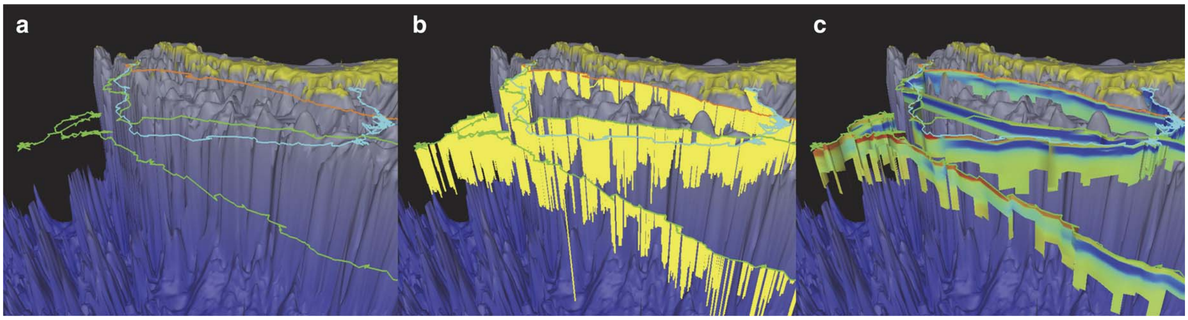

FIG. 3. Tracks of elephant seals in the Western Antarctic Peninsula help to inform the temperature and salinity profile of the southern ocean. Panels show (a) just the surface of the GPS track, (b) the surface track along with diving behavior, and (c) the temperature and salinity profile. The figure is reproduced, with copyright permission, from Costa et al. (2010: Fig. 1).

sampling intervals are usually too large (e.g., 15 minutes to 4 hours between locations) to capture the full suite of social interactions. Low-power GPS units that bypass the ephemeris and post-process the data on computers once they have been retrieved from the collar or tag (e.g., fastloc) are becoming increasingly available, allowing for sampling GPS locations every 1 second for a year or more under typical collar configurations.

Proximity loggers and GPS tags allow ecologists to better understand the underlying social ecology of various species. For instance, Prange et al. (2011) demonstrated that raccoons (*Procyon lotor*) fitted with proximity loggers exhibited considerably greater sociality than commonly recognized. Their social interactions were characterized by high fission–fusion dynamics with many short-term interactions and few long-term associations. In another study, Patzelt et al. (2014) used GPS collars with paired observations and genetic data to show that Guinea baboons live in multilevel social societies, not dissimilar from humans, in which unrelated males and their associated females team up with each other to form “gangs” that associate with each other cooperatively and share the same home range. Because this species was discovered to have a more hierarchical social system than other baboon species, the study suggests that the evolution of multi-tiered societies is not just a function of ecological processes such as resource distribution and predation risk, but also of stochastic changes in allele frequencies (so-called “gene surfing”) that occur during species range expansions.

Contact patterns among individuals in a population are also critical to understanding disease spread, and highly social individuals (so-called super spreaders) can be responsible for a very high proportion of the contacts that lead to disease spread (Lloyd-Smith et al. 2005). Outside of humans, however, little is known regarding the primary factors driving contact rates. Are contact rates driven by population density, social hierarchy, or environmental factors? To test this question, Cross et al. (2013) placed proximity loggers on 149 adult female elk (*Cervus canadensis*) across five different sites over three years in western Wyoming. At some of the locations, elk were fed supplemental food during the winter. Group sizes of the elk were also monitored visually throughout the study period. Cross et al. (2013) found that per capita contact rates increased with population density, but that identifying highly social individuals was less important than identifying environmental drivers (supplemental feeding in this case) in determining the rate of contact among individuals. They hypothesized that this might be a general pattern among social ungulates, but was unlikely to hold for species with multilevel societies such as elephants (Wittemyer et al. 2005) or primates.

CANARY IN THE COALMINE: USING WILD ANIMALS TO REMOTELY SENSE ENVIRONMENTAL CONDITIONS

The development and use of bio-logging devices for monitoring environmental and other external parameters is a relatively recent and novel extension of animal-borne sensors that is increasingly contributing to our understanding of a variety of environmental phenomena. In addition to sampling animal-specific data, animals themselves are used as sampling platforms, collecting data on a number of environmental measurements as they move throughout their home range. The utilization of animals as sampling platforms for external variables is widespread in marine ecology, where the vastness of the ocean environment in three dimensions can make data collection difficult. Utilizing these devices is particularly common in the polar oceans, where logistical difficulties can make access using research vessels impractical, and cloud cover or sea ice can interfere with the remote sensing capabilities of satellites (Costa et al. 2012).

Marine species have perhaps most frequently been used to measure ocean temperatures and salinity (Fig. 3). Data from conductivity–temperature–depth (CTD) recorders deployed on Antarctic fur seals (*Arctocephalus gazella*) have allowed researchers to investigate ocean-layer density structures and mixed-layer depths in the Southern Ocean (Hooker and Boyd 2003), and temperature profile data from the west Antarctic Peninsula have been collected from crabeater (*Lobodon carcinophagus*) and leopard (*Hydrurga leptonyx*) seals. These data, when compared to profiles obtained from ship-based measurements, had a broader spatiotemporal resolution than was possible using other sampling methods and were used to explore physical properties of the upper water column (Costa et al. 2008). Temperature data collected by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea had higher temporal and spatial resolution than ship-derived measurements. Researchers have suggested that integrating ship- and seal-derived data sets of environmental measurements could provide ocean temperature maps with a high degree of both scope and resolution (Nordstrom et al. 2013), which could aid in fine-scale descriptions of oceanographic processes.

Temperature data collected by time–temperature–depth recorders attached to King Penguins (*Aptenodytes patagonicus*) have provided highly detailed information on circulation patterns of waters in upper layers of the Southern Ocean, promoting better understanding of surface circulation of the Southern Ocean's Polar Front (Charrassin et al. 2002, 2004). Leatherback turtles in the Atlantic Ocean have helped to monitor ocean temperatures over long time series across a range of depths (McMahon et al. 2005), and white whales (*Delphinapterus leucas*) in the North Atlantic carrying CTD loggers have provided water temperature measurements of Arctic regions, permitting the study of oceanographic structure of Arctic fjords (Lydersen et al. 2002). Animal-borne sampling platforms were particularly useful in the latter study, during which whales collected measurements in areas with up to 90% ice cover, areas inaccessible by conventional (ship-based) means.

In fact, many marine predators capable of carrying environmental sensors routinely visit areas beyond the reach of research vessels. In ice zones near Antarctica in the Southern Ocean, instrumented seals have increased the number of hydrographic profiles in sea-ice zones 30-fold, filling in gaps in information for areas that cannot be reached by ships. Data from animal-borne sensors have generated estimates of sea-ice formation and pack ice expansion (Charrassin et al. 2008), in addition to measuring water mass changes and ocean structure (Sokolov et al. 2006, Charrassin et al. 2008). Sensors deployed during seal foraging bouts measure not only temperature profiles, but also diving depths. Southern elephant seals (*Mirounga leonina*) in this region regularly reach depths of more than 1000 m, and dive depth data from these mammals have improved maps of bathymetry of the Antarctic continental shelf. These data have identified significant troughs in otherwise poorly sampled regions, and this information has enhanced models of ocean circulation (Padman et al. 2010).

Recently, animal sampling platforms in marine environments have been extended to collect data on light penetration and fluorescence, which can be used to estimate chlorophyll concentration profiles. The distribution of chlorophyll throughout the water column is an indicator of spatiotemporal variability of primary productivity (Behrenfeld and Falkowski 1997), and is thus one of the most important biological parameters of the ocean. Notably, light attenuation profiles from light and depth sensors deployed on Pacific bluefin tuna (*Thunns orientalis*) in the eastern Pacific Ocean have been used to derive chlorophyll estimates comparable with records from the World Ocean Database (Teo et al. 2009). Bowhead whales (*Balaena mysticetus*) equipped with fluorometers in Greenland have also collected data characterizing chlorophyll concentrations in the water column. Chlorophyll measurements were obtained to depths below 200 m in an area for which primary production cannot be monitored with other methods due to icepack (Laidre et al. 2010), contributing significantly to understanding of primary productivity in this region.

Although more extensive methods to measure environmental variables exist, there is no question that animal-borne sensors have provided information critical to our understanding of natural and physical processes. There are now more than 1.4 million temperature and salinity profiles in the World Ocean Database from animal-borne sampling platforms, and approximately 70% of all oceanographic profiles south of 60° S have been provided by animals. Marine animals in Arctic waters are beginning to have a similar impact on oceanographic data in the North (Fedak 2013).

Although animal-borne environmental sensors are continually being used in new and exciting ways, further development of the field is needed to take full advantage of the technique. In particular, this technology has not been used extensively in terrestrial environments, despite promise for aiding data collection in these systems. Many of the challenges associated with observing terrestrial environments are analogous to those experienced in marine environments, and terrestrial ecologists stand to benefit from utilizing animals as sampling platforms in areas that are logistically difficult to access or study using conventional observation techniques. Wide-ranging species such as terrestrial predators, migratory ungulates, and migratory birds could provide a range of useful environmental data in the form of air quality measurements, temperature readings, species interactions, and estimates of resource abundance and distribution, among others. Imagine albatross sampling air quality across the Pacific, wolverines providing estimates of snowpack, wind speeds, and temperatures in remote mountain passes, or arboreal species in tropical forests sampling high-canopy microclimates. Greater exchange of expertise and collaboration between marine and terrestrial scientists could aid in development of these types of projects, potentially leading to advancements for both systems.

Concluding Thoughts

The use of animal-borne sensors has increased dramatically since the 1960s, allowing scientists to collect copious data on many aspects of wild animals' internal and external states. While the collection of such rich data quantifying how animals respond to the environment (i.e., the *y*'s, or dependent variables) can be viewed as an accomplishment in and of itself, answering the most interesting ecological questions will nearly always require fine-scale data on the ecological drivers (i.e., the *x*'s, or independent variables) of the behavioral and physiological measures that are being collected. The sampling of such predictor variables has generally lagged behind the collection of the response variables, but this is changing rapidly. As we have discussed, animals themselves can collect important environmental data (e.g., temperature or salinity) at an appropriately fine scale. Drones and UAVs can now be programed to locate instrumented animals via GPS and sample their surroundings (e.g., counting animal group sizes). LiDAR imagery obtained from planes can yield 1-m spatial resolution on canopy structure and understory biomass. Satellites such as MODIS can provide 8-day estimates of landscape-level changes in the environment such as vegetation phenology, and 1-m resolution multispectral data from Quickbird satellites can characterize vegetation composition. Camera arrays and/or traps can be set up in grids to provide estimates of biodiversity or animal abundance. And finally, there is still no substitution for good old-fashioned field data collected by humans.

To effectively carry out such research projects often necessitates an interdisciplinary team (e.g., animal physiologists, field ecologists, ecological modelers, engineers, and/or computer scientists). Such teams will likely carry out the best research in the years ahead. Ecologists often lament that increased use of technology is removing ecologists from the field and so causing a general decline in natural history skills. Our experience, however, has been the opposite. The more multidimensional and fine-scaled animal sensors become, the more time and effort is required by biologists in the field to collect the environmental covariates that are used to predict sensor output. Finally, better technology generally means more species and more individuals being captured and outfitted with animal-borne sensors. From the perspective of populations and species, this is no doubt a good thing; more knowledge about their critical needs will enable better conservation. From the perspective of those individuals wearing the tags or collars, the outcome is likely to be mixed. Collars can keep individual animals out of harm's way (e.g., by allowing wildlife managers to intervene if an animal wanders into an area where they are likely to get killed or find trouble), but inappropriate tags could do more harm than good (e.g., by disrupting behavior, etc.). As such, it is essential that ethical standards which seek to minimize the impact of animal-borne sensors to individuals continue to evolve in pace with technological development. Any time an animal is handled, researchers should think critically about whether the data are worth potentially jeopardizing that individual, and make sure they are taking all precautions to minimize risk. If the same data can be collected through noninvasive means, that is always preferable. When that is not possible, we have developed an amazing arsenal of tools that open avenues for ecological research and conservation that have never existed before.

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