

Using technology to monitor and improve zoo animal welfare

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Abstract

While the international zoological community is committed to enhancing the welfare of individual animals, researchers have yet to take full advantage of the tools available for non-invasively tracking behavioural and physiological indicators of welfare. We review technology currently being applied in studies of zoo, farm and laboratory animals to regularly monitor welfare status, as well as to evaluate responses to particular stimuli and situations. In terms of behavioural measures, we focus on automated assessments that offer insight into how animals — even those that are nocturnal or elusive — behave when humans are not present. Specifically, we provide an overview of how animal-attached technology (accelerometers, global positioning systems, radio frequency identification systems) can be implemented to generate activity budgets, examine use of space, conduct gait assessments, determine rates of movement and study social dynamics. We also emphasise the value of bioacoustics, as the rate and acoustic structure of certain vocalisations may vary across contexts and reflect an animal's internal state. While it can be challenging to identify non-invasive methods for investigating physiological welfare indicators, we discuss approaches (thermography, tracking measures of heart rate) that may be especially useful for monitoring affective states and psychophysiological functioning. Finally, we make a concerted effort to highlight tools that allow welfare scientists to consider measures of positive welfare. Ultimately, zoos can ensure that each animal has the opportunity to thrive by employing technology to create baseline behavioural and physiological profiles, conduct ongoing monitoring schemes and assess responses to specific conditions, events and stimuli.

Keywords: animal welfare, automated monitoring, behaviour, physiology, positive welfare, technology

Introduction

Recently, zoos and aquaria (hereafter zoos) have dramatically increased efforts to monitor and improve animal welfare (Walker *et al* 2014). Zoo associations across the globe, including the World Association of Zoos and Aquariums (WAZA), have expressed a commitment to proactively identifying and resolving welfare issues faced by populations and individual animals (Hosey *et al* 2009). Indeed, WAZA's World Zoo and Aquarium Animal Welfare Strategy offers guidance on attaining high welfare standards, outlines best practices, promotes research and encourages its members to serve as animal welfare leaders (Mellor *et al* 2015). Among organisations accredited by the Association of Zoos and Aquariums (AZA), a handful of centres have been established to examine welfare policy and/or implement welfare research (eg Chicago Zoological Society's Center for the Science of Animal Care and Welfare). Within the zoo community, there is a consensus that future research efforts must focus on identifying tools for systematically tracking and assessing animal welfare (Barber 2009; Hosey *et al* 2009; Butterworth *et al* 2011). Indeed, the mission of AZA's Animal Welfare Committee (AWC) includes, "encouraging the development of research

projects and assessment tools to advance and monitor animal welfare" (AZA 2015). This mission reflects a more widespread movement that urges the zoo industry to move beyond a resource-based approach to welfare assessment. While zoos traditionally have focused on outlining particular environmental requirements and management practices for accreditation purposes, welfare researchers emphasise the importance of incorporating animal-based measures (eg hormones, behaviour) that reflect an individual's physical and psychological states (Barber 2009; Butterworth *et al* 2011; Siegford 2013; Whitham & Wielebnowski 2013).

Over the past several decades, zoo welfare scientists have adopted a variety of valuable methods for assessing individual animal welfare. Most commonly, researchers have relied upon tracking hypothalamic-pituitary-adrenal axis (HPA) activity via non-invasive hormone monitoring, conducting behavioural observations (eg recording self-injurious behaviours), or documenting health indicators (Wielebnowski & Watters 2007; Hill & Broom 2009; Melfi 2009). While zoos have gained extensive knowledge by employing these approaches, there are certain limitations for those hoping to regularly monitor the welfare status of individual animals. For instance, it can be challenging to distin-

guish between an adaptive ‘stress response’ and chronic stress when using hormone monitoring, as adrenal responses are sometimes associated with events that do not negatively impact welfare over the long-term (eg breeding introductions). Moreover, an exposure to a stressor does not always result in increased adrenal activity (Wielebnowski 2003). Similarly, behavioural observations — often considered a vital component of welfare monitoring — may not provide a comprehensive view of welfare status when used independently. Often, exotic species do not overtly display indicators of poor welfare (Broom 2007). Even if signs of positive or negative welfare are expressed, researchers typically are limited to collecting data during zoo hours (unless cameras are employed) and observing only a few individuals at a given time. Furthermore, even trained personnel encounter visual obstructions, experience observer fatigue and have difficulty estimating variables, such as inter-individual distances (Hacker *et al* 2015). There clearly is a need for effective, reliable tools that allow zoos to monitor elusive, cryptic and nocturnal animals — especially when staff and visitors are not present. Moreover, measures and methods should be combined whenever possible to gain better insight into individual animal welfare. In a recent review, Whitham and Wielebnowski (2013) promote the integration of behavioural, physiological and biological indicators of *good* welfare (eg exploratory behaviours, certain vocalisations) and even touch on new technological breakthroughs for monitoring individual animals.

The current article reviews technology now being applied in zoos, farms and laboratories that can be combined with traditional measures to assess and enhance the welfare of individual animals. Specifically, we discuss technology that allows for the automatic recording of behaviour and the tracking of physiological indicators of welfare. While some of the tools described here can be employed in veterinary contexts (eg using accelerometers to detect lameness or infra-red thermography to identify inflammation), the goal is to highlight how technology can offer insight into an animal’s behaviour and/or affective states — either via continuous welfare monitoring or repeated assessments. Whenever possible, an attempt was made to present examples of tools that provide measures of positive welfare. Furthermore, because zoos care for exotic, endangered animals, we consider approaches that involve minimal restraint and handling rather than those that require surgical procedures or other invasive treatments (eg implantable loggers). This review also focuses primarily on tools that can be applied in naturalistic settings. In some cases, we describe measures for which inconspicuous, non-invasive technology is not yet available, with hopes that existing methods and materials can be modified for zoo animals. Even if equipment is available, technology evolves rapidly. Therefore, instead of recommending specific models for devices, we discuss some of the factors that must be considered when selecting equipment. Finally, while some tools can only be applied to terrestrial species, we include examples of how technology can be used to examine activity patterns, acute responses to the environment, chronic stress and overall welfare status for a wide range of taxa.

Technology for monitoring behaviour

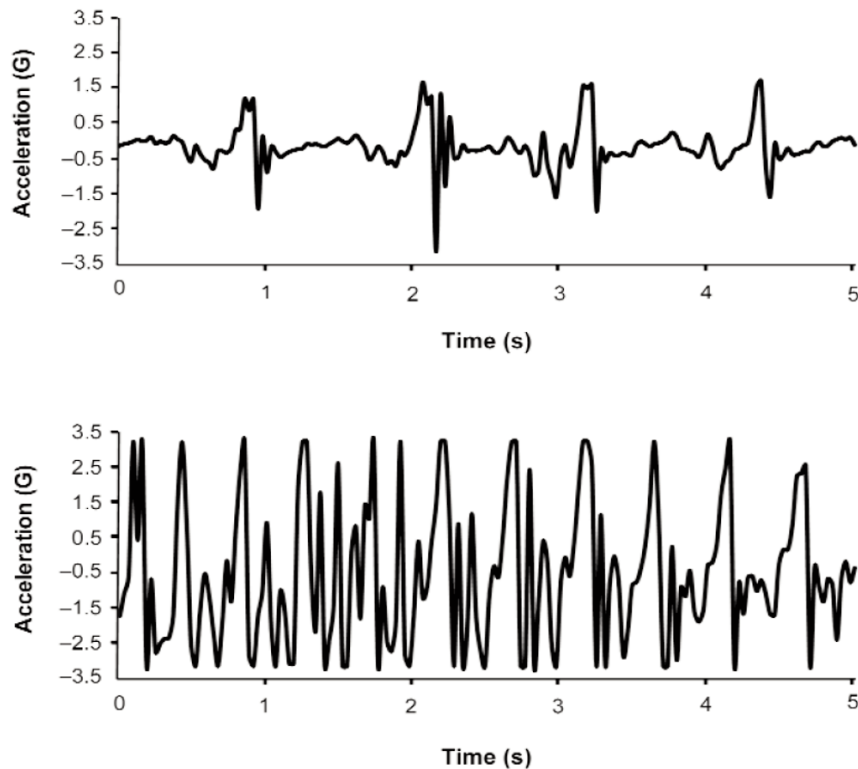
In recent years, welfare researchers have relied upon automated assessments to track animals that cannot be easily monitored by employing traditional methods. It is possible to use animal-attached technology to investigate postural behaviour, locomotor activity, movement patterns and even behaviours indicative of positive welfare. With this information, welfare scientists have the ability to generate activity budgets, calculate walking distances, analyse gait, track use of space and understand how an animal views its social and physical environments. These tools allow zoos to monitor animals that are elusive, nocturnal or live in large social groups. Indeed, many automated assessments can be performed regardless of visibility, terrain or time of day — making it possible to track animals even when staff and visitors are not present. Furthermore, researchers can collect data on behaviours that occur infrequently (eg vocalisations) and would otherwise be very time-consuming to investigate.

This article discusses only some of the technology now available for welfare monitoring. Many of the tools described below can be employed to create ‘baseline profiles’ for individual animals and then to evaluate responses to specific conditions or events. We do not review the technology available for conducting behavioural observations, though software and applications have been developed for recording behavioural states and events (eg Lincoln Park Zoo’s ZooMonitor, Tracks Software, Chicago, IL, USA; EthoTrak Observation System, Chicago Zoological Society, Brookfield, IL, USA; Animal Behaviour Pro, Nicholas Newton-Fisher, University of Kent, Canterbury, UK).

Accelerometers

Accelerometers are sensors that estimate body acceleration, either in intervals or continuously, along one to three axes (Wilson *et al* 2008; Brown *et al* 2013). Total acceleration represents the combination of both static (gravity-based) and dynamic (movement-based) components, allowing for the measurement of the animal’s orientation/posture and movement, respectively (Wilson *et al* 2014). The most precise information can be gained by using tri-axial accelerometers, which involves aligning three sensors orthogonally to measure sway (lateral acceleration), surge (front-back acceleration) and heave (up-down acceleration). While the sensors generate raw voltage data, patterns of waveforms can be used to develop ‘acceleration ethograms’ for particular behaviours and, ultimately, to create activity budgets (Brown *et al* 2013). Accelerometers are particularly useful for species that are difficult to observe due to nocturnal or crepuscular behaviour, visibility issues and/or inaccessible habitats, including species living in aerial and aquatic environments. According to a review conducted by Brown *et al* (2013), accelerometers have been used on over 120 species. Since the late 1990s, researchers have employed portable accelerometers to investigate energy expenditure, activity patterns and the postural behaviour of livestock, companion animals, free-ranging species, laboratory animals and zoo-housed species (eg Wilson *et al* 2008; Rushen *et al* 2012; Brown *et al* 2013).

Figure 1



Accelerometers can be used to differentiate gait types in dairy calves. Graphs represent acceleration of calves' legs in the vertical dimension. Individual steps can be identified for calves when walking (upper) and galloping (lower). Figure redrawn by Rushen *et al* (2012) from data presented in de Passillé *et al* (2010) with permission granted for re-use here by both.

One of the most common applications of accelerometers involves examining aspects of postural or locomotor behaviour to identify signs of lameness and discomfort. For example, by attaching two tri-axial accelerometers (one on the back, one on the hind leg) to gestating sows (*Sus domesticus*), Ringgenberg and colleagues (2010) were able to differentiate between standing, lying ventrally and lying laterally. The authors note that while observations of postural behaviour can be highly subjective, the 'postural time budgets' created by accelerometers not only provide insight into how much time an animal spends resting but also whether it is having difficulty shifting positions (eg lying down). Step counting, conducted via accelerometers and other sensors (eg pedometers), is frequently studied in the livestock industry to track locomotor activity, detect lameness and assess the adequacy of particular features of the environment, such as flooring (eg Platz *et al* 2008; Chapinal *et al* 2010; Ringgenberg *et al* 2010; Ouweltjes *et al* 2011; reviewed by Rushen *et al* 2012). Finally, accelerometers allow researchers to conduct gait analyses by measuring variables, such as stride length, stride frequency and speed (eg domestic dogs: Barthélémy *et al* 2009), as well as by attaching multiple devices to detect asymmetric stepping (eg dairy cows [*Bos taurus*]: Pastell *et al* 2009). Accelerometers can even be employed to differ-

entiate various forms of locomotion or gait types (eg dairy cows: de Passillé *et al* 2010; Figure 1). There is great potential for using accelerometers to regularly monitor baseline patterns of movement and to detect signs of pain, disease or discomfort in zoo animals.

In addition, there is evidence that accelerometers can differentiate between a wide range of behaviours and be used to create daily activity budgets. Researchers have employed lightweight accelerometers to identify the activities of hens (*Gallus gallus domesticus*) (Banerjee *et al* 2012), track the behaviour of goats (*Capra aegagrus hircus*) at pasture (Moreau *et al* 2009), estimate the activity of wild red deer (*Cervus elaphus*) (Löttker *et al* 2009), distinguish some common behaviours (eg eating, trotting, galloping) performed by free-ranging domestic cats (*Felis catus*) (Watanabe *et al* 2005), detect various sea turtle (*Chelonia mydas*) nesting behaviours (Nishizawa *et al* 2013) and monitor the behaviour of Adélie penguins (*Pygoscelis adeliae*) on land and at sea (Yoda *et al* 2001). In zoos, scientists have implemented accelerometers to study the behaviour of various mammalian species. Accelerometers proved to be especially useful for Sellers and colleagues (1998), who were able to distinguish between resting, leaping, walking and climbing for a mongoose lemur (*Eulemur mongoz*) fitted with a harness. The authors argue

that while behavioural observations are not always practical for nocturnal prosimians that spend large amounts of time out of view, researchers can develop 'locomotor budgets' based on the patterns of data generated by accelerometers. By using a harness fitted with a matchbook-sized accelerometer, Takahashi and colleagues (2009) determined that a koala's (*Phascolarctos cinereus*) activity levels were positively correlated with the occurrence of one oestrus behaviour (bellowing) and negatively associated with weekly weights. In a study of African elephants (*Loxodonta africana*), Soltis and colleagues (2012) found that tri-axial accelerometers, attached via collars, effectively distinguished between walking, feeding and even swaying, a repetitive behaviour. The researchers validated this method by comparing accelerometer data to videotaped behavioural observations and suggested that by doing so for various age/sex classes, accelerometers can be used to generate behavioural profiles for individual animals. These studies provide evidence that accelerometers can be a valuable tool for animal care staff looking to monitor baseline patterns of behaviour and movement regardless of the time of day, visibility of the animal or obstructions in the environment.

While compiling activity budget data is clearly worthwhile, we argue that accelerometers should be specifically used to highlight positive indicators of welfare. Wilson and colleagues (2014) demonstrated that different features of accelerometer data can provide information about how micro-movements are linked to internal states in humans, cockroaches (*Blaberus craniifer*) and African elephants. Specifically, these authors reported significant differences in the posture of African elephants experiencing positive versus negative affective states (ie walking between desired resources versus walking away from the dominant animal after being displaced). As discussed by Whitham and Wielebnowski (2013), it may also be possible to determine if an animal is experiencing positive affective states by monitoring sleep patterns (see also Langford & Cockram 2010). Studies on humans have shown that self-reported positive affect is associated with fewer sleep problems (eg number of occurrences of waking). By attaching a single accelerometer to the necks of calves, Hokkanen and colleagues (2011) successfully identified 90% of total sleeping time, including the occurrences and durations of sleeping bouts. Similarly, Holdgate and colleagues (Holdgate 2016a) attached anklets to Asian (*Elephas maximus*) and African elephants from 40 zoos and found that recumbence was associated with substrate type (for both species), the amount of space experienced by animals at night (for African elephants) and the amount of time spent alone at night (for Asian elephants). The authors note that recumbence is a proxy for sleep in elephants, and argue that understanding patterns of recumbence can inform management decisions. It may even be possible to use accelerometers to detect locomotor play, an indicator of good welfare for young individuals of many species (reviewed by Boissy *et al* 2007; Held & Špinka 2011). Rushen and de Passillé (2012) discovered that measures of acceleration could be used to estimate the duration of play

running in dairy calves. Indeed, it may be far more practical to rely upon accelerometers than behavioural observations when examining locomotor play, as play behaviours tend to occur relatively infrequently, particularly in adults (Held & Špinka 2011). By using accelerometers to track specific behaviours, especially those that may be difficult or time-consuming to observe, researchers can gain insight into how comfortable an animal is in its environment.

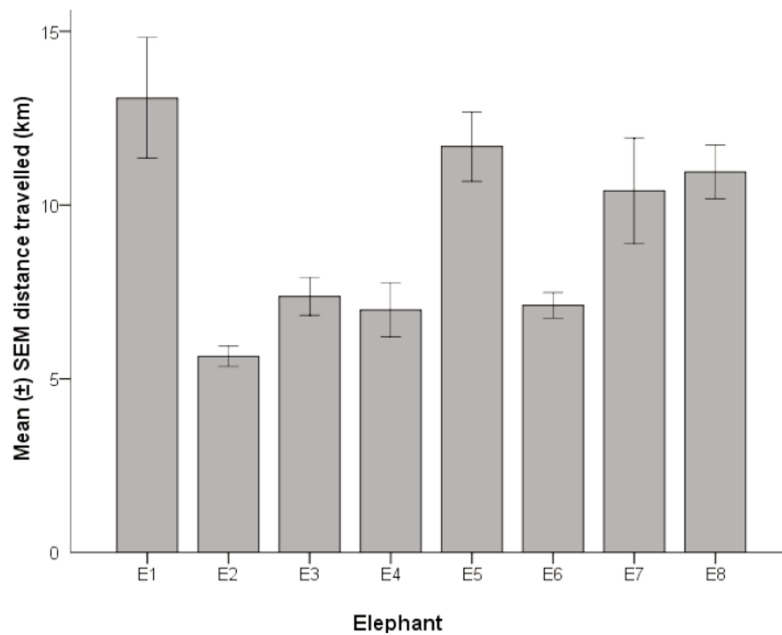
While accelerometers appeal to the zoo community due to the fact that they are affordable and lightweight, welfare scientists must consider several factors and potential limitations before implementing these devices (Brown *et al* 2013). Perhaps most importantly, the researcher must determine whether accelerometers have been validated for the species in question and, preferably, for particular age/sex classes. In fact, it may be necessary to collect behavioural data to validate the units for particular individuals, as Soltis and colleagues (2012) noted that behaviours such as swaying may vary across individuals (eg front-to-back vs side-to-side). Furthermore, accelerometers can be tested by hand-counting steps, as well as by attaching two devices to one animal to evaluate inter-unit agreement (eg Rothwell *et al* 2011). The researcher must also decide how to sample the data (continuously vs repeated bursts) and analyse the acceleration waveforms generated by the device (Brown *et al* 2013).

Before initiating a study, one must also ensure that the devices do not negatively impact the animals and, hence, skew the data. The researcher should work with animal care staff to determine how and where to attach the device. Common attachment methods include collars, anklets, harnesses and clamps, and the placement of the device will dictate the types of behaviours that can be monitored (Brown *et al* 2013). Furthermore, it is important to consider whether the subject or conspecifics can remove the device (Rothwell *et al* 2011) and whether factors such as colour, mass or shape affect the animal (Wilson *et al* 2008). In fact, researchers should train the animal to participate with attachment/removal procedures, allow time for habituation and collect behavioural data prior to and after attachment to rule out behavioural effects (Rushen *et al* 2012; Brown *et al* 2013). With careful planning, accelerometers can provide great insight into an animal's welfare by tracking postures, activity patterns and even specific behaviours over time.

Global positioning systems

Global positioning systems (GPS) technology is a satellite-based system that can pinpoint a subject's location by using receivers to triangulate signal information. Satellite telemetry gives researchers the ability to accurately track an animal's movement over a 24-h period by providing rapid position updates (Tomkiewicz *et al* 2010). By monitoring a subject's location over time, GPS units can provide information about habitat use, activity levels, rates of movement and distance travelled. Not surprisingly, these devices are being integrated into studies designed to track the distribution, grazing preferences and activities of free-ranging livestock (eg Ungar *et al* 2005; Tomkins & O'Reagain 2007; reviewed by Handcock *et al* 2009). In ecological

Figure 2



Examining daily distance travelled by implementing GPS technology. GPS technology can be employed to examine average daily distance travelled in a zoological environment. Data were collected on eight African elephants at the San Diego Zoo Safari Park. GPS locations were collected every 5 s to accurately calculate distance travelled over a 24-h period. Figure reprinted from data presented in Miller *et al* (2012).

studies of wild populations, researchers apply GPS technology to examine questions about home range, dispersal and patterns of movement (Cagnacci *et al* 2010). Cagnacci and colleagues (2010) argue that because “movement is the glue that ties ecological processes together”, GPS data offer insight into how and why individuals use particular resources, interact with conspecifics and prefer certain habitats (p 2159). GPS technology has even been applied to animals in marine environments (eg king penguins [*Aptenodytes patagonicus*], green sea turtles), small mammals and birds (reviewed by Tomkiewicz *et al* 2010). While this method can be very useful for large groups of animals, cryptic species, or those that are difficult to observe, most zoo research has focused on large mammals. Several zoo studies have investigated how GPS devices can be used to assess rates of movement, distance travelled and use of space in elephants (Leighty *et al* 2009, 2010; Horback *et al* 2012; Miller *et al* 2012; Hacker *et al* 2015). In a study of African elephants, Miller and colleagues (2012) found that GPS units — whether fitted to collars or anklets — accurately assessed walking rates and daily distance travelled (Figure 2). Similarly, Leighty and colleagues (2009) designed custom-made collars that included GPS devices to examine rates of movement in female African elephants. In addition to finding a positive correlation between rate of movement and mean temperature, their results suggest that elephants move at higher rates when living in complex social groups in relatively large enclosures. The same authors found that dominant females

used significantly more space, spent more time in particular parts of the enclosure (eg narrow, peripheral areas) and were more likely to use the watering hole than lower-ranking females (Leighty *et al* 2010). In a multi-institutional study of both African and Asian elephants, Holdgate and colleagues (2016b) used anklet-attached devices to determine that daily walking distances were impacted primarily by social and feeding-related variables. The authors reported that unpredictable feeding schedules and diverse methods of food presentation were associated with greater walking distances and suggested that dynamic feeding programmes may promote exploratory behaviour, an indicator of positive welfare (reviewed by Boissy *et al* 2007). GPS devices can help researchers explore associations between patterns/rates of movement and husbandry practices, health issues (eg obesity), physiological measures, environmental conditions and habitat complexity. GPS technology can even serve as a tool for examining social relationships, as the co-ordinates provide a measure of inter-individual distances. Hacker and colleagues (2015) conducted behavioural observations on African elephants while deploying GPS-fitted collars and discovered that individuals that spent more time in proximity to one another were more likely to exchange affiliative behaviours than dyads that spent less time in proximity. This relationship was specifically found when considering data collected during the evening hours, highlighting the value of this method for gaining insight into ‘true relationships’ that are not influenced by interactions with staff. This study also

revealed an association between GPS data and keeper input regarding social relationships. Overall, GPS technology offers a window into how animals interact with conspecifics and the environment when humans are not present.

As with accelerometers, researchers must consider several factors and limitations before initiating a GPS study. If this is the first time that GPS devices are being applied to the species of interest, one should review the specifications for available receiver modules. Units vary in multiple ways, such as size, operational life, number of available channels, power efficiency, voltage requirements and options for data storage and retrieval (Tomkiewicz *et al* 2010). It may be helpful to contact the manufacturer to discuss the mass of the animal, unit size and possible attachment methods (Tomkiewicz *et al* 2010). The general rule of thumb is that the device should not exceed 5% of the animal's body mass (Zekavat & Buehrer 2011). Also, it is important to note that the method and site of attachment can greatly influence system functionality and even the validity of the data, due to animal movement and interference. For instance, while there is evidence that both collars and anklets can be used to calculate the walking rates of African elephants, anklets may not be as accurate in determining exhibit use (due to the animal's body blocking location attempts), and collars may overestimate distance travelled for individuals that engage in repetitive swaying (Miller *et al* 2012). This highlights the importance of collecting behavioural data to validate the use of GPS technology for particular species and individuals. The accuracy of each wearable device can be evaluated in numerous ways, such as comparing position fixes to those produced by a hand-held GPS unit (eg Leighty *et al* 2009) and placing the device at pre-measured distances (eg Miller *et al* 2012). In addition, it is important to note that failed or delayed location attempts may occur due to environmental conditions (eg excessive cloud cover), physical obstructions (eg buildings) or atmospheric interference (Frair *et al* 2010; Tomkiewicz *et al* 2010). While it is not possible to obtain accurate readings when indoors, GPS systems can be combined with dead-reckoning to continuously track fine-scale movements in extreme conditions, underground or underwater (Wilson *et al* 2007, 2008). As technology evolves and new devices emerge, many of the limitations described in this paper will very likely be addressed.

Most of the same guidelines for minimising the impact of accelerometers on behaviour are applicable to GPS devices. Researchers should set time aside for training attachment/removal procedures, habituation and conducting behavioural observations to ensure that the devices are not influencing behaviour. While Horback and colleagues' (2012) study of African elephants found that GPS collars did not significantly affect the rates of behavioural events or percent of time spent in particular behavioural states, there are cases in which GPS devices have impacted behaviour and overall welfare status (discussed by Tomkiewicz *et al* 2010 and Horback *et al* 2012). However, by choosing the appropriate device, site and attachment methods, we can better comprehend how each individual views its social and physical environments. Fortunately, GPS devices are becoming increasingly affordable, as commercial applications (eg navigation, social media 'tagging') are now quite common.

Radio frequency identification systems

Like GPS technology, radio frequency identification (RFID) systems provide detailed location information, yet can be applied to a wider range of taxa (eg insects) in a variety of settings (eg indoors, burrows, nests). RFID is an automatic identification and data transmission system that relies on unique animal-borne tags and a reader (ie receiver) that detects and stores the data (Roberts *et al* 2006; Krause *et al* 2013). As opposed to active tags, passive tags do not have an internal power source and must be energised by the reader's electromagnetic field to transmit signals (Bonter & Bridge 2011). While passive tags have a more limited read range, they theoretically have an unlimited operational life and are generally cheaper, smaller, and more lightweight (Roberts *et al* 2006). In fact, some are small enough to be referred to as 'powder' and 'dust' tags and can be deployed for years without disrupting the subjects (Ruhil *et al* 2013). RFID technology allows for multiple tags to be read simultaneously, functions in extreme conditions (eg snow, fog) and does not require a line-of-sight between the tag and reader (Roberts *et al* 2006; Ruhil *et al* 2013). The livestock industry has used RFID systems (mainly active, re-writable tags with storage capability) for numerous purposes, including tracking animals throughout the lifecycle and tracing individuals following a disease outbreak (Voulodimos *et al* 2010; Ruiz-Garcia & Lunadei 2011; Ruhil *et al* 2013). However, this technology has also been used to investigate use of space, resource selection, daily/seasonal variation in feeding rates, mate choice, provisioning behaviour (in birds) and social dynamics (Dyo *et al* 2010; Bonter & Bridge 2011; Krause *et al* 2013).

Most commonly, RFID technology has been used to monitor the movements and activities of individual animals. Catarinucci and colleagues (2014) recently designed an RFID tracking system — with an antenna matrix placed underneath animal cages — to record the location and movements of small laboratory animals. By gluing passive tags to bumblebees (*Bombus terrestris*) and placing a reader at the nest entrance, Streit and colleagues (2003) could track exactly how much time each bee spent out of the nest (ie foraging) and the total number of trips. RFID also serves as a valuable tool for those conducting preference testing. For instance, Ringgenberg and colleagues (2015) investigated the factors influencing nest choice in hens by attaching passive tags to the birds' legs and designing antennae-lined nests. In a study of laboratory mice, RFID data were used not only to track the amount of time individuals spent within particular areas of a testing apparatus, but also to monitor general activity (Howerton *et al* 2012). In fact, the authors found that RFID readings for individual mice were correlated with the number of minutes spent 'active' and could serve as a proxy for activity. They proposed using RFID to examine environmental preferences and to detect 'depression-like phenotypes' when activity levels deviate from baseline patterns. Finally, Dallas Zoo monitors its African elephants via active tags (attached to anklets) and a network of receivers placed around the perimeter of the

enclosure (N Scott, personal communication 2015). By calculating positions using trilateration, zoo staff can track individual differences in distance travelled, use of space and locomotory patterns, as well as how these measures are influenced by social and seasonal variables. This approach could be extended to a variety of zoo species.

RFID technology can also be used to extract information about social relationships. Similar to GPS, RFID systems allow for 'indirect encounter mapping', as co-occurrence records from particular readers reflect potential associations (Krause *et al* 2013). By using passive microtransponders weighing less than 9 µg, Robinson and colleagues (2009) recorded ants' (*Temnothorax albipennis*) exits and entrances to the nest and discovered that returning ants stimulate others to leave. In a study of free-ranging European badgers (*Meles meles*), researchers analysed pairwise co-locations from receiver records to determine where and when dyads interacted, and ultimately to identify communities (Dyo *et al* 2010). It is even possible to conduct social network analyses to investigate topics such as pair formation, the exchange of social information (eg how social connectedness influences the likelihood of discovering novel food patches) and inter-specific dynamics (reviewed by Krause *et al* 2013).

While relatively little effort is required during data collection once tags (especially passive tags) have been deployed, a considerable amount of time must be devoted to research design. The researcher must decide whether to use passive or active tags and then explore non-invasive attachment methods (eg collars, anklets, ear-tags, glue). Clearly, careful consideration must be given to the placement of the readers, as data can only be collected from these locations and some passive tags must pass within centimeters of the reader for a fix to occur (Roberts *et al* 2006). One should also collect behavioural data to ensure that the RFID readings are accurate and reliable (eg Ringgenberg *et al* 2015). Unfortunately, missed detections do occur, especially with passive tags, due to multiple individuals arriving at the reader simultaneously, interference from adjacent readers and electromagnetic noise caused by certain features of the environment (Roberts *et al* 2006; Howerton *et al* 2012). Furthermore, a tag may not be detected due to its orientation or may be detected multiple times if the animal is moving slowly (Robinson *et al* 2009). Before analysis, researchers should review the raw data to remove erroneous readings and create 'rules' for generating a meaningful dataset (eg consecutive readings less than 5 s apart should be considered a single fix) (eg Robinson *et al* 2009). Data analysis may be laborious, especially if trying to extract social information from co-occurrence records (see Krause *et al* 2013). Still, RFID technology can be an extremely useful tool when researching species that are difficult or even impossible to observe using traditional methods.

Bioacoustics

Another way to gain an impression of an animal's inner state is to investigate vocal behaviour, which can reflect both physiological and psychological aspects of welfare (Weary & Fraser 1995; Watts & Stookey 2000; Manteuffel *et al* 2004; Boissy *et al* 2007). There is evidence that vocal behaviour is associated with activation of the HPA axis (Rushen *et al* 1999) and measures of autonomic nervous system (ANS) activity (Marchant-Forde *et al* 2001). Indeed, studies of human infant vocalisations have shown that because certain acoustic features are associated with measures of respiration and heart rate, vocal prosody (ie variations in rhythm and pitch) can serve as a 'sensitive index of autonomic activity' (Stewart *et al* 2013). Calls can be recorded by placing microphones or hydrophones in enclosures or via animal-attached recording devices (eg collars), and recent advances in software allow for real-time sound analyses. This means that health and/or welfare status can be monitored continuously and particular sounds, such as coughs (Ferrari *et al* 2008) and stress-related calls (Schön *et al* 2001), can be detected automatically.

Most studies have examined the types, rates and acoustic structures of vocalisations produced in negative contexts, such as experiencing pain, stress or social isolation (eg Weary *et al* 1997). Typically, calls generated in these contexts are emitted at high rates and characterised by high frequencies, durations and amplitudes (Manteuffel *et al* 2004). Siebert and colleagues (2011) found that the vocalisations of dwarf goats (*Capra hircus*) are influenced by degree of social isolation, with animals exhibiting fewer high bleats but greater low bleats when completely isolated, as compared to partially isolated. The authors suggest that when completely isolated, the low bleats may represent a form of auto-communication and serve a self-calming mechanism. In a study of beluga whales (*Delphinapterus leucas*), a hydrophone was used to examine the acoustic activity of animals in response to environmental stressors (Castellote & Fossa 2006). Specifically, vocalisation rates decreased after transportation to a new facility, as well as following the introduction of harbour seals (*Phoca vitulina*), and remained low for weeks (four and two weeks, respectively). It is important to note that food intake was not impacted by these stressors, and that acoustic activity remained low even after behavioural indicators of negative welfare (as reported by trainers) disappeared. Acoustic activity can be a reliable indicator of an individual's comfort level and be used to evaluate the effects of animal transfers, introductions and changes to the environment.

While it is less common to study vocalisations produced in positive contexts, several welfare scientists highlight the value of investigating calls that may reflect good or great welfare (Boissy *et al* 2007; Fraser 2008). Indeed, Fraser (2008) suggests that researchers should consider the sounds emitted when 'all's well', such as when pigs generate 'snuffly' sounds and hens sing. The vocal repertoires of animals may include calls that reflect positive arousal, such

as the ultrasonic chirps produced by rats in some social contexts (eg playing) and the ‘laughter’ of great apes (rats: Panksepp & Burgdorf 2003; great apes: Davila Ross *et al* 2009). With the use of directional microphones and spectrographic analysis, Briefer and colleagues (2015) discovered vocal indicators of valence when comparing the calls emitted by goats in positive, negative and neutral situations. Specifically, the calls produced during positive situations had less variable fundamental frequencies than those emitted in negative situations. Similarly, by using collars fitted with microphones, Soltis and colleagues (2009) found that the ‘rumbles’ produced by low-ranking African elephants in calm social contexts had lower and less variable fundamental frequencies, as well as lower amplitudes and durations, than rumbles generated when interacting with dominant individuals. While a follow-up study determined that rumbles primarily express the intensity of affect (regardless of the valence of the situation), the authors argue that “...the unique combination of acoustic features observed in the positive social context may constitute a ‘vocal signature’ of positive affect that is distinguishable from neutral and negative affective states” (Soltis *et al* 2011; p 1064). Studies such as this highlight the importance of adopting a ‘dimensional approach’ which considers both affect quality or valence (positive versus negative) and affect intensity (the degree of arousal: from low to high) (Soltis *et al* 2011). Essentially, researchers should identify acoustic features that occur in positive contexts, so that these valence indicators can later be used to distinguish between positive and negative affective states.

While bioacoustics is clearly a valuable tool for gaining insight into an animal’s welfare status, researchers must invest a considerable amount of effort into exploring options for recording and analysing vocalisations. First, the researcher should conduct preliminary observations and review the available natural history literature to identify the most appropriate calls for assessing welfare (Weary & Fraser 1995). Next, these calls should be validated by collecting behavioural and/or physiological data (Manteuffel *et al* 2004; Soltis *et al* 2011). If possible, it is best to design experiments to elicit and then analyse calls spectrographically to highlight associations between particular acoustic features and affective states. However, it is critical to note that certain states (eg excessive lethargy) may not evoke any vocalisations and that even individual animals are not always consistent in their vocal responses (Manteuffel *et al* 2004). Furthermore, while vocalisations may accurately reflect an animal’s ‘immediate experiences’ (Boissy *et al* 2007), it may be more challenging to integrate bioacoustics into studies of long-term, persistent states (eg chronic stress), once again highlighting the need to combine measures when monitoring welfare.

Finally, there are obvious technological considerations and limitations. The recording equipment that one chooses will depend primarily upon the species of interest, as some animals produce infrasonic or ultrasonic calls and devices are sensitive to particular frequencies (Blumstein *et al* 2011). The researcher must also decide whether to employ

directional or omnidirectional microphones, choose a sampling rate (determines spectral range) and consider bit depth requirements (determines dynamic range and size of acoustic files) (Blumstein *et al* 2011). While animal-attached technology may be preferred for monitoring individuals, this may not be feasible for all species. It may not even be possible to distinguish the calls of individual animals when using hydrophones on group-living animals in a marine environment. Finally, while discussions of spectrographic analyses and the physiological mechanisms impacting vocal output are beyond the scope of this paper, these topics should be reviewed before initiating a study (Manteuffel *et al* 2004; Taylor & Reby 2010). Once calls of interest (positive and/or negative) have been identified, they can be monitored on a regular basis to determine baseline rates for individuals. It is also possible to compare rates and call features across various contexts or following changes to the environment or routine.

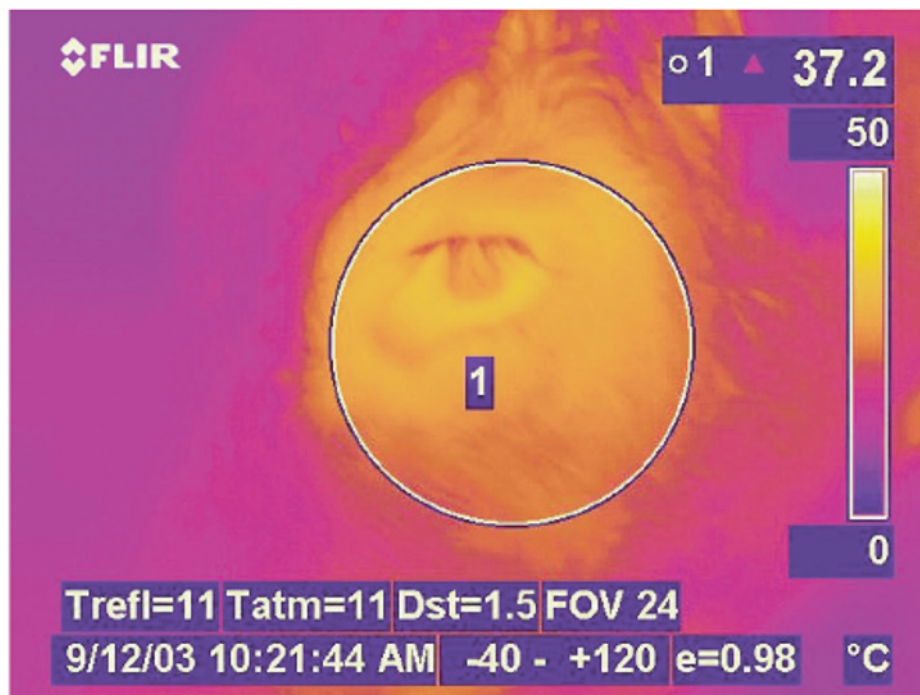
Technology for monitoring physiological states

To supplement behavioural measures, non-invasive assessments of ANS activity can provide insight into an individual’s physiological functioning and even affective states. This can be accomplished by examining measures of heart rate, body surface humidity, respiration and peripheral body temperature. This section focuses primarily on approaches that are best for monitoring psychophysiological aspects of welfare. For instance, while core body temperature can be monitored using ingestible ‘pills’ (eg iButtons: Kinahan *et al* 2007; Harlow *et al* 2010), body surface temperature is a more sensitive measure of changes that result from stress (Church *et al* 2009). Also, while researchers have monitored respiratory activity using microwave Doppler radar (eg Suzuki *et al* 2009), laser distance sensors (eg Pastell *et al* 2006) and extendable belts (Reefmann *et al* 2009), there is some evidence that, as compared to other measures of ANS activity, this may be a less-promising approach for distinguishing between negative and positive states (Reefmann *et al* 2009). Still, there is great potential for integrating all of the measures listed above into welfare-related research. Furthermore, an attempt should be made to combine measures whenever possible to create the most comprehensive view of welfare status, as some reflect the activity of the parasympathetic nervous system (eg heart rate variability) while others (eg body surface humidity and temperature) reflect the activity of the sympathetic nervous system (Reefmann *et al* 2009).

Thermography

Measuring changes in skin temperature can serve as an objective, reliable method for assessing the physical and emotional well-being of animals (Stewart *et al* 2005; McCafferty 2007). Infra-red thermography (IRT) devices measure radiated heat from particular body parts, without the need for restraint or handling, from distances less than 1 m to greater than 1,000 m (Church *et al* 2009). IRT images, which can be viewed as single frames or in video format, provide a

Figure 3



Detecting disease using infra-red thermography and an electronic identification system. Infra-red thermography (IRT) can be utilised to detect disease non-invasively in livestock, such as cattle. This photograph was captured using an infra-red camera aimed at a water trough. By coupling this infra-red scanning station with an electronic ID detection plate, farm managers can automatically identify individuals while collecting infra-red images of the eye region. Measuring eye temperature allows for the early detection of certain diseases, such as bovine viral diarrhoea. Figure reprinted with permission from Stewart *et al* (2005).

map of the variation in temperature across a particular surface (McCafferty 2007; Church *et al* 2009). Devices range from small, hand-held units to scanning stations (integrated into feeders/troughs) that can regularly capture infra-red images of the eye for multiple individuals (Stewart *et al* 2005; Figure 3). IRT technology has been applied to a wide range of mammals, birds, reptiles and insects in a variety of settings (McCafferty 2007). Common applications include using IRT to detect signs of inflammation, oestrus, disease and infection but researchers have also employed devices to conduct population surveys, assess fertility, diagnose pregnancy and to examine how temperature change is associated with particular affective states (Stewart *et al* 2005; McCafferty 2007, 2011; Church *et al* 2009). IRT has numerous veterinary applications, as a change in temperature may reflect circulatory problems, an inflammatory response or an infection. In fact, IRT can detect inflammation of the tendons and joints two weeks before the presentation of clinical signs (Church *et al* 2009), making it a valuable tool for identifying lameness and injuries (eg Eddy *et al* 2001; Nikkhah *et al* 2005). Similarly, by employing IRT to measure eye temperature, bovine viral diarrhoea can be diagnosed as early as day one of infection and before the appearance of clinical signs (Schaefer *et al* 2007). A decade ago, Kouba and Willard (2005) recommended using IRT on zoo animals for a variety of purposes, such as collecting baseline 'heat signatures' of feet to detect lameness, gauging thermal comfort and monitoring for signs of disease.

There is also potential for using IRT to gain insight into an individual's emotional state, though most studies have examined how temperature change is associated with negative arousal. For instance, when an animal experiences fear, the sympathetic nervous system is activated which results in vasoconstriction and subsequent cooling of the extremities (Stewart *et al* 2008). By using IRT, Nakayama and colleagues (2005) discovered that the nasal skin temperature of rhesus macaques (*Macaca mulatta*) decreased when approached by a potentially threatening person. Similarly, fear-conditioned rats placed (but not shocked) in a foot-shock chamber experienced a significant decrease in paw and tail temperature, but an increase in other regions such as the eyes (Vianna & Carrive 2005). Eye temperature also increased significantly for horses participating in a novel object test, with larger increases recorded for those which did not re-approach the object (Dai *et al* 2015). IRT has even been used to detect stress in horses participating in sports competitions, as Valera and colleagues (2012) found that eye temperature increased following showjumping events. However, it should be noted that a rapid decrease in eye temperature was reported for cattle exposed to unpredictable, aversive stimuli (Stewart *et al* 2008) and temporary social isolation (Stewart *et al* 2007). Stewart and colleagues (2008) argue that a very frequent sampling interval may be necessary to capture this sudden decrease in eye temperature that occurs before any subsequent increases. Furthermore, methodological differences — as well as

confounding factors (eg handling, invasive sampling) — may explain why studies offer conflicting results regarding the relationship between eye temperature and particular affective states, as well as whether an association exists between eye temperature and HPA activity (Cook *et al* 2001; Stewart *et al* 2007). Nonetheless, there is strong evidence that IRT is a useful tool for highlighting negative arousal. Moreover, as Stewart and colleagues (2008) argue, “its use may be extended to other situations where activity of the autonomic nervous system is changed, such as during pleasure or positive responses...” (p 392).

Before initiating a study that involves IRT, researchers must consider several animal-related and environmental factors. While the research question and species of interest will determine which part of the body to measure, common sites include the eye, muzzle and dorsal surface (Stewart *et al* 2005). As discussed above, the fact that some body parts increase in temperature in response to particular stimuli while others decrease highlights the importance of validation. Next, the researcher must evaluate the effects of exercise and consider the circadian rhythms of the selected region (Berry *et al* 2003). If measuring areas covered with fur, measurements should be collected when coats are relatively clean and dry (Stewart *et al* 2005). Moreover, the researcher should control for seasonal differences due to molting, as temperature readings are affected by the thickness and quality of the coat (McCafferty 2007). It is also necessary to consider how weather conditions (eg sunlight, wind draughts) influence coat temperature (Stewart *et al* 2005). For instance, a zebra's (*Equus burchelli*) black stripes are at least 10°C warmer than its white stripes when in direct sunlight (McCafferty 2007). Finally, McCafferty (2007) suggests reducing the amount of thermal radiation generated by the environment by avoiding small spaces with features that emanate heat. Fortunately, zoo researchers often have the ability to control the setting and husbandry practices (eg brushing coats) to ensure that IRT data are as accurate as possible.

Measures of heart rate

Another method for gaining insight into an animal's welfare status and even its emotional state, is to consider measures of heart rate (Boissy *et al* 2007). Most studies have examined how negative emotional states (eg stress) influence heart rate. In fact, there is evidence that a wide range of taxa, including reptiles, exhibit an increase in heart rate when experiencing negative events (Cabanac & Cabanac 2000). Research has also shown that positive states and pleasurable events are associated with reduced heart rates. For example, decreases in heart rate were reported for horses (*Equus caballus*) being groomed (by humans) on particular areas of the body (Feh & de Mazières 1993) and for rhesus macaques receiving grooming from conspecifics (Aureli *et al* 1999). It is important to note that most studies have measured mean heart rate, which reflects the combined activity of both the sympathetic and parasympathetic nervous systems.

In recent years, many researchers have promoted the use of heart-rate variability (HRV), which measures the balance between sympathetic and parasympathetic tone, as a reliable indicator of emotion regulation (Mohr *et al* 2002; Marchant-Forde *et al* 2004; Boissy *et al* 2007; von Borell *et al* 2007). For instance, welfare scientists have measured HRV to explore how vagal activity and changes in sympathovagal balance are associated with housing conditions, exposure to novel objects, environmental stressors, husbandry practices and cognitive challenges (eg Mohr *et al* 2002; Désiré *et al* 2004; Langbein *et al* 2004; reviewed by von Borell *et al* 2007). There is also evidence that HRV may be influenced by positive affective states (reviewed by Boissy *et al* 2007; Kreibitz 2010). For example, McCraty and colleagues (1995) discovered that self-induced positive emotional states in humans resulted in an increase in HRV. Similarly, in an eloquent study designed to assess the emotional states of sheep, Reefmann and colleagues (2009) found that HRV (measured with a Holter recorder) was higher when sheep were subjected to a positive situation (being groomed by humans) than a negative situation (separation from conspecifics). When experiencing positive situations, the sheep also exhibited lower variability in body surface humidity and a decrease in heart rate. The authors recommend combining physiological measures whenever possible to distinguish between positive and negative emotional states.

Most commercially available ambulatory cardiac monitors are only applicable to a narrow range of zoo-housed species. Von Borell and colleagues (2007) describe available technology for monitoring cardiac activity in laboratory, farm and companion animals. Most studies rely on either Holter systems, which record electrocardiogram (ECG) signals and are commonly used on humans, or monitors that detect inter-beat intervals (IBI) specifically (eg Polar recorders). While the latter are more affordable, they are less reliable because without the complete record of ECG signals, errors in IBI measurements cannot be identified (eg Marchant-Forde *et al* 2004; reviewed by von Borell *et al* 2007). It may also be possible to use an ingestible ‘pill’ fitted with a submersible microphone to capture measures of heart rate (Martinez *et al* 2006). After choosing a device, the researcher should evaluate how changes are influenced by the subject's diurnal rhythms, current level of fitness and recent physical activity and then attempt to standardise conditions for data collection. In addition, it is important to note that changes in cardiac activity may occur before a particular behaviour is displayed and that the cardiac response may continue after its expression (von Borell *et al* 2007). It is clearly necessary to habituate the animal to the device before assessing how cardiac activity is associated with other welfare indicators (eg HPA activity, behaviour) and influenced by environmental conditions, the husbandry routine or particular events. See von Borell and colleagues (2007) for a more thorough discussion about available equipment, data editing and data analysis.

Animal welfare implications

The goal of this review is to highlight the most promising tools currently available for monitoring the welfare of zoo animals. Technologies that allow for automated assessments of postural behaviour, movement, activity patterns and even vocalisations may be especially useful when caring for species that are challenging to monitor with traditional methods. Moreover, many of these tools can provide insight into how animals behave when visitors, caretakers and observers are not present. By creating baseline movement or behaviour profiles for individual animals, it is possible to evaluate the effects of environmental conditions (eg ambient temperature), social variables (eg group composition) and changes to the routine or enclosure (eg new enrichment devices). The non-invasive sampling of physiological measures is less common than behavioural research — and is typically more challenging to apply in zoo settings (as demonstrated by the relative lengths of these two sections of the paper) — but can help evaluate the impact of specific events or conditions. Indeed, welfare scientists may be able to examine measures of ANS activity to determine whether animals are expressing positive or negative affect in particular contexts. Whether hoping to continuously monitor the welfare status of individual animals, or determine responses to particular stimuli, the technology described above can supplement the approaches currently being applied in zoos.

Conclusion

While the zoo community is committed to enhancing animal welfare, researchers have yet to take full advantage of the tools available for monitoring and assessing the welfare of individual animals. To gain the most comprehensive view of an animal's welfare status, researchers should combine methods for tracking behavioural and physiological indicators. For instance, collars can be affixed with GPS units, accelerometers and audio-recording devices (Soltis *et al* 2012), as well as sensors for measuring environmental variables (eg temperature) (reviewed by Brown *et al* 2013). Depending on the species, it may be possible to simultaneously measure body temperature, respiration and heart rate (Reefmann *et al* 2009). Marine mammals can be fitted with tags that include sensors for depth, temperature, orientation and audio recordings (Johnson & Tyack 2003). By combining these measures whenever possible, and continuing to employ traditional methods (eg behavioural data collection, non-invasive hormone monitoring), researchers will be able to take a holistic approach to welfare assessment.

Of course, technology evolves rapidly, with companies constantly designing new devices and models that show improved reliability, efficiency and functionality. As you read this, technologies are surfacing that still require further validation, especially in zoo settings, including: loggers for wirelessly monitoring EEG activity, sensors for measuring body surface humidity, force plates for detecting signs of discomfort, systems for continuously monitoring mobility and Bluetooth technology for tracking small-bodied species. As technological advancements continue to occur

in the field of human and animal welfare science, it will become feasible for zoos to monitor entire collections in a time-efficient manner. Since technology is continually transforming our approach to welfare monitoring, it is impossible to predict exactly what the future holds in terms of monitoring particular species. However, if the previous ten years are any indication of the potential impact of technology on the field of animal welfare science, zoos will be able to ensure that each animal has the opportunity to thrive.

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References

- Aureli F, Preston SD and de Waal F** 1999 Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): a pilot study. *Journal of Comparative Psychology* 113: 59-65. <http://dx.doi.org/10.1037/0735-7036.113.1.59>
- AZA (Association of Zoos and Aquariums)** 2015 *Animal Welfare Committee Mission*. <http://www.aza.org/Membership/detail.aspx?id=378>
- Banerjee D, Biswas S, Daigle C and Siegford JM** 2012 Remote activity classification of hens using wireless body mounted sensors. In: Yang G (ed) *Ninth International Workshop on Wearable and Implantable Body Sensor Networks* pp 107-112. 9-12 May 2012, IEEE, London, UK
- Barber JCE** 2009 Programmatic approaches to assessing and improving animal welfare in zoos and aquariums. *Zoo Biology* 28: 519-530. <http://dx.doi.org/10.1002/zoo.20260>
- Barthélemy I, Barrey E, Thibaud JL, Uriarte A, Voit T, Blot S and Hogrel JY** 2009 Gait analysis using accelerometry in dystrophin-deficient dogs. *Neuromuscular Disorders* 19: 788-796. <http://dx.doi.org/10.1016/j.nmd.2009.07.014>
- Berry RJ, Kennedy AD, Scott SL, Kyle BL and Schaefer AL** 2003 Daily variation in the udder surface temperature of dairy cows measured by infrared thermography: potential for mastitis detection. *Canadian Journal of Animal Science* 83: 687-693. <http://dx.doi.org/10.4141/A03-012>
- Blumstein DT, Mennill DJ, Clemins P, Girod L, Yao K, Patricelli G, Deppe JL, Krakauer AH, Clark C, Cortopassi KA, Hanser SF, McCowan B, Ali AM and Kirschel ANG** 2011 Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. *Journal of Applied Ecology* 48: 758-767. <http://dx.doi.org/10.1111/j.1365-2664.2011.01993.x>
- Boissy A, Manteuffel G, Bak Jensen M, Oppermann Moe R, Spruijt B, Keeling LJ, Winckler C, Forkman B, Dimitrov I, Langbein J, Bakken M, Veissier I and Aubert A** 2007 Assessment of positive emotions in animals to improve their welfare. *Physiology & Behavior* 92: 375-397. <http://dx.doi.org/10.1016/j.physbeh.2007.02.003>
- Bonter DN and Bridge ES** 2011 Applications of radio frequency identification (RFID) in ornithological research: a review. *Journal of Field Ornithology* 82: 1-10. <http://dx.doi.org/10.1111/j.1557-9263.2010.00302.x>

- Briefer EF, Tettamanti F and McElligott AG** 2015 Emotions in goats: mapping physiological, behavioural and vocal profiles. *Animal Behaviour* 99: 131-143. <http://dx.doi.org/10.1016/j.anbehav.2014.11.002>
- Broom DM** 2007 Quality of life means welfare: how is it related to other concepts and assessed? *Animal Welfare* 16(S): 45-53
- Brown DD, Kays R, Wikelski M, Wilson R and Klimley AP** 2013 Observing the unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry* 1: 20. <http://dx.doi.org/10.1186/2050-3385-1-20>
- Butterworth A, Mench JA and Wielebnowski N** 2011 Practical strategies to assess (and improve) welfare. In: Appleby MC, Mench JA, Olsson IAS and Hughes BO (eds) *Animal Welfare, Second Edition* pp 200-214. CABI Publishing: Cambridge, MA, USA
- Cabanac A and Cabanac M** 2000 Heart rate response to gentle handling of frog and lizard. *Behavioural Processes* 52: 89-95. [http://dx.doi.org/10.1016/S0376-6357\(00\)00108-X](http://dx.doi.org/10.1016/S0376-6357(00)00108-X)
- Cagnacci F, Boitani L, Powell RA and Boyce MS** 2010 Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2157-2162. <http://dx.doi.org/10.1098/rstb.2010.0107>
- Castellote M and Fossa F** 2006 Measuring acoustic activity as a method to evaluate welfare in captive beluga whales (*Delphinapterus leucas*). *Aquatic Mammals* 32: 325-333. <http://dx.doi.org/10.1578/AM.32.3.2006.325>
- Catarinucci L, Colella R, Mainetti L, Patrono L, Pieretti S, Sergi I and Tarricone L** 2014 Smart RFID antenna system for indoor tracking and behavior analysis of small animals in colony cages. *IEEE Sensors Journal* 14: 1198-1206. <http://dx.doi.org/10.1109/JSEN.2013.2293594>
- Chapinal N, de Passillé AM, Rushen J and Wagner S** 2010 Automated methods for detecting lameness and measuring analgesia in dairy cattle. *Journal of Dairy Science* 93: 2007-2013. <http://dx.doi.org/10.3168/jds.2009-2803>
- Church JS, Cook NJ and Schaefer AL** 2009 Recent applications of infrared thermography for animal welfare and veterinary research: everything from chicks to elephants. *InfraMation 2009 Proceedings*. 19-22 October 2009, Las Vegas, USA
- Cook NJ, Schaefer AL, Warren L, Burwash L, Anderson M and Baron V** 2001 Adrenocortical and metabolic responses to ACTH injection in horses: an assessment by salivary cortisol and infrared thermography of the eye. *Canadian Society of Animal Science* 81: 621 (Abstract)
- Dai F, Cogi NH, Heinzl EUL, Dalla Costa E, Canali E and Minero M** 2015 Validation of a fear test in sport horses using infrared thermography. *Journal of Veterinary Behavior: Clinical Applications and Research* 10: 128-136. <http://dx.doi.org/10.1016/j.jveb.2014.12.001>
- Davila Ross M, Owren MJ and Zimmermann E** 2009 Reconstructing the evolution of laughter in great apes and humans. *Current Biology* 19: 1106-1111. <http://dx.doi.org/10.1016/j.cub.2009.05.028>
- de Passillé AM, Jensen MB, Chapinal N and Rushen J** 2010 Technical note: use of accelerometers to describe gait patterns in dairy calves. *Journal of Dairy Science* 93: 3287-3293. <http://dx.doi.org/10.3168/jds.2009-2758>
- Désiré L, Veissier I, Després G and Boissy A** 2004 On the way to assess emotions in animals: do lambs (*Ovis aries*) evaluate an event through its suddenness, novelty, or unpredictability? *Journal of Comparative Psychology* 118: 363-374. <http://dx.doi.org/10.1037/0735-7036.118.4.363>
- Dyo V, Ellwood SA, Macdonald DW, Markham A, Mascolo C, Pásztor B, Scellato S, Trigoni N, Wohlers R and Yousef K** 2010 Evolution and sustainability of a wildlife monitoring sensor network. *Proceedings of the 8th ACM Conference on Embedded Networked Sensor Systems* pp 127-140. 3-5 November 2010, Zurich, Switzerland. ACM: New York City, USA. <http://dx.doi.org/10.1145/1869983.1869997>
- Eddy AL, Van Hoogmoed LM and Snyder JR** 2001 The role of thermography in the management of equine lameness. *The Veterinary Journal* 162: 172-181. <http://dx.doi.org/10.1053/tvj.2001.0618>
- Feh C and de Mazières J** 1993 Grooming at a preferred site reduces heart rate in horses. *Animal Behaviour* 46: 1191-1194. <http://dx.doi.org/10.1006/anbe.1993.1309>
- Ferrari S, Silva M, Guarino M, Aerts JM and Berckmans D** 2008 Cough sound analysis to identify respiratory infection in pigs. *Computers and Electronics in Agriculture* 64: 318-325. <http://dx.doi.org/10.1016/j.compag.2008.07.003>
- Frair JL, Fieberg J, Hebblewhite M, Cagnacci F, De Cesare N and Pedrotti L** 2010 Resolving issues of imprecision and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2187-2200. <http://dx.doi.org/10.1098/rstb.2010.0084>
- Fraser D** 2008 *Understanding Animal Welfare: The Science in its Cultural Context*. Wiley-Blackwell: Oxford, UK
- Hacker CE, Horback KM and Miller LJ** 2015 GPS technology as a proxy tool for determining relationships in social animals: an example with African elephants. *Applied Animal Behaviour Science* 163: 175-182. <http://dx.doi.org/10.1016/j.applanim.2014.12.005>
- Handcock RN, Swain DL, Bishop-Hurley GJ, Patison KP, Wark T, Valencia P, Corke P and O'Neill CJ** 2009 Monitoring animal behaviour and environmental interactions using wireless sensor networks, GPS collars and satellite remote sensing. *Sensors* 9: 3586-3603. <http://dx.doi.org/10.3390/s90503586>
- Harlow HJ, Purwandana D, Jessop TS and Phillips JA** 2010 Size-related differences in the thermoregulatory habits of free-ranging Komodo dragons. *International Journal of Zoology* 2010: 1-9. <http://dx.doi.org/10.1155/2010/921371>
- Held SDE and Špinko M** 2011 Animal play and animal welfare. *Animal Welfare* 81: 891-899. <http://dx.doi.org/10.1016/j.anbehav.2011.01.007>
- Hill SP and Broom DM** 2009 Measuring zoo animal welfare: theory and practice. *Zoo Biology* 28: 531-544. <http://dx.doi.org/10.1002/zoo.20276>
- Hokkanen AH, Hänninen L, Tiisanen J and Pastell M** 2011 Predicting sleep and lying time of calves with a support vector machine classifier using accelerometer data. *Applied Animal Behaviour Science* 134: 10-15. <http://dx.doi.org/10.1016/j.applanim.2011.06.016>

- Holdgate MR, Meehan CL, Hogan JN, Miller LJ, Rushen J, de Passillé AM, Soltis J, Andrews J and Shepherdson DJ** 2016a Recumbence behavior in zoo elephants: determination of patterns and frequency of recumbent rest and associated environmental and social factors. *PLoS ONE* 11(7): e0153301. <http://dx.doi.org/10.1371/journal.pone.0153301>
- Holdgate MR, Meehan CL, Hogan JN, Miller LJ, Soltis J, Andrews J and Shepherdson DJ** 2016b Walking behavior of zoo elephants: associations between GPS-measured daily walking distances and environmental factors, social factors, and welfare indicators. *PLoS ONE* 11(7): e0150331. <http://dx.doi.org/10.1371/journal.pone.0150331>
- Horback KM, Miller LJ, Andrews J, Kuczaj SA and Anderson M** 2012 The effects of GPS collars on African elephant (*Loxodonta africana*) behavior at the San Diego Zoo Safari Park. *Applied Animal Behaviour Science* 142: 76-81. <http://dx.doi.org/10.1016/j.applanim.2012.09.010>
- Hosey G, Melfi V and Pankhurst S** 2009 *Zoo Animals: Behaviour, Management, and Welfare*. Oxford University Press: Oxford, UK
- Howerton CL, Garner JP and Mench JA** 2012 A system utilizing radio frequency identification (RFID) technology to monitor individual rodent behavior in complex social settings. *Journal of Neuroscience Methods* 209: 74-78. <http://dx.doi.org/10.1016/j.jneumeth.2012.06.001>
- Johnson MP and Tyack PL** 2003 A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering* 28: 3-12. <http://dx.doi.org/10.1109/JOE.2002.808212>
- Kinahan AA, Inge-Moller R, Bateman PW, Kotze A and Scantlebury M** 2007 Body temperature daily rhythm adaptations in African savanna elephants (*Loxodonta africana*). *Physiology & Behavior* 92: 560-565. <http://dx.doi.org/10.1016/j.physbeh.2007.05.001>
- Kouba A and Willard S** 2005 What's new and hot in zoo technology: thermography. *Communiqué (American Zoo & Aquarium Association) March*: 10-13
- Krause J, Krause S, Arlinghaus R, Psorakis I, Roberts S and Rutz C** 2013 Reality mining of animal social systems. *Trends in Ecology & Evolution* 28: 541-551. <http://dx.doi.org/10.1016/j.tree.2013.06.002>
- Kreibig SD** 2010 Autonomic nervous system activity in emotion: a review. *Biological Psychology* 84: 394-421. <http://dx.doi.org/10.1016/j.biopsycho.2010.03.010>
- Langbein J, Nürnberg G and Manteuffel G** 2004 Visual discrimination learning in dwarf goats and associated changes in heart rate and heart rate variability. *Physiology & Behavior* 82: 601-609. <http://dx.doi.org/10.1016/j.physbeh.2004.05.007>
- Langford FM and Cockram MS** 2010 Is sleep in animals affected by prior waking experiences? *Animal Welfare* 19: 215-222
- Leighty KA, Soltis J and Savage A** 2010 GPS assessment of the use of exhibit space and resources by African elephants (*Loxodonta africana*). *Zoo Biology* 29: 210-220.
- Leighty KA, Soltis J, Wesolek CM, Savage A, Mellen J and Lehnhardt J** 2009 GPS determination of walking rates in captive African elephants (*Loxodonta africana*). *Zoo Biology* 28: 16-28. <http://dx.doi.org/10.1002/zoo.20199>
- Löttker P, Rummel A, Traube M, Stache A, Šustr P, Müller J and Heurich M** 2009 New possibilities of observing animal behaviour from a distance using activity sensors in GPS-collars: an attempt to calibrate remotely collected activity data with direct behavioural observations in red deer *Cervus elaphus*. *Wildlife Biology* 15: 425-434. <http://dx.doi.org/10.2981/08-014>
- Manteuffel G, Puppe B and Schön PC** 2004 Vocalization of farm animals as a measure of welfare. *Applied Animal Behaviour Science* 88: 163-182. <http://dx.doi.org/10.1016/j.applanim.2004.02.012>
- Marchant-Forde JN, Whittaker X and Broom DM** 2001 Vocalisations of the adult female domestic pig during a standard human approach test and their relationships with behavioural and heart rate measures. *Applied Animal Behaviour Science* 72: 23-39. [http://dx.doi.org/10.1016/S0168-1591\(00\)00190-8](http://dx.doi.org/10.1016/S0168-1591(00)00190-8)
- Marchant-Forde RM, Marlin DJ and Marchant-Forde JN** 2004 Validation of a cardiac monitor for measuring heart rate variability in adult female pigs: accuracy, artefacts and editing. *Physiology & Behavior* 80: 449-458. <http://dx.doi.org/10.1016/j.physbeh.2003.09.007>
- Martinez A, Schoenig S, Andresen D and Warren S** 2006 Ingestible pill for heart rate and core temperature measurement in cattle. *Proceedings of the 28th Annual International Conference of the IEEE - Engineering in Medicine and Biology Society* pp 3190-3193. 30 August-3 September 2006, IEEE, New York City, USA
- McCafferty DJ** 2007 The value of infrared thermography for research on mammals: previous applications and future directions. *Mammal Review* 37: 207-223. <http://dx.doi.org/10.1111/j.1365-2907.2007.00111.x>
- McCraty R, Atkinson M, Tiller WA, Rein G and Watkins AD** 1995 The effects of emotions on short-term power spectrum analysis of heart rate variability. *The American Journal of Cardiology* 76: 1089-1093. [http://dx.doi.org/10.1016/S0002-9149\(99\)80309-9](http://dx.doi.org/10.1016/S0002-9149(99)80309-9)
- Melfi VA** 2009 There are big gaps in our knowledge, and thus approach, to zoo animal welfare: a case for evidence-based zoo animal management. *Zoo Biology* 28: 574-588. <http://dx.doi.org/10.1002/zoo.20288>
- Mellor DJ, Hunt S and Gusset M** 2015 *Caring for Wildlife: The World Zoo and Aquarium Animal Welfare Strategy*. WAZA Executive Office: Gland, Switzerland
- Miller LJ, Andrews J and Anderson M** 2012 Validating methods to determine walking rates of elephants within a zoological institution. *Animal Welfare* 21: 577-582. <http://dx.doi.org/10.7120/09627286.21.4.577>
- Mohr E, Langbein J and Nurnberg G** 2002 Heart rate variability: a noninvasive approach to measure stress in calves and cows. *Physiology & Behavior* 75: 251-259. [http://dx.doi.org/10.1016/S0031-9384\(01\)00651-5](http://dx.doi.org/10.1016/S0031-9384(01)00651-5)
- Moreau M, Siebert S, Buerkert A and Schlecht E** 2009 Use of a tri-axial accelerometer for automated recording and classification of goats' grazing behaviour. *Applied Animal Behaviour Science* 119: 158-170. <http://dx.doi.org/10.1016/j.applanim.2009.04.008>
- Nakayama K, Goto S, Kuraoka K and Nakamura K** 2005 Decrease in nasal temperature of rhesus monkeys (*Macaca mulatta*) in negative emotional state. *Physiology & Behavior* 84: 783-790. <http://dx.doi.org/10.1016/j.physbeh.2005.03.009>

- Nikkhah A, Plaizier JC, Einarson MS, Berry RJ, Scott SL and Kennedy AD** 2005 Infrared thermography and visual examination of hooves of dairy cows in two stages of lactation. *Journal of Dairy Science* 88: 2749-2753. [http://dx.doi.org/10.3168/jds.S0022-0302\(05\)72954-4](http://dx.doi.org/10.3168/jds.S0022-0302(05)72954-4)
- Nishizawa H, Noda T, Yasuda T, Okuyama J, Arai N and Kobayashi M** 2013 Decision tree classification of behaviors in the nesting process of green turtles (*Chelonia mydas*) from tri-axial acceleration data. *Journal of Ethology* 31: 315-322. <http://dx.doi.org/10.1007/s10164-013-0381-1>
- Ouweltjes W, van der Werf JTN, Frankena K and van Leeuwen JL** 2011 Effects of flooring and restricted freestall access on behavior and claw health of dairy heifers. *Journal of Dairy Science* 94: 705-715. <http://dx.doi.org/10.3168/jds.2010-3208>
- Panksepp J and Burgdorf J** 2003 "Laughing" rats and the evolutionary antecedents of human joy? *Physiology & Behavior* 79: 533-547. [http://dx.doi.org/10.1016/S0031-9384\(03\)00159-8](http://dx.doi.org/10.1016/S0031-9384(03)00159-8)
- Pastell M, Aisla AM, Hautala M, Poikalainen V, Praks J, Veermäe I and Ahokas J** 2006 Contactless measurement of cow behavior in a milking robot. *Behavior Research Methods* 38: 479-486. <http://dx.doi.org/10.3758/BF03192802>
- Pastell M, Tiusanen J, Hakojärvi M and Hänninen L** 2009 A wireless accelerometer system with wavelet analysis for assessing lameness in cattle. *Biosystems Engineering* 104: 545-551. <http://dx.doi.org/10.1016/j.biosystemseng.2009.09.007>
- Platz S, Ahrens F, Bendel J, Meyer HHD and Erhard MH** 2008 What happens with cow behavior when replacing concrete slatted floor by rubber coating: a case study. *Journal of Dairy Science* 91: 999-1004. <http://dx.doi.org/10.3168/jds.2007-0584>
- Reefmann N, Wechsler B and Gygas L** 2009 Behavioural and physiological assessment of positive and negative emotion in sheep. *Animal Behaviour* 78: 651-659. <http://dx.doi.org/10.1016/j.anbehav.2009.06.015>
- Ringgenberg N, Bergeron R and Devillers N** 2010 Validation of accelerometers to automatically record sow postures and stepping behaviour. *Applied Animal Behaviour Science* 128: 37-44. <http://dx.doi.org/10.1016/j.applanim.2010.09.018>
- Ringgenberg N, Fröhlich EK, Harlander-Matauschek A, Toscano MJ, Würbel H and Roth BA** 2015 Effects of variation in nest curtain design on pre-laying behaviour of domestic hens. *Applied Animal Behaviour Science* 170: 34-43. <http://dx.doi.org/10.1016/j.applanim.2015.06.008>
- Roberts CM** 2006 Radio frequency identification (RFID). *Computers & Security* 25: 18-26. <http://dx.doi.org/10.1016/j.cose.2005.12.003>
- Robinson EJ, Richardson TO, Sendova-Franks AB, Feinerman O and Franks NR** 2009 Radio tagging reveals the roles of corpulence, experience and social information in ant decision making. *Behavioral Ecology and Sociobiology* 63: 627-636. <http://dx.doi.org/10.1007/s00265-008-0696-z>
- Rothwell ES, Bercovitch FB, Andrews J and Anderson M** 2011 Estimating daily walking distance of captive African elephants using an accelerometer. *Zoo Biology* 30: 579-591. <http://dx.doi.org/10.1002/zoo.20364>
- Ruhil AP, Mohanty TK, Rao SV, Lathwal SS and Subramanian VV** 2013 Radio-frequency identification: a cost effective tool to improve livestock sector. *Indian Journal of Animal Sciences* 83: 871-879
- Ruiz-Garcia L and Lunadei L** 2011 The role of RFID in agriculture: applications, limitations and challenges. *Computers and Electronics in Agriculture* 79: 42-50. <http://dx.doi.org/10.1016/j.compag.2011.08.010>
- Rushen J, Boissy A, Terlouw EMC and de Passillé AMB** 1999 Opioid peptides and behavioural and physiological responses of dairy cows to social isolation in unfamiliar surroundings. *Journal of Animal Science* 77: 2918-2924. <http://dx.doi.org/10.2527/1999.77112918x>
- Rushen J, Chapinal N and de Passillé AM** 2012 Automated monitoring of behavioural-based animal welfare indicators. *Animal Welfare* 21: 339-350. <http://dx.doi.org/10.7120/09627286.21.3.339>
- Rushen J and de Passillé AM** 2012 Automated measurement of acceleration can detect effects of age, dehorning and weaning on locomotor play of calves. *Applied Animal Behaviour Science* 139: 169-174. <http://dx.doi.org/10.1016/j.applanim.2012.04.011>
- Schaefer AL, Cook NJ, Church JS, Basarab J, Perry B, Miller C and Tong AKW** 2007 The use of infrared thermography as an early indicator of bovine respiratory disease complex in calves. *Research in Veterinary Science* 83: 376-384. <http://dx.doi.org/10.1016/j.rvsc.2007.01.008>
- Schön PC, Puppe B and Manteuffel G** 2001 Linear prediction coding analysis and self-organizing feature map as tools to classify stress calls of domestic pigs (*Sus scrofa*). *The Journal of the Acoustical Society of America* 110: 1425-1431. <http://dx.doi.org/10.1121/1.1388003>
- Sellers WI, Varley JS and Waters SS** 1998 Remote monitoring of locomotion using accelerometers: a pilot study. *Folia Primatologica* 69: 82-85. <http://dx.doi.org/10.1159/000052700>
- Siebert K, Langbein J, Schön PC, Tuchscherer A and Puppe B** 2011 Degree of social isolation affects behavioural and vocal response patterns in dwarf goats (*Capra hircus*). *Applied Animal Behaviour Science* 131: 53-62. <http://dx.doi.org/10.1016/j.applanim.2011.01.003>
- Siegford JM** 2013 Multidisciplinary approaches and assessment techniques to better understand and enhance zoo nonhuman animal welfare. *Journal of Applied Animal Welfare Science* 16: 300-318. <http://dx.doi.org/10.1080/10888705.2013.827914>
- Soltis J, Blowers TE and Savage A** 2011 Measuring positive and negative affect in the voiced sounds of African elephants (*Loxodonta africana*). *The Journal of the Acoustical Society of America* 129: 1059-1066. <http://dx.doi.org/10.1121/1.3531798>
- Soltis J, Leighty KA, Wesolek CM and Savage A** 2009 The expression of affect in African elephant (*Loxodonta africana*) rumble vocalizations. *Journal of Comparative Psychology* 123: 222-225. <http://dx.doi.org/10.1037/a0015223>
- Soltis J, Wilson RP, Douglas-Hamilton I, Vollrath F, King LE and Savage A** 2012 Accelerometers in collars identify behavioral states in captive African elephants *Loxodonta africana*. *Endangered Species Research* 18: 255-263. <http://dx.doi.org/10.3354/esr00452>
- Stewart AM, Lewis GF, Heilman KJ, Davila MI, Coleman DD, Aylward SA and Porges SW** 2013 The covariation of acoustic features of infant cries and autonomic state. *Physiology & Behavior* 120: 203-210. <http://dx.doi.org/10.1016/j.physbeh.2013.07.003>
- Stewart M, Schaefer AL, Haley DB, Colyn J, Cook NJ, Stafford KJ and Webster JR** 2008 Infrared thermography as a non-invasive method for detecting fear-related responses of cattle to handling procedures. *Animal Welfare* 17: 387-393

- Stewart M, Webster JR, Schaefer AL, Cook NJ and Scott SL** 2005 Infrared thermography as a non-invasive tool to study animal welfare. *Animal Welfare* 14: 319-325
- Stewart M, Webster JR, Verkerk GA, Schaefer AL, Colyn JJ and Stafford KJ** 2007 Non-invasive measurement of stress in dairy cows using infrared thermography. *Physiology & Behavior* 92: 520-525. <http://dx.doi.org/10.1016/j.physbeh.2007.04.034>
- Streit S, Bock F, Pirk CW and Tautz J** 2003 Automatic life-long monitoring of individual insect behavior now possible. *Zoology* 106: 169-171. <http://dx.doi.org/10.1078/0944-2006-00113>
- Suzuki S, Matsui T, Kawahara H and Gotoh S** 2009 Development of a noncontact and long-term respiration monitoring system using microwave radar for hibernating black bear. *Zoo Biology* 28: 259-270. <http://dx.doi.org/10.1002/zoo.20229>
- Takahashi M, Tobey JR, Pisacane CB and Andrus CH** 2009 Evaluating the utility of an accelerometer and urinary hormone analysis as indicators of estrus in a zoo-housed koala (*Phascolarctos cinereus*). *Zoo Biology* 28: 59-68. <http://dx.doi.org/10.1002/zoo.20212>
- Taylor AM and Reby D** 2010 The contribution of source-filter theory to mammal vocal communication research. *Journal of Zoology* 280: 221-236. <http://dx.doi.org/10.1111/j.1469-7998.2009.00661.x>
- Tomkiewicz SM, Fuller MR, Kie JG and Bates KK** 2010 Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2163-2176. <http://dx.doi.org/10.1098/rstb.2010.0090>
- Tomkins N and O'Reagain P** 2007 Global positioning systems indicate landscape preferences of cattle in the subtropical savannas. *The Rangeland Journal* 29: 217-222. <http://dx.doi.org/10.1071/RJ07024>
- Ungar ED, Henkin Z, Gutman M, Dolev A, Genizi A and Ganskopp D** 2005 Inference of animal activity from GPS collar data on free-ranging cattle. *Rangeland Ecology & Management* 58: 256-266. [http://dx.doi.org/10.2111/1551-5028\(2005\)58\[256:IOAAFJ\]2.0.CO;2](http://dx.doi.org/10.2111/1551-5028(2005)58[256:IOAAFJ]2.0.CO;2)
- Valera M, Bartolomé E, Sánchez MJ, Molina A, Cook N and Schaefer AL** 2012 Changes in eye temperature and stress assessment in horses during show jumping competitions. *Journal of Equine Veterinary Science* 32: 827-830. <http://dx.doi.org/10.1016/j.jevs.2012.03.005>
- Vianna DM and Carrive P** 2005 Changes in cutaneous and body temperature during and after conditioned fear to context in the rat. *European Journal of Neuroscience* 21: 2505-2512. <http://dx.doi.org/10.1111/j.1460-9568.2005.04073.x>
- von Borell E, Langbein J, Després G, Hansen S, Leterrier C, Marchant-Forde J, Marchant-Forde R, Minero M, Mohr E, Prunier A, Valance D and Veissier I** 2007 Heart rate variability as a measure of autonomic regulation of cardiac activity for assessing stress and welfare in farm animals: a review. *Physiology & Behavior* 92: 293-316. <http://dx.doi.org/10.1016/j.physbeh.2007.01.007>
- Voulodimos AS, Patrikakis CZ, Sideridis AB, Ntakis VA and Xylouri EM** 2010 A complete farm management system based on animal identification using RFID technology. *Computers and Electronics in Agriculture* 70: 380-388. <http://dx.doi.org/10.1016/j.compag.2009.07.009>
- Walker M, Diez-Leon M and Mason G** 2014 Animal welfare science: recent publication trends and future research priorities. *International Journal of Comparative Psychology* 27: 80-100
- Watanabe S, Izawa M, Kato A, Ropert-Coudert Y and Naito Y** 2005 A new technique for monitoring the detailed behaviour of terrestrial animals: a case study with the domestic cat. *Applied Animal Behaviour Science* 94: 117-131. <http://dx.doi.org/10.1016/j.applanim.2005.01.010>
- Watts JM and Stookey JM** 2000 Vocal behaviour in cattle: the animal's commentary on its biological processes and welfare. *Applied Animal Behaviour Science* 67: 15-33. [http://dx.doi.org/10.1016/S0168-1591\(99\)00108-2](http://dx.doi.org/10.1016/S0168-1591(99)00108-2)
- Weary DM and Fraser D** 1995 Signalling need. Costly signals and animal welfare assessment. *Applied Animal Behaviour Science* 44: 159-169. [http://dx.doi.org/10.1016/0168-1591\(95\)00611-U](http://dx.doi.org/10.1016/0168-1591(95)00611-U)
- Weary DM, Ross S and Fraser D** 1997 Vocalizations by isolated piglets: a reliable indicator of piglet need directed towards the sow. *Applied Animal Behaviour Science* 53: 249-257. [http://dx.doi.org/10.1016/S0168-1591\(96\)01173-2](http://dx.doi.org/10.1016/S0168-1591(96)01173-2)
- Whitham JC and Wielebnowski N** 2013 New directions for zoo animal welfare science. *Applied Animal Behaviour Science* 147: 247-260. <http://dx.doi.org/10.1016/j.applanim.2013.02.004>
- Wielebnowski N** 2003 Stress and distress: evaluating their impact for the well-being of zoo animals. *Journal of the American Veterinary Medical Association* 223: 973-977. <http://dx.doi.org/10.2460/javma.2003.223.973>
- Wielebnowski N and Watters J** 2007 Applying fecal endocrine monitoring to conservation and behavior studies of wild mammals: important considerations and preliminary tests. *Israel Journal of Ecology and Evolution* 53: 439-460. <http://dx.doi.org/10.1560/IJEE.53.3.439>
- Wilson RP, Grundy E, Massy R, Soltis J, Tysse B, Holton M, Cai Y, Parrott A, Downey LA, Qasem L and Butt T** 2014 Wild state secrets: ultra-sensitive measurement of micro-movement can reveal internal processes in animals. *Frontiers in Ecology and the Environment* 12: 582-587. <http://dx.doi.org/10.1890/140068>
- Wilson RP, Liebsch N, Davies IM, Quintana F, Weimerskirch H, Storch S, Lucke K, Siebert U, Zankl S, Müller G, Zimmer I, Scolaro A, Campagna C, Plötz J, Bornemann H, Teilmann J and McMahon CR** 2007 All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. *Deep Sea Research Part II: Topical Studies in Oceanography* 54: 193-210. <http://dx.doi.org/10.1016/j.dsr2.2006.11.017>
- Wilson RP, Shepard ELC and Liebsch N** 2008 Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* 4: 123-137. <http://dx.doi.org/10.3354/esr00064>
- Yoda K, Naito Y, Sato K, Takahashi A, Nishikawa J, Ropert-Coudert Y, Kurita M and Le Maho Y** 2001 A new technique for monitoring the behaviour of free-ranging Adélie penguins. *Journal of Experimental Biology* 204: 685-690
- Zekavat R and Buehrer RM** 2011 *Handbook of Position Location: Theory, Practice and Advances Volume 27*. John Wiley & Sons: Hoboken, USA. <http://dx.doi.org/10.1002/9781118104750>