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PERSPECTIVES AND NOTES

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A review of factors to consider when using camera traps to study animal behavior to inform wildlife ecology and conservation

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Abstract

Camera traps (CTs) are an increasingly popular method of studying animal behavior. However, the impact of cameras on detected individuals—such as from mechanical noise, odor, and emitted light—has received relatively little attention. These impacts are particularly important in behavioral studies in conservation that seek to ascribe changes in behavior to relevant environmental factors. In this article, we discuss three sources of bias that are relevant to conservation behavior studies using CTs: (a) disturbance caused by cameras; (b) variation in animal-detection parameters across camera models; and (c) biased detection across individuals and age, sex, and behavioral classes. We propose several recommendations aimed at mitigating responses to CTs by wildlife. Our recommendations offer a platform for the development of more rigorous and robust behavioral studies using CT technology and, if adopted, would result in greater applied benefits for conservation and management.

KEYWORDS

conservation behavior, management, observer bias, remote sensing, wildlife

1 | INTRODUCTION

Detecting changes in species behavior in response to environmental stimuli is key to understanding the mechanisms behind individual and, ultimately, species responses to global change, including land use changes, habitat and biodiversity loss, and climate change (Wong & Candolin, 2015). Behavioral change can serve as an early warning sign for demographic impacts (Wiley & Ridley, 2016), shed light on species adaptations to changing environments (Rabaiotti & Woodroffe, 2019), and highlight potential conservation interventions (Anthony & Blumstein, 2000). Advances in technology, declining costs, methodological versatility, and the potential for collecting a substantial amount of data with comparatively little survey effort, mean that remotely activated camera traps (CTs, hereafter) are becoming increasingly popular in studies of animal behavior (Burton et al., 2015; Caravaggi et al., 2017; Sanz & Morgan, 2007). For example, CTs have been used to describe activity patterns (e.g., Rowcliffe, Kays, Kranstauber, Carbone, & Jansen, 2014), foraging (e.g., Delgado-V, Arias Alzate, Botero, & Sanchez Londono, 2011), social behavior (e.g., Leuchtenberger, Zucco, Ribas, Magnusson, & Mourao, 2014), denning (Bridges, Vaughan, & Klenzendorf, 2004), and anti-predator behaviors (Carthey & Banks, 2016). Changes to these behaviors can affect individual survivorship and fitness and, given sufficient frequency and effect size, population dynamics. However, all these analyses assume behaviors of detected species are independent of the detector (i.e., CTs). The degree to which this assumption is met or violated is rarely considered or articulated. This problem has the potential to affect conclusions and conservation measures derived from behavioral analyses.

Behavioral studies of wildlife conducted via direct human observation are subject to observer bias, that is, the tendency of observers to interpret behaviors in the light of their own prior knowledge, expectations, and feelings. Indeed, field studies of behavior are often undertaken, and observations filtered, by researchers with a priori preconceptions about the focal animal's ecology and environment. Conversely, CTs allow researchers to escape at least some of those biases by recording direct observations of wildlife, for extended periods of time and at multiple locations simultaneously, without requiring a potentially confounding human presence in the field (apart from activities required for camera deployment and maintenance). Researchers' activities and presence may have long-term consequences for the local ecology or focal species' behavior (Hobaiter et al., 2017), and human observers may bias data collection where researchers choose which individuals to obtain data from or when to record footage, or when an observed animal reacts to the observer. In contrast, CTs collect data from any animals moving through the detection zone, and are thus likely to be less biased—or, at worst, systematically biased based on measureable factors—with regard to sampling of individuals. Each detection thus becomes a voucher specimen from which recorded behavior can be reviewed by several researchers, allowing enhanced replicability and even reduced data processing time by engaging volunteer citizen-scientists through internet-based platforms (Hsing et al., 2018). Cameras also allow the collation of standardized data from spatially and/or temporally independent studies (e.g., Caravaggi et al., 2018; Kalan et al., 2019; Stewart et al., 2016), facilitating more broadly applicable ethological inferences on how species respond to various stimuli. This approach is exemplified by successful projects on citizen science platforms (e.g., Chimp&See, www.chimpandsee.org; MammalWeb, www.mammalweb.org; Snapshot Serengeti, www.zooniverse.org/projects/zooniverse/snapshot-serengeti). There, public volunteers can contribute to large-scale efforts for identifying and classifying species, individuals, and behaviors from thousands of CT photos and videos (Kalan et al., 2019). It is then possible to assess degrees of inter-observer reliability (Martin & Bateson, 1986) and aggregate classifications from multiple participants to improve accuracy in resulting datasets (Hsing et al., 2018; Swanson et al., 2015). CT data can also be archived for future reference (e.g., eMammal, https://emammal.si.edu/).

Although CTs provide many advantages, biases persist (Hofmeester et al., 2019). These biases are particularly key to behavioral studies in conservation, wherein we seek to ascribe changes in behavior to anthropogenic impacts in the environment (e.g., Stewart et al., 2016). Cameras can be their own source of anthropogenic impact. Here, we review and discuss three sources of bias that are of particular relevance to behavioral conservation studies conducted via CTs and how they might affect the reliability of behavioral inferences: (a) disturbance caused by cameras; (b) variation in animal-detection parameters across camera models; and (c) biased detection across individuals and age, sex, and behavioral classes.

2 | DISTURBANCE CAUSED BY CAMERAS

While CTs mitigate several methodological risks, the impacts of CT technology itself on wildlife have been given limited attention (but see Séquin, Jaeger, Brussard, & Barrett, 2003; Schipper, 2007; Gibeau & McTavish, 2009; Meek et al., 2014; Meek, Ballard, Fleming, & Falzon, 2016; Kalan et al., 2019). For instance, contrary to the common labeling of CTs as nonintrusive or noninvasive (e.g., Bahaa-el-din & Cusack, 2018; Hackett et al., 2007; Karanth & Nichols, 2010; Long, MacKay, Zielinski, & Ray, 2008; Monterroso, Alves, & Ferreras, 2011; Velli, Bologna, Silvia, Ragni, & Randi, 2015), CTs are mechanical devices that emit light and sound, carry human scent, and have a tangible and novel presence in the environment. Indeed, some behavioral studies actually use CT systems as a source of experimental disturbance against which animal responses can be measured (e.g., Kalan et al., 2019; Suraci et al., 2017). It is no surprise, then, that a wide range of species have been observed to detect and investigate CT units (see Figure 1 for examples). CTs that use visible light to illuminate wildlife are more likely to be detected than those that use infrared and, as a result, have greater potential to disrupt natural behavior (Meek et al., 2014; Wegge, Pokheral, & Jnawali, 2004), particularly for wary species such as wolves, *Canis lupus* (Gibeau & McTavish, 2009) or coyotes, *Canis latrans* (Larrucea, Brussard, Jaeger, & Barrett, 2007). Further, Apparent differences in diurnal versus nocturnal behaviors need to be evaluated particularly carefully since nocturnal illumination ranges are typically reduced. Moreover, the sound produced by CTs may be undetectable by humans, but often elicits a reaction from other species (Meek et al., 2016).

Similarly, a CT represents a new visual and chemical element in the environment that is often detectable by wildlife (e.g., Kalan et al., 2019; Larrucea et al., 2007). Animals vary in their response to scent (e.g., Kalan et al., 2019; Muñoz, Kapfer, & Olfenbuttel, 2014) and it is possible that human scents on equipment will affect the behavior of some species or individuals more than others. This influence may be exacerbated by clearing immediate vegetation to reduce false triggers, potentially leaving behind additional cues of recent human presence. Many CT studies use bait or lure to bring animals into the camera's detection zone, thus increasing the probability of detecting particular species, typically carnivores, and have the potential to alter species behavior (Braczkowski et al., 2015, 2016; Burton et al., 2015; Holinda, Burgar, & Burton, 2020; Mills, Fattebert, Hunter, & Slotow, 2019). Bait designed to attract carnivores can also result in the avoidance of the camera location by prey species, resulting in fewer detections (Rocha, Ramalho, & Magnusson, 2016). Hence, both baited and unbaited cameras could have particular implications for observations of species that use odor for communication, navigation, or to detect predators and/or prey (Mills et al., 2019). Moreover, we consider it possible that the use of attractants could increase local potential for human–wildlife conflicts if animals come to associate the attractant and camera system with humans (sensu Newsome, & Van Eeden, 2017).

3 | VARIATION BETWEEN CAMERA MODELS

There is considerable variation in the physical design, structure, and technical specifications of CT models (Rovero, Zimmermann, Berzi, & Meek, 2013; Rovero & Zimmermann, 2016; Trolliet et al., 2014). For example, CTs vary in the sensitivity of their passive infrared detection band, leading to marked differences in how animals are detected given their speed, position, time of day, and ambient temperature (Rovero et al., 2013; Rovero & Zimmermann, 2016). Variation between and within models when using different settings can result in differences in animal detectability due to variation in trigger speed, sensitivity, detection zone, and field of view (Apps & McNutt, 2018; Glen, Warburton, Cruz, & Coleman, 2014; Meek, Ballard, & Fleming, 2015), leading to missed detections (Wellington et al., 2014; Lepard et al., 2019). More importantly, for behavioral studies, such variation can affect detectability of behavioral states within a species, such as oversampling resting and undersampling fleeing, that could, subsequently lead to spurious conclusions about behavior. Similarly, there is considerable variation in the amount of noise—including ultrasonic sound when still images are taken—produced between camera models, almost all of which is within the hearing range of most mammals (Meek et al., 2014). Any noise produced by a camera could therefore increase the probability of the unit being detected by an animal and influence subsequent behavior. Variance in noise emission between individual cameras is a further potential confounding factor that remains untested.

There appears to be no substantial difference in the wavelengths of infrared illumination produced between many CT models. However, contrary to the claims of some manufacturers that animals cannot see infrared light, many animals are in fact able to see the infrared illumination used by many CTs in low light (Meek et al., 2014) and the flash produced by some units is bright enough to be visible to humans under some conditions (T. R. Hofmeester, personal observation).

Differences between camera models may be particularly relevant when recording video footage. When camera units are set to record video, for instance, the detected animal is illuminated for a longer length of time, thus increasing the likelihood of the camera being detected. While still images have been favored in the majority of CT studies—due to faster trigger speeds, recovery times, and easier processing—advances in technology have led to improved video performance and a corresponding increase in video use, particularly for behavioral studies (e.g., Caravaggi et al., 2017; Sanz & Morgan, 2007; Tattoni, Bragalanti, Groff, &

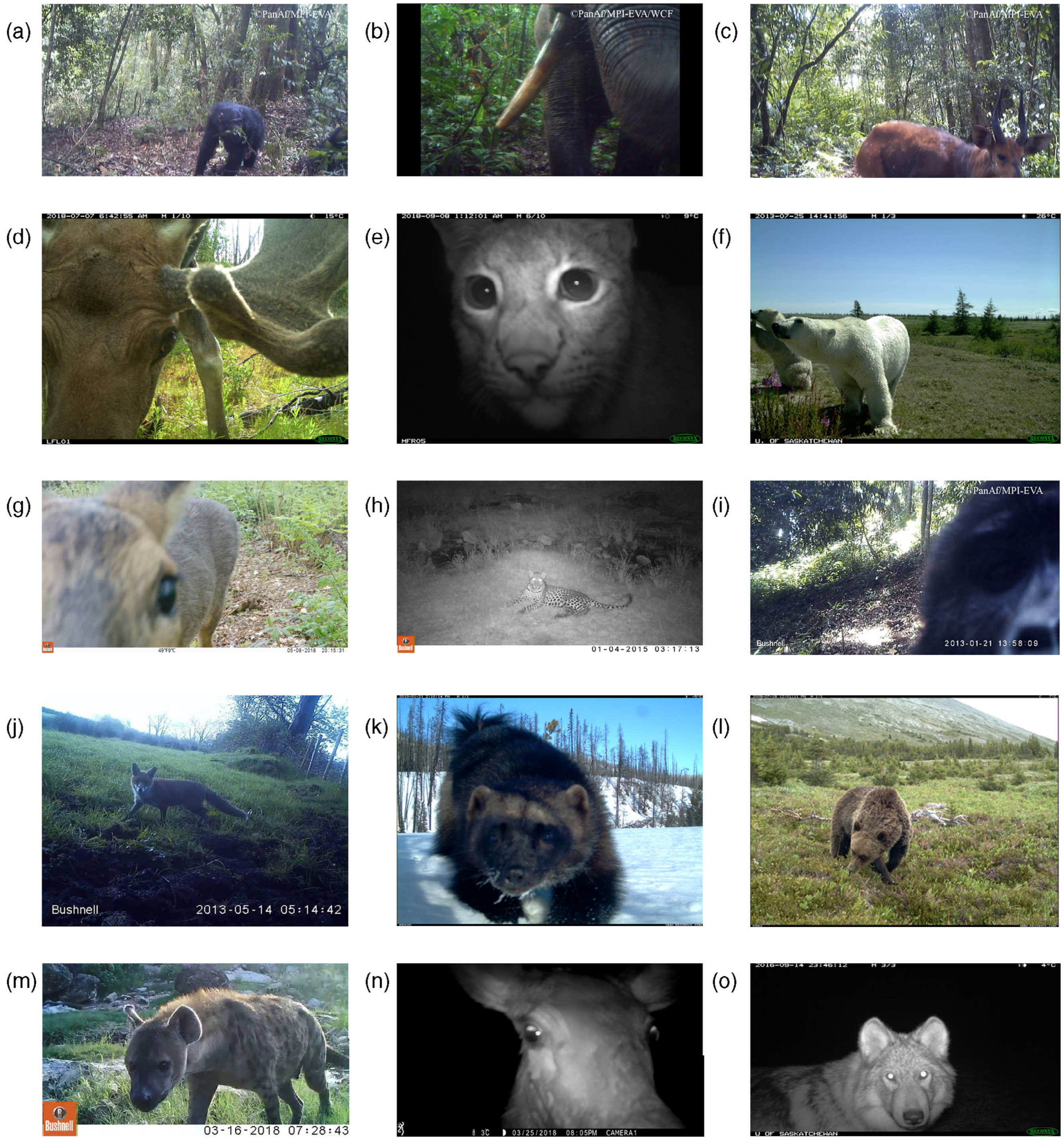

FIGURE 1 Examples of mammals detecting camera traps and/or olfactory cues associated with camera traps. (a) Chimpanzee, *Pan troglodytes*; (b) African elephant, *Loxodonta africana*; (c) sitatunga, *Tragelaphus spekii*; (d) moose, *Alces alces*; (e) Eurasian lynx, *Lynx lynx*; (f) polar bear, *Ursus maritimus*; (g) roe deer, *Capreolus capreolus*; (h) African leopard, *Panthera pardus*; (i) mountain gorilla, *Gorilla beringei*; (j) red fox, *Vulpes vulpes*; (k) wolverine, *Gulo gulo*; (l) grizzly bear, *Ursus arctos*; (m) spotted hyena, *Crocuta crocuta*; (n) red deer, *Cervus elaphus*; (o) grey wolf, *Canis lupus*. Images provided by Ammie K. Kalan (a–c,i), T. R. H. (d,e), D. R. (f,o), S. G. (g,n), A. C. (h,j), J. T. F. (k,l), A. G. (m). Visit https://doi.org/10.6084/m9.figshare.c.4593902.v1 for selected source videos

Rovero, 2015). It is important, therefore, that researchers choose the most appropriate camera model and settings for their study species, taking into account relevant biological factors such as auditory and visual acuity, as well as mechanical traits inherent to the cameras themselves.

4 | DETECTION BIAS

While cameras sample a population without making a priori decisions about which individuals to sample, study design and methodological protocols (e.g., camera array structure, or camera sensitivity and trigger-speed settings) may, nevertheless, bias which animals are detected (Larrucea et al., 2007) and which behaviors are recorded. Indeed, the application of different sampling methodologies (e.g., systematic versus [pseudo-]random placement) can result in very different detection probabilities (e.g., Cusack et al., 2015; Després-Einspenner, Howe, Drapeau, & Kühl, 2017; Kays et al., 2020; Kolowski & Forrester, 2017; Rovero et al., 2013; Srbek-Araujo & Chiarello, 2013). For example, anthropogenic features such as roads can act as corridors facilitating species' movement or represent disturbances to be avoided, inflating or deflating the number of detections depending on species-specific responses to the feature (Di Bitetti, Paviolo, & de Angelo, 2014; Rovero & Zimmermann, 2016). Furthermore, CTs sample a vanishingly small fraction of the territory of many target species, perhaps just a few square meters. Even where locations have been selected as being of particular interest to the species (e.g., food or water sources), it remains probable, simply as a function of encounter rate between the individual and the relatively insignificant area of coverage of even the immediate area around the CT, that many encounters at CT locations are missed.

Movement is a fundamental component of detection for mammals (Broadley, Burton, Avgar, & Boutin, 2019; Neilson, Avgar, Burton, Broadley, & Boutin, 2018; Stewart, Volpe, & Fisher, 2019) and CT data have been found to be biased against detecting small, fast-moving species (Glen et al., 2014). Within-species differences in site fidelity, for example, around specific resources, decreases use of space and, hence, increases the probability of detection at specific camera locations (e.g., Sanz & Morgan, 2007). The same can be true of interspecific interactions (Fisher, Wheatley, & Mackenzie, 2014). Similarly, intraspecific variation in behavior and the frequency with which certain behavioral classes are expressed, for example, movement versus mating behavior, can affect the detectability of individuals and, as a result, which behaviors are recorded. Some taxa, indeed, individuals, may be intrinsically more neophobic or neophilic toward novel cues (Glickman & Sroges, 1966), including CTs (Kalan et al., 2019). There may even be differences between age and sex classes within species (Braczkowski et al., 2015). Some species such as wolverines, *Gulo gulo* (J. T. Fisher, personal observation) and elephants, *Elephantidae*, may seek out and even attack CTs, whereas others such as wolves appear to avoid them (Gibeau & McTavish, 2009). Indeed, the detection of CTs by target species may subsequently impact the detection of those individuals by the CTs, as well as the behavior captured. For example, species with binocular vision, such as primates, are more likely to detect and, hence, respond to devices when they are facing and traveling toward the CT rather than away from or parallel to it (Kalan et al., 2019). For some studies, it may be necessary to allow animals to become habituated to CTs over a longer period of time before reliable data can be collected.

Species' behaviors can also vary seasonally (Caravaggi et al., 2018; Larrucea et al., 2007; Popescu, de Valpine, & Sweitzer, 2014) and annually, resulting in time-varying patterns in diurnal activity (Frey, Fisher, Burton, & Volpe, 2017), movement (Broadley et al., 2019), habitat use (Kalle, Ramesh, Qureshi, & Sankar, 2014), and social behaviors (Hongo, Nakashima, Akomo-Okoue, & Mindonga-Nguelet, 2016). For example, gregarious species are more likely to be detected by CTs (Treves, Mwima, Plumptre, & Isoke, 2010), but group sizes can vary throughout the year. Environmental variation such as differences in habitat structure, altitude, or vegetation (Hofmeester et al., 2019), could result in certain behaviors being more frequently detected in some habitats or under different environmental conditions. It is also worth considering that behavior relative to cameras could vary with predictor variables of interest, such as human disturbance (as observed for wolverines; Stewart et al., 2016) or perceived predation risk, and also according to sampling design (e.g., cameras set on-trail versus off-trail, or at specific microhabitat features).

5 | WHAT ARE THE SOLUTIONS?

While CTs are a powerful tool for research and conservation, improved understanding of their detection biases and their impacts on behaviors of sampled individuals is necessary to avoid inaccurate inferences from CT data sets. The extent of these biases remains poorly understood yet their potential importance cannot be understated, especially when the impact of the detection process is misconstrued as resulting from the environmental stimuli under investigation. To avoid erroneous conclusions (particularly false positives), it is incumbent upon CT researchers to ensure that study designs anticipate potential sources of bias and measure or mitigate them whenever possible. Where there is considerable uncertainty in the degree, or even direction, of potential biases, further focused research should be undertaken to measure and model that uncertainty in a study's specific context.

At present there is little we can do in the field to mitigate the immediate impacts of the novel cues we introduce by placing CTs in the environment on observed behavior. Indeed, novel cues may even be necessary to achieve sufficient detection rates to support analyses. We therefore propose the following recommendations for mitigating CT detection bias and improving the measurement of behavior in species and ecosystems of conservation importance. First, test for the period over which animals become habituated to CTs and truncate data for behavioral inferences accordingly, bearing in mind that even low-impact observational methods of habituation for direct observation may change natural behavior for years, or even decades (e.g., chimpanzees: Hobaiter et al., 2017). Second, test the impacts of olfactory cues on the behavioral patterns of focal species and classes (e.g., age, sex) within those species (e.g., du Preez, Loveridge, & Macdonald, 2014). Third, use white-light flashes only when the light is absolutely needed to illuminate focal behaviors: supplementary triggers or illuminators may reduce the need for visible illumination. In such sequences, the first record alone should be used in behavioral analysis, with a subsequent truncation of data until habituation returns. Fourth, exclude from analyses any pronounced responses to CTs that disrupt or change behaviors of interest. Fifth, measure additional relevant factors (e.g., habitat structure, climate, seasonality) and use these as covariates in statistical analyses.

Finally, researchers can mitigate the problems identified herein by acknowledging and accounting for such issues in their statistical analyses of camera data. By recording site, species, seasonal, or age-class responses to the camera specifically—in addition to the "natural" behaviors of ecological focus being studied—and including these in analyses as covariates, researchers may partition these sources of variance, subsequently identifying "nuisance" variables. Factors underlying relative, interspecific detectability, such as variation in detectability between individuals of different sexes (Srbek-Araujo, 2018), ages (Kalan et al., 2019), or social status (Séquin et al., 2003), should be explicitly tested in an appropriate experimental and statistical framework. Partitioning false absences (i.e., the failure to detect species, even when present) using occupancy models (MacKenzie et al., 2017) is already a focus for many CT researchers (Burton et al., 2015). In probing the apparent problem of false absences further, new insights into the ecological and behavioral factors affecting detectability have been revealed (Stewart et al., 2019; Stewart, Fisher, Burton, & Volpe, 2018). We suggest that, at a minimum, all behavioral studies using CTs must demonstrate how they have accounted for species' responses to CTs in analysis by partitioning variance introduced by the factors described, above. Explicitly state the assumptions underlying behavioral CT studies, and any potential violations thereof. We encourage researchers to undertake investigations into the reasons why differential behavioral responses to these anthropogenic cues can occur, as these may yield valuable insights. In this sense, the CT becomes a part of the experiment, as well as the detector.

It is impossible that we, as observers of a system, will ever remove ourselves fully from that system. However, our presence is a part of the variable environment animals encounter, and, hence, a contributor to the variance in species' behaviors. Minimizing the specific effects of remote detection methods such as CTs will at least remove some of the variance attributed to observation, prevent directionality in that variance and hence bias, and increase confidence in our conclusions. Failing to account for inter- and intra-specific variability in behavioral responses to CTs could lead to spurious conclusions about behavior, particularly where behaviors are assumed to apply across populations, but only a subset of individuals or behaviors are detected. As a result, conclusions used to inform conservation decisions may not be well founded. By adopting and building on our recommendations, researchers can ensure that behavioral studies utilizing CT technology are more rigorous and robust, deliver more accurate data, and yield greater applied benefits for conservation and management.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

6 | AUTHOR CONTRIBUTIONS

Anthony Caravaggi: Conceived, organized, and compiled the manuscript, contributed to the text and contributed videos and images for Figure 1. Ammie K. Kalan, Tim R. Hofmeester, Daniella Rabaiotti, Sian Green, Jason T. Fisher, and Amelia Grass: Contributed to the text, along with videos and images for Figure 1. A. Cole Burton, Douglas A. Clark, Catherine Hobaiter, and Danielle Rivet: Contributed to the text.

DATA AVAILABILITY STATEMENT

No data were explicitly analyzed in the production of this work. However, selected source videos associated with Figure 1 can be found at https://doi.org/10.6084/m9.figshare.c.4593902.v1.

7 | ETHICS STATEMENT

All camera trapping undertaken featured in this work (see Figure 1) was compliant with institutional/organizational ethics guidelines. Landowner permission was obtained where required.

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