

A review of camera trapping for conservation behaviour research

Caravaggi, A.; Banks, P.B.; Burton, A.C. ; Finlay, C.M.V.; Haswell, Peter;
Hayward, Matthew; Rowcliffe, J.M.; Wood, M.D.

Remote Sensing in Ecology and Conservation

DOI:
[/10.1002/rse2.48](https://doi.org/10.1002/rse2.48)

Published: 01/09/2017

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):
Caravaggi, A., Banks, P. B., Burton, A. C., Finlay, C. M. V., Haswell, P., Hayward, M., Rowcliffe, J. M., & Wood, M. D. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, 3(3), 109-122. <https://doi.org/10.1002/rse2.48>

Hawliau Cyffredinol / General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1 Review

2 **A review of camera trapping for conservation behaviour research**

3 Caravaggi, A.¹, Banks, P.B.², Burton, A.C.³, Finlay, C.M.V.⁴, Haswell, P.M.⁵, Hayward,
4 M.W.^{5,6}, Rowcliffe, J.M.⁷, Wood, M.D.⁸

5

6 ¹ School of Biological Sciences, Queen's University Belfast, Belfast, BT9 7BL, UK

7 ² School of Life and Environmental Sciences, The University of Sydney, NSW 2006

8 ³ Department of Forest Resources Management, University of British Columbia, 2215 - 2424
9 Main Mall, Vancouver, BC, Canada, V6T 1Z4

10 ⁴ Ulster Wildlife, McClelland House, 10 Heron Road, Belfast, BT3 9LE

11 ⁵ School of Biological Sciences, Bangor University, Bangor, Gwynedd, LL57 2UW, UK.

12 ⁶ Centre for African Wildlife Ecology, Nelson Mandela University, Port Elizabeth 6031
13 South Africa; and Centre for African Wildlife Ecology, University of Pretoria, Pretoria, 0001
14 South Africa

15 ⁷ ZSL Institute of Zoology, Regent's Park, London NW 4RY, UK

16 ⁸ School of Environment & Life Sciences, University of Salford, Manchester, M5 4WT, UK

17

18 **Corresponding author email:** acaravaggi01@qub.ac.uk

19

20 **Running title:** Camera traps and conservation behaviour

21

22 **Word count**

23 **Abstract:** 211

24 **Main text:** 4,488

25 **Acknowledgments:** 95

26 **References:** 3,656

27 **Tables:** 562

28 **Figures:** 113

29

30 **Tables:** 2

31

32 **Figures:** 1

33

34

35 **Abstract**

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

54
55 **Key words:** Ethology, remote sensing, anthropogenic impacts, behavioural indicators,
56 monitoring, management
57

58 **Introduction**

59 Animal behaviour is an important component of conservation biology (Berger-Tal et al. 2011),
60 and, hence, is of considerable interest to researchers and wildlife managers (Caro and Durant
61 1995). For example, behavioural studies can increase our understanding of species' habitat
62 requirements (Pienkowski 1979), reproductive behaviour (Cant 2000) and dispersal or
63 migration (Doerr et al. 2011), and elucidate impacts of habitat fragmentation (Merckx and Van
64 Dyck 2007) or climate change (Moller 2004). Animal behaviour can also be a useful
65 monitoring tool, with individual and group-level responses used to evaluate the impacts of
66 management (Morehouse et al. 2016). It is important, therefore, to incorporate behaviour into
67 conservation planning; its omission limits efficacy of conservation actions and could lead to
68 failure (Berger-Tal et al. 2011). The confluence of conservation biology and ethology has come
69 to be known as 'conservation behaviour', wherein conservation problems are addressed by the
70 application of behavioural research (Blumstein and Fernández-Juricic 2004; Berger-Tal et al.
71 2011).

72 Quantifying the behaviour of wild animals presents significant challenges. Direct
73 observation of animals can allow the evaluation of individual responses to environmental
74 stimuli. Such studies may be weakened, however, by the influence of the human observer on
75 focal animals (Nowak et al. 2014) and limited by small sample size and logistical constraints
76 (Bridges and Noss 2011). Furthermore, only a limited number of species and habitats are
77 amenable to direct, field-based observations (e.g. larger species and those that can be
78 habituated; and in open and accessible habitats). Many of these have already been the focus of
79 direct behavioural research (Schaller 1967; Kruuk 1972; Caro 1994) or may be atypical of more
80 common habitats and can lead to inconsistent results (Laurenson 1994 vs Mills and Mills 2014).
81 In cases where focal animal(s) cannot easily be directly observed, the vast majority of field-
82 based behavioural studies have used radio (VHF) or satellite (GPS) telemetry, activity sensors

83 and/or biologgers (e.g. Lewis et al. 2002; Grignolio et al. 2004; Shamoun-Baranes et al. 2012;
84 Bouten et al. 2013). The advantages and disadvantages of these methods, which are currently
85 the gold-standards for obtaining spatio-temporal behavioural data, are summarised in Table 1,
86 highlighting that while these devices can provide powerful insights, they also have significant
87 logistical and inferential limitations. Consequently, the suite of species that have had their
88 behaviour quantified is biased and limited. New methods of obtaining behavioural data are,
89 therefore, urgently required.

90 Camera traps (i.e. cameras that are remotely activated via an active or passive sensor;
91 hereafter referred to as CTs) offer a reliable, minimally-invasive, visual means of surveying
92 wildlife that substantially reduces survey effort. CTs are increasingly popular in ecological
93 studies (Burton et al. 2015; Rovero and Zimmermann 2016) and provide a wealth of
94 information that is often of considerable conservation value (e.g. Ng et al. 2004; Di Bitetti et
95 al. 2006; Caravaggi et al. 2016). Continued technological improvements and decreasing
96 equipment costs (Tobler et al. 2008a), combined with their demonstrated versatility (Rovero et
97 al. 2013), mean that CTs will only continue to grow in popularity. CT data take the form of a
98 still image or video of an individual or a group of individuals, of one or more species, which
99 have been detected within the camera and location-specific zone of detection. These images
100 can be linked with additional information, including the date, time and location at which the
101 image was recorded. CT surveys have been effectively used to quantify species diversity
102 (Tobler et al. 2008b), relative abundance (Carbone et al. 2001; Villette et al. 2017) and
103 population parameters (Karanth et al. 2006; Rowcliffe et al. 2008), demonstrate site occupancy
104 of rare or cryptic species (Linkie et al. 2007) and describe species replacement processes
105 (Caravaggi et al. 2016). CTs have also been used in behavioural studies (Bridges and Noss
106 2011; Maffei et al. 2005). In a recent review of 266 CT studies, Burton et al. (2015)

107 characterized one-third as addressing behavioural questions (e.g. activity patterns, diet; Table
108 2).

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

115

116 **Current applications of camera traps to animal behaviour**

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

131 Many types of animal behaviours have been studied with CTs (Table 2), including
132 foraging (Otani 2001), daily activity patterns (Tan et al. 2013), scent marking (Delgado-V. et
133 al. 2011), movement (Ford et al. 2009), livestock depredation (Bauer et al. 2005), and use of a
134 variety of habitat features including dens/burrows (Clapham et al. 2014), urban habitats (Marks
135 and Duncan 2009), corridors (LaPoint et al. 2013) and waterholes (Hayward and Hayward
136 2012). CT studies have often yielded key behavioural insights that may otherwise have
137 remained unknown, many of which could be important to conservation processes. For example,
138 studies investigating the efficacy of highway crossings in Banff National Park, Canada,
139 described the effectiveness of under- and over-passes, an expensive and controversial means
140 of impact mitigation (Clevenger and Waltho 2000; Ford et al. 2009), which is now being
141 duplicated in other parts of the world. Picman and Schriml (1994) observed the predators of
142 quail (*Coturnix coturnix*) nests in a variety of habitats, elucidating temporal variation and
143 relative importance of each predatory species. The application of this method to the study of
144 threatened avifauna has clear conservation benefits via the identification of direct impacts on
145 egg success and the development of appropriate mitigation and monitoring techniques.
146 Similarly, cameras provide more accurate post-hibernation den-emergence estimates for
147 American black bears (*Ursus americanus*) than conventional methods, i.e. den visits and radio
148 telemetry (Bridges et al. 2004). Long-term monitoring of emergence relative to climate may
149 yield important insights into the effects of climate change on black bears and other hibernating
150 species (*sensu* Bridges and Noss 2011).

151 The majority of ethological CT studies conducted thus far have been primarily
152 curiosity-driven, rather than being motivated by applied conservation-focussed hypotheses.
153 This is not to say that a large number of these studies do not have conservation value. On the
154 contrary, the conservation relevance of the data is often explicitly discussed. It is apparent,
155 however, that there is an increasing need for conservation-driven studies. CTs are among the

156 most promising and flexible tools available and we are only beginning to explore their
157 potential.

158

159 **Emerging directions in camera-based conservation behaviour**

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

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

178

179 *Anthropogenic impacts*

180

181 An important area of conservation research lies in understanding the influence of
182 anthropogenic stressors on animal behaviours and predicting the resulting population-level
183 responses in order to inform management practices. Stressors such as habitat fragmentation,
184 disturbance, the creation of ecological traps and the introduction of non-native species can have
185 significant effects on behaviour (Robertson and Hutto 2006) and, hence, fitness (Berger-Tal et
186 al. 2011). For example, animals may exhibit increasing wariness in areas of greater disturbance
187 (Stewart et al. 2016) and may change their daily activity patterns in close proximity to human
188 populations (Carter et al. 2012). While anthropogenic impacts are generally negative, some
189 species show benefits such as increased occupancy in fragmented landscapes (Fleschutz et al.
190 2016), or using human activity to evade apex predators (Muhly et al. 2011; Steyaert et al. 2016).
191 Impacts on one species may also have spillover effects on the wider ecological community
192 (Wright et al. 2010; Clinchy et al. 2016).

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

202 The disruption of dispersal behaviour can lead to the endangerment and potential
203 extinction of isolated populations by various mechanisms, including changes to genetic
204 diversity and structure (Keyghobadi 2007), stochastic threats (Fischer and Lindenmayer 2007)

205 and long-term displacement effects (Ewers and Didham 2005). Using CTs to document
206 dispersal behaviour can improve understanding of responses to movement disruption
207 (Blumstein and Fernández-Juricic 2004) and inform design and implementation of mitigation
208 measures that encourage dispersal. Individual-level analysis of dispersal is potentially possible
209 for animals with individually-identifiable markings or tags, although designing such a study
210 may be challenging as dispersal routes and, hence, appropriate locations for CT deployment,
211 may not be known *a priori*. Inferences about dispersal, however, can also be drawn without
212 individual identification. For example, cameras are well suited to quantifying use of presumed
213 dispersal routes or movement corridors, including mitigations designed to promote
214 connectivity (e.g. highway crossings; Clevenger and Waltho 2005; Ford et al. 2009). CTs can
215 also be used to identify colonization of new habitat patches (including range expansions or
216 species invasions) and parameterize landscape connectivity models (Brodie et al. 2015).

217 No studies have integrated environmental sensors into CT studies investigating
218 anthropogenic impacts on behaviour, and we believe this is a promising area for future
219 development. Local temperature, precipitation and humidity can readily be recorded, and
220 phenocams can be used to document vegetation and environmental changes (Brown et al.
221 2016). Collecting such information alongside CT-based behavioural data will allow us to
222 increase our understanding of how animals respond to changing conditions at both large
223 (population) and small (localities within home ranges) spatial scales. This is particularly
224 important given the rapid changes that are predicted to occur under climate change.

225

226 *Behaviour-based management*

227 Berger-Tal et al. (2011) suggested that behaviour-sensitive management and behavioural
228 modification are two key pathways through which ethology can inform active management for

229 conservation. The former considers animal behaviour in the design of reserves and corridors,
230 planning species reintroductions and translocations, and epidemiology with the goal of
231 stabilising or increasing threatened populations or controlling pest or invasive species.
232 Behavioural modification focuses on changing or preserving key behaviours within a focal
233 population. CT surveys have the potential to inform both of these areas.

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

254 potential bias with calibration by direct observation or other methods and placing observations
255 in appropriate contexts is therefore important.

256 SNA has the potential to increase our understanding of disease or pathogen
257 transmission and individual or group vulnerability (Krause et al. 2007), an issue of particular
258 relevance to the conservation of species which are susceptible to outbreaks (e.g. Hamede et al.
259 2009). SNA studies have demonstrated that the removal of certain individuals (e.g. via hunting)
260 can have a considerable effect on the stability of the social network (e.g. Flack et al. 2006),
261 thus demonstrating their potential utility in elucidating the impacts of the bushmeat trade on
262 inter- and intra-group dynamics in primates, for example. Furthermore, SNA has implications
263 for reintroduction programmes, where the (re)construction of cohesive social structures in a
264 captive setting would be necessary for the return of the focal species to the wild (Abell et al.
265 2013). Studies of the relationships between individuals, therefore, can help us to understand
266 how social behaviour is influenced by a variety of factors and, hence, provide an additional
267 means by which practitioners can build an evidence base to address conservation questions.

268 CTs can also be applied to studies of behavioural modification. For example, Davies et
269 al. (2016) used CTs to investigate responses of African herbivores to changes in predation risk
270 resulting from recently-reintroduced lions. Cameras are also well suited to monitoring animal
271 responses to conflict mitigation measures and have been used to demonstrate the efficacy of
272 bees as a deterrent of crop-raiding elephants (Ngama et al. 2016).

273

274 *Behavioural indicators*

275 The ways in which animals adapt their foraging behaviour in human-impacted environments
276 have important implications for their abilities to adapt and persist under increasing pressures.
277 Behavioural indicators can be used to assess the state of animals and the environments they

278 inhabit, highlighting important conservation issues such as population decline or habitat
279 degradation, or being used to monitor the efficacy of management (Berger-Tal et al. 2011).
280 Behaviour effectively acts as an early-warning system, indicating changes to processes before
281 they are evident through, for example, population decline.

282 The giving up density (GUD; i.e. the amount of food left behind from a known starting
283 quantity; Brown 1988) is one such behavioural indicator that has been used to study predation
284 risk (Orrock 2004; Severud et al. 2011), energetic costs (Nolet et al. 2006), forager state and
285 forage quality (Hayward et al. 2015), plant toxins (Emerson and Brown 2015), competition
286 (Brown et al. 1997) and predator-prey dynamics (Andruskiw et al. 2008). It is also central to
287 describing the “landscape of fear” (i.e. relative levels of predation risk within an area of use)
288 of an animal and its habitat preferences, which are direct behavioural indicators with significant
289 conservation implications (Kotler et al. 2016). CTs offer a relatively reliable way of using the
290 GUD technique to ask more in-depth questions of conservation relevance. For example, CTs
291 have been used to calculate GUDs for multiple species (Lerman et al. 2012), examine (Mella
292 et al. 2015), and differentiate individual versus group foraging habits (Carthey and Banks
293 2015). These observations can then be used to inform the development of hypotheses relating
294 to the broader effects of local food and predator abundance, predation pressure and inter- and
295 intra-specific competition. With advancements in CT technology and creative experimental
296 design, a wealth of conservation-focussed GUD applications are now possible.

297 A key strength of CTs lies in collecting data on multiple species, either as bycatch in a
298 focal study, or as part of a specific multi-taxa investigation. Accordingly, there has been an
299 increasing focus on assessing species interactions and niche partitioning via comparisons of
300 co-occurrence and activity patterns (de Almeida Jacomo et al. 2004; Kukielka et al. 2013;
301 Farris et al. 2014; Wang et al. 2015; Bu et al. 2016; Cusack et al. 2016; Sweitzer and Furnas
302 2016). Animal activity patterns are shaped by a number of factors, including foraging

303 efficiency (Lode 1995), predator/prey activity (Middleton et al. 2013), photoperiodism
304 (McElhinny et al. 1997), and competition (Rychlik 2005). Conservation-focussed studies using
305 these methodologies, however, are scarce. Changes in the way species interact and use the
306 landscape may be indicative of responses to changing environmental pressures and, hence, can
307 direct development of early conservation strategies. For example, brown bears (*Ursus arctos*;
308 Ordiz et al. 2013) altered their movement patterns and wolverines (*Gulo gulo*; Stewart et al.
309 2016) behaved differently when faced with human disturbance, potentially impacting their
310 ecosystem roles and, hence, associated species and habitats. Disturbance of the activity patterns
311 of one or more species in a dynamic interaction, particularly ecological competitors or
312 predators and prey, can therefore be interpreted as indicative of environmental changes and,
313 hence, suggest additional lines of enquiry and highlight areas of conservation concern.

314

315 *Scaling-up*

316 Cameras can be used to monitor large-scale biodiversity conservation processes (O'Brien et al.
317 2010; Ahumada et al. 2013) and investigate animal behaviour on a landscape scale. Scaling-up
318 CT networks would provide stronger, larger-scale inferences on spatio-temporal variation in
319 behaviours (Steenweg et al. 2016). Studies conducted on a broader scale have inherent
320 limitations, however, that are not necessarily considerations for more localised investigations.
321 The trade-off between the scale of investigation and camera array density has spatio-temporal
322 implications which must be considered when designing a study, formulating hypotheses and
323 deriving inferences from resultant data. Broad-scale studies are also ostensibly limited by the
324 number of researchers available to place and check cameras and process data. The recruitment
325 of volunteers (i.e. citizen scientists), however, offers a means of expanding the scope of
326 research (Cohn 2008), greatly expanding spatial coverage and delivering a wealth of temporally

327 comparable data (McShea et al. 2016). Emerging large-scale camera monitoring initiatives,
328 such as Snapshot Serengeti (www.snapshotserengeti.org; Swanson et al. 2015) and Wildcam
329 Gorongosa (www.wildcamgorongosa.org) demonstrate the benefits of this approach. CT
330 projects utilising citizen science have the potential to deliver a substantial amount of
331 behavioural data (McShea et al. 2016) and inform conservation processes. However, few large-
332 scale studies utilising citizen science involve behavioural analyses. CT video data can produce
333 vast amounts of video footage but the extraction of key behavioural data from video footage is
334 time consuming, imposing a major obstacle. Crowdsourcing video interpretations can
335 overcome this limitation, however, and the use of robust ethograms, simple training regimes
336 and blinding of observers to treatments can assuage concerns about the reliability of citizen
337 science interpretations (e.g. Carthey 2013).

338 Synthesising across projects offers another means of conducting broader analyses
339 (Steenweg et al. 2016). We recommend that researchers embrace emerging CT metadata
340 standards and associated opportunities to use common data repositories such as Wildlife
341 Insights (www.wildlifeinsights.org; Forrester et al. 2016), thus increasing the potential for the
342 synthesis of inferences across large scales. The value of current data repositories is reduced,
343 however, by their reliance on static images and omission of video. Expenses notwithstanding,
344 it is in the interests of conservation behaviour researchers to establish a digital repository for
345 video data.

346

347

348 **Relevant limitations and considerations**

349 Despite the great promise of new insights in conservation behaviour from CTs, it is important
350 to consider potential limitations. CTs are passive instruments; thus, while it is possible to

351 identify animals according to species, age-class (Clapham et al. 2014), sex (Bezerra et al. 2014)
352 or, indeed, identify individuals (Karanth et al. 2006; Zheng et al. 2016), the collection of
353 biometric, genetic and other data of interest requires the application of supplementary or
354 alternative methodologies. Furthermore, CTs are frequently considered to be non-intrusive,
355 causing little to no disturbance. However, while the sound produced by recording units is
356 largely inaudible to humans, it is frequently detected by wildlife (Meek et al. 2014a). Similarly,
357 CTs which utilise visible light (as opposed to infra-red) increase the chances of the camera
358 being detected by animals, potentially disrupting their natural behaviour (Meek et al. 2016a).

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

366 Researchers utilising CTs have the option of recording data in the form of still images
367 or video footage. In many cases, still images are adequate; it is possible to derive important
368 behavioural data from them and, indeed, the format offers some obvious benefits. For example,
369 still images require considerably less memory than video footage (Glen et al. 2013) and, hence,
370 may be more suitable for studies which require CTs to be deployed, without intervention, for
371 a prolonged period of time. However, similar capture success rates can be achieved with either
372 format (Glen et al. 2013) and the majority of operational limitations apply equally to both. For
373 example, some cameras have a slow trigger time meaning that initial behaviours, which might
374 be the most important in terms of measuring detection of a stimulus (rather than the response),
375 can be missed. Furthermore, many cameras offer only a limited number of high-speed ‘burst’

376 (i.e. sequentially captured) images or length of video (e.g. 60 seconds), requiring the camera to
377 be retriggered to continue the capture of the behaviours and, hence, creating gaps in the
378 observation. However, video footage opens up new opportunities, e.g. observing interactions
379 at focal sites, or measuring the duration of behavioural bouts. While both formats can be
380 effectively used in most of the applications described herein (SNA being the one exception,
381 with video being preferred), videos are undoubtedly more informative and an important future
382 direction for CT-based behavioural research.

383 . Sampling the behaviours of small species can be particularly challenging, with CTs
384 typically designed for deer-sized game species (Weerakoon et al. 2014), a problem that will
385 require novel solutions. For example, flash-illuminated images are frequently obscured by
386 overexposure when close enough to small mammals to observe behaviour clearly, whereas at
387 the correctly exposed distance, animals can be too far away to reliably identify species or
388 discern behaviours. Furthermore, understanding the reliability of camera surveys for
389 addressing multi-species objectives remains an important area of methodological research (see
390 Burton et al. 2015). Multi-taxa studies also require careful planning to ensure that CTs are
391 appropriately located and adequately spaced to maximise the chances of capturing a diverse
392 species assemblage while meeting analytical assumptions such as independence of sampling
393 sites. The choice and placement of cameras should, therefore, be dictated by the objectives of
394 the study, the ecology of the study species, the statistical sampling framework and associated
395 considerations.

396 An oft-repeated concern relates to study repeatability; specific details of study design
397 (e.g. how survey sites were chosen, use of lures) and camera protocols (e.g. camera model,
398 deployment details) are often lacking (Meek et al. 2014b; Burton et al. 2015). A number of
399 factors influence the detection of individuals (see Burton et al. 2015) and sampling details may
400 have important implications for analytical assumptions such as effective sampling area and site

401 independence (Harmsen et al. 2010; Mccoy et al. 2011; du Preez et al. 2014; Newey et al.
402 2015). Comprehensive methodological descriptions and utilisation of emerging CT metadata
403 standards (Forrester et al. 2016) are important for facilitating reproduction, comparison and
404 synthesis across studies.

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

412

413

414 **Conclusions**

415 CTs are rapidly increasing in popularity, and their application to conservation behaviour is
416 growing. Recent efforts to coordinate camera studies across large-scales through
417 methodological standardization and/or better reporting of methodologies and metadata will
418 facilitate broader ethological inferences on species' behavioural responses to environmental
419 change. The development and application of new techniques and analytical methods explicitly
420 focussed on anthropogenic impacts, behaviour-based management and behavioural indicators
421 would undoubtedly benefit conservation programmes. CTs are not a panacea, but they confer
422 many benefits to researchers and the diversity of possible applications is gradually being
423 realised. We hope that this paper will act as a catalyst, advancing the adoption of CT technology
424 within conservation behaviour. It is important, therefore, that potentially profitable avenues of

425 investigation are identified and pursued if we are to maximise the generation of valuable data
426 and, hence, improve the conservation outlook for the ever-increasing number of threatened or
427 endangered species.

428

429 **Acknowledgments**

430 The authors thank the journal for their encouragement and support of this review and,
431 specifically, the editor and reviewers for their valuable comments which strengthened the final
432 manuscript. Authors are ordered alphabetically by surname, except for A. Caravaggi who
433 conceived, organised and compiled the manuscript. The contribution of M.D. Wood was
434 supported by the TREE project (www.ceh.ac.uk/TREE) funded by the Natural Environment
435 Research Council (NERC), Environment Agency and Radioactive Waste Management
436 Limited. The contributions of C.M.V. Finlay were supported by the Red Squirrels United
437 project (<http://www.redsquirrelsunited.org.uk/>) funded by EU Life and Heritage Lottery Fund.

438

439 **References**

440

441 Abell, J. et al. 2013. A social network analysis of social cohesion in a constructed pride:
442 implications for ex situ reintroduction of the African lion (*Panthera leo*). *PLoS ONE* 8(12), p.
443 e82541.

444 Ahumada, J.A. et al. 2013. Monitoring the status and trends of tropical forest terrestrial
445 vertebrate communities from camera trap data: a tool for conservation. *PLoS ONE* 8(9), p.
446 e73707.

447 de Almeida Jacomo, A.T. et al. 2004. Niche separation between the maned wolf (*Chrysocyon*
448 *brachyurus*), the crab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) in
449 central Brazil. *Journal of Zoology* 262(1), pp. 99–106.

450 Andruskiw, M. et al. 2008. Habitat-mediated variation in predation risk by the American
451 marten. *Ecology* 89(8), pp. 2273–2280.

452 Archie, E.A. et al. 2006. Dominance rank relationships among wild female African elephants,
453 *Loxodonta africana*. *Animal Behaviour* 71(1), pp. 117–127.

454 Azlan, J.M. and Sharma, D.S.K. 2006. The diversity and activity patterns of wild felids in a
455 secondary forest in Peninsular Malaysia. *Oryx* 40(01), p. 36.

456 Barron, D.G. et al. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology:
457 Meta-analysis of avian transmitter effects. *Methods in Ecology and Evolution* 1(2), pp. 180–
458 187.

459 Bauer, J.W. et al. 2005. Scavenging behaviour in puma. *The Southwestern Naturalist* 50(4),
460 pp. 466–471.

461 Berger-Tal, O. et al. 2011. Integrating animal behavior and conservation biology: a conceptual
462 framework. *Behavioral Ecology* 22(2), pp. 236–239.

463 Bezerra, B.M. et al. 2014. Camera trap observations of nonhabituated critically endangered
464 wild blonde capuchins, *Sapajus flavius* (formerly *Cebus flavius*). *International Journal of*
465 *Primatology* 35(5), pp. 895–907.

466 Blumstein, D.T. and Fernández-Juricic, E. 2004. The emergence of conservation behavior.
467 *Conservation Biology* 18(5), pp. 1175–1177.

468 Bouten, W. et al. 2013. A flexible GPS tracking system for studying bird behaviour at multiple
469 scales. *Journal of Ornithology* 154(2), pp. 571–580.

470 Bowler, M.T. et al. 2016. Estimating mammalian species richness and occupancy in tropical
471 forest canopies with arboreal camera traps. *Remote Sensing in Ecology and Conservation*.
472 Available at: <http://doi.wiley.com/10.1002/rse2.35> [Accessed: 7 December 2016].

473 Bridges, A.S. et al. 2004. Seasonal variation in American black bear *Ursus americanus* activity
474 patterns: quantification via remote photography. *Wildlife Biology* 10(4), pp. 277–284.

475 Bridges, A.S. and Noss, A.J. 2011. Behaviour and activity patterns. In: O’Connell, A. F. et al.
476 eds. *Camera traps in animal ecology: Methods and analyses*. New York: Springer, pp. 57–69.

- 477 Brodie, J. et al. 2012. Climate change intensification of herbivore impacts on tree recruitment.
478 *Proceedings of the Royal Society B: Biological Sciences* 279(1732), pp. 1366–1370.
- 479 Brodie, J.F. et al. 2015. Evaluating multispecies landscape connectivity in a threatened tropical
480 mammal community: multispecies habitat corridors. *Conservation Biology* 29(1), pp. 122–132.
- 481 Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and
482 competition. *Behavioral Ecology and Sociobiology* 22(1), pp. 37–47.
- 483 Brown, J.S. et al. 1997. Competition between birds and mammals: a comparison of giving-up
484 densities between crested larks and gerbils. *Evolutionary Ecology* 11(6), pp. 757–771.
- 485 Bu, H. et al. 2016. Spatial co-occurrence and activity patterns of mesocarnivores in the
486 temperate forests of southwest China. *PLOS ONE* 11(10), p. e0164271.
- 487 Burton, A.C. et al. 2015. Wildlife camera trapping: a review and recommendations for linking
488 surveys to ecological processes. *Journal of Applied Ecology* 52(3), pp. 675–685.
- 489 Cant, M.A. 2000. Social control of reproduction in banded mongooses. *Animal Behaviour*
490 59(1), pp. 147–158.
- 491 Caravaggi, A. et al. 2016. An invasive-native mammalian species replacement process captured
492 by camera trap survey random encounter models. *Remote Sensing in Ecology and Conservation*
493 2(1), pp. 45–58.
- 494 Carbone, C. et al. 2001. The use of photographic rates to estimate densities of tigers and other
495 cryptic mammals. *Animal conservation* 4(01), pp. 75–79.
- 496 Caro, T. and Durant, S.M. 1995. The importance of behavioral ecology for conservation
497 biology: examples from Serengeti carnivores. In: Sinclair, A. R. E. and Arcese, P. eds.
498 *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem*. Chicago: University
499 of Chicago, pp. 451–472.
- 500 Caro, T.M. 1994. *Cheetahs of the Serengeti Plains: group living in an asocial species*. Chicago:
501 University of Chicago Press.
- 502 Carter, N.H. et al. 2012. Coexistence between wildlife and humans at fine spatial scales.
503 *Proceedings of the National Academy of Sciences* 109(38), pp. 15360–15365.
- 504 Carthey, A.J.R. 2013. Naivete, novelty and native status: mismatched ecological interactions
505 in the Australian environment. Australia: University of Sydney.
- 506 Carthey, A.J.R. and Banks, P.B. 2015. Foraging in groups affects giving-up densities: solo
507 foragers quit sooner. *Oecologia* 178(3), pp. 707–713.
- 508 Carthey, A.J.R. and Banks, P.B. 2016. Naiveté is not forever: responses of a vulnerable native
509 rodent to its long term alien predators. *Oikos* 125(7), pp. 918–926.
- 510 Clapham, M. et al. 2014. Scent-marking investment and motor patterns are affected by the age
511 and sex of wild brown bears. *Animal Behaviour* 94, pp. 107–116.

- 512 Claridge, A.W. et al. 2004. Use of infrared digital cameras to investigate aspects of the social
513 behaviour of cryptic species. *Wildlife Research* 31(6), p. 645.
- 514 Clevenger, A.P. and Waltho, N. 2000. Factors influencing the effectiveness of wildlife
515 underpasses in Banff National Park, Alberta, Canada. *Conservation Biology* 14(1), pp. 47–56.
- 516 Clevenger, A.P. and Waltho, N. 2005. Performance indices to identify attributes of highway
517 crossing structures facilitating movement of large mammals. *Biological Conservation* 121(3),
518 pp. 453–464.
- 519 Clinchy, M. et al. 2016. Fear of the human ‘super predator’ far exceeds the fear of large
520 carnivores in a model mesocarnivore. *Behavioral Ecology*, p. arw117.
- 521 Cohn, J.P. 2008. Citizen science: can volunteers do real research? *BioScience* 58(3), p. 192.
- 522 Coulombe, M. et al. 2006. Quantification and accuracy of activity data measured with VHF
523 and GPS telemetry. *Wildlife Society Bulletin* 34, pp. 81–92.
- 524 Creel, S. 1997. Handling of African wild dogs and chronic stress: reply to East et al.
525 *Conservation Biology* 11(6), pp. 1454–1456.
- 526 Crook, N. et al. 2013. Bare-nosed wombats (*Vombatus ursinus*) use drainage culverts to cross
527 roads. *Australian Mammalogy* 35(1), p. 23.
- 528 Cusack, J.J. et al. 2016. Revealing kleptoparasitic and predatory tendencies in an African
529 mammal community using camera traps: a comparison of spatiotemporal approaches. *Oikos*.
530 Available at: <http://doi.wiley.com/10.1111/oik.03403> [Accessed: 18 December 2016].
- 531 Dalloz, M.F. et al. 2012. Positional behaviour and tail use by the bare-tailed woolly opossum
532 *Caluromys philander* (Didelphimorphia, Didelphidae). *Mammalian Biology - Zeitschrift für*
533 *Säugetierkunde* 77(5), pp. 307–313.
- 534 Davies, A.B. et al. 2016. Limited spatial response to direct predation risk by African herbivores
535 following predator reintroduction. *Ecology and Evolution* 6(16), pp. 5728–5748.
- 536 Delgado-V., C.A. et al. 2011. Behaviour of the Tayra *Eira barbara* near Medellín, Colombia:
537 preliminary data from a video-capturing survey. *Small Carnivore Conservation* 44(2011), pp.
538 19–21.
- 539 Di Bitetti, M.S. et al. 2006. Density, habitat use and activity patterns of ocelots (*Leopardus*
540 *pardalis*) in the Atlantic Forest of Misiones, Argentina. *Journal of Zoology* 270, pp. 153–163.
- 541 Diete, R.L. et al. 2014. Burrowing behaviour of the northern hopping-mouse (*Notomys aquilo*):
542 field observations. *Australian Mammalogy*. Available at:
543 <http://www.publish.csiro.au/?paper=AM13039> [Accessed: 26 March 2017].
- 544 Doerr, V.A.J. et al. 2011. Connectivity, dispersal behaviour and conservation under climate
545 change: a response to Hodgson et al.: Connectivity and dispersal behaviour. *Journal of Applied*
546 *Ecology* 48(1), pp. 143–147.

- 547 Edwards, S. et al. 2015. Spatiotemporal resource partitioning of water sources by African
548 carnivores on Namibian commercial farmlands: Carnivore resource partitioning at water
549 sources. *Journal of Zoology* 297(1), pp. 22–31.
- 550 Emerson, S.E. and Brown, J.S. 2015. The influence of food chemistry on food-safety tradeoffs
551 in samango monkeys. *Journal of Mammalogy* 96(1), pp. 237–244.
- 552 Emmons, L.H. et al. 2004. Bathing behavior of giant anteaters (*Myrmecophaga tridactyla*).
553 *Edentata* 6(1), p. 41.
- 554 Ewers, R.M. and Didham, R.K. 2005. Confounding factors in the detection of species responses
555 to habitat fragmentation. *Biological Reviews* 81(01), p. 117.
- 556 Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology,*
557 *Evolution, and Systematics* 34(1), pp. 487–515.
- 558 Farris, Z.J. et al. 2014. Predator–primate distribution, activity, and co-occurrence in relation to
559 habitat and human activity across fragmented and contiguous forests in northeastern
560 Madagascar. *International Journal of Primatology* 35(5), pp. 859–880.
- 561 Fischer, J. and Lindenmayer, D.B. 2007. Landscape modification and habitat fragmentation: a
562 synthesis. *Global Ecology and Biogeography* 16(3), pp. 265–280.
- 563 Flack, J.C. et al. 2006. Policing stabilizes construction of social niches in primates. *Nature*
564 439(7075), pp. 426–429.
- 565 Fleschutz, M.M. et al. 2016. Response of a small felid of conservation concern to habitat
566 fragmentation. *Biodiversity and Conservation* 25(8), pp. 1447–1463.
- 567 Ford, A.T. et al. 2009. Comparison of methods of monitoring wildlife crossing-structures on
568 highways. *Journal of Wildlife Management* 73(7), pp. 1213–1222.
- 569 Forrester, T. et al. 2016. An open standard for camera trap data. *Biodiversity Data Journal* 4,
570 p. e10197.
- 571 Glen, A.S. et al. 2013. Optimising camera traps for monitoring small mammals. *PLoS ONE*
572 8(6), p. e67940.
- 573 Grignolio, S. et al. 2004. Seasonal variations of spatial behaviour in female Alpine ibex (*Capra*
574 *ibex ibex*) in relation to climatic conditions and age. *Ethology Ecology & Evolution* 16(3), pp.
575 255–264.
- 576 Haddad, N.M. et al. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems.
577 *Science Advances* 1(2), p. e1500052.
- 578 Hamede, R.K. et al. 2009. Contact networks in a wild Tasmanian devil (*Sarcophilus harrisii*)
579 population: using social network analysis to reveal seasonal variability in social behaviour and
580 its implications for transmission of devil facial tumour disease. *Ecology Letters* 12(11), pp.
581 1147–1157.

- 582 Harmsen, B.J. et al. 2010. Differential use of trails by forest mammals and the implications for
583 camera-trap studies: a case study from Belize: trail use by Neotropical forest mammals.
584 *Biotropica* 42(1), pp. 126–133.
- 585 Hayward, M.W. et al. 2015. Risk perception by endangered European bison *Bison bonasus* is
586 context (condition) dependent. *Landscape Ecology* 30(10), pp. 2079–2093.
- 587 Hayward, M.W. and Hayward, M.D. 2012. Waterhole use by African fauna. *South African*
588 *Journal of Wildlife Research* 42(2), pp. 117–127.
- 589 Heavener, S.J. et al. 2014. Competitive naïveté between a highly successful invader and a
590 functionally similar native species. *Oecologia* 175(1), pp. 73–84.
- 591 Jachowski, D.S. et al. 2015. Monitoring landscape-level distribution and migration phenology
592 of raptors using a volunteer camera-trap network. *Wildlife Society Bulletin* 39(3), pp. 553–563.
- 593 Jacoby, D.M.P. and Freeman, R. 2016. Emerging Network-Based Tools in Movement Ecology.
594 *Trends in Ecology & Evolution* 31(4), pp. 301–314.
- 595 Johnson, A. et al. 2006. Effects of human-carnivore conflict on tiger (*Panthera tigris*) and prey
596 populations in Lao PDR. *Animal Conservation* 9(4), pp. 421–430.
- 597 Karanth, K.U. et al. 2006. Assessing tiger population dynamics using photographic capture-
598 recapture sampling. *Ecology* 87(11), pp. 2925–2937.
- 599 Keyghobadi, N. 2007. The genetic implications of habitat fragmentation for animals. *Canadian*
600 *Journal of Zoology* 85(10), pp. 1049–1064.
- 601 Kotler, B.P. et al. 2016. Direct behavioral indicators as a conservation and management tool.
602 In: Berger-Tal, O. and Saltz, D. eds. *Conservation Behavior*. Cambridge: Cambridge
603 University Press, pp. 307–351.
- 604 Krause, J. et al. 2007. Social network theory in the behavioural sciences: potential applications.
605 *Behavioral Ecology and Sociobiology* 62(1), pp. 15–27.
- 606 Kruuk, H. 1972. *The Spotted Hyaena*. Chicago: University of Chicago Press.
- 607 Kukielka, E. et al. 2013. Spatial and temporal interactions between livestock and wildlife in
608 South Central Spain assessed by camera traps. *Preventive Veterinary Medicine* 112(3–4), pp.
609 213–221.
- 610 LaPoint, S. et al. 2013. Animal behavior, cost-based corridor models, and real corridors.
611 *Landscape Ecology* 28(8), pp. 1615–1630.
- 612 Laurenson, M.K. 1994. High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its
613 consequences for maternal care. *Journal of Zoology* 234(3), pp. 387–408.
- 614 Lerman, S.B. et al. 2012. Linking foraging decisions to residential yard bird composition. *PLoS*
615 *ONE* 7(8), p. e43497.
- 616 Leuchtenberger, C. et al. 2014. Activity patterns of giant otters recorded by telemetry and
617 camera traps. *Ethology Ecology & Evolution* 26(1), pp. 19–28.

- 618 Lewis, S. et al. 2002. Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings*
619 *of the Royal Society of London B: Biological Sciences* 269(1501), pp. 1687–1693.
- 620 Linkie, M. et al. 2007. Estimating occupancy of a data deficient mammalian species living in
621 tropical rainforests: Sun bears in the Kerinci Seblat region, Sumatra. *Biological Conservation*
622 137(1), pp. 20–27.
- 623 Lode, T. 1995. Activity pattern of polecats *Mustela putorius* L. in relation to food habits and
624 prey activity. *Ethology* 100(4), pp. 295–308.
- 625 Lusseau, D. et al. 2006. Quantifying the influence of sociality on population structure in
626 bottlenose dolphins. *Journal of Animal Ecology* 75(1), pp. 14–24.
- 627 Maffei, L. et al. 2005. Ocelot (*Felis pardalis*) population densities, activity, and ranging
628 behaviour in the dry forests of eastern Bolivia: data from camera trapping. *Journal of Tropical*
629 *Ecology* 21(3), pp. 349–353.
- 630 Marks, B.K. and Duncan, R.S. 2009. Use of forest edges by free-ranging cats and dogs in an
631 urban forest fragment. *Southeastern Naturalist* 8(3), pp. 427–436.
- 632 Martin, E.H. et al. 2015. Modelling fine-scale habitat associations of medium-to-large forest
633 mammals in the Udzungwa Mountains of Tanzania using camera trapping. *Tropical Zoology*
634 28(4), pp. 137–151.
- 635 McCoy, J.C. et al. 2011. Bias associated with baited camera sites for assessing population
636 characteristics of deer. *The Journal of Wildlife Management* 75(2), pp. 472–477.
- 637 McElhinny, T.L. et al. 1997. Patterns of body temperature, activity, and reproductive behavior
638 in a tropical murid rodent, *Arvicanthis niloticus*. *Physiology & Behavior* 62(1), pp. 91–96.
- 639 McShea, W.J. et al. 2016. Volunteer-run cameras as distributed sensors for macrosystem
640 mammal research. *Landscape Ecology* 31(1), pp. 55–66.
- 641 Meek, P.D. et al. 2014. Camera traps can be heard and seen by animals. *PLoS ONE* 9(10), p.
642 e110832.
- 643 Meek, P. D. et al. 2014. Recommended guiding principles for reporting on camera trapping
644 research. *Biodiversity and Conservation* 23(9), pp. 2321–2343.
- 645 Meek, P.D. et al. 2016. Are we getting the full picture? Animal responses to camera traps and
646 implications for predator studies. *Ecology and Evolution* 6(10), pp. 3216–3225.
- 647 Meek, Paul D. et al. 2016. The higher you go the less you will know: placing camera traps high
648 to avoid theft will affect detection Rowcliffe, M. and De Angelo, C. eds. *Remote Sensing in*
649 *Ecology and Conservation* 2(4), pp. 204–211.
- 650 Mella, V.S.A. et al. 2015. Personality affects the foraging response of a mammalian herbivore
651 to the dual costs of food and fear. *Oecologia* 177(1), pp. 293–303.
- 652 Merckx, T. and Van Dyck, H. 2007. Habitat fragmentation affects habitat-finding ability of the
653 speckled wood butterfly, *Pararge aegeria* L. *Animal Behaviour* 74(4), pp. 1029–1037.

- 654 Middleton, A.D. et al. 2013. Linking anti-predator behaviour to prey demography reveals
655 limited risk effects of an actively hunting large carnivore. *Ecology Letters* 16(8), pp. 1023–
656 1030.
- 657 Mills, M.G.L. and Mills, M.E.J. 2014. Cheetah cub survival revisited: a re-evaluation of the
658 role of predation, especially by lions, and implications for conservation. *Journal of Zoology*
659 292(2), pp. 136–141.
- 660 Moller, A.P. 2004. Protandry, sexual selection and climate change. *Global Change Biology*
661 10(12), pp. 2028–2035.
- 662 Morehouse, A.T. et al. 2016. Nature vs. nurture: evidence for social learning of conflict
663 behaviour in grizzly bears. *PLOS ONE* 11(11), p. e0165425.
- 664 Muhly, T.B. et al. 2011. Human activity helps prey win the predator-prey space race. *PLoS*
665 *ONE* 6(3), p. e17050.
- 666 Newey, S. et al. 2015. Limitations of recreational camera traps for wildlife management and
667 conservation research: A practitioner’s perspective. *Ambio* 44(S4), pp. 624–635.
- 668 Ng, S.J. et al. 2004. Use of highway undercrossings by wildlife in southern California.
669 *Biological Conservation* 115(3), pp. 499–507.
- 670 Ngama, S. et al. 2016. How bees deter elephants: beehive trials with forest elephants
671 (*Loxodonta africana cyclotis*) in Gabon. *PLOS ONE* 11(5), p. e0155690.
- 672 Nolet, B.A. et al. 2006. Foraging costs and accessibility as determinants of giving-up densities
673 in a swan-pondweed system. *Oikos* 112(2), pp. 353–362.
- 674 Norris, D. et al. 2010. Habitat patch size modulates terrestrial mammal activity patterns in
675 Amazonian forest fragments. *Journal of Mammalogy* 91(3), pp. 551–560.
- 676 Nowak, K. et al. 2014. Human observers impact habituated samango monkeys’ perceived
677 landscape of fear. *Behavioral Ecology* 25(5), pp. 1199–1204.
- 678 Nyakaana, S. et al. 2001. DNA evidence for elephant social behaviour breakdown in Queen
679 Elizabeth National Park, Uganda. *Animal Conservation* 4(3), pp. 231–237.
- 680 O’Brien, T.G. et al. 2010. The Wildlife Picture Index: monitoring top trophic levels. *Animal*
681 *Conservation* 13(4), pp. 335–343.
- 682 Ordiz, A. et al. 2013. Lasting behavioural responses of brown bears to experimental encounters
683 with humans. *Journal of Applied Ecology* 50(2), pp. 306–314.
- 684 Orrock, J.L. 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation
685 risk. *Behavioral Ecology* 15(3), pp. 433–437.
- 686 Otani, T. 2001. Measuring fig foraging frequency of the Yakushima macaque by using
687 automatic cameras. *Ecological Research* 16(1), pp. 49–54.
- 688 Picman, J. and Schriml, L.M. 1994. A camera study of temporal patterns of nest predation in
689 different habitats. *The Wilson Bulletin*, pp. 456–465.

- 690 Pienkowski, M.W. 1979. Differences in habitat requirements and distribution patterns of
691 plovers and sandpipers as investigated by studies of feeding behaviour. *Verhandlungen der*
692 *Ornithologische Gesellschaft in Bayern* 23, pp. 105–124.
- 693 du Preez, B.D. et al. 2014. To bait or not to bait: a comparison of camera-trapping methods for
694 estimating leopard *Panthera pardus* density. *Biological Conservation* 176, pp. 153–161.
- 695 Robertson, B.A. and Hutto, R.L. 2006. A framework for understanding ecological traps and an
696 evaluation of existing evidence. *Ecology* 87(5), pp. 1075–1085.
- 697 Romero-Muñoz, A. et al. 2010. Temporal separation between jaguar and puma in the dry
698 forests of southern Bolivia. *Journal of Tropical Ecology* 26(03), pp. 303–311.
- 699 Rovero, F. et al. 2013. ‘Which camera trap type and how many do I need?’ A review of camera
700 features and study designs for a range of wildlife research applications. *Hystrix, the Italian*
701 *Journal of Mammalogy* 24(2), pp. 148–156.
- 702 Rovero, F. and Zimmermann, F. 2016. *Camera Trapping for Wildlife Research*. Pelagic
703 Publishing Ltd.
- 704 Rowcliffe, J.M. et al. 2008. Estimating animal density using camera traps without the need for
705 individual recognition. *Journal of Applied Ecology* 45(4), pp. 1228–1236.
- 706 Rowcliffe, J.M. et al. 2014. Quantifying levels of animal activity using camera trap data.
707 *Methods in Ecology and Evolution* 5(11), pp. 1170–1179.
- 708 Rowcliffe, J.M. et al. 2016. Wildlife speed cameras: measuring animal travel speed and day
709 range using camera traps. *Remote Sensing in Ecology and Conservation* 2(2), pp. 84–94.
- 710 Rowell, T.E. 1966. Hierarchy in the organization of a captive baboon group. *Animal Behaviour*
711 14(4), pp. 430–443.
- 712 Rychlik, L. 2005. Overlap of temporal niches among four sympatric species of shrews. *Acta*
713 *Theriologica* 50(2), pp. 175–188.
- 714 Schaller, G.B. 1967. *The Deer and the Tiger: A Study of Wildlife in India*. Chicago: University
715 of Chicago Press.
- 716 Severud, W.J. et al. 2011. Predator cues reduce American beaver use of foraging trails. *Human-*
717 *Wildlife Interactions* 5, pp. 296–305.
- 718 Shamoun-Baranes, J. et al. 2012. From sensor data to animal behaviour: an oystercatcher
719 example. *PLoS ONE* 7(5), p. e37997.
- 720 Steenweg, R. et al. 2016. Scaling up camera traps: monitoring the planet’s biodiversity with
721 networks of remote sensors. *Frontiers in Ecology and the Environment*.
- 722 Stewart, F.E.C. et al. 2016. Wolverine behavior varies spatially with anthropogenic footprint:
723 implications for conservation and inferences about declines. *Ecology and Evolution* 6(5), pp.
724 1493–1503.

- 725 Steyaert, S.M.J.G. et al. 2016. Human shields mediate sexual conflict in a top predator.
726 *Proceedings of the Royal Society B: Biological Sciences* 283(1833), p. 20160906.
- 727 Sueur, C. et al. 2011. How can social network analysis improve the study of primate behavior?
728 *American Journal of Primatology* 73(8), pp. 703–719.
- 729 Suraci, J.P. et al. 2016. A new Automated Behavioural Response system to integrate playback
730 experiments into camera trap studies. *Methods in Ecology and Evolution*. Available at:
731 <http://doi.wiley.com/10.1111/2041-210X.12711> [Accessed: 22 December 2016].
- 732 Suselbeek, L. et al. 2014. Food acquisition and predator avoidance in a Neotropical rodent.
733 *Animal Behaviour* 88, pp. 41–48.
- 734 Swanson, A.M. et al. 2015. Snapshot Serengeti, high-frequency annotated camera trap images
735 of 40 mammalian species in an African savanna. *Scientific Data* 2.
- 736 Sweitzer, R.A. and Furnas, B.J. 2016. Data from camera surveys identifying co-occurrence and
737 occupancy linkages between fishers (*Pekania pennanti*), rodent prey, mesocarnivores, and
738 larger predators in mixed-conifer forests. *Data in Brief* 6, pp. 783–792.
- 739 Tan, C.L. et al. 2013. Into the night: camera traps reveal nocturnal activity in a presumptive
740 diurnal primate, *Rhinopithecus brelichi*. *Primates* 54(1), pp. 1–6.
- 741 Tobler, M.W. et al. 2008a. An evaluation of camera traps for inventorying large- and medium-
742 sized terrestrial rainforest mammals. *Animal Conservation* 11(3), pp. 169–178.
- 743 Tobler, M.W. et al. 2008b. Further notes on the analysis of mammal inventory data collected
744 with camera traps. *Animal Conservation* 11(3), pp. 187–189.
- 745 Villette, P. et al. 2017. Evaluating camera traps as an alternative to live trapping for estimating
746 the density of snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus*
747 *hudsonicus*). *European Journal of Wildlife Research* 63(7). Available at:
748 <http://link.springer.com/10.1007/s10344-016-1064-3> [Accessed: 18 December 2016].
- 749 Voelkl, B. and Kasper, C. 2009. Social structure of primate interaction networks facilitates the
750 emergence of cooperation. *Biology Letters* 5(4), pp. 462–464.
- 751 Vogt, K. et al. 2014. Scent-marking behaviour and social dynamics in a wild population of
752 Eurasian lynx *Lynx lynx*. *Behavioural Processes* 106, pp. 98–106.
- 753 Wang, Y. et al. 2015. Mesopredator spatial and temporal responses to large predators and
754 human development in the Santa Cruz Mountains of California. *Biological Conservation* 190,
755 pp. 23–33.
- 756 Ware, J.V. et al. 2015. Validation of mercury tip-switch and accelerometer activity sensors for
757 identifying resting and active behavior in bears. *Ursus* 26(2), pp. 86–96.
- 758 Weerakoon, M.K. et al. 2014. Can camera traps be used to estimate small mammal population
759 size. In: Fleming, P. et al. eds. *Camera trapping: wildlife management and research*. CSIRO
760 Publishing, pp. 307–316.

- 761 Wey, T. et al. 2008. Social network analysis of animal behaviour: a promising tool for the study
762 of sociality. *Animal Behaviour* 75(2), pp. 333–344.
- 763 Whitehead, H. 2008. *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social*
764 *Analysis*. University of Chicago Press.
- 765 Wilson, R.P. et al. 1986. Recording devices on free-ranging marine animals: does measurement
766 affect foraging performance? *Ecology* 67(4), pp. 1091–1093.
- 767 Wolf, J.B.W. et al. 2007. Social structure in a colonial mammal: unravelling hidden structural
768 layers and their foundations by network analysis. *Animal Behaviour* 74(5), pp. 1293–1302.
- 769 Wright, J.T. et al. 2010. Native species behaviour mitigates the impact of habitat-forming
770 invasive seaweed. *Oecologia* 163(2), pp. 527–534.
- 771 Zheng, X. et al. 2016. Individual identification of wild giant pandas from camera trap photos -
772 a systematic and hierarchical approach. *Journal of Zoology* 300, pp. 247–256.

773

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 (still images and video footage, equally).

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

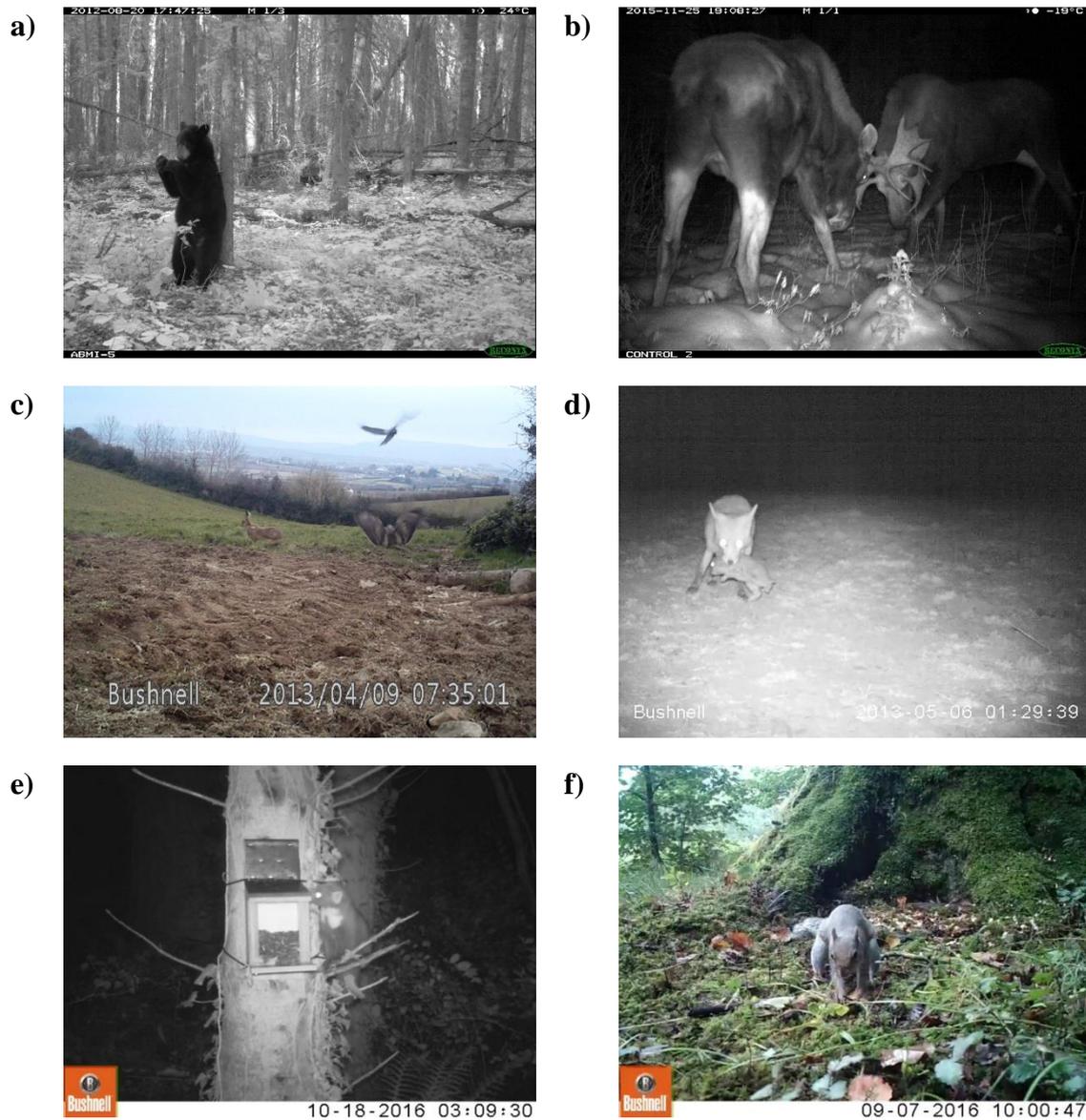


Figure 1. Examples of animal behaviour captured by camera traps: **a)** Scent marking by an American black bear (*Ursus americanus*); **b)** intraspecific competition in moose (*Alces alces*); **c)** interspecific interactions between a European hare (*Lepus europaeus*; anti-predator response), a common 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).