

REVIEW

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Observing the unwatchable through acceleration logging of animal behavior

Danielle D Brown^{1*}, Roland Kays^{2,3,4}, Martin Wikelski^{4,5,6}, Rory Wilson⁷ and A Peter Klimley⁸**Abstract**

Behavior is an important mechanism of evolution and it is paid for through energy expenditure. Nevertheless, field biologists can rarely observe animals for more than a fraction of their daily activities and attempts to quantify behavior for modeling ecological processes often exclude cryptic yet important behavioral events. Over the past few years, an explosion of research on remote monitoring of animal behavior using acceleration sensors has smashed the decades-old limits of observational studies. Animal-attached accelerometers measure the change in velocity of the body over time and can quantify fine-scale movements and body postures unlimited by visibility, observer bias, or the scale of space use. Pioneered more than a decade ago, application of accelerometers as a remote monitoring tool has recently surged thanks to the development of more accessible hardware and software. It has been applied to more than 120 species of animals to date. Accelerometer measurements are typically collected in three dimensions of movement at very high resolution (>10 Hz), and have so far been applied towards two main objectives. First, the patterns of accelerometer waveforms can be used to deduce specific behaviors through animal movement and body posture. Second, the variation in accelerometer waveform measurements has been shown to correlate with energy expenditure, opening up a suite of scientific questions in species notoriously difficult to observe in the wild. To date, studies of wild aquatic species outnumber wild terrestrial species and analyses of social behaviors are particularly few in number. Researchers of domestic and captive species also tend to report methodology more thoroughly than those studying species in the wild. There are substantial challenges to getting the most out of accelerometers, including validation, calibration, and the management and analysis of large quantities of data. In this review, we illustrate how accelerometers work, provide an overview of the ecological questions that have employed accelerometry, and highlight the emerging best practices for data acquisition and analysis. This tool offers a level of detail in behavioral studies of free-ranging wild animals that has previously been impossible to achieve and, across scientific disciplines, it improves understanding of the role of behavioral mechanisms in ecological and evolutionary processes.

Keywords: Accelerometer, Activity, Animal behavior, Bio-logging, Dead reckoning, Energy expenditure, Ethogram, Remote observation, Telemetry

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Abstract

Resumen: El comportamiento es un mecanismo importante de la evolución y que se paga a través del gasto de energía. Sin embargo, los biólogos de campo raramente observan los animales durante más de una fracción de sus actividades y los intentos de cuantificar el comportamiento para el modelado de los procesos ecológicos a menudo excluyen eventos crípticos pero importantes. En los últimos años se produjeron avances importantes en el monitoreo remoto del comportamiento de los animales, utilizando sensores de telemetro de aceleración (acelerómetros) que empujan los límites tradicionales de los estudios observacionales. Acelerómetros unidos a los animales miden el cambio de la velocidad del cuerpo en el tiempo y pueden cuantificar los movimientos a escala fina y posturas corporales ilimitadas por la visibilidad, el sesgo del observador, o la escala de la utilización del espacio. Como pionero hace más de una década, la aplicación de los acelerómetros como una herramienta de monitoreo remoto ha aumentado recientemente debido al desarrollo de hardware y software más accesibles. Se ha aplicado a más de 120 especies de animales hasta hoy. Medidas de los acelerómetros se recogen típicamente en tres dimensiones de movimiento a muy alta resolución (>10 Hz), y hasta ahora se han aplicado hacia dos objetivos principales. Primero, los patrones de las formas de los acelerómetros de onda se pueden utilizar para deducir comportamientos específicos a través de movimiento de los animales y la postura corporal. Segundo, se ha demostrado que la variación en las medidas de forma de los acelerómetros de onda se ha demostrado que se correlaciona con el gasto de energía, abriendo una serie de preguntas de carácter científico sobre especies muy difíciles de observar en la naturaleza. Hasta la fecha, los estudios de las especies acuáticas silvestres superan a las especies terrestres silvestres, y los análisis de los comportamientos sociales son muy pocos en número. Los investigadores de las especies domésticas y en cautiverio tienden a reportar metodología más completa que los que estudian las especies silvestres. Hay retos importantes para conseguir el máximo rendimiento de los acelerómetros, incluyendo la validación, calibración y gestión y análisis de grandes cantidades de datos. En esta revisión se ilustra cómo funciona el acelerómetro, se proporciona una visión general de las investigaciones ecológicas que han empleado los acelerómetros y se destacan las mejores prácticas emergentes para la adquisición y análisis de datos. Esta herramienta ofrece un nivel de detalle en los estudios de comportamiento de los animales salvajes que han sido hasta ahora imposibles de alcanzar y, en todas las disciplinas científicas, que mejora la comprensión del papel de los mecanismos de comportamiento de los procesos ecológicos y evolutivos.

Palabras claves: Acelerómetro, actividad, bio-registro, comportamiento animal, gasto energético, etograma, navegación a estima, observación a distancia, telemetría.

Review

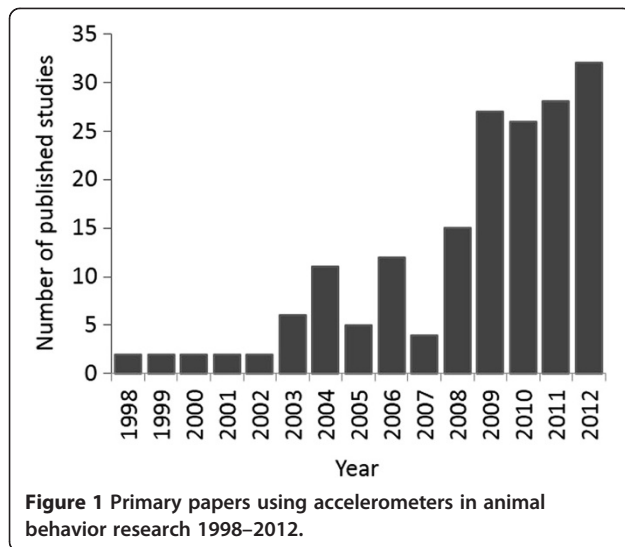
“Man goes to nature to learn what nature is, but, in so doing, he introduces possibilities of distortion through his own presence.” – T.C. Schneirla (p. 1022, [1]).

Naturalists have long been aware that their presence can affect animal behavior [1,2]. Direct observation presents obvious difficulties when animals perceive humans as predators [3] or when they are naturally secretive and elusive [4,5]. Habituating individuals to an observer is sometimes possible but it is labor-intensive, and can require long-term study [6,7]. Furthermore, though the subjects under study may be habituated, human presence can still affect their behavioral interactions with other non-habituated predator, prey or competitor species [8]. The observer is rarely undetectable and even animals that do not appear to react to human presence may still change their behavior in subtle ways [9,10]. Direct observations are also biased by our own physical limitations [11-13] and tendencies to attend to some events and subjects more than others [14].

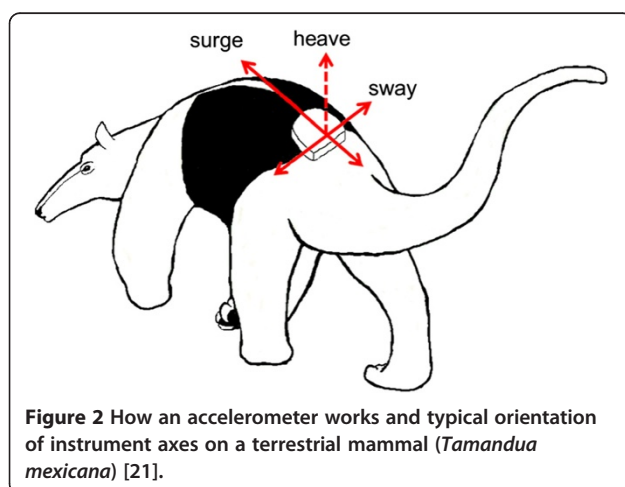
The field of biotelemetry grew out of the need to locate animals at will and observe and record their habits despite their abilities to travel rapidly and widely in inclement

weather, underwater, or at night [12,13,15]. Locating animals in space has progressed from manual tracking of animal-borne radio- or acoustic signals to automated depth and geomagnetic loggers and satellite-based positioning systems that practically eliminate the observer effect and can now provide precise worldwide locations with few temporal or spatial constraints [11,16]. Nevertheless, a record of animal locations or a depth profile tells where the animal was and how long it stayed there, but the behavioral context is absent and must either be inferred or demands a return to direct observation methods [17]. These issues underscore the need for remote measurement of animal behavior to reduce or eliminate the potential effects of observer presence while maintaining a high level of detail in data recording that is comparable to direct observation [18]. Over the past few years, there has been an explosion of research on remote monitoring of animal behavior using measurements of acceleration (Figure 1) [19,20]. This tool, the accelerometer, has repeatedly circumvented many of the age-old limits of direct observation of animals in the field.

Figure 2 provides a basic explanation of how an accelerometer works [21]. An accelerometer is a spring-like



piezoelectric sensor. When deformed, the sensor generates a wave-like voltage signal that is proportional to the acceleration (change in velocity) it experiences [22]. The sensor is deformed both by gravitational acceleration as well as inertial acceleration due to movement. From one to three of these sensors are aligned orthogonally to one another and affixed to an animal so that each sensor measures acceleration in a single plane, or dimension, of movement (surge, heave, and sway (Figure 2)). All three sensors collecting simultaneous measurements can represent three-dimensional movement realistically [20,23]. The sensors can be user-programmed to sample acceleration at frequencies ranging from 0.5 to 10,000 Hz, and can be set to record continuously or in repeated bursts (e.g., every 2 min). The voltage signals, also known as raw accelerometer output, may be used in their raw state, or converted to actual acceleration if the unit is



carefully calibrated (measured in g ; $1 g = 9.8 m/s^2$). Under static circumstances, such as during rest or after death, the accelerometer signal only represents the gravitational force acting on the sensors. When an animal is moving, sensor output represents acceleration due to gravity combined with the inertial acceleration generated by movement [23]. Accelerometers typically incorporate a microprocessor and digital memory to store logged measurements until the instrument is retrieved [24].

Measurement of acceleration is a well-established research tool in biomechanics [25,26] and exercise science [27,28]. The first (wired) accelerometers were used to examine the biomechanics of movement in humans [29] and fish [30] and then to ascertain the correlation between bodily acceleration and oxygen consumption in human subjects [28]. The introduction of air-bag technology in passenger vehicles lead to the development of relatively inexpensive accelerometers that use very little power [31]. These were quickly adopted for studies outside the laboratory environment, because they are “small, low-cost instruments that provide quantitative [and objective] measurements [of activity]” p. 679, [32]. Animal studies using these modern, truly portable acceleration sensors did not appear in the literature until the late 1990s [33,34]. Initially, animal studies were confined to captive and domesticated species, as well as aquatic taxa, for whom few other behavioral observation methods were possible [12,35,36]. Since then, the ongoing reduction in the size of computer microprocessors and improvements in battery size, weight, and longevity combined with these small solid-state acceleration sensors have resulted in a modern accelerometer that can weigh 0.7 g (without a battery) and measure $9.5 \times 15 \times 4$ mm (available from: <http://www.technosmart.eu/axy.php>). Modern accelerometers also consume very little digital memory with each measurement [37], so data collection and data storage on-board the instrument itself is possible for up to several months or years, depending on the sampling schedule. Accelerometers that simply log their data must be retrieved after the sampling period, as with other types of telemetric data loggers. However, some accelerometers incorporate ultra-high frequency data download technology in similar frequency bandwidths as those used in cellular phones [38]. This feature makes it possible to download the data from the accelerometer from a reasonable distance (up to 500 m, personal observation) even if the device and its bearer are not visible or the instrument cannot be retrieved because it has been discarded in a tree cavity, for example [21]. Radio or acoustic beacons are commonly used on loggers that must be retrieved [21,24].

Movement is the fundamental behavioral response to both internal motivations and the external environment [13,17]. Using accelerometers, biologists can measure the movement behavior of wild animals over biologically and

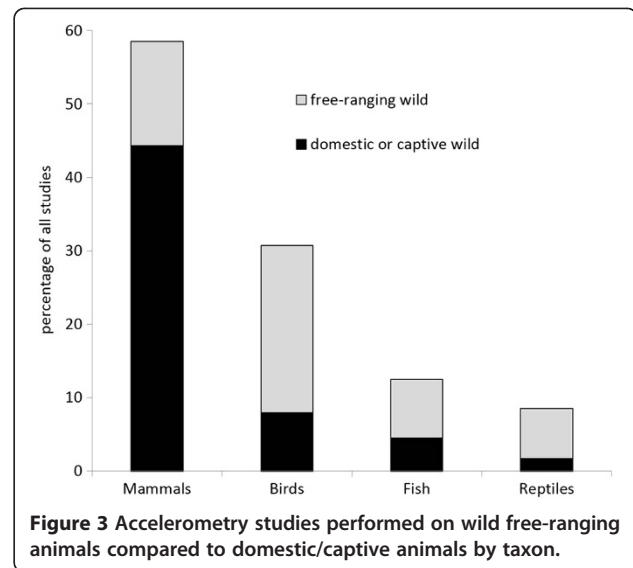
ecologically significant events and periods, practically unlimited by visibility, observer bias, or geographic scale. Accelerometers can be deployed with other sensors, such as those recording location (GPS, acoustic telemetry, water depth), physiological measurements (heart rate, body temperature), and environmental variables like air temperature, light levels and magnetic heading [24,39,40]. Particularly when combined with other instruments, measurements of acceleration can provide a wide range of detailed information on the environmental context of animal behavior and physiology that can exceed the descriptive abilities of the human observer and deepen our knowledge even for well-known species such as domestic animals. Here, we review how accelerometers have been used to date in the study of animal behavior, including the taxonomic and research trends in the literature and we illustrate the type of data produced by this technology from instruments deployed on a variety of species. Further, we provide a summary of the currently available techniques for data calibration, management and analysis, and suggest key directions for future research.

Methods

We accessed BIOSIS® Previews and ISI Web of Knowledge® online and ran searches for any publication containing references to accelerometry in the title, abstract or keywords. We limited our analysis to primary research published in peer-reviewed journals and book chapters through December 2012. From those, we selected studies utilizing animal-borne sensors applied to non-human species. We assessed the resulting works for the following: i) study purpose; ii) species and whether subjects were captive/domestic or free-ranging, and aquatic or terrestrial; iii) number of acceleration axes; iv) sampling frequency utilized; v) the behavioral resolution of the resulting measurements; vi) the parameters of the accelerometer data used for analysis; vii) whether or not behavioral classification accuracy was reported (if pertinent); and viii) whether accelerometry was combined with other telemetry sensors. Results are presented as percentages; not all percentages will sum to 100 because not all categories were mutually exclusive.

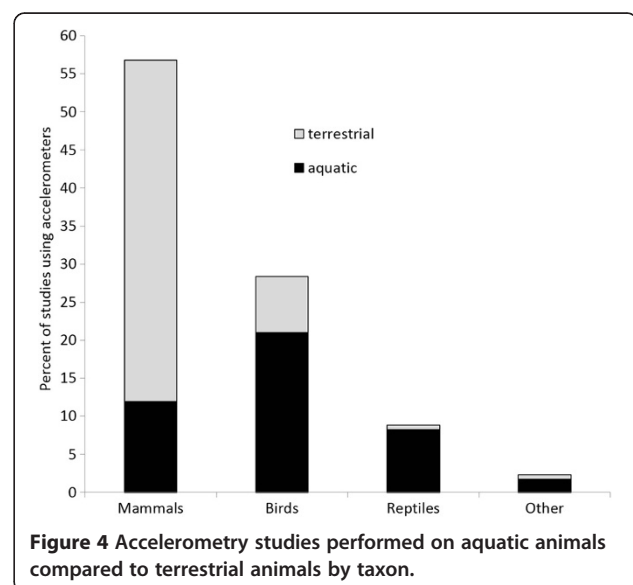
Results

We discovered 176 accelerometry studies and counted 125 animal species that have borne accelerometers (Additional file 1). Studies were relatively evenly split between aquatic (48.3%) and terrestrial (52.8%) habitats and between free-ranging wild animals (50%) and domesticated/captive wild animals (33/27.3%), but there were biases among taxa for these categories (Figures 3 and 4). Mammals represented 45.6% of all study species with domestic cattle and Pinnipeds being the most-studied among the mammals (14% of studies and 18% of species, respectively). Birds comprised



33.6% of all study species and 38% of avian species were either Sphenisciformes or Suliformes. Fishes included 11.2% of species and half of all fish species were Elasmobranch sharks. Eight reptile species, five of them Chelonians, comprised 6.4% of study subjects. Giant cuttlefish (*Sepia apama*), Humboldt squid (*Dosidicus gigas*), King scallop (*Pecten maximus*) and Cane toad (*Bufo marinus*) were the four study species remaining outside of these four taxon categories.

More than half of all studies (62.3%) utilized 3-axis accelerometers; 90.3% of studies utilized either 2- or 3-axis accelerometers. Sampling frequencies ranged from 0.5 Hz to 10,000 Hz, with 60% of studies using one of the following most common sampling frequencies of 8, 10, 16, 32, 64 or 100 Hz. Forty-eight percent of studies collected



acceleration data continuously and 13.3% collected data in discrete bursts or intervals; 38.7% of studies did not clearly report their collection method. Sixty-three percent of studies combined an accelerometer with other telemetric instruments; however, free-ranging wild species were 3 times more likely than captive wild species and 6 times more likely than domesticated species to be outfitted with telemetry devices that contained multiple sensors. The most common remote sensors used in tandem with accelerometers measured depth (35.6% of studies), travel speed (16% of studies) and temperature (14.7% of studies).

Survey of questions currently served by accelerometry: body posture and body movement

The acceleration waveforms over short (millisecond) to long (minutes) periods can be used to deduce behavior-specific body postures and body movements (Figures 5 and 6) [41,42]. Across taxa, 36.4% of studies reported acceleration ethograms or acceleration-based descriptions of behavior. Just under half (46.6%) of all studies utilized the accelerometer waveforms to determine activity budgets. As shown graphically in Figure 5, accelerometer voltage output of inactive or rest behavior is more or less constant, while whole-body movement of any kind produces fluctuating acceleration waveforms with high levels of variance among measurements. Of the studies examining activity budgets, 35% of authors used this variance characteristic of accelerometer waveforms to simply identify the timing of activity vs. rest [43-46]. Sixty-five percent of authors identified distinct waveforms for specific behaviors and then estimated the amount of time animals spent engaged in these behaviors such as chasing prey or feeding, flight, swimming,

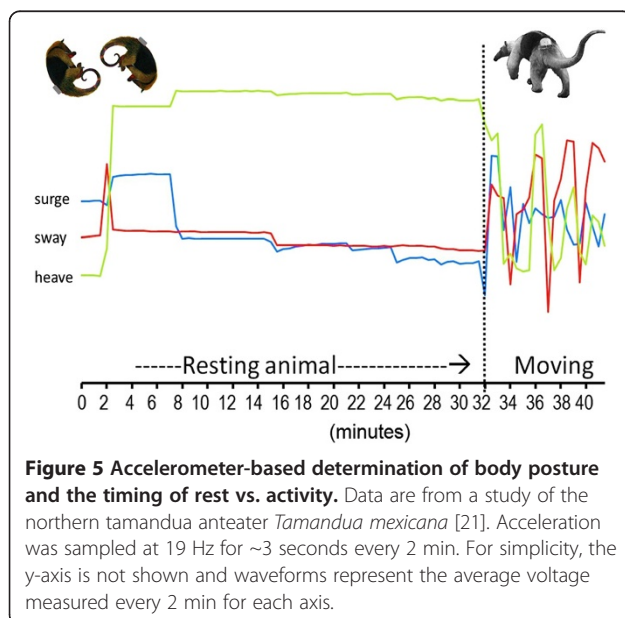


Figure 5 Accelerometer-based determination of body posture and the timing of rest vs. activity. Data are from a study of the northern tamandua anteater *Tamandua mexicana* [21]. Acceleration was sampled at 19 Hz for ~3 seconds every 2 min. For simplicity, the y-axis is not shown and waveforms represent the average voltage measured every 2 min for each axis.

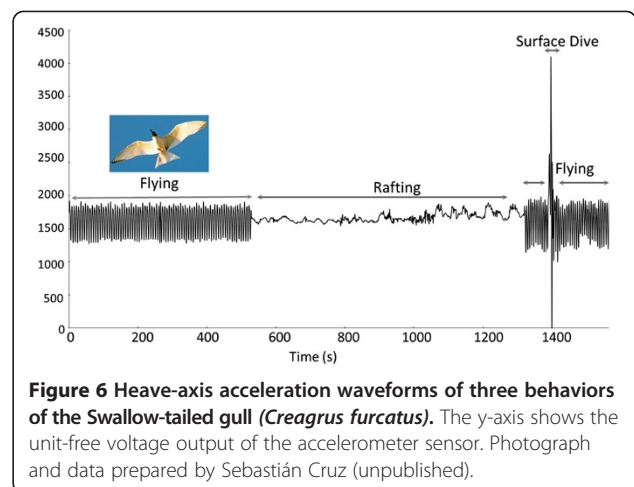


Figure 6 Heave-axis acceleration waveforms of three behaviors of the Swallow-tailed gull (*Creagrurus furcatus*). The y-axis shows the unit-free voltage output of the accelerometer sensor. Photograph and data prepared by Sebastián Cruz (unpublished).

walking, running, climbing, standing, lying down, thermoregulation and sleeping. Quantifying foraging effort is an application of accelerometry that few other telemetry technologies can accomplish and is particularly useful for animals that forage or hunt out of sight. Researchers have documented foraging strategies that differ by species, age or sex [47-52]. Other studies placed accelerometer sensors on the head/mandible to directly measure attempts at food capture [53], although foraging effort did not necessarily correlate with foraging success [54]. There are several methods for identifying and categorizing waveforms that represent specific behaviors (see 'Best Practices', below). On average, these studies were able to identify four distinct acceleration waveform profiles (range 2 to 7), typically falling under the broad behavioral categories of locomotion, resting, and feeding/foraging [55-57]. In general, while the accelerometer patterns of active locomotory behaviors (walking, running, climbing, swimming and flying) are clearly distinguishable from inactive behaviors such as sleep, thermoregulation and digestion, the waveforms of these types of relatively immobile behaviors are not particularly distinct from one another [19].

When an accelerometer is combined with other sensors on a tagged animal, researchers can describe the broader ecological context of accelerometer-determined behaviors. Light level and ambient temperature sensors in tandem with accelerometry permit examination of activity timing in relation to environmental conditions [58-61]. Accelerometers and remotely-sensed location via GPS, compass, depth or acoustic sensors provide the spatial distributions of accelerometer-determined behaviors [62-66] and can lead to novel insights about species' behavioral ecology. For example, traditional observation-only research of the little-known oilbird (*Steatornis caripensis*) led to the hypothesis that these nocturnal frugivorous birds were not seed dispersers because the seeds from their diet were regurgitated in the dark caves where the birds roost. Holland

et al. [38] determined that oilbirds outfitted with GPS/acceleration loggers spent only every third day in caves, otherwise remaining in the rainforest where they regurgitated seeds onto the forest floor at considerable distances from both feeding sites and cave roosts. The authors maintained that oilbirds should be reconsidered as an important long-distance seed disperser in Neotropical forests, a novel hypothesis for the ecology of that ecosystem.

Behavioral analysis applied to monitor animal welfare was a significant component of accelerometry research on terrestrial animals; 80% of the terrestrial studies (and 25% of all studies) examined the welfare of domesticated species. Typically, authors used accelerometry to monitor behavioral changes associated with reproduction [67,68] or behavioral responses to veterinary or husbandry practices [69-74]. In studying welfare of free-ranging wild species, mortality sensors are a common feature of telemeters and typically provide a special signal to alert researchers to the animal's demise [75]. The advantage of using accelerometers to detect mortality is that it includes a record of behavior leading up to the time of death, providing a richer context than a simple location and time of death often do not. For example, Krone *et al.* [76] were able to identify a change in activity and, ultimately, the moment of death, due to toxin exposure in a white-tailed sea eagle (*Haliaeetus albicilla*).

What is largely absent from this body of 82 articles about activity budgets is the measurement of social behaviors. While numerous studies compared behavior budgets during particular reproductive states and reported ethograms for brooding or nest preparation [52,57,66,77-81], only two studies examined whether mating behavior had a characteristic acceleration profile [82,83]. The scarcity of published accelerometry ethograms for aggressive interactions, territorial or courtship displays, and play and parent-offspring behavior [84,85] could be because these social behaviors were generally rare in the majority of the species that have been studied, the acceleration waveforms of social behaviors were indistinguishable from those of non-social behaviors, or because it was not feasible to tag multiple animals in the same group. Inter-individual telemetry, with animals bearing tags that are able to record the date and time of proximity to other tagged animals has recently been reported for acoustic transmitters [86]. The application of accelerometers to studies of social behavior would benefit mightily from accelerometer tags that have the ability to record proximity, identity or even behavior of tagged individuals in contact with the animal that bears the primary tag.

Survey of questions currently served by accelerometry: biomechanics and the energetics of movement

Energetics have long been of interest to behavioral ecologists [87,88] because all movements require energy, and

prudent allocation of energy to specific activities such as foraging has direct consequences for fitness and natural selection [77,89,90]. Prior to the recent developments in accelerometry, measuring energy expenditure in wild animals in the field involved doubly-labeled water or heart rate telemetry, both of which have logistical limitations that have restricted their use [91,92]. Accelerometer technology has dramatically advanced our understanding of the role of energy in behavioral strategies by making it possible to study fine-scale, behavior-specific energy expenditure outside the laboratory in diverse taxa [93]. Wilson and Halsey *et al.* have tested for correlations between bodily acceleration and oxygen consumed (assuming at least predominantly aerobic metabolic pathways) across a wide range of species from aquatic mammals [94,95], birds [64,77,96-99], fishes [100,101], reptiles [52,102-104] and a bivalve [105], to terrestrial mammals, birds [56,106-108] and one amphibian [109]. Although the strength of the relationship between bodily acceleration and oxygen consumption (as a proxy for metabolic rate) varies and depends on a number of factors, the relationship is valid across all species examined to date [110]. Wilson's metric 'Overall Dynamic Body Acceleration' (ODBA) [77] has become the most commonly used acceleration-based proxy of metabolic rate (energy expenditure) and several articles have been devoted to standardizing this proxy or variants of it [19,106,110-112]. The current available research indicates that bodily acceleration can qualitatively assess how the amount of mechanical work performed by the body differs among active locomotive behaviors, a distinct improvement on older techniques that were not behavior-specific (Figure 7) [110].

Seventy-three articles applied accelerometry to biomechanical research (42.7% of all articles examined). A small minority of these studies (7), eschewed applications to metabolism and instead remained within the traditional realm of evaluating performance: running in racehorses [113-117], swimming in sea snakes [118], and flight in Procellariiform sea birds [119]. The remaining 90% of articles focused on energy efficiency during locomotion for travel or foraging [31,35,94,120-124]. In order to better understand the selection pressures on current patterns of locomotor behavior, researchers compared movement energetics across species, movement strategies, demographic classes and behaviors [42,48,102,107,122-127].

There was a strong habitat bias in existing accelerometry-based research on biomechanical energetics, with a heavy emphasis on marine diving animals such as Pinnipeds and Cetaceans [36,95,128,129], penguins [97,130,131], Pelicaniform birds [77,99,126,131-133], and marine turtles [79,134]. Terrestrial taxa, mainly birds, were represented in only five (of 66) studies of movement energetics [56,106-108]. Of the terrestrial species, we were able to identify only a single published field study of energetics for non-volant terrestrial animals: cane toads (*Bufo marinus*)

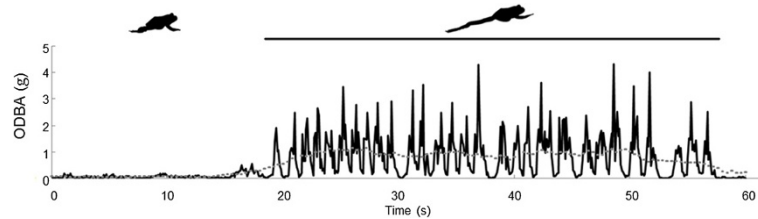


Figure 7 Overall dynamic body acceleration shown for a hopping and non-hopping cane toad *Bufo marinus*. This study was the first to use accelerometry to establish a behavioral time budget and assign energy costs to those behaviors for a non-volant terrestrial animal. Graphic reprinted with permission from [109].

[109]. Battery size and weight still mostly preclude accelerometry energetics studies of the smallest wild mammals (particularly bats) and birds. A further limitation is that accelerometers do not appear to be a particularly good proxy of energy expended during immobile but still energetically costly behaviors such as thermoregulation or gestation [107,135].

Potential application of accelerometry: position and location

Acceleration measurements can be used to derive animal speed, which, together with compass and depth/altitudinal information, could be used to 'dead-reckon' an animal's position. There are several existing methods for locating animals in space and time including radio telemetry [136], satellite or geographic positioning systems [11,137,138] and acoustic arrays [139]. None of these methods works for all species and habitats and, consequently, travel paths are frequently reconstructed by bridging sporadic points and have low spatio-temporal resolution [140,141].

Dead-reckoning (also known as path integration) uses vector calculations from velocity and the change in height or depth together with a known start position (usually the animal release point) to derive new positions with respect to those previously known [24,142]. Locations obtained by dead-reckoning, therefore, are not subject to the same constraints of receiver location or satellite access and represent an alternative method for studying movement paths when radio- or satellite-based telemetry methods are unsuitable. Dead-reckoning uses sensors on-board the telemetry tag that record heading/direction (usually measured with magnetometers), altitude or depth (usually measured with pressure sensors), and speed. In theory, speed can be calculated by taking the derivative of acceleration over a known time interval [130] or by using a known stride length and the accelerometer-measured stride frequency [142]. However, speed determined in this way can be subject to large errors due to variation in slope and substrate during travel [67,139]. These errors are particularly unpredictable in

aquatic or volant species, due to drift caused by water and wind currents rather than animal locomotion [142]. In terrestrial systems, terrain incline and substrate impact stride length, affect speed calculations and consequently the determination of distance moved. Furthermore, these errors accumulate over time, making location estimates increasingly worse further from the last known location. Because of these problems, dead-reckoning from accelerometry data has been used infrequently and most researchers interested in movement speed have added separate speed sensors (small external propellers) to the telemetry tags [24,137,141-144]. As GPS technology becomes more widely integrated into accelerometer tags, the greatest potential for dead-reckoned animal location comes in recreating the exact travel path between subsequent GPS locations collected at short intervals e.g., <15 min [24,139].

Best practices in data acquisition and data analysis: tag attachment and tandem sensors

Attaching telemetry tags to animals is a complicated and delicate process that requires care to reduce the influence of the equipment to the animal. Consultation with experienced field biologists and tag companies, not to mention proper literature review, is critical during the planning stage of any tagging study. In addition to the standard concerns of attachment longevity, device retrieval and whether tag attachment affects animal behavior [138], tag attachment for accelerometer sensors is especially sensitive because shifts of the tag relative to the position of the animal could impact the interpretation of the three-axis data. Extensive preliminary research on readily observable animals is often needed to fine-tune a new attachment method for a given species [145]. Common methods of accelerometer tag attachment include neck collars [20,55], leg bracelets [146], harnesses [109,145], and tape- [118], clamp- [147] or glue-on tags (Figure 2) [21,102]. A rigid attachment ensures that once the tag is deployed, the axes, or dimensions, of movement being measured do not change over the deployment period and that acceleration of the tag

independent of the animal (by a collar bouncing up and down on the neck, for example) is kept to a minimum [111]. For species that must wear collars or bracelets, a completely rigid attachment is not possible unless the collar can be prevented from turning around the neck/leg [55], which may present a welfare concern for free-ranging animals. For some questions, for example the timing of activity/rest, the requirement of rigid attachment may be relaxed. Finally, accelerometer tags can also be deployed inside the body cavity of some species [61,148], which may reduce concerns about tag movements that are irrelevant to the research question. Internal deployments may provide the advantage of recording accelerations due to physiological processes such as heartbeat and movements of smooth muscle during digestion [148], but can also have the disadvantage of necessitating surgical procedures for tag deployment and retrieval/removal, which can affect animal behavior and well-being.

The orientation of axes is typically placed so that the surge axis is aligned with the longitudinal body axis and sway with the horizontal body axis (Figure 2) [20]. Ensuring that tag position is as similar as possible between individuals, especially those of very different body sizes, improves the signal-to-noise ratio of the accelerometer output and minimizes errors in interpretation [20,63,101,131]. Beyond its orientation on the body, the specific anatomical location of the attached accelerometer tag largely determines, what behaviors can be distinguished by their accelerometry patterns. Both species morphology and tag placement will determine the number and type of behaviors with distinct acceleration profiles [44]. For example, tags attached to an animal's back, as in Figure 2 [38,109], will not provide acceleration patterns of fine-scale feeding behaviors that only involve movement of the mouth. On the other hand, accelerations of chewing movements may be detectable with neck collars [33,55]. In humans, it has been well established that precise accelerometer-based descriptions of full-body movement require at least five acceleration sensors, one mounted on the trunk of the body and one on each extremity [26]. Studies of free-ranging wild animal are typically limited to one telemetry tag per individual; however, multiple accelerometer instruments have been used on domesticated animals [149-152] and in a handful of wild marine species [53,54,153-157], improving the precision of behavior measurements.

Even when contained in a single tag, most modern accelerometers are combined with other types of sensors to enhance the amount of information collected simultaneously from the environment, such as light, air/water pressure, external air/water temperature, relative humidity and magnetic field [24], as well as from the animal, such as body temperature, heart rate and mouth/jaw movements [79,99,101,133,134,157-160]. In modern telemetry tags, each of these data sensors, including each axis of the

accelerometer, have their own separate channels for data recording, so that accelerometer data are collected independently of other information like GPS [24,160]. As a result, even if one sensor malfunctions or cannot acquire information momentarily (for example, the GPS unit spends several minutes attempting to access satellites and obtain a location), the other sensors continue to record data on schedule. In some tags, the activity levels of the animal as determined by the accelerometer can be used to set the recording schedules of other sensors dynamically. For example, the GPS schedule is set to acquire locations more frequently during active behaviors such as foraging and travel and less frequently during rest, improving the overall performance and battery longevity of the telemeter [21].

Best practices in data acquisition and data analysis:

sampling axes, sampling interval and sampling frequency
Sampling of all three axes of acceleration (tri-axial) is the most accurate and precise way of measuring behavior that occurs in three dimensions as well as estimating energy expenditure [20,161]. For some research questions or for relatively immobile species, one or two axes may be sufficient to characterize the behavior(s) of interest [23,80]. However, the efficiency of modern accelerometer sensors mean that little is gained, in terms of battery life, by using fewer axes.

The majority of studies in the literature sampled acceleration continuously, at frequencies above 1 Hz [97]. This type of sampling produces an extremely high volume of data; because each accelerometer axis is separate, three axes recording at 1 Hz produce three measurements per second, which rapidly accumulate into millions of logged measurements for a tag deployed over several days. In practice, continuous data are typically subsampled or averaged over several seconds' worth of measurements to create a running mean [111] so an alternative to continuous sampling is to record for a few seconds at intervals of one or more minutes. By recording at high resolution (e.g., 60 Hz) but short duration (e.g., 1 to 3 sec) this strategy aims to sample just one behavior type and avoid behavioral transitions (e.g., resting to walking) that could complicate automated classification statistics. Each discrete sampling period is then called a "burst" or an "epoch" [22,158]. Because burst studies record fewer data over the entire study period it is possible to download the data remotely through wireless connections [21,40], whereas continuous accelerometer data typically are logged over days or weeks and manually downloaded upon tag retrieval [143]. If animals are expected to remain within the vicinity of a fixed receiver, then continuous data may be transmitted wirelessly at intervals [161]. If proximity to a receiver is problematic, as with marine animals that can range over very long distances, data can still be collected at high resolution (high sampling frequency and continuous sampling

interval) as long as the entire sampling period matches device storage capacity, or there is periodic offloading of data via mobile receivers such as satellites.

Generally, the smaller the subject, the faster the movement and the higher the sampling frequency necessary to accurately characterize the pattern of acceleration [98,123,137]. From signal processing theory we have the rule-of-thumb that for adequate reconstruction of a continuous waveform such as acceleration, the sampling frequency ought to be at least twice that of the highest frequency movement being classified [162]. Sato *et al.* [123] measured the dominant stroke frequencies for several species of aquatic birds and marine mammals and they ranged from 0.2 Hz for sperm whales to 9.3 Hz in guillemots. Meanwhile, the three most common sampling frequencies in the literature were 10, 16, and 32 Hz but there was little a priori justification for the choice of sampling frequency. Halsey *et al.* found that accelerometer-sampling frequencies of 2 to 10 Hz were adequate for characterizing energy expenditure in chickens [19]. These studies suggest that sampling frequencies higher than 50 to 60 Hz are probably unnecessary for most research questions and that in such cases the additional data generated is wasteful of digital storage space. However, authors recommended that the research question and desired tempo-spatial resolution of the data should ultimately dictate the sampling frequency (and sampling interval) [19].

Best practices in accelerometer data analysis: describing the waveforms

For both continuous and burst sampling schemes, irrespective of sampling frequency, acceleration sensors produce raw data in a wave-like signal with units in voltage. Prior to analysis, researchers may use calibration equations to convert this signal into actual acceleration measured in m/s^2 or g units where $1g = 9.80665 m/s^2$ [57,127,154,159]. This calibration and conversion may be required for measuring the actual biomechanical forces experienced by animals during different movements, for example, the air to water transition for a diving seabird, or the strike force on horses' hooves when running. The dynamic body acceleration metrics also use the signal converted to acceleration as the proxy for metabolic exertion [96]. Alternatively, for simple acceleration ethograms or determining activity budgets, the signal may be used in the raw voltage state as depicted in Figure 6.

To describe the acceleration waveform patterns, researchers then calculate a wide variety of summary statistics using each burst's population of values or subsamples of the continuous measurements (Table 1). The statistics listed in Table 1 could be calculated for each axis individually or combined to represent multiple axes simultaneously [149].

There is a dichotomy in the literature on how researchers process and describe the wave-like properties

Table 1 Statistics used to describe acceleration waveforms

Summary statistic	Representative source(s)
Mean	[20,23,38]
Running mean for continuous data	[107,111]
Minimum, Maximum, Range	[125,130,163]
Variance	[23,36,112]
Standard deviation	
Inverse coefficient of variation	[62,112]
Resultant	
Overall dynamic body acceleration	[79,103]
Vector dynamic body acceleration	[112]
Subsequent-measurement autocorrelation	[62]
Trend (linear regression coefficient through axis data)	
Pair-wise correlations between axes data	
Inclination, azimuth of resultant and their circular variances	
Frequency power spectrum	Fast Fourier transformation [43,48,57,126,129] Continuous wavelet transformation [164]
Δ acceleration	[20]
Δ frequency	
Waveform frequency	[43,130]
Waveform period and amplitude	[32,164]
Area under the waveform curve	[163]
Skewness and kurtosis of the waveform	[165]
Signal magnitude area	[166]
Waveform length	
Waveform inheritance	

of accelerometer output. Some researchers have utilized simple waveform statistics, such as the number of peaks (frequency of the movement), the mean value of the waveform (body angle), and their variances [23,35,121,131,146,160]. Others have used specialized programs to perform complex analyses on the waveforms, resulting in a large number of additional descriptive statistics [34,46,55,127,130,144,156,161,165]. There are numerous complex techniques for analyzing data that, like acceleration, exist in a time series [167,168]. The most commonly used method with accelerometer data is the fast Fourier transformation. Fourier transformations identify the individual frequencies that are present in the raw acceleration waveform and determine the power spectral densities of those frequencies, i.e., how much of the total signal is present in each frequency [162]. Another complex approach is continuous wavelet transformation, which identifies not only which frequencies are present, but also

when during the signal they are present [164]. Shepard *et al.* [20] and Laich *et al.* [23] suggest that these complex analyses are not essential and that simpler statistics are both intuitively and practically more accessible for the broadest range of potential users. However, they acknowledged that when behaviors “are transitory and/or highly variable” p. 36 [23], or are measured using only one axis of acceleration, the more complicated techniques and the additional statistics they provide may prove helpful for identifying or distinguishing different behaviors.

Data filters for separating gravitational acceleration from inertial acceleration

Recall that the accelerometer waveform output during movement is a combination of acceleration due to gravity and inertial acceleration due to animal movement (dynamic acceleration). When isolated, gravitational acceleration can be used to determine the orientation of the body in space (posture or body angle) [23,55,57]. The gravitational component can be isolated by: i) applying a low-pass filter such as 0.1 Hz that removes high frequency acceleration [41,78,79,121,164]; or ii) by smoothing (i.e., calculating a running mean) over a large set of measurements [57]. For acceleration sampled over a few seconds in a burst, taking the mean value of a single burst’s measurements can suffice for isolating momentary gravitational acceleration, or body angle [21]. One can see how this works in Figure 5; note the relatively flat slope of voltage output for all three axes when the animal is more or less motionless (left side designated ‘resting’). Between minutes 2 and 4, the mean value of the heave axis shifts dramatically as the animal changed position during rest from a ‘feet-up’ posture to a ‘feet-down’ posture. The change in the mean value of the heave axis represents a change in voltage output stimulated by gravitational acceleration after the tag (the animal) changed orientation. Determining exact body angle requires calibration of accelerometer voltage output as the tag is passed through 360 degrees along each axis. Using this method, researchers calculated body “pitch” angle from the heave or surge axes and body “roll” angle from the sway axis, also correcting for the position of the tag on the animal [41,163].

Conversely, researchers used high-pass filters to examine accelerations due to movement in isolation from the gravitational component of acceleration [63,159]. This dynamic component was used to calculate the measures of dynamic body acceleration in the majority of the studies on energetics [19,20,24,77,97,107,109,111,142,159]. Frequency filters were also used to reduce the noise in the acceleration signal created by non-rigid attachments of accelerometer collars [31] and to isolate the pattern of one particular type of dynamic behavior that occurred simultaneously with other movements, namely prey capture events during swimming [155,156]. Spectral and other waveform analyses discussed

in the previous section are often conducted on dynamic acceleration after its isolation by high-pass frequency filtering.

Best practices in accelerometer data analysis: validation and assigning characteristic waveforms to behavior

The advantage of accelerometers is that they provide a remotely collected record of behavior: large sets of acceleration waveforms that were mostly not observed by the human eye. To understand how the acceleration record and the statistical properties of the waveforms relate to observable behavior, researchers using this tool must have a way of assigning the waveforms to specific behaviors or behavioral categories with a high degree of accuracy (validation). This task requires some prior knowledge of the behaviors animals perform and studies, to date, have generally obtained this information from deployments on similar domesticated animals, captive individuals and brief periods of observation on free-ranging wild animals, some via video [36]. Carefully synchronized observations and accelerometer recordings validate what behaviors correspond to what accelerometer measurements, for example, the relatively flat waveforms that occur during rest compared to the variable waveforms that occur during activity (Figure 5). This process also must quantify to what extent accelerometer waveforms for the same behavior vary within an individual, or between individuals or species [19,109]. This validation process is a critically important part of using accelerometers. The accuracy of the conclusions drawn from assigning behaviors or energy expenditures to accelerometer waveforms depend enormously on the accuracy of the assignments (see discussion below on methods reporting).

This fact notwithstanding, wild animals, particularly aquatic species, may not be observed at all between release and tag recovery [42]. Even when animals are being observed directly, it is hard to be certain that all possible relevant behaviors have been witnessed [169], especially when extrapolating behavior in captivity to behavior in the wild. As accelerometry has matured, researchers have developed special software tools to address this obstacle and reduce the time and labor necessary for direct observation [164,170]. With knowledge of i) general body shape, ii) form of locomotion (bipedal, quadrupedal, etc.), and iii) how the tag is attached to the body, these software programs can help researchers visualize the movement of their study animals according to the accelerometer signals recorded during tag deployment [170].

Manual examination of accelerometer data is essential in the pilot phases of a study, but an automatic system to categorize waveform patterns and assign them to different behaviors quickly becomes necessary due to the large size of the acceleration data sets. After calculating waveform characteristics such as those listed in Table 1, there are two major approaches to automatic waveform classification in the literature. The first is to use statistical

algorithms to cluster accelerometer waveforms with similar characteristics and then assign each cluster to a general behavioral group [163]. For example, Sakamoto *et al.* [164] used an unsupervised k-means clustering algorithm to assign accelerometer waveforms from a diving seabird to 20 different groups, which they matched to simultaneously recorded depth profiles and then labeled with different behavior groups including ‘in flight’, ‘underwater diving’ and ‘on land’. The second, more common approach is to use the accelerometer waveforms generated from known (observed) behaviors of similar domesticated or captive individuals to train an algorithm that will assign the remaining waveforms in the dataset to those specific behavioral categories. For example, Nathan *et al.* [56] observed wild and captive vultures exhibit a variety of behaviors while wearing accelerometer tags and then used various supervised statistical algorithms to categorize the accelerometer waveforms as either active flight, passive flight (soaring-gliding), eating, lying down, preening, standing or running. Both methods lessen the burdens of extended direct observations and manual analysis of accelerometer data, however, the former has the potential to detect previously unknown or unobserved behaviors and behavioral sequences while the latter has the advantage that behavioral categories correspond directly to observations. Both rely on the validation process for accurate conclusions. Table 2 summarizes the assignment methods and algorithms represented in the literature; Nathan *et al.* [56] reviews and compares several of the supervised algorithms in detail.

Regardless of the method used to assign accelerometer waveforms to behaviors, each group of researchers develops its own set of waveform statistics to feed to what are largely custom-designed automatic classification systems. Algorithms that deal with one particular domain

of activities (e.g., diving in aquatic animals) may not be easily adapted for a different environment or different set of movements [32]. Furthermore, 58% of scientists working with domestic species and 47.6% of those working with captive wild species reported the performance and reliability of their chosen automated classification systems [55,72], while only 9.1% of those studying wild species did so [23,44,57,83]. Lack of methods reporting, from the accelerometer-recording schedule to whether and how accelerometer data is validated, stymies direct comparisons between studies and between analytical approaches. As previously discussed, validation is an essential part of using accelerometer as a stand-in for direct observation. If accelerometers are to achieve widespread use in studies of free-ranging wild species, there will have to be more complete reporting of methods, particularly for the classification phase of analysis.

Best practices in accelerometer data analysis: data visualization and storage

We noted earlier that the high resolution of accelerometry results in a large volume of data accumulating over a short period. For example, a single-axis accelerometer tag recording continuously at 8 Hz for 8 hours and 40 minutes resulted in 249,988 measurements [170]. When combined with the data from sensors deployed in tandem with tri-axial accelerometry, such as GPS, depth, or temperature telemeters, the dataset in its entirety can easily overwhelm basic spreadsheet and statistical programs and it becomes difficult to visualize more than one data stream at a time. ‘Igor Pro’ (WaveMetrics, Lake Oswego, OR, USA), ‘R’ (R Foundation for Statistical Computing, Vienna, Austria) and ‘Matlab’ (MathWorks, Natick, MA, USA) are commonly used for acceleration data analysis and can handle large datasets [83,164,165], although all three programs have a considerable learning curve. We are aware of two web-based options geared towards animal-borne telemetry data visualization, storage and analysis. *MOVEBANK* (available at <https://www.movebank.org/>) is a free, online database of animal tracking data that helps researchers to manage, selectively share, protect, analyze and archive their data. With *MOVEBANK*, researchers can link animal behavior from accelerometer data with animal location data from GPS and information from global environmental datasets, such as weather models and satellite imagery, making it easier to explore how animals’ movements relate to their environment. Gao *et al.* presented another online accelerometer data storage and analysis system, the Semantic Annotation and Activity Recognition system [166]. Their interactive web interface enables ecologists to visualize and correlate tri-axial accelerometer data streams while also facilitating accelerometer data analysis with a support vector machine classification algorithm. A major benefit to using these web-based repositories is that the

Table 2 Methods for assigning accelerometer waveforms to behavioral categories based on waveform statistics

Method	Representative source(s)
Manual	
Reference patterning	[34,98,108,127,171]
Fixed-threshold	[31,57,83,161]
Unsupervised machine learning algorithms	
Cluster analysis	[164]
Supervised machine learning algorithms	
Classification and regression trees	[24,77,172]
Random forests	[55]
Linear or quadratic discriminant analysis	[55,132,149]
Logistic regression	[55,148]
Support vector machines	[162,172]
Artificial neural networks	[55,172]

average biologist tracking a handful of animals gets access to collaborations with other biologists, statisticians, engineers and computer programmers who can collectively continue to develop this tool and the hardware and software that make the most of accelerometry's potential.

Conclusions and future directions

Accelerometry is a tool for fine-scale observations of behavior, unlimited by animal visibility, terrain, climate, observer bias or the scale of space use. To date, accelerometer tags have been applied to more than 120 species in diverse taxa in order to deduce body postures, behaviors and energetics in the field. Accelerometry also shows potential as a method to 'dead reckon' an animal's exact travel path when applied in tandem with satellite-based location systems. In all of the research described, accelerometry provided fine-scale behavioral measurements that, prior to its development, were rarely attainable outside of the laboratory setting and without the influence of the researchers' presence.

The literature shows several taxonomic biases in what research questions have been examined and how the results have been reported. Studies of wild aquatic species outnumber studies of wild terrestrial species. Research on aquatic animals (whether captive or wild) has focused on describing the biomechanics and energetic consequences of behavior, while in terrestrial systems the focus was on determining activity budgets. Both at sea and on land, feeding, locomotion, and activity/rest were the behavior categories most frequently analyzed; social behaviors (parental care, territorial, mating and courtship behaviors, and antagonistic exchanges) are nearly absent from both ethograms and energy budgets. Researchers of domestic and captive species tended to report analysis methods more thoroughly than those studying species in the wild.

There are substantial challenges to getting the most out of accelerometer data, including device retrieval and data calibration, validation, management and analysis. Numerous techniques for addressing these challenges have already been published in both human and animal studies and new methods continue to develop and are awaiting broad application to the field. With more thorough reporting of methodology and habitual use of web-based data repositories, universal practices are bound to emerge as hardware and software continues to mature and become more broadly available across research groups.

Future directions

The rapid development of this tool in the field, thus far, leads us to anticipate two promising breakthrough applications that will open even more doors in behavioral research. The first is the incorporation of inter-individual telemeters in the study of social behavior. Device-to-device data sharing and proximity sensors exist in the consumer electronics

industry and have already been incorporated into acoustic telemeters [86]. Most modern telemetry tags have multiple data channels and could be modified to include these features. Accelerometer tags that have the ability to record proximity, identity and even behavior of tagged individuals in contact with the animal that bears the primary tag, would reduce the burden of extensive direct observation, yet permit scientists to directly question how individuals interact and how those interactions shape behavior across a large number of social and territorial species. Secondly, we recommend that researchers entering the field of wildlife telemetry look to explicitly link energetic expenditure in wild animals with behavioral responses to human-altered habitats [163]. Whether considering climate change, resource competition or anti-predator defenses, the potential toll on fitness should manifest in energetic expenditure and allow a window onto the longer-term consequences of our impacts on other long-lived species. Accelerometry offers a level of detail in behavioral studies of free-ranging wild animals that has previously been impossible to achieve and it has proven itself in furthering our understanding of the role of behavioral mechanisms in ecological and evolutionary processes.

Additional file

Additional file 1: Spreadsheet of all studies analyzed for this review. Column headings indicate the information taken from the study, studies are listed in rows by first author.

Competing interests

APK, MW, and RW are on the editorial board of *Animal Biotelemetry*. The authors declare that they have no other competing interests.

Author's contributions

DB collected the articles used in this review, carried out the data analysis, and drafted the manuscript and Figures 1 to 5. RK initially conceived of the idea to write a review of the subject and heavily influenced the organization of the information. MW, RW, and APK made critical revisions to drafts for comprehensiveness and presentation of the information. All authors read and approved the final manuscript.

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