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Biotelemetry: a mechanistic approach to ecology

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Remote measurement of the physiology, behaviour and energetic status of free-living animals is made possible by a variety of techniques that we refer to collectively as 'biotelemetry'. This set of tools ranges from transmitters that send their signals to receivers up to a few kilometers away to those that send data to orbiting satellites and, more frequently, to devices that log data. They enable researchers to document, for long uninterrupted periods, how undisturbed organisms interact with each other and their environment in real time. In spite of advances enabling the monitoring of many physiological and behavioural variables across a range of taxa of various sizes, these devices have yet to be embraced widely by the ecological community. Our review suggests that this technology has immense potential for research in basic and applied animal ecology. Efforts to incorporate biotelemetry into broader ecological research programs should yield novel information that has been challenging to collect historically from free-ranging animals in their natural environments. Examples of research that would benefit from biotelemetry include the assessment of animal responses to different anthropogenic perturbations and the development of life-time energy budgets.

Fundamental to basic and applied ecology is an understanding of the physiology, behaviour and energetic status of unrestrained organisms in their natural environment. Although terminology has varied, the set of techniques most appropriate for monitoring these variables remotely can be referred to as BIOTELEMETRY (see Glossary). The last major reviews on biotelemetry [1,2] concluded that, throughout the 1990s, we could anticipate major advances in our understanding of how animals interact with each other and their environment owing to these technologies. Indeed, refinements and advances in TELEMETRY equipment (including RECEIVERS, TRANSMITTERS and ARCHIVAL LOGGERS) and techniques are currently enabling the precise and simultaneous positioning of organisms in real time in most environments; these forms of automated and manual TRACKING are now common in basic and applied ecology and are discussed in detail elsewhere [3]. However, the advancement of remote monitoring of physiological and behavioural variables (i.e. biotelemetry) and its actual or potential contribution to ecological research is less clear. Several recent papers have identified biotelemetry as a tool that should be considered for studies in behavioural [4] and physiological [5–7] ecology, but few provide a comprehensive synthesis including a critical analysis of its limitations (see [8]). Here, we provide an overview of recent advances in biotelemetry that are relevant to basic and applied ecology. Our approach is taxonomically inclusive, covering all major animal groups

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Glossary

Archival loggers: a device that records and stores information on some recording medium or in memory for later retrieval. In some cases, loggers must be recovered for data retrieval, but data are being stored increasingly on board and transmitted to a satellite.

Biotelemetry: remote measurement of physiological, behavioural or energetic data. Typically, this involves monitoring a signal that originates from within the animal that requires amplification (e.g. electrocardiogram) or measurement of a binary activity, such as a tail beat or wing beat. Some researchers have used the term 'physiological telemetry' to define this suite of tools, but this seems to restrict the meaning to physiological variables. Our broader definition of biotelemetry can also include measurements of activity that are more relevant to behaviour (e.g. chewing, audio) or measurements of environmental conditions that are relevant to organismal physiology (e.g. body temperature). However, our definition of biotelemetry excludes simple locational or positional telemetry often referred to as 'tracking'.

Receiver: an apparatus that collects (receives) information emitted by a transmitter. Some receivers have data-logging capability, whereas others simply display or amplify the signal.

Telemetry: remote measurement of data. Strictly speaking, this might be transmission via a wire or cable, but, for the purposes of this review, our focus is on nontethered animals. Telemetry generally has been assumed to include devices that store data onboard (archival data loggers) for later downloading or transmission. Our working definition here includes nontethered transmitters and archival loggers carried by the animal. (A larger telemetry glossary is available from the Laboratory for Applied Biotelemetry and Biotechnology at Texas A&M University at http://www.tamug.edu/labb/LABB_frame.htm).

Tracking: the most basic type of telemetry that involves determining where an animal is located spatially (sometimes referred to as locational or positional telemetry). Using fixed receiving stations, it is possible to determine fine-scale movement and activity patterns.

Transmitter: a device that transmits (sends) information to a receiver.

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(and environments) for which these technologies are utilized currently. We conclude with a synthesis of what can be learned from this technology and a critical assessment of the factors that are retarding its widespread adoption. Greater application of biotelemetry to basic ecological research as well as applied issues in conservation, management and environmental monitoring will further advance our knowledge of the natural world and the human impact upon it.

Research activities for major animal taxa

We provide a brief overview of several recent ecologically relevant studies that employ biotelemetry on different animal taxa and show how biotelemetry has enabled characteristic features of the taxa to be studied in greater detail than was possible previously.

Invertebrates

Among invertebrates, many ecological issues exist that could benefit from biotelemetry, including biological control and predator-prey interactions. However, in terrestrial and low-conductivity freshwater environments, only the largest arthropods and gastropods are robust enough to carry simple pulsed-radio transmitters (Box 1). Telemetry of physiological and behavioural variables, which requires more complex circuits than does simple tracking (but see Box 2), has been limited to a few studies of large insects owing to the size of the transmitters. Even so, biotelemetry has given us insight into the role of proprioreceptors in the flight of the desert locust *Schistocerca gregaria* [9] and how flight mechanics change as locusts mature into the swarm-migrating form [10,11]. This information could lead to the development of effective biological control techniques for this species, where the flight capabilities of migratory locusts leads to population booms that can devastate wide areas. In another example, tiny transmitters coupled with video have revealed zigzag motor patterns that underlie pheromone-mediated mate-finding maneuvers in the hawkmoth *Agrius convolvuli* [12] and that presumably assist in locating sparsely distributed mates.

In the past decade, the invertebrate targeted most frequently for ecological study by remote-data techniques has probably been the blue crab *Callinectes sapidus* [13]. In spite of the importance of this crab both as a fishery stock and as an estuarine predator, many aspects of its basic biology became accessible only when a variety of transmitters able to send information on activity and energetics up from turbid waters were developed. Spatial and temporal patterns of foraging and the modulation of

Box 1. Size constraints

Biotelemetry presents technological challenges for researchers investigating small organisms. The rule of thumb is that to minimize artifacts such as increased energetic expenditure or altered behaviour, a telemetry device should weigh $<2\%$ of the body weight of the subject (e.g. [61,62,67]). For small animals, size and mass of input modules such as biopotential amplifiers limits the kind or number of variables that can be measured [13]. Battery size is also a constraint. Batteries tiny enough for small animals might be exhausted so quickly (minutes to hours) by the continuous-wave transmission of physiological data that records are too short to be useful [67]. For very long deployments on somewhat larger animals, there have been attempts to replace some of the battery weight with lighter components that draw power from the environment (e.g. solar cells). In the future, improvements in storage battery technology might increase the use of these techniques.

The output stages of transmitters have different characteristics (size and mass) in terrestrial and freshwater systems, in which radio frequencies (RF) propagate well, compared with ocean and estuarine waters, in which ultrasound must be used as the carrier. RF provides good range for a given power output and the high frequencies allow sufficient bandwidth for complex signals. The radiating elements (antennas) are light and simple, but might be limited to inefficient designs (e.g. small loops) on small organisms that would be encumbered by trailing whip antennas. By contrast, ultrasonic transmitters achieve only modest range –(up to 1 km for typical designs, much less in the presence of background noise) and suffer from strong attenuation and multipath (i.e. reflection or refraction of valid signals). Transmitting complex data ultrasonically is challenging because of the lower carrier frequencies and hence available bandwidth. Also, the radiating elements (piezoceramic transducers) are bulky and heavy.

The difficulty of remaining close enough to a target animal to record continuous data has created a niche for loggers that store rather than transmit data. Data must be physically retrieved from these loggers unless the latter include radio transmitters to download the data via satellite, a heavy and costly alternative. Thus, investigators of large vertebrates are limited only by their imaginations, whereas the load-carrying capacity of smaller animals limits the complexity of data that can be telemetered. Investigators of invertebrates on land are limited to those few species robust enough to carry radio transmitters (e.g. crayfishes, big insects and snails) [13,67]. In marine environs, only a few invertebrates (mainly crustaceans and molluscs) are large enough to carry complex devices; most are too small for even the tiniest ultrasonic transmitters [13].

Box 2. Opportunities from precise tracking

Recent developments in real-time monitoring provide precise fixes of the positions of the subject animals using two- and three-dimensional arrays of antennas or hydrophones. Numerous individuals can also be monitored simultaneously using coded digital transmitters. Animal locations can be automatically computed using the time-of-arrival of the transmitted signal to at least three receiving stations (i.e. hyperbolic navigation) or by comparisons among different directional antennas to yield crossed bearings. For animals that undertake long-distance migrations (e.g. birds, marine mammals and pelagic fish), satellite transmitters have enabled the description of nearly complete migration routes for animals such as Atlantic bluefin tuna *Thunnus thynnus* [68]. More accurate and cheaper global positioning system receivers will provide even greater detail.

There are also several telemetry observatories that have been deployed to monitor the behaviour and interspecific interactions of communities of animals. In Panama, a terrestrial telemetry observatory (radio technology) has been deployed in a tropical forest (http://www.princeton.edu/~wikelski/research/index.htm). At the Queen's University Biological Station in Ontario, an aquatic telemetry observatory (ultrasonic technology) was recently installed in a small lake [Partnership between Lotek Engineering Inc. (http://www.lotek.com/) and Queen's University] and efforts are underway to initiate a continental scale marine telemetry system (ultrasonic technology) for the Pacific coast of North America (http://www.postcoml.org/). Using these observatories, multiple users can release different transmitter-equipped animals and monitor locations using the same receiving infrastructure. These systems can be interfaced with physiological or environmental sensors to link spatial and temporal patterns of behaviour and activity. Data from these projects are forthcoming and will undoubtedly provide novel information relevant to animal ecology, conservation, and management.

Figure 1. Biotelemetry in ecological research. **(a)** Blue crab *Callinectes sapidus* equipped with an externally mounted ultrasonic transmitter for assessment of chewing activity (myopotentials of mandible muscles [13]; T.G. Wolcott). **(b)** Sockeye salmon *Oncorhynchus nerka* equipped with an internal EMG transmitter in a swim tunnel respirometer (S. Larsson). The respirometer is used for determining the relationship between transmitter output and swimming speed, tail beats, and oxygen consumption [18,19]. Calibration of biotelemetry devices is often required, especially when inferring energetic data from a correlate such as heart rate [8] or locomotory activity [18]. **(c)** Largemouth bass *Micropterus salmoides* equipped with an external ultrasonic heart-rate transmitter. The fish is being angled by rod and reel to assess the consequences of catch-and-release fishing. Knowledge derived from this type of study can be used to develop or refine conservation and management strategies ([24]; S. Cooke). **(d)** Leatherback sea turtle *Dermochelys coriacea* instrumented with data loggers to record dive depth, swim speed, heart rate, and subcarapace and stomach temperature (R. Andrews). These measurements will help to reveal the causes for the sharp population decline of the critically endangered Pacific population [30]. **(e)** Spotted antbird *Hylophylax naivoides* equipped with an external heart-rate transmitter that can be interfaced with a fixed receiving system to couple heart-rate measurements with position and movement (M. Wikelski). This device weighs <1 g, enabling energetic assessments of small birds and bats [35].

foraging efficiency by aggressive interactions with conspecifics were investigated by telemetering threat postures and chewing (via myopotentials of mandible muscles; see Figure 1a). Microhabitat requirements for the molting stages were explored using transmitters that signaled the molting events, thereby yielding information on the crucial habitats that require protection during that vulnerable life stage [14–16].

In pelagic marine environments, cephalopods (especially squid and cuttlefish) have been targeted for biotelemetry studies because of their size and ecological importance as a food source for whales. To understand foraging ranges and transport costs (hence energetics, food requirements), a few studies have telemetered ventilation frequency and pressures in the mantle (and propulsive jet) of cephalopods [17], revealing that they increase locomotor efficiency by exploiting fine-scale oceanographic features.

Fish

In fish, biotelemetry has enabled the acquisition of basic information on their behaviour and physiology in nature to enable the development of bioenergetic models and the identification of stressors. The variables most commonly telemetered are locomotor activity and energetics using radio electromyogram (EMG) transmitters [18]. These devices have revolutionized our thinking about the migration ecology and management of sockeye salmon *Oncorhynchus nerka* by revealing how they utilize energy to maximize survival and fitness. EMG telemetry has enabled investigators to measure swim speeds and estimate energetic costs of migration [19,20] (Figure 1b), and has provided insights into the relative fitness costs of size and dominance on spawning grounds [21]. It has also been used to evaluate how fishways (a device that facilitates the passage of fish around a barrier) and channel reconfiguration (management actions intended to help migrations) affect salmon behaviour [19,22]. Using these data, mortality-risk models have been developed to predict the likelihood of migration success depending on river flow and temperature conditions and to predict the consequences of climate change [20].

Findings from biotelemetry have also revealed that patterns of parental effort and energy use in bass *Micropterus* spp. do not always conform to parental care theory or to empirical observational assessments (e.g. snorkeling) [23]. To assist in developing conservation and management strategies for minimizing stress and mortality associated with recreational fishing, heart rate and EMG transmitters have been used to assess disturbance and recovery patterns of angled largemouth bass *Micropterus salmoides* [24,25]. Post-release recovery of heart rate was confounded by movement, predator avoidance, and digestion [24] (Figure 1c). During the parental-care period, nest-guarding ability of parental bass was also impaired [25]. These findings will promote management actions that will ensure the sustainability of fish populations.

Amphibians and reptiles

Answering questions about how amphibians and reptiles manage their body temperature and survive with an energy metabolism that is one tenth that of similar-sized birds and mammals in the same environment will help us to understand the physiological and ecological tradeoffs in the evolution of endothermy. Understandably therefore, thermal ecology has been the most common focus of biotelemetry studies on amphibians and reptiles. It is known that one way that reptiles ameliorate their lack of endogenous heat production is to manage heat flow from the environment most efficiently. For instance, as first discovered in the laboratory [26,27], reptiles show an interesting heart-rate hysteresis (i.e. capacity to control thermal conductance by changing cardiovascular activity) during heating and cooling. Recently, however, researchers [28] discovered using heart-rate telemetry that lizards also exhibit a reverse hysteresis pattern at high body temperatures to prevent overheating, revealing physiological adaptations for thermoregulation that enable reptiles to extend their activity into very hot environments. Ecologists have also utilized thermally sensitive transmitters to determine that thermoregulatory behaviour of black rat snakes, *Elaphe obsoleta*, in a challenging northern climate contradicts conventional cost-benefit thermoregulation models that predict that ectotherms should stop thermoregulating when the costs outweigh the benefits [29].

Use of heart-rate telemetry has yielded several interesting results. Leatherback turtles *Dermochelys coriacea* achieve dive records rivaling those of marine mammals (e.g. seals), but using heart rates as low as 1 beat per min [30] (Figure 1d). This is paradoxical considering the extreme amount of locomotor activity required to dive to depth. Apparently, muscle mechanics and cardiovascular physiology (assessed with biotelemetry) in turtles differ greatly from mammals [30], providing insight into how different animals achieve the same behaviour. Heart-rate telemetry has also been applied to the emerging field of disturbance biology to quantify the stress responses of free-ranging frogs and lizards to human-induced stressors [31]. Researchers have also evaluated the ability of heart-rate and body-temperature measurements to estimate the field energetics of reptiles such as the Galapagos marine iguana *Amblyrhynchus subcristata* [32]. As a result, it is now possible to use lizard model systems to address questions that were difficult or impossible to study before in lizards, such as the energetic costs of mate choice. Knowing the precise amount of energy expended on certain activities further enables researchers to determine the level of allostatic load (i.e. the cumulative physiological costs of repetitive or chronic exposure to stress) [33] in free-living animals. Because the human influence on natural systems is continually increasing, it is imperative to understand precisely the factors that cause severe stress in animals and thus can contribute to allostatic overload. For amphibians in particular, because anthropogenic stress can lead to population declines, biotelemetry has immense potential for conserving biodiversity.

Birds

It has only become possible to study bird flight in any detail with the advent of small telemetric and data-storage techniques. Pioneering studies of the flight physiology of birds used radio transmitters attached to their backs, but were limited to only a few seconds of data collection because of the relatively large mass and drag of the transmitters. Researchers overcame these early limitations by implanting relatively small transmitters (<10 g) into the abdominal cavity of barnacle geese *Branta leucopsis* [34]. More recently, an even smaller (0.6 g) transmitter has been developed [35] (Figure 1e) that enables the concurrent measurement of heart rate, wing beat and respiration in small vertebrates such as songbirds or bats [36]. Because it is not always convenient, or indeed possible, to be sufficiently close to a subject to record data via a radio link, still other technologies are required. An example is implantable data loggers weighing <25 g that have been used to record heart rate and body temperature (for a year or more) to estimate metabolic rate in wild barnacle geese before, during and after the migration from their breeding grounds in the high Arctic to their wintering area in southern Scotland, a distance of some 2500 km [37,38].

Implantable radio-transmitters and data loggers have also been used to study the behaviour, physiology and field energetics of diving birds [39,40]. These studies have demonstrated that freely diving birds expend little more energy when diving as they do when resting in water, and that there is invariably a substantial reduction in temperature in the abdominal cavity in marine birds, which might be important in minimizing metabolic rate and, therefore, the rate at which stored oxygen is used. Most loggers providing behavioural data have been attached externally (e.g. pressure sensors to monitor depth of diving, accelerometers or impellers to monitor speed) and have provided information about the use of buoyancy by Adélie *Pygoscelis adeliae* and king penguins *Aptenodytes patagonicus* [41]. Hall sensors have also been used to determine movement of the flippers and patterns of respiration in swimming penguins [42].

Body temperature has been recorded remotely in many bird species in the context of thermoregulation [43], time and energy budgets [44], and circadian and circa-annual rhythms [38]. An intriguing aspect of thermoregulation in some species is selective brain cooling (i.e. when the brain temperature is lower than that of the blood in the carotid artery). The first study to examine hypothalamic temperature in free-living ostriches *Struthio camelus* in nature used a data logger implanted subcutaneously and concluded that selective brain cooling was not present in all individuals and was not tightly coupled to body temperature [43]. Thus, the functional significance of selective brain cooling in ostriches could include protecting the brain from heat stress or whole body thermoregulation; alternatively, it might serve no current function.

Marine mammals

Visual observation of marine mammals at sea is limited largely to their brief excursions to the surface. Biotelemetry, therefore, has been crucial in advancing our understanding of their behaviour, physiology, and ecology [45]. Given the many population declines that have occurred recently, some of which are unexplained, biotelemetry is also an important tool for conservation biologists and managers. For example, remote measurements of dive behaviour have led to the conclusion that some sea lions are operating routinely at or close to their maximum physiological capacity, possibly limiting their ability to respond to natural or anthropogenic environmental changes [46].

One leading hypothesis for the dramatic population decline of Steller sea lions *Eumetopias jubatus* since the 1960s [47] is nutritional stress from a change in the distribution, abundance or type of their prey. Remote monitoring of prey ingestion using stomach-temperature telemetry and archival data loggers [48] showed that adult female sea lions do not appear to be food limited during the summer [49], which contradicts the leading hypothesis. For Weddell seals *Leptonychotes weddellii,* prey ingestion has also been measured by recording jaw opening [50], and even more directly by video recording with animal-borne cameras [51]. Combining such data with remotely sensed physical and biological oceanographic data has enabled investigation of the effects of environmental variables on animals even when they are thousands of kilometers from the nearest research station or vessel [52]. It is also now possible to gather not just information on the physiology of the animals, but also about their physical environments using onboard CTDs (conductivity, temperature and depth sensors; [53]).

Energy expenditure in marine mammals has also been estimated with biotelemetry devices, where, if properly calibrated, heart rate can be a good indicator of metabolic rate [8]. Although heart rate is usually recorded with biopotential electrodes, it was shown recently that acoustic recorders could pick up both heart beat and breathing sounds from free-ranging marine mammals [54]. Acoustic tags have enabled studies of the effect of depth on sound production and the effect of anthropogenic noise on behaviour [55,56]. Attachment of three-dimensional orientation data loggers to the critically endangered North Atlantic right whale *Eubalaena glacialis* has shown that their positive buoyancy leads to dive behaviour that makes them very susceptible to boat collisions [57].

Non-marine mammals

In non-marine mammals, thermometric telemetry has been applied frequently to understand patterns of activity and energy use in the context of endothermy. It used to be thought, for example, that mammalian hibernation and torpor (i.e. controlled lowering of the thermoregulatory set-point resulting in a lowering of body temperature and metabolic rate) was restricted to species in cold regions. However, the use of thermometric transmitters on fat-tailed dwarf lemurs *Cheirogaleus mediushas* has shown that it also occurs in species inhabiting warm climates [58]. Likewise, telemetering of the temperature of blood in the carotid artery of several free-ranging African ungulates has undermined the generally accepted theory that large arid-zone mammals store body heat during the day to reduce water loss through evaporative cooling [59]. Moreover, some of these animals that utilize selective brain cooling are able to shut off this function quickly to excite evaporative heat loss [59], which could reduce the risk of potentially lethal hyperthermia during and after the sudden intense exercise required by flight and fright responses.

Other forms of biotelemetry have not been applied often to non-marine mammals outside of the biomedical field. Heart-rate telemetry, with its enormous potential as an indirect measure of field metabolic rate, received considerable interest in the 1970s and 1980s, but there are few recent examples. Such energetic assessments would enable both the quantification of allostatic load and the division of energy estimates into behaviour-specific components such as mobility, food acquisition, or reproduction [8]. Heart-rate telemetry coupled with thermometric loggers has been used to understand how large ungulates cope with winter food shortages and cold [60]. Red deer, *Cervus elaphus*, exhibited an overall reduction in heart rate as well as a unique nocturnal lowering of metabolism associated with peripheral cooling. This previously

Table 1. Types of variables that can be measured remotely and their relative usage in different taxa[a]

Taxa	Locomotory activity[b]	Refs	Ventilation	Refs	Heart rate	Refs	Blood pressure	Refs	Precise location[c]	Refs	Thermal properties[d]	Refs
Invertebrates	C	[13,17]	U	[13,17]	U	[13]	N		C	[67]	U	[13]
Fish	C	[18,69]	U	[66]	C	[24,66]	N		C	[68]	C	[70,71]
Birds	C	[2,34]	U	[2,34]	C	[2,8]	U	[72]	C	[36]	C	[37,43]
Amphibians and reptiles	U	[30]	N		U	[30,31]	N		U	[73]	C	[27,29]
Marine mammals	C	[45]	C	[2,45]	C	[2,54]	U	[72]	C	[45]	C	[48]
Non-marine mammals	U	[2,3]	U	[2]	U	[2,60]	U	[74]	C	[75]	C	[58,59]

[a]Abbreviations: C, common; N, not attempted to our knowledge; U, uncommon.
[b]Includes measures such as appendage beats (i.e. tail or wing), jet propulsion, electromyogram activity and velocity recorders.
[c]Includes measures of real-time position in two or three dimensions (Box 2).
[d]Includes the environment within and adjacent to an organism.

unknown mechanism of energy conservation (i.e. reducing endogenous heat production) might represent a common survival strategy of endothermic organisms to energetically challenging situations.

Conclusion

Biotelemetry provides a powerful set of tools for addressing mechanistic issues in animal ecology. As is evident from the examples above, biotelemetry techniques

Table 2. Categories of biological variables that can be telemetered, appropriate sensors and their application to ecological research[a]

Desired variable	Sensor details	Applications	Refs
Sound, vibration	Electret and dynamic microphones, piezoceramic benders, piezo films	Measurement of feeding activity in chewing mammals; recording communication among animals such as birds and marine mammals	[54–56,76]
Pressure in body cavities, depth in water, barometric pressure	Micromachined Si pressure transducers	Assessment of opercular rate in fish; pericardial pressure; frequency and amplitude of tail beats in water; jet pressure of squid and blood pressure in numerous animals; depth of diving animals	[2,17,69]
Acceleration, locomotor rhythms, activity	Micromachined (multi-axis) accelerometers, Hg tip switches, body temperature (death or torpor indicator for endotherms)	Assessment of movement and swimming dynamics of aquatic animals in two or three dimensions; used primarily in fish and marine mammals	[77]
Salinity of milieu, ionic strength of body fluids	Conductivity cells	Reveals information on the environmental conditions faced by the animal; assessment of the ionoregulatory status during migration of fish between salt and fresh waters; assessment of ionic balance of mammals and reptiles in arid environments	[53]
Imagery	Miniaturized versions of commercially available image capture technology such as still cameras and video	Provides the ‘animal’s perspective’, enabling the coupling of behaviour and physiology; animal borne video is frequently used on marine mammals	[51]
Blood flow rates, swimming or flying speed	Magnetically or optically sensed rotors, drag and strain gauges, heated thermistors, ultrasonic (piezoelectric) Doppler	Quantification of several flow and speed related variables such as cardiac output (which is highly correlated with metabolic rate)	[1–3]
Position (e.g. of body parts), orientation	Magnetic reed switches, Hall-effect sensors, variable resistors, optical interrupter modules, ultrasound, Hall-effect magnetic field angle encoders, fluxgate compasses	Document movement of appendages, such as flippers, wings and tails; mandibular movement indicating feeding activity; migration biology	[13,42,78]
Light	Photocells, phototransistors and photodiodes, integrated circuits (light to voltage, light to frequency, some with ability to measure in several wavelength bands)	Assessment of diel activity patterns, hibernation, pollination ecology; bioluminescence of marine organisms encountered by fish or marine mammals; geolocation	[79]
Temperature	Thermistors, transistor junctions, thermocouples, heat flux sensors	Detection of gross and tissue specific temperatures associated with thermal ecology; feeding activity in marine mammals and birds	[29,43,48,59,70,71]
Chemistry of body fluids or external milieu	Fluors or colorimetric compounds located at tips of optical fibers or on exterior of glass capsules and excited or measured by LEDs and phototransistors; ion-specific electrodes	Quantification of blood chemistry in free-ranging animals; currently few examples of applications to ecological research although muchopportunity; includes remote collection of blood samples for later analysis	[2,80]
Biopotentials[b] (ECG, EMG, EEG)	Biocompatible electrodes, high input impedance amplifiers	Assessment of gross patterns of locomotor activity (EMG), estimate energetics (EMG, ECG), record neural activity (EEG, neural activity); relevant to many types of animal	[8,18,81]

[a]Sensors are constantly being developed that could provide the ability to quantify or measure other variables. The list provided is intended to summarize some of the more common types of sensors used and to quantify some of the more commonly telemetered physiological variables. Similarly, the applications listed are intended to provide several examples and are not exhaustive.
[b]Abbreviations: ECG, electrocardiogram; EMG, electromyogram; EEG, electroencephalogram.

Table 3. Benefits and limitations of techniques for remotely monitoring animals with biotelemetry

Desirable characteristics and benefits		**Refs**
Partnering of physiology with field behavioural measures	Enables the linking of the behaviour and physiology of free-ranging animals in their own environment. Few other techniques enable researchers to determine the energetic cost of specific behaviours at ecologically meaningful timescales	[8,66]
Individual-based	It is possible to characterize the variation among individuals and to recognize the plasticity of the responses. Ideal tool for linking individual behaviour with physiology and energy status	
Continuous, real-time	Continuous data streams eliminate unknowns during periods when animals are not monitored and facilitate the detection of trends through time. Data can be collected on a diel basis and in harsh environmental conditions for extended periods without requiring continuous human support	[51,65]
Multi-scale	Provides opportunity to focus on animal behaviour and physiology that occur at a variety of scales (e.g. temporal, spatial or system)	
Energetic equivalents	Energy is a common currency in ecology and is essential for inferring the bioenergetic costs of different behaviours. Enables estimation of metabolic rate in the field	[8,17,18]
Unrestrained animals	In nature, animals face a suite of site-specific biotic (e.g. predation or habitat heterogeneity) and abiotic (e.g. weather) conditions that cannot be adequately replicated in a laboratory. Monitoring of unrestrained free-ranging animals in their own environment eliminates laboratory artifacts	[24]
Potential to study endangered animals	Enables data collection without further imperilment from animals the populations of which are threatened with extinction; can eliminate the need for laboratory confinement	[49,57]
Limitations and challenges		
Understanding patterns in the data	Produces large volumes of data and interpreting patterns can be extremely difficult; is most powerful when coupled with other techniques, including detailed visual and/or video observations, blood sampling, tissue biopsies or combining multiple sensors	
Unfamiliarity with technological options	Most researchers are unfamiliar with options that modern microelectronics has provided for transducing behavioural, physiological and microenvironmental variables. Greater communication and collaboration among researchers working in different fields and on different taxa might promote effective use of biotelemetry	[13]
Cost	Cost can be high, in some cases leading to low sample sizes. However, must be contrasted with the benefit derived from data that cannot be collected using other techniques	
Accuracy of energetic estimates	Some forms might fail to estimate accurately the rate of energy expenditure. Many current approaches (e.g. activity telemetry) fail to quantify anaerobic activity, which can be an important component of energy budgets although some have attempted to correct for anaerobiosis in their biotelemetry-based energy models. Because aerobic metabolism is usually involved in the removal of anaerobic metabolites, heart-rate telemetry can be used to estimate this cost	[8,20]
Need for calibration	Generally desirable to calibrate transmitters (usually to some energetic equivalent) and to verify their proper function using parallel laboratory techniques (Figure 1b). This aspect is important, but can be costly	[8,18]
Statistical analysis and interpretation of autocorrelated time series	Because data can be collected in real time, there is the danger of collecting data sets that are difficult to manage. Because time series represent the repeated sampling of data from the same individual, data are nonindependent and could require complex statistical techniques that are poorly suited to these types of data. Can be addressed by monitoring large numbers of individuals with repeated measure designs, although larger budgets are then required	
Burden on animal	Battery size and longevity continue to limit research on small organisms or long-term monitoring and also limits the complexity (mass) of the required circuitry (Box 1). The types of transmitter and sensor, and the biology of the organism of interest will determine whether telemetry devices will be fully implantable or require the use of transcutaneous connections. Where possible, transcutaneous connections should generally be avoided owing to potential for damage or dislodging of transmitters and sensors, and possibility of infection	[67]
Specialized skills	Biotelemetry requires an understanding of basic electronics as well as a more specialized understanding of the fundamental biological variable being measured (i.e. use of heart-rate telemetry requires a basic understanding of cardiovascular physiology). Surgical implantation requires specific training that might require enlisting veterinarians for higher vertebrates	
Ethical issues	It is usually necessary to obtain ethical approval for invasive techniques on higher vertebrates	
Translation to ecological scale problems	Some researchers whose work focuses on populations, communities, or ecosystems could find it difficult to view individual-based physiological or behavioural data in the context of broader ecological scale problems	
Availability and/or customization	The lack of commercial suppliers for much of the biotelemetry apparatus can impede new researchers from adopting these techniques, so efforts must be taken to share technology among researchers. Where commercial equipment is available, the costs are high and will remain so until more researchers start using these technologies	

are used with differing frequency for different taxa based largely on constraints of size and environment (Table 1). Collectively, several physiological and behavioural variables can be monitored remotely for most taxa (Table 2). However, as with all techniques, a suite of challenges and limitations exist that must be balanced against its many positive aspects (Table 3). Interestingly, in spite of major technological advances and the ability to monitor an increasing number of variables for increasingly smaller organisms, biotelemetry has still not been widely embraced by the ecological community.

We are confident that some of the most interesting and informative findings in ecology will be derived from research that incorporates telemetered or logged field measurements. For example, biotelemetry has much to offer for estimating the energetic cost of behaviours, which can be incorporated into bioenergetic models and tests of life-history theory. We also anticipate that biotelemetry will be an important tool for evaluating the effects of different stressors on individuals and populations in the wild. Our review is intended to stimulate those activities and to serve as a key resource for those considering or unaware of the modern capabilities of biotelemetry. An increasing number of biotelemetry devices are now commercially available, and many methodological studies detail or synthesize their design and function, and present preliminary data on deployments, including assessments of the effects of the transmitter on the organism (e.g. [61,62]). In our opinion, the two principle factors retarding the widespread adoption of biotelemetry methods are the lack of commercial development for many applications, and, to a lesser extent, cost. Increased demand for these devices would reduce production costs and enable companies to invest more in research for novel technologies. In reality, the benefits outweigh the costs as these devices enable the collection of data not available using other techniques.

Here, we have revealed the power and robustness of these technologies, while pointing out limitations and practical issues that have retarded their widespread adoption. When biotelemetry fails to deliver on its promise to provide physiological and behavioural information from free-living animals, it often is not because the electronics fail, but because the researcher needs a clearer understanding of how to match electronic technology to the question, the animal and the environment. As the ecological research community becomes more acquainted with the kinds of questions to which telemetry systems can provide novel answers, we expect the technology to be applied to more complex research issues and used to test long-standing ecological theory using empirical data collected from free-ranging animals. Even evolutionary biology is benefiting from data derived from biotelemetry in areas such as understanding the evolution of mammalian endothermy [63] and diving responses in marine mammals [64]. By providing information about how real animals interact with their real (normal) environments, this technology also will address applied issues in animal conservation. Telemetered animals can serve as proxies for monitoring how natural or anthropogenic environmental conditions as well as conservation strategies could affect animal populations, as well as facilitating a bioenergetic approach to quantifying stress [65]. Finally, data derived from biotelemetry could benefit intensively managed animal populations through development of predictive models, refinement of bioenergetic models and understanding of population-level processes [66].

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