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Review

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Abstract

An understanding of animal behaviour is important if conservation initiatives are to be effective. However, quantifying the behaviour of wild animals presents significant challenges. Remote-sensing camera traps are becoming increasingly popular survey instruments that have been used to non-invasively study a variety of animal behaviours, yielding key insights into behavioural repertoires. They are well-suited to ethological studies and provide considerable opportunities for generating conservation-relevant behavioural data if novel and robust methodological and analytical solutions can be developed. This paper reviews the current state of camera-trap-based ethological studies, describes new and emerging directions in camera-based conservation behaviour, and highlights a number of limitations and considerations of particular relevance for camera-based studies. Three promising areas of study are discussed: i) documenting anthropogenic impacts on behaviour; ii) incorporating behavioural responses into management planning; and iii) using behavioural indicators such as giving up densities and daily activity patterns. We emphasise the importance of reporting methodological details, utilising emerging camera trap metadata standards and central data repositories for facilitating reproducibility, comparison and synthesis across studies. Behavioural studies using camera traps are in their infancy; the full potential of the technology is as yet unrealised. Researchers are encouraged to embrace conservation-driven hypotheses in order to meet future challenges and improve the efficacy of conservation and management processes.

Key words: Ethology, remote sensing, anthropogenic impacts, behavioural indicators, monitoring, management

Introduction

Animal behaviour is an important component of conservation biology (Berger-Tal et al. 2011), and, hence, is of considerable interest to researchers and wildlife managers (Caro and Durant 1995). For example, behavioural studies can increase our understanding of species' habitat requirements (Pienkowski 1979), reproductive behaviour (Cant 2000) and dispersal or migration (Doerr et al. 2011), and elucidate impacts of habitat fragmentation (Merckx and Van Dyck 2007) or climate change (Moller 2004). Animal behaviour can also be a useful monitoring tool, with individual and group-level responses used to evaluate the impacts of management (Morehouse et al. 2016). It is important, therefore, to incorporate behaviour into conservation planning; its omission limits efficacy of conservation actions and could lead to failure (Berger-Tal et al. 2011). The confluence of conservation biology and ethology has come to be known as 'conservation behaviour', wherein conservation problems are addressed by the application of behavioural research (Blumstein and Fernández-Juricic 2004; Berger-Tal et al. 2011).

Quantifying the behaviour of wild animals presents significant challenges. Direct observation of animals can allow the evaluation of individual responses to environmental stimuli. Such studies may be weakened, however, by the influence of the human observer on focal animals (Nowak et al. 2014) and limited by small sample size and logistical constraints (Bridges and Noss 2011). Furthermore, only a limited number of species and habitats are amenable to direct, field-based observations (e.g. larger species and those that can be habituated; and in open and accessible habitats). Many of these have already been the focus of direct behavioural research (Schaller 1967; Kruuk 1972; Caro 1994) or may be atypical of more common habitats and can lead to inconsistent results (Laurenson 1994 vs Mills and Mills 2014). In cases where focal animal(s) cannot easily be directly observed, the vast majority of field-based behavioural studies have used radio (VHF) or satellite (GPS) telemetry, activity sensors and/or biologgers (e.g. Lewis et al. 2002; Grignolio et al. 2004; Shamoun-Baranes et al. 2012; Bouten et al. 2013). The advantages and disadvantages of these methods, which are currently the gold-standards for obtaining spatio-temporal behavioural data, are summarised in Table 1, highlighting that while these devices can provide powerful insights, they also have significant logistical and inferential limitations. Consequently, the suite of species that have had their behaviour quantified is biased and limited. New methods of obtaining behavioural data are, therefore, urgently required.

Camera traps (i.e. cameras that are remotely activated via an active or passive sensor; hereafter referred to as CTs) offer a reliable, minimally-invasive, visual means of surveying wildlife that substantially reduces survey effort. CTs are increasingly popular in ecological studies (Burton et al. 2015; Rovero and Zimmermann 2016) and provide a wealth of information that is often of considerable conservation value (e.g. Ng et al. 2004; Di Bitetti et al. 2006; Caravaggi et al. 2016). Continued technological improvements and decreasing equipment costs (Tobler et al. 2008a), combined with their demonstrated versatility (Rovero et al. 2013), mean that CTs will only continue to grow in popularity. CT data take the form of a still image or video of an individual or a group of individuals, of one or more species, which have been detected within the camera and location-specific zone of detection. These images can be linked with additional information, including the date, time and location at which the image was recorded. CT surveys have been effectively used to quantify species diversity (Tobler et al. 2008b), relative abundance (Carbone et al. 2001; Villette et al. 2017) and population parameters (Karanth et al. 2006; Rowcliffe et al. 2008), demonstrate site occupancy of rare or cryptic species (Linkie et al. 2007) and describe species replacement processes (Caravaggi et al. 2016). CTs have also been used in behavioural studies (Bridges and Noss 2011; Maffei et al. 2005). In a recent review of 266 CT studies, Burton et al. (2015)

characterized one-third as addressing behavioural questions (e.g. activity patterns, diet; Table 2).

In this paper, we review some of the recent literature on animal behaviour as elucidated by camera trapping studies. We then describe a number of common issues encountered by researchers undertaking such surveys and, finally, suggest future avenues of research that may be of considerable benefit to conservation initiatives. This review serves as a point of reference for researchers and practitioners undertaking conservation-oriented CT surveys of animal behaviour.

Current applications of camera traps to animal behaviour

CTs are well-suited to ethological studies, providing increasing opportunities to undertake extensive and detailed sampling of wild animal behavioural repertoires (see Fig. 1 and Table 2 for examples). The nature of the technology confers a number of important benefits. For example, CTs facilitate detailed studies of behaviours in species that were previously considered too small or elusive to be reliably observed in the field. CTs have been used to understand burrowing behaviour in <40g northern hopping-mice (*Notomys aquilo*; Diete et al. 2014) and olfactory communication in native and introduced <120g rats (*Rattus* sp.; Heavener et al. 2014). The use of CTs may also lead to a reduction in observer bias as, while a human observer is required to review collected images and assign individual and/or species identities and behaviours, cameras allow independent verification and recurrent analysis of observations. This is in contrast to conventional field methods for documenting behaviour, where it is rarely possible for another scientist to independently verify observational data.

Many types of animal behaviours have been studied with CTs (Table 2), including foraging (Otani 2001), daily activity patterns (Tan et al. 2013), scent marking (Delgado-V. et al. 2011), movement (Ford et al. 2009), livestock depredation (Bauer et al. 2005), and use of a variety of habitat features including dens/burrows (Clapham et al. 2014), urban habitats (Marks and Duncan 2009), corridors (LaPoint et al. 2013) and waterholes (Hayward and Hayward 2012). CT studies have often yielded key behavioural insights that may otherwise have remained unknown, many of which could be important to conservation processes. For example, studies investigating the efficacy of highway crossings in Banff National Park, Canada, described the effectiveness of under- and over-passes, an expensive and controversial means of impact mitigation (Clevenger and Waltho 2000; Ford et al. 2009), which is now being duplicated in other parts of the world. Picman and Schriml (1994) observed the predators of quail (*Coturnix coturnix*) nests in a variety of habitats, elucidating temporal variation and relative importance of each predatory species. The application of this method to the study of threatened avifauna has clear conservation benefits via the identification of direct impacts on egg success and the development of appropriate mitigation and monitoring techniques. Similarly, cameras provide more accurate post-hibernation den-emergence estimates for American black bears (*Ursus americanus*) than conventional methods, i.e. den visits and radio telemetry (Bridges et al. 2004). Long-term monitoring of emergence relative to climate may yield important insights into the effects of climate change on black bears and other hibernating species (*sensu* Bridges and Noss 2011).

The majority of ethological CT studies conducted thus far have been primarily curiosity-driven, rather than being motivated by applied conservation-focussed hypotheses. This is not to say that a large number of these studies do not have conservation value. On the contrary, the conservation relevance of the data is often explicitly discussed. It is apparent, however, that there is an increasing need for conservation-driven studies. CTs are among the most promising and flexible tools available and we are only beginning to explore their potential.

Emerging directions in camera-based conservation behaviour

The growth in popularity and application of CT surveys and novel solutions to non-behavioural questions of animal ecology (e.g. Rowcliffe et al. 2008; Martin et al. 2015; Bowler et al. 2016) suggests that creative methodological and analytical solutions will be increasingly used to investigate animal behaviours. If these novel studies are to be developed, it is important that researchers strive for true experimental designs focussed on conservation behaviour. A particular strength of CT surveys is the potential for multiple studies to be carried out concurrently (e.g. estimation of focal species population density and the species richness of the surveyed area). Thus, behaviour can be recorded alongside other important parameters, thereby facilitating insight into processes such as density-dependent behaviours and responses to climate change. New approaches are also being developed to move beyond correlational approaches and incorporate CTs into manipulative experiments, such as measuring animal behavioural responses to introduced stimuli (e.g. predator calls; Suraci et al. 2016).

Berger-Tal et al. (2011) described three ways in which behavioural research can be of conservation benefit: i) identifying the impact of anthropogenic environmental changes on behaviour; ii) considering behavioural aspects of conservation initiatives (‘behaviour-based management’); and iii) identifying behavioural indicators which are suggestive of changes in populations or the environment. We use this framework as a basis for our recommendations, below.

Anthropogenic impacts

An important area of conservation research lies in understanding the influence of anthropogenic stressors on animal behaviours and predicting the resulting population-level responses in order to inform management practices. Stressors such as habitat fragmentation, disturbance, the creation of ecological traps and the introduction of non-native species can have significant effects on behaviour (Robertson and Hutto 2006) and, hence, fitness (Berger-Tal et al. 2011). For example, animals may exhibit increasing wariness in areas of greater disturbance (Stewart et al. 2016) and may change their daily activity patterns in close proximity to human populations (Carter et al. 2012). While anthropogenic impacts are generally negative, some species show benefits such as increased occupancy in fragmented landscapes (Fleschutz et al. 2016), or using human activity to evade apex predators (Muhly et al. 2011; Steyaert et al. 2016). Impacts on one species may also have spillover effects on the wider ecological community (Wright et al. 2010; Clinchy et al. 2016).

Habitat fragmentation, the division of large, connected habitats into small, isolated fragments separated by dissimilar habitats, is a major conservation issue (Haddad et al. 2015). Fragmentation has a wide range of potential impacts on species and ecosystems (e.g. via edge effects, patch size, shape and complexity and distance from other patches; Fahrig 2003), and these impacts may be mediated through effects on animal behaviour. CTs provide new opportunities for documenting behavioural responses to fragmentation. For example, the activity patterns of nine-banded armadillos (*Dasypus novemcinctus*) varied in association with forest patch size, among other factors, while patch time-since-isolation was predictive of agouti (*Dasyprocta leporina*) activity (Norris et al. 2010).

The disruption of dispersal behaviour can lead to the endangerment and potential extinction of isolated populations by various mechanisms, including changes to genetic diversity and structure (Keyghobadi 2007), stochastic threats (Fischer and Lindenmayer 2007) and long-term displacement effects (Ewers and Didham 2005). Using CTs to document dispersal behaviour can improve understanding of responses to movement disruption (Blumstein and Fernández-Juricic 2004) and inform design and implementation of mitigation measures that encourage dispersal. Aimed at species with individually-identifiable markings or tags, individual-level analysis is potentially possible, although inferences about dispersal can also be drawn without individual identification. For examples, cameras are well suited to quantifying use of presumed dispersal routes or movement corridors, including mitigations designed to promote connectivity (e.g. highway crossings; Clevenger and Waltho 2005; Ford et al. 2009). CTs can also be used to identify colonization of new habitat patches (including range expansions or species invasions) and parameterize landscape connectivity models (Brodie et al. 2015).

No studies have integrated environmental sensors into CT studies investigating anthropogenic impacts on behaviour, and we believe this is a promising area for future development. Local temperature, precipitation and humidity can readily be recorded, and phenocams can be used to document vegetation and environmental changes (Brown et al. 2016). Collecting such information alongside CT-based behavioural data will allow us to increase our understanding of how animals respond to changing conditions at both large (population) and small (localities within home ranges) spatial scales. This is particularly important given the rapid changes that are predicted to occur under climate change.

Behaviour-based management

Berger-Tal et al. (2011) suggested that behaviour-sensitive management and behavioural modification are two key pathways through which ethology can inform active management for conservation. The former considers animal behaviour in the design of reserves and corridors, planning species reintroductions and translocations, and epidemiology with the goal of stabilising or increasing threatened populations or controlling pest or invasive species. Behavioural modification focuses on changing or preserving key behaviours within a focal population. CT surveys have the potential to inform both of these areas.

Considering social dynamics is one important area in which CT surveys can inform behaviour-sensitive management. Social species, i.e. those that interact and/or live together, often exhibit complex inter-group relationships and social structure (Rowell 1966; Creel 1997; Archie et al. 2006; Wolf et al. 2007; Wey et al. 2008), that are susceptible to rapid change via the social displacement or death of one or more individuals. This can have severe consequences for the species and/or their environment (e.g. Nyakaana et al. 2001). Social Network Analysis (SNA) facilitates the study of relationships between nodes (i.e. individuals), within networks (i.e. social groups; Sueur et al. 2011). The methodology is increasingly used to study animal behaviour (Lusseau et al. 2006; Whitehead 2008; Voelkl and Kasper 2009; Jacoby and Freeman 2016). Examples of SNA demonstrating a direct benefit to conservation, however, are few. SNA studies are limited in that they require the reliable identification of individuals and, hence, are only applicable with CTs where animals exhibit individual characteristics or markings, or where marks (e.g. tags) can be attached. However, placing cameras in areas frequented by social groups such as feeding or resting sites, and with a sufficient number of units, could yield a considerable amount of important data for behaviour-sensitive management. Such site-specific studies have some limitations and incur biases that require evaluation. For example, individuals may not be equally detectable, or full groups may not be observed. Furthermore, it would be difficult to account for behaviours and social interactions which occur while away from the focal site. However, SNA analyses do not require constant observation of all group members to be effective (see Jacoby and Freeman 2016). Assessing potential bias with calibration by direct observation or other methods and placing observations in appropriate contexts is therefore important.

SNA has the potential to increase our understanding of disease or pathogen transmission and individual or group vulnerability (Krause et al. 2007), an issue of particular relevance to the conservation of species which are susceptible to outbreaks (e.g. Hamede et al. 2009). SNA studies have demonstrated that the removal of certain individuals (e.g. via hunting) can have a considerable effect on the stability of the social network (e.g. Flack et al. 2006), thus demonstrating their potential utility in elucidating the impacts of the bushmeat trade on inter- and intra-group dynamics in primates, for example. Furthermore, SNA has implications for reintroduction programmes, where the (re)construction of cohesive social structures in a captive setting would be necessary for the return of the focal species to the wild (Abell et al. 2013). Studies of the relationships between individuals, therefore, can help us to understand how social behaviour is influenced by a variety of factors and, hence, provide an additional means by which practitioners can build an evidence base to address conservation questions.

CTs can also be applied to studies of behavioural modification. For example, Davies et al. (2016) investigated responses of African herbivores to changes in predation risk resulting from recently-reintroduced lions. Cameras could also be used to monitor animal responses to conflict mitigation measures such as the use of bees or chilli to deter crop-raiding elephants (Karidozo and Osborn 2015; Ngama et al. 2016).

Behavioural indicators

The ways in which animals adapt their foraging behaviour in human-impacted environments have important implications for their abilities to adapt and persist under increasing pressures. Behavioural indicators can be used to assess the state of animals and the environments they inhabit, highlighting important conservation issues such as population decline or habitat degradation, or being used to monitor the efficacy of management (Berger-Tal et al. 2011). Behaviour effectively acts as an early-warning system, indicating changes to processes before they are evident through, for example, population decline.

The giving up density (GUD; i.e. the amount of food left behind from a known starting quantity; Brown 1988) is one such behavioural indicator that has been used to study predation risk (Orrock 2004; Severud et al. 2011), energetic costs (Nolet et al. 2006), forager state and forage quality (Hayward et al. 2015), plant toxins (Emerson and Brown 2015), competition (Brown et al. 1997) and predator-prey dynamics (Andruskiw et al. 2008). It is also central to describing the "landscape of fear" (i.e. relative levels of predation risk within an area of use) of an animal and its habitat preferences, which are direct behavioural indicators with significant conservation implications (Kotler et al. 2016). CTs offer a relatively reliable way of using the GUD technique to ask more in-depth questions of conservation relevance. For example, CTs have been used to calculate GUDs for multiple species (Lerman et al. 2012), examine (Mella et al. 2015), and differentiate individual versus group foraging habits (Carthey and Banks 2015). These observations can then be used to inform the development of hypotheses relating to the broader effects of local food and predator abundance, predation pressure and inter- and intra-specific competition. With advancements in CT technology and creative experimental design, a wealth of conservation-focussed GUD applications are now possible.

A key strength of CTs lies in collecting data on multiple species, either as bycatch in a focal study, or as part of a specific multi-taxa investigation. Accordingly, there has been an increasing focus on assessing species interactions and niche partitioning via comparisons of co-occurrence and activity patterns (de Almeida Jacomo et al. 2004; Kukielka et al. 2013; Farris et al. 2014; Wang et al. 2015; Bu et al. 2016; Cusack et al. 2016; Sweitzer and Furnas 2016). Animal activity patterns are shaped by a number of factors, including foraging efficiency (Lode 1995), predator/prey activity (Middleton et al. 2013), photoperiodism (McElhinny et al. 1997), and competition (Rychlik 2005). Conservation-focussed studies using these methodologies, however, are scarce. Changes in the way species interact and use the landscape may be indicative of responses to changing environmental pressures and, hence, can direct development of early conservation strategies. For example, brown bears (*Ursus arctos*; Ordiz et al. 2013) altered their movement patterns and wolverines (*Gulo gulo*; Stewart et al. 2016) behaved differently when faced with human disturbance, potentially impacting their ecosystem roles and, hence, associated species and habitats. Disturbance of the activity patterns of one or more species in a dynamic interaction, particularly ecological competitors or predators and prey, can therefore be interpreted as indicative of environmental changes and, hence, suggest additional lines of enquiry and highlight areas of conservation concern.

Scaling-up

Cameras can be used to monitor large-scale biodiversity conservation processes (O'Brien et al. 2010; Ahumada et al. 2013) and investigate animal behaviour on a landscape scale. Scaling-up CT networks would provide stronger, larger-scale inferences on spatio-temporal variation in behaviours (Steenweg et al. 2016). Studies conducted on a broader scale have inherent limitations, however, that are not necessarily considerations for more localised investigations. The trade-off between the scale of investigation and camera array density has spatio-temporal implications which must be considered when designing a study, formulating hypotheses and deriving inferences from resultant data. Broad-scale studies are also ostensibly limited by the number of researchers available to place and check cameras and process data. The recruitment of volunteers (i.e. citizen scientists), however, offers a means of expanding the scope of research (Cohn 2008), greatly expanding spatial coverage and delivering a wealth of temporally comparable data (McShea et al. 2016). Emerging large-scale camera monitoring initiatives, such as Snapshot Serengeti (www.snapshotserengeti.org; Swanson et al. 2015) and Wildcam Gorongosa (www.wildcamgorongosa.org) demonstrate the benefits of this approach. CT projects utilising citizen science have the potential to deliver a substantial amount of behavioural data (McShea et al. 2016) and inform conservation processes. However, few large-scale studies utilising citizen science involve behavioural analyses. CT video data can produce vast amounts of video footage but the extraction of key behavioural data from video footage is time consuming, imposing a major obstacle. Crowdsourcing video interpretations can overcome this limitation, however, and the use of robust ethograms, simple training regimes and blinding of observers to treatments can assuage concerns about the reliability of citizen science interpretations (e.g. Carthey 2013).

Synthesising across projects offers another means of conducting broader analyses (Steenweg et al. 2016). We recommend that researchers embrace emerging CT metadata standards and associated opportunities to use common data repositories such as Wildlife Insights (www.wildlifeinsights.org; Forrester et al. 2016), thus increasing the potential for the synthesis of inferences across large scales. The value of current data repositories is reduced, however, by their reliance on static images and omission of video. While it is possible to derive important behavioural data from still images, videos are undoubtedly more informative and an important future direction for CT-based behavioural research. Expenses notwithstanding, it is in the interests of conservation behaviour researchers to establish a digital repository for video data.

Relevant limitations and considerations

Despite the great promise of new insights in conservation behaviour from CTs, it is important to consider potential limitations. CTs are passive instruments; thus, while it is possible to identify animals according to species, age-class (Clapham et al. 2014), sex (Bezerra et al. 2014) or, indeed, identify individuals (Karanth et al. 2006; Zheng et al. 2016), the collection of biometric, genetic and other data of interest requires the application of supplementary or alternative methodologies. Furthermore, CTs are frequently considered to be non-intrusive, causing little to no disturbance. However, while the sound produced by recording units is largely inaudible to humans, it is frequently detected by wildlife (Meek et al. 2014a). Similarly, CTs which utilise visible light (as opposed to infra-red) increase the chances of the camera being detected by animals, potentially disrupting their natural behaviour (Meek et al. 2016a).

Camera failure, although rare, can result in the loss of large quantities of data. Similarly, camera theft is becoming increasingly common (Meek et al. 2016b). It is therefore necessary to balance the frequency of visits to maintain CTs with risk of data loss. To accommodate this, it is advisable to build some redundancy into the study design, such as the use of cameras that allow the transmission of images via Global Packet Radio Service (GRPS) and/or Wi-Fi and can therefore facilitate remote data collection and inform the timing of maintenance visits.

Detailed analysis of a target species' behavioural repertoire requires the use of video footage which often exposes the technical limitations of CT equipment. Many cameras offer only limited length of videos (e.g. 60 seconds), requiring the camera to be retriggered to continue the capture of the behaviours and, hence, creating gaps in the observation. Some cameras have a slow trigger time meaning that initial behaviours, which might be the most important in terms of measuring detection of a stimulus (rather than the response), can be missed. Sampling the behaviours of small species can be particularly challenging, with CTs typically designed for deer-sized game species (Weerakoon et al. 2014), a problem that will require novel solutions. For example, flash-illuminated images are frequently obscured by overexposure when close enough to small mammals to observe behaviour clearly, whereas at the correctly exposed distance, animals can be too far away to reliably identify species or discern behaviours. Furthermore, understanding the reliability of camera surveys for addressing multi-species objectives remains an important area of methodological research (see Burton et al. 2015). Multi-taxa studies also require careful planning to ensure that CTs are appropriately located and adequately spaced to maximise the chances of capturing a diverse species assemblage. The choice and placement of cameras should, therefore, be dictated by the objectives of the study, the ecology of the study species, the statistical sampling framework and associated considerations.

An oft-repeated concern relates to study repeatability; specific details of study design (e.g. how survey sites were chosen, use of lures) and camera protocols (e.g. camera model, deployment details) are often lacking (Meek et al. 2014b; Burton et al. 2015). A number of factors influence the detection of individuals (see Burton et al. 2015) and sampling details may have important implications for analytical assumptions such as effective sampling area and site independence (Harmsen et al. 2010; Mccoy et al. 2011; du Preez et al. 2014; Newey et al. 2015). Comprehensive methodological descriptions and utilisation of emerging CT metadata standards (Forrester et al. 2016) are important for facilitating reproduction, comparison and synthesis across studies.

Finally, as with any survey method, observations from CTs are incomplete and may contain biases that affect inferences. As noted above, species and individuals may vary in their detectability by CTs according to attributes such as body size, movement speed, curiosity and wariness. Behaviours observed by CTs may also not always be representative of behaviours more generally. It is thus incumbent upon researchers to remain vigilant for potential biases and test CT-based inferences through comparison and calibration with more established ethological methods.

Conclusions

CTs are rapidly increasing in popularity, and their application to conservation behaviour is growing. Recent efforts to coordinate camera studies across large-scales through methodological standardization and/or better reporting of methodologies and metadata will facilitate broader ethological inferences on species' behavioural responses to environmental change. The development and application of new techniques and analytical methods explicitly focussed on anthropogenic impacts, behaviour-based management and behavioural indicators would undoubtedly benefit conservation programmes. CTs are not a panacea, but they confer many benefits to researchers and the diversity of possible applications is gradually being realised. We hope that this paper will act as a catalyst, advancing the adoption of CT technology within conservation behaviour. It is important, therefore, that potentially profitable avenues of investigation are identified and pursued if we are to maximise the generation of valuable data and, hence, improve the conservation outlook for the ever-increasing number of threatened or endangered species.

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Table 1. Potential advantages and disadvantages of three conventional methods commonly used to collect animal behavioural data. These are not necessarily contextual constants. For example, GPS accuracy is affected by vegetation density. Similarly, activity sensors may return detailed or simplistic data, depending on the device used. VHF = Radio telemetry tags; GPS = Global Positioning System tags; ACC = activity sensors; CT = camera traps.

	Method			
Advantages	**VHF**	**GPS**	**ACC**	**CT**
Allows independent data verification			✓	✓
Collection of biometric data during deployment	✓	✓	✓	
Combined analysis of movement and trait-based data	✓[1,2]	✓	✓	✓
Detailed data[2,3,4*]		✓	✓	✓
Habitat associations	✓	✓		✓
Identification of specific behaviours			✓*	✓
Landscape-scale	✓	✓		✓
Low cost			✓	✓*
Low survey effort		✓*	✓*	✓*
Multi-taxa surveys				✓
Range analyses	✓	✓		✓
Disadvantages				
Bias from handling focal animal(s)[5,8]	✓	✓	✓	
Disturbance effects				✓*
Expensive	✓	✓		✓*
Limited sample size	✓	✓	✓	
Negative impacts on focal animal(s) during backpack/collar deployment[7]	✓	✓	✓	
Requires ground-truthing to avoid inferential error[4,5,6]			✓	
Simplistic data*	✓	✓	✓[9]	✓
Stationary				✓
Technological failure	✓	✓	✓	✓
Triangulation/location error[5]	✓	✓		

* Device, environment and/or species-dependent

[1] Grignolio et al. (2004)
[2] Lewis et al. (2002)
[3] Bouten et al. (2013)
[4] Shamoun-Baranes et al. (2012)
[5] Bridges and Noss (2011)
[6] Ware et al. (2015)
[7] Barron et al. (2010)
[8] Wilson et al. (1986)
[9] Coulombe et al. (2006)

Table 2. Examples of behavioural observations of wildlife via camera trapping. Species are ordered chronologically following the date of corresponding references.

Behaviour	Species	References
Active period	Agouti (*Dasyprocta punctata*) and ocelot (*Leopardus pardalis*)	Suselbeek et al. 2014
	Guizhou snub-nosed monkey (*Rhinopithecus brelichi*)	Claridge et al. 2004
	Spotted-tailed quoll (*Dasyurus maculatus*)	Tan et al. 2013
Antipredator responses	Bush rat (*Rattus fuscipes*)	Carthey and Banks 2016
Bathing/wallowing	Giant anteater (*Myrmecophaga tridactyla*)	Emmons et al. 2004
Crossing roads	Bare-nosed wombats (*Vombatus ursinus*)	Crook et al. 2013
Daily activity	Clouded leopard (*Neofelis nebulosa*), golden cat (*Catopuma temminckii*), and 4 other felids	Azlan and Sharma 2006
	Tayra (*Eira barbara*)	Delgado-V. et al. 2011
	Giant otter (*Pteronura brasiliensis*)	Leuchtenberger et al. 2014
	12 terrestrial mammal species	Rowcliffe et al. 2014
Denning	American black bear (*Ursus americanus*)	Bridges et al. 2004
Foraging	Yakushima macaque (Macaca fuscata yakui)	Otani 2001
	Tayra (*Eira barbara*)	Delgado-V. et al. 2011
Migration	Bald eagle (*Haliaeetus leucocephalus*), black vulture (*Coragyps atratus*) and 5 other birds of prey	Jachowski et al. 2015
Nest predation	Predators exploiting quail (*Coturnix coturnix*) eggs	Picman and Schriml 1994
Phenological changes	Elk (*Cervus elaphus*)	Brodie et al. 2012
Positional behaviour	Bare-tailed woolly opossum (*Caluromys philander*)	Dalloz et al. 2012
Resource partitioning	Cape fox (*Vulpes chama*), caracal (*Caracal caracal*), honey badger (*Mellivora capensis*) and 9 other carnivores	Edwards et al. 2015
Response to human-animal conflict	Tiger (*Panthera tigris*) and associated prey species	Johnson et al. 2006
Scent marking	Tayra (*Eira barbara*)	Delgado-V. et al. 2011
	Eurasian lynx (*Lynx lynx*)	Vogt et al. 2014
Social behaviour	Blonde capuchin (*Sapajus flavius*)	Bezerra et al. 2014
	Giant otter (*Pteronura brasiliensis*)	Leuchtenberger et al. 2014
Temporal avoidance	Jaguar (*Panthera onca*) and puma (*Puma concolor*)	Romero-Muñoz et al. 2010
Travel speed	12 terrestrial mammal species	Rowcliffe et al. 2016
Waterhole use	15 species of ungulates, 5 birds, 3 mega-herbivores, 2 primates and 5 carnivores	Hayward and Hayward 2012

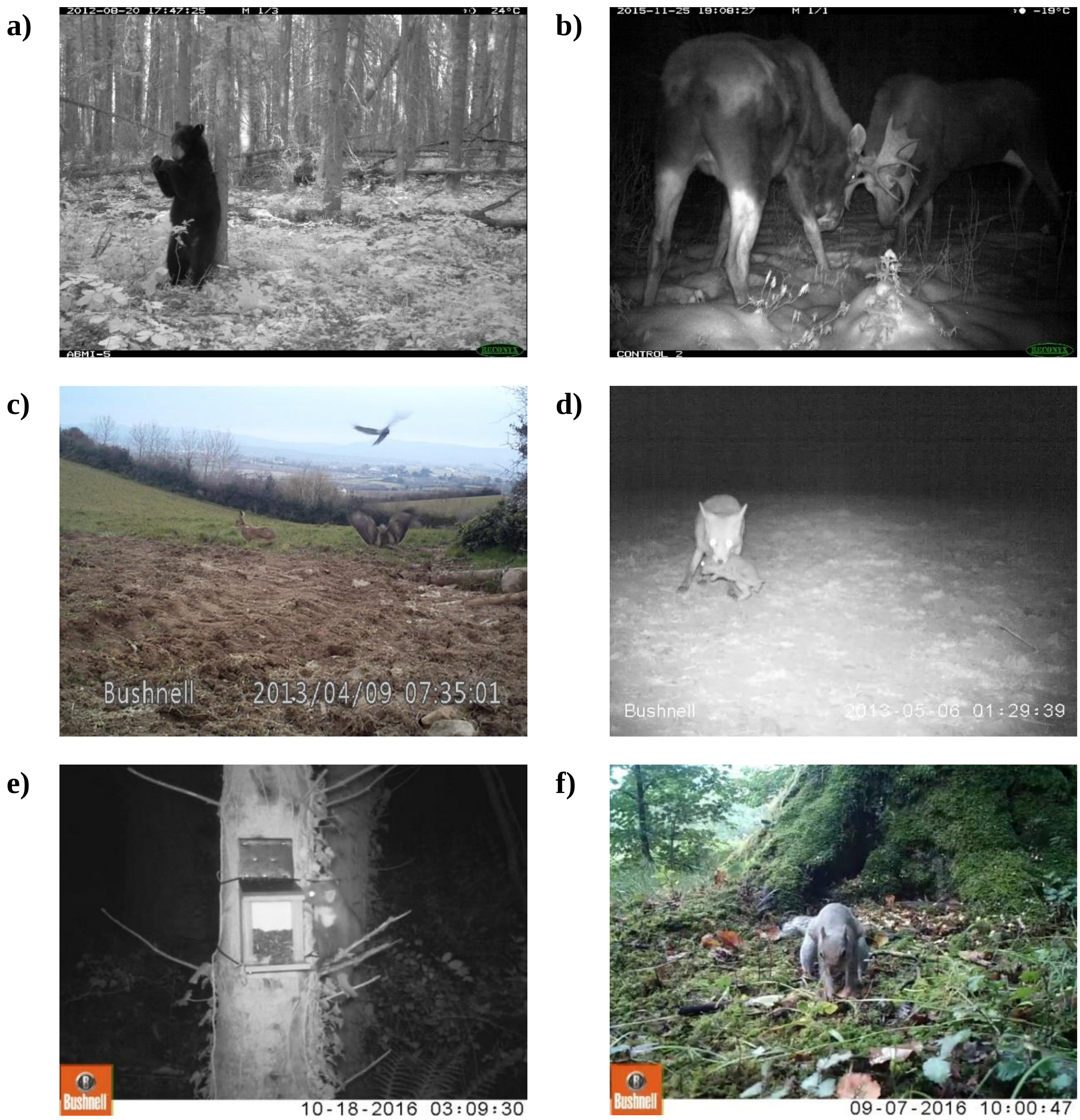

Figure 1. Examples of animal behaviour captured by camera traps: **a)** Scent marking by an American black bear (*Ursus americanus*); **b)** intraspecific competition in moose (*Alces alces*); **c)** interspecific interactions between a European hare (*Lepus europaeus*; anti-predator response), a common buzzard (*Buteo buteo*; avoidance and attempted predation) and a hooded crow (*Corvus cornix*; anti-predator behaviour) captured on video (available at 10.6084/m9.figshare.4508369); **d)** predation of a European rabbit (*Oryctolagus cuniculus*) by a red fox (*Vulpes vulpes*); **e)** investigation of a squirrel feeding station by a pine marten (*Martes martes*); **f)** nut caching by a grey squirrel (*Sciurus carolinensis*). Images provided by A.C. Burton (a, b), A. Caravaggi (c, d) and C.M.V. Finlay (e, f).