

REVIEW

Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes

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Summary

1. Reliable assessment of animal populations is a long-standing challenge in wildlife ecology. Technological advances have led to widespread adoption of camera traps (CTs) to survey wildlife distribution, abundance and behaviour. As for any wildlife survey method, camera trapping must contend with sources of sampling error such as imperfect detection. Early applications focused on density estimation of naturally marked species, but there is growing interest in broad-scale CT surveys of unmarked populations and communities. Nevertheless, inferences based on detection indices are controversial, and the suitability of alternatives such as occupancy estimation is debatable.

2. We reviewed 266 CT studies published between 2008 and 2013. We recorded study objectives and methodologies, evaluating the consistency of CT protocols and sampling designs, the extent to which CT surveys considered sampling error, and the linkages between analytical assumptions and species ecology.

3. Nearly two-thirds of studies surveyed more than one species, and a majority used response variables that ignored imperfect detection (e.g. presence–absence, relative abundance). Many studies used opportunistic sampling and did not explicitly report details of sampling design and camera deployment that could affect conclusions.

4. Most studies estimating density used capture–recapture methods on marked species, with spatially explicit methods becoming more prominent. Few studies estimated density for unmarked species, focusing instead on occupancy modelling or measures of relative abundance. While occupancy studies estimated detectability, most did not explicitly define key components of the modelling framework (e.g. a site) or discuss potential violations of model assumptions (e.g. site closure). Studies using relative abundance relied on assumptions of equal detectability, and most did not explicitly define expected relationships between measured responses and underlying ecological processes (e.g. animal abundance and movement).

5. *Synthesis and applications.* The rapid adoption of camera traps represents an exciting transition in wildlife survey methodology. We remain optimistic about the technology's promise, but call for more explicit consideration of underlying processes of animal abundance, movement and detection by cameras, including more thorough reporting of methodological details and assumptions. Such transparency will facilitate efforts to evaluate and improve the reliability of camera trap surveys, ultimately leading to stronger inferences and helping to meet modern needs for effective ecological inquiry and biodiversity monitoring.

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Introduction

The problem of reliably assessing animal populations has challenged wildlife ecologists and managers for decades (Caughley 1977). A wide variety of field and analytical approaches have been developed and refined (Krebs 1999; Williams, Nichols & Conroy 2002; Long *et al.* 2008), but the use of camera trapping to survey and monitor wildlife has increased dramatically in recent years (O’Connell, Nichols & Karanth 2011). From pioneering photos captured with bulky cameras and tripwires, technological advances in infrared sensors and digital photography have led to cost-effective, noninvasive means of generating reliable detection of elusive wildlife (Kucera & Barrett 2011). Camera trap (CT) methodology now encompasses a wide range of equipment and ecological applications: CTs are now being used to assess wildlife distribution, abundance, behaviour and community structure (Rovero *et al.* 2013; Meek *et al.* 2014b). Such widespread applications are generating a profusion of new data, and the potential for methodological standardization has led to calls to use CTs as a cornerstone of global biodiversity monitoring initiatives (O’Brien *et al.* 2010; Ahumada, Hurtado & Lizcano 2013; Linkie *et al.* 2013).

While the adoption of new survey technologies such as camera trapping can open avenues for novel insights, it could convey a false sense of progress if data collection outpaces rigorous sampling designs and statistical analyses (cf. Hebblewhite & Haydon 2010). Although CTs show great promise for facilitating standardized surveys, increasing knowledge on data-deficient species and capturing public attention, concerns about substandard applications and weak inferences have been raised (O’Connell, Nichols & Karanth 2011; Meek, Ballard & Fleming 2015). As with any wildlife survey methodology, CT surveys must address common sources of sampling error, particularly the problem of imperfect detection – where individuals or species present within a sampling area are not always detected (Anderson 2001; Williams, Nichols & Conroy 2002). CT surveys target mobile species and thus must contend with imperfect detection at two spatial scales: first, individuals passing through the relatively small camera detection zone may not be detected; secondly, individuals using some larger area that the camera is assumed to sample may not enter the detection zone (Fig. 1). Probability of detection can be affected by many factors operating across these scales, including a camera’s detection zone, sensitivity and specific placement; habitat characteristics or attractants at a camera; ambient and animal temperatures; timing and duration of sampling; and animal density and behaviour in the landscape

(Figs 1 and 2). This complexity necessitates a careful accounting of the relationship between CT detections and underlying ecological processes of interest (e.g. Rowcliffe *et al.* 2011; Claridge & Paull 2014).

Carefully planned sampling protocols can help minimize detection bias, but analytical approaches to contend with imperfect detection are also needed (Williams, Nichols & Conroy 2002; MacKenzie *et al.* 2006). Formal statistical modelling of detectability in CT surveys began with the use of capture–recapture (CR) methods to estimate density of individually identifiable species – typically large, patterned carnivores such as tigers *Panthera tigris* and leopards *Panthera pardus* (Karanth & Nichols 1998; Fig. 2). Such CR applications continue to develop rapidly, particularly with the advent of spatially explicit CR methods (SCR; Royle *et al.* 2014). Nevertheless, the majority of wildlife species are not easily individually identifiable from photos, rendering CR approaches difficult and leading to widespread interest in alternate analytical approaches for ‘unmarked’ species (Fig. 2). Furthermore, CT surveys typically collect data on a wide range of species, generating a desire for metrics applicable to multispecies surveys (Tobler *et al.* 2008), particularly given the growing demand for multispecies monitoring in support of large-scale biodiversity conservation (O’Brien *et al.* 2010; Ahumada, Hurtado & Lizcano 2013).

Several analytical approaches have been proposed for population surveys of unmarked species using CTs. Indices of relative abundance, such as detection rates, have been widely used (e.g. Carbone *et al.* 2001; O’Brien, Kinnaird & Wibisono 2003; Bengsen *et al.* 2011), but have also been critiqued for their implicit assumption that detection probability is constant across areas, time or species (Jennelle, Runge & MacKenzie 2002; Harmsen *et al.* 2010; Sollmann *et al.* 2013a). In the absence of individual identification, detection rates confound abundance and detectability – they may reflect both the number and behaviour of animals, as well as nuisance factors related to sampling error (Fig. 1; O’Brien 2011; Rowcliffe *et al.* 2011). There is thus a need to explicitly consider these ecological and observational processes in order to make robust inferences about abundance. Promising approaches to modelling detection rates while accounting for animal movement and detectability have been proposed (Rowcliffe *et al.* 2008; Chandler & Royle 2013), but their broader reliability for CT surveys remains to be more thoroughly tested (Rowcliffe *et al.* 2011; Sollmann *et al.* 2013b; Zero *et al.* 2013).

The rise of occupancy modelling as a method to account for imperfect detection has led to its application in CT surveys as a surrogate for abundance (MacKenzie

Fig. 1. The detection of animals by camera traps is affected by ecological and observational processes occurring at both the local scale of the camera trap detection zone and the broader scale of the surrounding landscape. Explicitly accounting for these underlying processes is an important challenge for wildlife surveys with camera traps. (Image by Jeff Dixon).

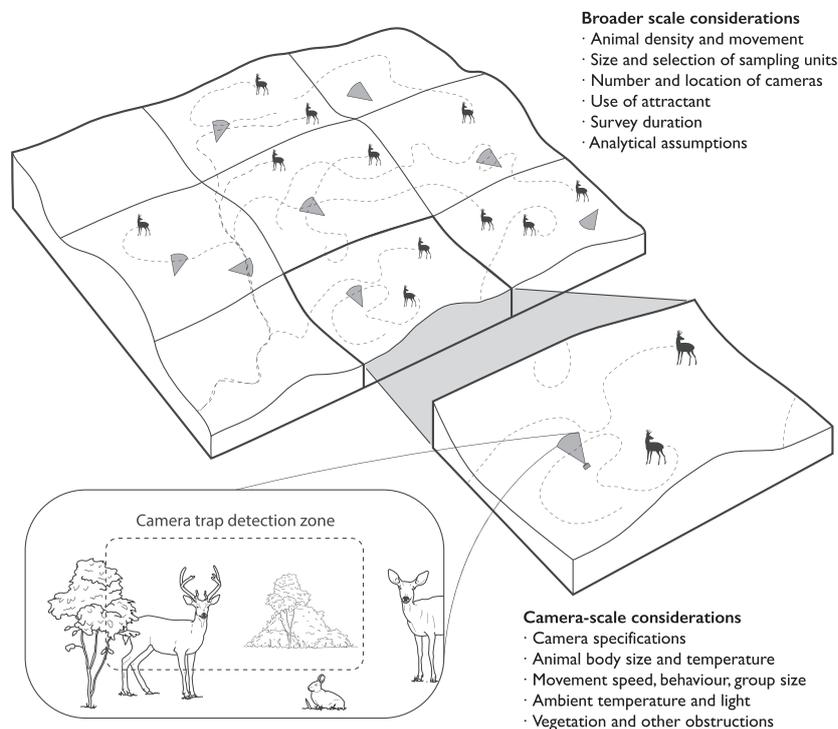
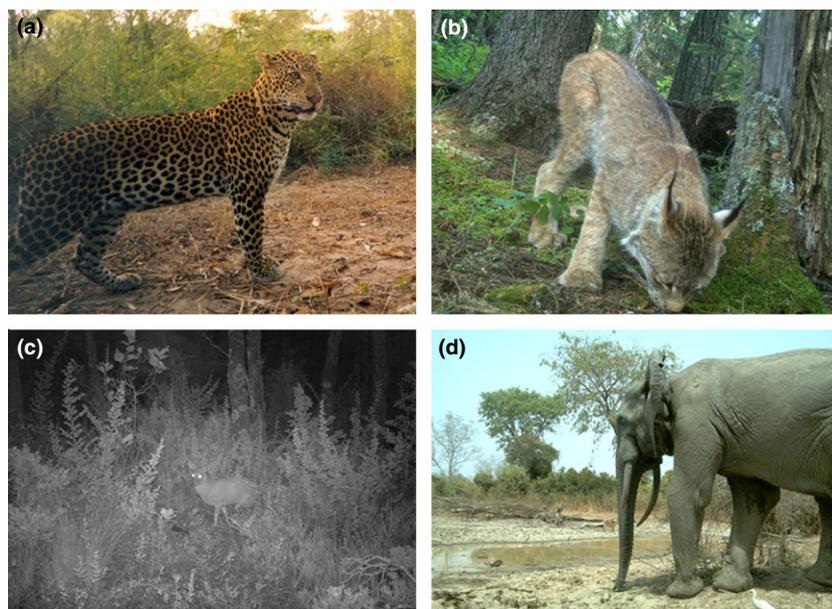


Fig. 2. Examples of the diverse wildlife species surveyed with camera traps. Methods for density estimation mostly rely on individual identification of species with unique patterns (such as (a) leopard *Panthera pardus*), whereas estimation methods for 'unmarked' species are less established (e.g. (b) lynx *Lynx canadensis*; (c) pudu *Pudu pudu*; (d) elephant *Loxodonta africana*). Camera trap detections are affected by many factors that may vary widely across species, sites, sampling periods and protocols. These include species body size and movement range (as shown in (c) vs. (d)); size and composition of the detection zone and field of view (as shown in (b) narrow or (c) densely vegetated vs. (d) wide and open) and use of attractants such as roads for (a), scent lure for (b) or water sources for (d).



et al. 2006; O'Brien *et al.* 2010; Ahumada, Hurtado & Lizcano 2013). The flexible occupancy framework has also been applied to multispecies CT assessments, such as species interactions (Steinmetz, Seaturien & Chutipong 2013) and community dynamics (Burton *et al.* 2012), as well as other parameters, for example reproductive success (Fisher, Wheatley & Mackenzie 2014). Nevertheless, occupancy models were initially formulated for systems with discrete, independent sites closed to changes in occupancy over a sampling period (MacKenzie *et al.* 2002), while CT surveys often target species that range widely in continu-

ous habitat – typically far beyond the 'site' covered by a camera's detection zone (Figs 1 and 2). The consequences of violating occupancy model assumptions for CT applications have received little attention, but recent studies suggest they should be more carefully considered (e.g. Rota *et al.* 2009; Efford & Dawson 2012). Ultimately, interpretation of occupancy model parameters and associated biological inference depends on meeting model assumptions, which in turn depends on definitions of critical design features such as sampling units and occasions (Bailey, MacKenzie & Nichols 2014).

Careful sampling design is also necessary to contend with another key source of sampling error: spatial variability (Krebs 1999; Williams, Nichols & Conroy 2002). Most wildlife surveys do not cover an entire area of interest and therefore require a sample of locations chosen in a manner permitting inference to unsampled locations. In principle, spatial variation can be addressed in CT surveys like any other plot-based or trap-based method: by defining a target population of sampling units for inference (e.g. grid cells or individual territories in a survey area) and deploying cameras following a probability-based design (e.g. random sampling). In practice, target populations and associated sampling units may differ depending on the objective for which CTs are used (e.g. abundance vs. distribution); thus, CT sampling designs should be explicitly linked to survey objectives. For instance, CT surveys focused on CR density estimation have frequently chosen camera locations that maximize detection probabilities for a particular species (e.g. roads, trails), but such a targeted sampling design may not be appropriate for other survey objectives such as occupancy or richness (O'Connell & Bailey 2011; Wearn *et al.* 2013). Furthermore, sampling details such as use of lures or camera spacing may have important implications for analytical assumptions such as effective sampling area and site independence.

Given the rapidly growing use of CTs to survey an increasing diversity of wildlife, and the challenges of dealing with common sources of sampling error, we identified a need to assess the current state of CT practice. We suggest that to achieve their potential for improving large-scale biodiversity monitoring and ecological understanding, CT surveys must be reliable, repeatable and transparent in their approaches to measuring ecological processes. Recent studies have reviewed general patterns in CT usage and technologies, providing examples and recommendations for specific protocols and designs (e.g. Rovero *et al.* 2013; Meek *et al.* 2014a), but an explicit evaluation of linkages between CT surveys and the ecological processes they are intended to quantify has not been undertaken. We therefore aimed to systematically characterize objectives and methodologies of recently published CT studies, with a focus on evaluating whether and how survey designs, protocols and analyses dealt with imperfect detection and spatial variability, particularly with respect to population-level and community-level assessments of unmarked species. Our ultimate goal was to provide recommendations and identify directions for further research to improve camera trapping methods for wildlife research and monitoring.

Materials and methods

We searched the Web of Science™ (Science Citation Index Expanded) for papers published between 2008 and 2013 to obtain a broad sample of recent CT studies. We used the following topic search terms: (camera trap* OR remote camera*) AND (wildlife

OR mammal* OR bird*), with an initial search completed on 28 June 2013 and updated on 20 February 2014. We reviewed the resulting list of 359 papers and excluded studies that did not collect CT data to make inferences on animal occurrence, abundance or behaviour. We also excluded studies unavailable in English, using only video surveillance, presenting only review, opinion or meta-analysis, or focusing only on methodological tests of equipment or data processing. Our final set for assessment included 266 published studies (Table S1 Supporting information).

To characterize the diversity of CT applications for assessing wildlife, we summarized a set of variables detailing basic features of the published studies, such as focal taxa, geographic location, analytical objectives and response variables used (Table S1). For studies that used CTs as one of multiple survey methods, we focused only on details of the CT methods. We quantified the degree of consistency in implementing and reporting features of CT protocols and study design that might affect detectability and sampling error (e.g. camera type and settings, spatial and temporal sampling effort, use of attractants; Table S1). These details are fundamental to interpreting results of CT studies and assessing their reliability, repeatability and suitability for broader comparison or synthesis (Meek *et al.* 2014a). We then assessed in more detail subsets of papers that focused on estimating density or occupancy (*sensu* MacKenzie *et al.* 2006), or used indices of relative abundance, in order to further characterize application of these differing approaches to assessing populations – particularly the degree of attention devoted to model assumptions.

We also collated information on average body and home range sizes for a subset of species surveyed in the reviewed studies in order to better quantify the functional diversity of wildlife being sampled by CTs and to evaluate the degree to which CT methodologies were tailored to focal species. Trait data were obtained for 181 species from 174 studies, including the majority of single-species studies and a random selection from multispecies studies (Table S2; Appendix S1, Supporting information).

Breadth of camera trap research

The 266 CT studies we reviewed were published in 95 journals and at an increasing rate over the 6-year period (Fig. 3; Table S1). Studies focused on a range of ecological objectives and response metrics, including relative abundance (43.6%), presence–absence (41.4%), behaviour (32.3%, e.g. activity patterns, diet), population density (15.8%) and occupancy (15.4%). Roughly half of the studies (49.6%) used CT data to address multiple analytical objectives (e.g. presence–absence and behaviour).

The majority of studies in our sample focused on mammal species (94.8%), but birds were also represented (11.9%) and a few studies included reptiles (1.1%), amphibians (0.74%) and plants (0.74%). Mammalian carnivores were the most frequently targeted group (64.7%) – particularly large felids – followed by ungulates (40.2%), small mammals (e.g. lagomorphs, rodents; 24.1%) and primates (10.5%; Fig. 4a). Species surveyed with CTs spanned a broad array of body sizes and movement ranges: average body mass ranged from 1.3 g to 4750 kg (median = 12.1 kg) across 179 species (from 173

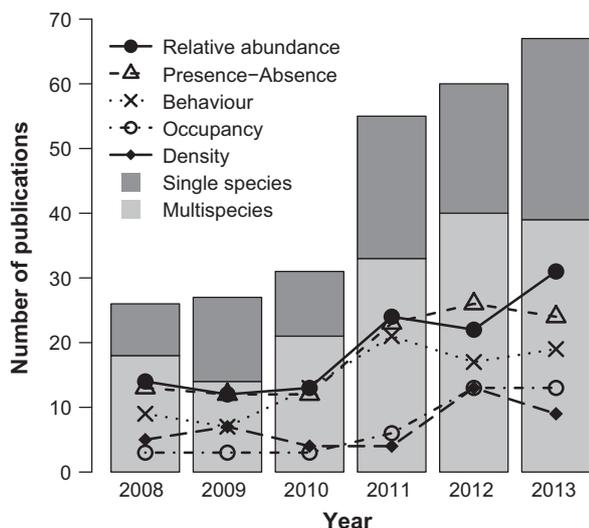


Fig. 3. Annual number and type of camera trap publications in the reviewed sample, with studies classified by their focus on single species vs. multispecies and their analytical objectives (50% had multiple objectives).

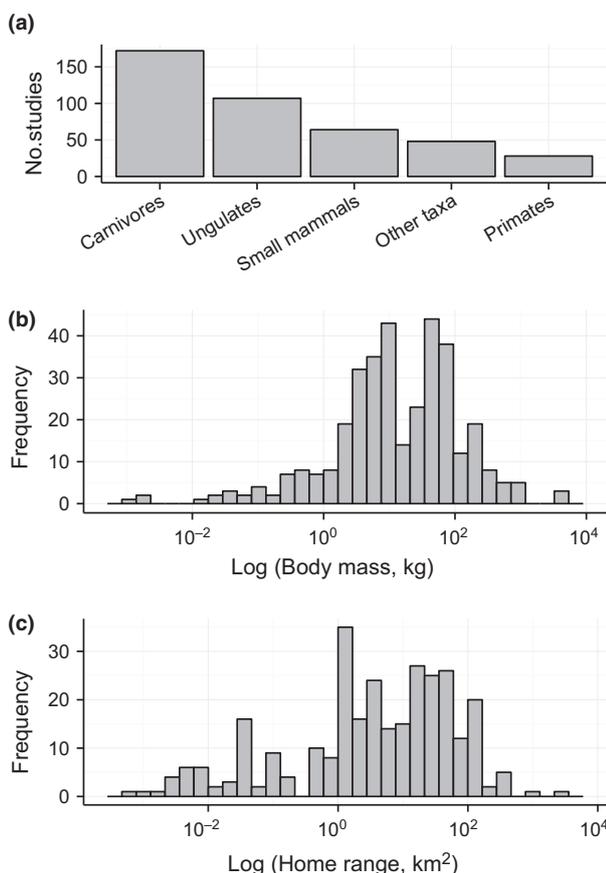


Fig. 4. Diversity of wildlife surveyed in the reviewed camera trap publications. (a) Mammalian carnivores were most commonly targeted, although many other taxonomic groups were surveyed. (b) Species spanning a wide range of body sizes were detected. (c) Home range sizes of species detected were diverse. Trait data were taken from a sample of 181 species from 174 studies; Table S2.

studies) for which we obtained data, and average home range size varied from 655 m² to 2800 km² (median = 4.8 km², 138 species from 157 studies; Fig. 4b, c; Table S2). Nearly two-thirds of studies focused on more than one species (61.3%; Fig. 3), with species traits often varying considerably within multispecies studies. For instance, body mass varied by a median of 40 kg in 62 multispecies studies examined (range 0.03–4705; mean of 3.8 species evaluated per study; Table S2), and home range size varied by a median of 29 km² within 57 studies (range 0.004–2796; mean of 3.4 species per study).

Geographically, CT studies were reported from 60 countries and were most common in the USA (17.1%), Brazil (13.8%) and Australia (5.6%; Fig. S1, Supporting information). By continent, the majority of studies took place in Asia (28.6%) and the Americas (North = 28.8%, South = 23.0%), with fewer from Africa (12.3%) and Europe (8.1%).

Camera trap equipment and protocols

The make and model of CT equipment, and the settings and deployment protocols used, have important consequences for species detectability and the interpretation and repeatability of CT results (Rovero *et al.* 2013; Meek, Ballard & Fleming 2015). For instance, standardized tests of popular CT models indicate order-of-magnitude variation in key metrics such as size of the detection zone and trigger speed (e.g. www.trailcampro.com), and field comparisons confirm that such differences translate into significant effects on detectability (e.g. Wellington *et al.* 2014). Across the studies we reviewed, more than 100 CT models from 41 brands were used, with 21.4% of studies using multiple models and 16.2% not specifying camera type. Many studies did not report specific CT settings such as sensitivity (e.g. high vs. low; reported in 10.6% of studies), delay between consecutive triggers (47.8%) and camera height (48.5%). Where reported, these settings varied considerably (e.g. mean camera height = 80.4 cm, SD = 102.3, range = 15–600; range in trigger delay = 0–60 min) and were not consistently tailored to surveyed species; for example, camera height was not correlated to species body mass across a subset of studies for which data were available ($r_s = 0.16$, $P = 0.16$, $n = 78$; Fig. S2). We hypothesize that the large amount of variation in CT equipment and protocols could cause significant heterogeneity in species detectability, particularly across studies but even within studies where protocols were not consistent, yet very few studies explicitly considered such potential influences on the interpretation of their results (cf. Meek, Ballard & Fleming 2015).

Sampling design

Whereas CT equipment and protocols can have important consequences for detectability, details of sampling design are central to the interpretation and extrapolation of survey

results. The approach to choosing camera locations, and their number, spacing and duration of deployment, affects the interpretation of the processes being sampled, their statistical treatment and the strength of inference (Fig. 1; O'Brien 2011; O'Connell & Bailey 2011). A large proportion of the reviewed studies (40.2%; Fig. S3) did not use a probability-based sampling design, relying instead on opportunistic or targeted approaches for choosing camera locations (e.g. based on site accessibility or expectations of animal occurrence). A further 21.4% provided almost no details on sampling design. Some form of systematic design was reported in 22.2% of studies (e.g. regular spacing of cameras), and 15.4% described a random (or stratified random) selection of sampling sites.

Overall survey areas, when reported, ranged from 1 hectare to more than 200 000 km² (median = 182 km², $n = 119$). Most studies did not explicitly define a sampling unit, which we interpreted as implicitly using individual camera stations as sampling units. This can in turn be ambiguously interpreted anywhere from the size of the camera detection zone (e.g. on the order of 100 m²) to some maximum, unknown area containing animals with some chance of moving into that detection zone during the sampling period (Fig. 1; Efford & Dawson 2012). A small proportion (7.9%) of studies used specific features as sampling units (e.g. fruiting trees, water sources, dens, seed plots), while 11.3% described a specific area as the sampling unit (varying from 100 m² to over 100 km² and often lacking strong biological justification). The presence of natural or artificial attractants may draw animals in to a CT (Fig. 2), increasing its effective sampling area, and 59.8% of studies reported positioning cameras at some form of attractant to increase detection probabilities, including many different food baits (22.9%) and scent lures (9.0%), as well as natural attractants such as trails, roads, water sources or other specific habitat features. Spacing between adjacent camera stations, when reported, varied from 20 m to 8 km (mean = 1.3 km, SD = 1.3 km, $n = 136$), with sampling independence typically assumed but rarely tested. Few studies gave an explicit rationale for the choice of design, sampling unit or spacing criteria – we noted only 13.2% that specifically related camera distribution to the spatial ecology of target species. Nevertheless, there were significant correlations between average home range size and camera spacing ($r_s = 0.40$, $P < 0.01$, $n = 88$; Fig. S2), sampling unit area ($r_s = 0.46$, $P = 0.02$, $n = 27$) and overall survey area ($r_s = 0.43$, $P < 0.01$, $n = 74$) across studies for which data were available.

The scale of spatial and temporal sampling effort – and its reporting – also varied considerably across studies. The number of camera stations in a study varied from only 1 up to 1174 (median = 31, $n = 229$), with camera density ranging from 10 per hectare to <1 per 1000 km² (median = 1 per 2.9 km², $n = 104$). Reported survey durations varied from <1 month to over 13 years (median = 8 months, $n = 211$), with total trap-days of sampling effort varying from 29 to 52 900 (median = 2055, $n = 173$;

Fig. S3). Nearly one-third (28.9%) of studies that reported sampling effort had fewer than 1000 total trap-days, which is likely to be insufficient to detect rare species in a study area (Carbone *et al.* 2001; Tobler *et al.* 2008; Wearn *et al.* 2013). Despite the influence of both spatial and temporal sampling effort on inferences, very few of the reviewed studies reported using *a priori* simulation or power analysis to inform sampling design or effort (e.g. Bailey *et al.* 2007).

Analytical approaches to population assessment

DENSITY ESTIMATION

Population density is often a state variable of primary interest in wildlife surveys (Williams, Nichols & Conroy 2002; O'Brien 2011). Of the CT studies we reviewed, 42 (15.8%) estimated density or absolute abundance (Fig. 3). More than half of these (54.8%) used conventional CR methods to account for imperfect detection based on capture histories of marked individuals (e.g. Karanth & Nichols 1998). One-third applied SCR methods, all published since 2011, indicating the increasing adoption of spatially explicit models, which were deemed superior to non-spatial CR methods in several comparative studies (e.g. Blanc *et al.* 2013). Four studies (9.5%) did not correct for detectability but used the minimum number of detected individuals to estimate density, and three (7.1%) used ad hoc methods to infer density from a combination of detection rates, occupancy estimates and home range sizes. Only three studies produced density estimates accounting for imperfect detection without the need to identify individuals, and all three used the random encounter model (REM; including its original developers Rowcliffe *et al.* 2008). The majority of density studies focused on carnivores (76.2%), particularly on uniquely patterned species, although several surveyed patterned ungulates (e.g. Grevy's zebra *Equus grevyi*; Zero *et al.* 2013), and some applied CR approaches to species with less obvious markings (e.g. red fox *Vulpes vulpes*; Sarmiento *et al.* 2009). A few studies used mark–resight models on populations in which only a subset of animals could be individually identified (e.g. antlered males; Watts *et al.* 2008; collared individuals; Sollmann *et al.* 2013b).

As in the full sample of CT studies, there was variation in sampling design and protocols among density estimation studies. Most used either a systematic (38.1%) or opportunistic (33.3%) approach to distributing cameras in the study area, with only 3 studies (7.1%) using a randomized design. One-half stated that cameras were set at natural attractants, with another 16.7% using bait or lure. A quarter (26.2%) used the same design to estimate density for multiple species, and nearly half (47.6%) estimated density as well as other response variables (e.g. occupancy, relative abundance, activity patterns). We noted only 28.6% of density studies that explicitly related

sampling design to focal species ecology. Other authors have highlighted implications of biased sampling designs and heterogeneous detection probabilities for density estimation with CTs (e.g. Foster & Harmsen 2012; Royle *et al.* 2014), and we recommend that future studies devote more attention to evaluating their analytical assumptions.

OCCUPANCY MODELLING

Given the challenge of estimating abundance of unmarked species with CTs, the use of occupancy modelling to estimate detection probabilities and provide an index of abundance has been proposed (e.g. O'Brien *et al.* 2010; O'Connell & Bailey 2011). In our sample, 41 studies (15.4%) applied occupancy models to CT data across a diversity of species (Fig. 3). Most used the single-species, single-season modelling framework originally formulated by MacKenzie *et al.* (2002), although many applied these models to more than one species (65.8%) and over relatively long sampling periods. While detectability is estimated as part of the occupancy framework, specific treatment of imperfect detection varied across occupancy studies and was rarely well described. Few studies explicitly defined key components of the framework in terms of underlying processes of animal abundance, movement and detection by CTs. That is, most did not delineate the specific area being occupied, describe the period of occupancy or discuss how 'occupancy' and 'detectability' were defined and distinguished for the target system (Fig. 1; Eford & Dawson 2012; Bailey, MacKenzie & Nichols 2014).

The overall survey area (i.e. statistical target population) was specified in only 21 occupancy studies (51.2%; range in area = 3–25 000 km², median = 187), and sampling units or 'sites' for which occupancy was being estimated were clearly defined in only nine studies (21.9%; range = 314–32 000 m², median = 1 km²). Nearly half (41.5%) of the studies either did not use a probabilistic sampling scheme to estimate site occupancy (proportion of area occupied) or did not report details of sampling design. Sixteen studies (39.0%) followed a systematic approach to selecting camera locations and ten (24.4%) used a randomized design. Almost two-thirds (65.9%) targeted cameras at an attractant, including some form of lure or bait in 34.1%. Only nine studies (21.9%) explicitly related their sampling design to the size of target species' home ranges, with two others using defined habitat patches. Camera spacing varied considerably across studies (0.1–5 km, median = 1.3, $n = 32$) and was not significantly correlated with home range size of surveyed species ($r_s = 0.32$, $P = 0.12$, $n = 26$). The duration of occupancy surveys ranged from 1 to 38 months (median = 8, $n = 31$), with survey occasions defined in 32 studies (78.0%) and varying from 1 to 15 camera-days (median = 5). Less than one-third of studies explicitly mentioned assumptions of spatial and temporal independence of detections (MacKenzie *et al.* 2006).

An assumption of site closure across repeated survey occasions is required to estimate detectability with occupancy models; that is, sites are assumed to be either always occupied or unoccupied by a species over the survey period (MacKenzie *et al.* 2006). This assumption was explicitly mentioned in less than half of the occupancy studies (41.5%), despite the fact it is almost certainly violated in most CT studies (Fig. 1). Some studies stated that sites were not closed and followed MacKenzie *et al.* (2006) generalization that 'occupancy' be considered habitat use, and detectability includes availability for detection, with the associated assumption that animal movement into or out of the site is random (e.g. Burton *et al.* 2012). Another key assumption of occupancy models is that there is no unmodelled heterogeneity in occupancy or detectability across sites. Eleven of the occupancy studies (26.8%) implicitly assumed that probability of detection was constant across all spatial and temporal replicates (i.e. CT stations and survey occasions). The other 30 studies (73.2%) used a wide variety of covariates to model variation in detection probability, including habitat descriptors (31.7%; e.g. vegetation cover), anthropogenic disturbances (24.4%; e.g. land use, distance to settlement), temporal variation (34.1%; e.g. survey, season), protocol details (31.7%, e.g. camera type, attractant) and other environmental variables (22%; e.g. temperature, precipitation). One-third of these studies used the same covariates to model detectability as for occupancy, often without clearly distinguishing the underlying hypotheses in terms of ecological processes. Most occupancy studies (78%) used AIC model selection to assess relative support for different model specifications (e.g. different covariates on occupancy and detection), but we noted only 15 (36.6%) that explicitly evaluated the adequacy of models at explaining observed heterogeneity (most using MacKenzie & Bailey (2004) goodness-of-fit test or inspecting coefficient confidence intervals).

RELATIVE ABUNDANCE

Studies that did not estimate density or occupancy relied instead on response variables that did not explicitly account for imperfect detection, including presence-absence (PA; 41.4% of studies) and various measures of relative abundance (RA; 43.6%). PA has been called 'naïve' occupancy and will underestimate true occurrence of a species when detection probabilities are <1 , thereby potentially confusing observational and ecological processes (MacKenzie *et al.* 2006). We defined RA broadly as any measure comparing CT detection rates across sites, species or surveys, reflecting its ambiguity as an index that confounds underlying processes of animal abundance and behaviour (Fig. 1). The most commonly reported index was the number of detection events per 100 CT-days of sampling effort (O'Brien, Kinnaird & Wibisono 2003), but we noted use of 18 different indices, including total detections, detections standardized by other measures of effort

(e.g. CT-hour, total CT-days, survey weeks or months), proportion of sites with detections, proportion of total photos and latency to detection. There was also considerable variation in criteria used to define independent detection 'events' for the purpose of calculating indices. Typically, a threshold of elapsed time between consecutive photographs was used (most commonly 30 or 60 min, but varying from no threshold up to 1 day), along with other criteria such as non-consecutive photos of the same species, or determinations of different individuals (O'Brien, Kinnaird & Wibisono 2003).

The variety of approaches to calculating detection indices reflect the diverse usage of RA. For instance, RA measures were frequently used to infer differences in abundance between species or sites (e.g. Kuprewicz 2013), but were also used to describe variation in habitat use, foraging behaviour, activity patterns or species interactions (e.g. Switalski & Nelson 2011; Wang & Fisher 2012). Similarly, RA studies used a wide range of CT protocols and sampling designs (reflected in summaries given above). While the use of RA indices is valid when assumptions of constant detectability hold (O'Brien 2011), there are many suggestions in the literature that this is unlikely to be true (e.g. Harmsen *et al.* 2010; Sollmann *et al.* 2013a). Nevertheless, we noted few RA studies that explicitly considered imperfect detection, such as using N-mixture models to estimate site abundance (e.g. Brodie & Giordano 2013), or that evaluated the reliability of their index by comparing with an alternative measure of abundance (e.g. Rovero & Marshall 2009). The lack of index standardization or evaluation of detection bias renders the use of RA indices for broader, cross-study synthesis problematic.

Towards more effective camera trap surveys

Camera trapping is increasingly used around the world to assess the occurrence, abundance and behaviour of a diverse range of mammal species and other taxa. Scientific uses of CTs are expanding rapidly beyond basic species inventories and traditional CR estimates of population density for uniquely marked carnivores. Our review demonstrates a large number of CT studies focused on multispecies surveys (Fig. 3), and growing use of estimation methods directed at unmarked species, highlighting the great potential of CTs to contribute to broad-scale ecological inquiry and global biodiversity monitoring. Nevertheless, our results also reveal considerable inconsistency in CT approaches and interpretations, even among studies focused on similar species and questions, suggesting shortcomings of the current state of CT practice and revealing opportunities for significant improvement.

IMPROVED METHODOLOGICAL REPORTING

A first opportunity for improvement is more consistent reporting of methodological details (Meek *et al.* 2014a). A

substantial proportion of CT studies that we reviewed omitted basic information such as the type of camera used, how and when they were deployed at a site, the number of sites sampled and how those sites were defined and chosen. Given the influence of CT protocols and sampling designs on the detectability of individuals and species (e.g. Srbek-Araujo & Chiarello 2013; du Preez, Loveridge & Macdonald 2014; Wellington *et al.* 2014) and the interpretation of detections with respect to broader ecological processes of interest, we maintain that more thorough and consistent reporting is needed to assess the reliability of CT inferences. This attention to experimental design would also increase the potential for comparison and synthesis of results across studies (e.g. Linkie *et al.* 2013). We recommend not only that CT studies include details on camera equipment, sampling design and data analysis (cf. Meek *et al.* 2014a), but perhaps more importantly that they explicitly relate methodological specifications to survey objectives. For instance, studies should report on camera sensitivity in the context of focal species detectability (e.g. body size, movement speed), and on camera location with respect to the spatial sampling unit and target population. Measuring and accounting for the effective detection zone of individual CT stations would be useful (Rowcliffe *et al.* 2011; Glen *et al.* 2013), particularly if this zone is expected to vary across features of interest such as species or habitats. Relating sampling design to the ecology of focal species is also vital (e.g. number and spacing of cameras relative to expected home range size) and warrants particular attention in multispecies surveys.

LINKING CAMERA DETECTIONS TO ECOLOGICAL PROCESSES

Explicitly defining expected relationships between CT sampling and underlying ecological processes is perhaps the most important area for improvement in CT studies. Given the range of study objectives and focal taxa, there is no one-size-fits-all approach to designing CT surveys or interpreting detections. However, many of the studies we reviewed relied on poorly supported assumptions about the relationship between CT detections and ecological parameters of interest. For example, many studies continue to ignore the problem of imperfect detection by implicitly assuming that all species are equally detectable or that the number of observed detections has a direct and consistent relationship to abundance across space, time and species. But when considered explicitly, we know that detection rates at a camera will be affected by many factors other than abundance (Fig. 1). Similarly, detection rates aggregated across an array of cameras may reflect not only population abundance but also relationships between camera siting (e.g. random vs. targeted), spacing and animal movement behaviours (e.g. home range size and exclusivity, habitat selection, movement routes, interspecific interactions). This ambiguity is reflected in the

fact that some researchers used detection rates to infer abundance while others used similar metrics to describe behaviour. We therefore recommend that researchers be explicit about the ecological processes they intend to measure with CT detections and the assumptions required to relate detections to those processes.

Directly estimating detection probabilities is an important step towards avoiding the problematic assumption of perfect or equal detectability (Anderson 2001; MacKenzie *et al.* 2002). However, there are no silver bullets, and uncritical application of statistical models that account for detectability without due consideration of associated model assumptions may not ultimately be better than ignoring detectability (Johnson 2008). Accounting for imperfect detection in CT surveys of unmarked species remains a key challenge. Our review highlights increasing application of occupancy modelling in CT studies, particularly in surveys targeting multiple, unmarked species. While this framework explicitly models the detection process separately from that of occupancy, it may not be well suited to CT surveys of wide-ranging wildlife in continuous habitat (Efford & Dawson 2012). Ultimately, interpretation of occupancy and detectability depends on definitions of a site, sampling occasion and season (Bailey, MacKenzie & Nichols 2014). For instance, 'occupancy' of a small area immediately surrounding a camera is quite different than of a 10-km² grid cell within which it is situated, yet such disparate contexts are not clearly distinguished in many current studies. Similarly, 'occupancy' measured during 1 month is not equivalent to that during one year, and a detection probability estimated for an occasion of one camera-day is not equivalent to that estimated over an occasion spanning fifteen camera-days. It is difficult to imagine a CT study of most mammal species where the site surveyed by a camera station remains closed to changes in occupancy over weeks or months, or where movement of individuals in and out of the site is truly random. As such, basic interpretation of 'occupancy' and 'detectability' should be more clearly defined in the context of CT surveys, particularly when considering those sampling a range of different species.

We recognize that it is not straightforward to define the area effectively sampled by a camera trap over time, and we do not advocate arbitrary specification of fixed sampling units simply to meet assumptions of an occupancy framework. However, there is a need for more explicit consideration of the relationship between animal space use and occupancy sampling frameworks, and for more research focused on the issue of effective sampling area. The consequences of violating key model assumptions, such as site closure, spatial and temporal independence of detections, or adequate modelling of heterogeneity in detection and occupancy also require greater attention. As noted above for detection rates, we recommend that applications of occupancy modelling to CT surveys be accompanied by clear explanation of expected relationships between ecological processes and model parameters,

and the plausibility of associated assumptions. We also call for more empirical and simulation-based testing of the effects of different CT sampling designs and protocols on estimates of detectability and occupancy. Multimethod evaluations (e.g. O'Connell *et al.* 2006) and the linking of animal movement models derived from telemetry studies with camera trap designs hold great promise in this regard.

Better accounting of animal movements also holds promise for improving density estimation with CTs. The use of CR methods with CT data on individually identifiable species continues to improve with development and application of spatially explicit approaches that facilitate modelling of individual movement behaviours and heterogeneous detection probabilities (Royle *et al.* 2014). However, density estimation for unmarked species remains a major challenge for CT surveys, and it is clear that most recent efforts to estimate abundance continue to focus on marked species. Many studies seek creative ways of individually identifying less obviously marked species (e.g. Magoun *et al.* 2011), and while encouraging, such approaches require careful testing of identification methods along with means of analytically accounting for probabilities of misidentification (Foster & Harmsen 2012). More promising may be recent developments applicable to partially marked populations (e.g. Sollmann *et al.* 2013b), as well as methods designed for unmarked populations (e.g. Rowcliffe *et al.* 2008; Chandler & Royle 2013). However, reliable accounting of movement behaviours of unmarked individuals is difficult, particularly when considering potential complexities of movement dynamics, such as behaviours dependent on habitat or density. For example, if density estimation requires assumptions about movement rates or home range characteristics, and these vary with density (e.g. Kjellander *et al.* 2004), they will need to be estimated as part of the density estimation analysis. Exploration of relationships between movement and density, as well as empirical and simulation testing of unmarked density estimation methods, is crucial to the advancement of CT survey methodology.

Conclusion

The explosion of camera trapping represents a grand experiment in modern wildlife survey methodology. There is great potential for CTs to generate important new data, spur analytical innovation and capture public attention (O'Connell, Nichols & Karanth 2011). This potential engenders much optimism, but we suggest a cautious optimism that recognizes the inherent challenges of accurately and precisely evaluating elusive wildlife. Advances in CT capabilities and cost-effectiveness have stimulated new surveys, but robust ecological inquiry requires more than rapid accumulation of novel data and insightful images. CT practitioners must heed the lessons learned through decades of quantitative assessment of animal populations (e.g. Krebs 1999; Anderson 2001; Williams, Nichols & Conroy 2002).

Indeed, many of the issues we have raised – e.g. imperfect detection, effective sampling area, occupancy model assumptions, multispecies inference – are common to other wildlife survey methods, including widely used noninvasive techniques such as genetic tagging, track stations and natural sign surveys (Long *et al.* 2008). Continued development of CT survey methods should entail an explicit focus on the underlying processes of animal abundance, movement and detection by cameras and include more thorough treatment of methodological details and assumptions. Such transparency will facilitate collaborative efforts to evaluate, test and improve the reliability of CT surveys, leading to stronger inferences and more powerful syntheses, and ultimately helping to fill crucial gaps in ecological inquiry and wildlife conservation.

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Data accessibility

Bibliographic details and data for camera trap studies and species traits are in Supporting Information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Distribution of reviewed camera trap studies by country.

Fig. S2. Relationships between species traits and sampling attributes.

Fig. S3. Summary of sampling designs and effort.

Appendix S1. Bibliographic details of references used to obtain data on species body sizes and home range sizes (data contained in Table S2).

Table S1. Bibliographic details and data summarized from camera trap publications included in the review.

Table S2. Data on body size and home range size for a sample of surveyed species.