

Commentary

A Critique of Density Estimation From Camera-Trap Data

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ABSTRACT Densities of elusive terrestrial mammals are commonly estimated from camera-trap data. Typically, this is a 2-step process involving 1) fitting conventional closed population capture–recapture models to estimate abundance, and 2) using ad hoc methods to determine the effective trapping area. The methodology needs to be accurate, robust, and reliable when results are used to guide wildlife management. We critically review 47 published studies and discuss the problems associated with contemporary population estimates of elusive species from camera-trap data. In particular we discuss 1) individual identification, 2) sample size and capture probability, 3) camera location and spacing, 4) the size of the study area, and 5) ad hoc density estimation from the calculation of an effective trapping area. We also discuss the recently developed spatially explicit capture–recapture (SECR) models as an alternative approach that does not require the intermediate step of estimating an effective trapping area. We recommend 1) greater transparency in study design and quality of the data, 2) greater rigor when reviewing manuscripts, and 3) that more attention is given to the survey design to ensure data are of sufficient quality for analysis. © 2011 The Wildlife Society.

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The use of camera traps to study elusive species was pioneered by Griffiths and van Schaik (1993) while studying the activity patterns of rainforest mammals. They recommended the method be used for abundance estimation via a capture–recapture (C–R) framework. The cameras allow for high capture rates (photographs) of species that are otherwise rarely detected in the wild by human observers and are difficult to live-trap. The method took off as a wildlife monitoring tool following the landmark work of Karanth and Nichols (1998) in which they estimated tiger densities in 4 reserves. Capture–recapture analysis of camera-trap data has since become a common method of estimating population density of elusive terrestrial mammals, particularly in the tropics. Most published studies have focused on felids, and, more recently, the method has been used for other carnivore families, armadillos, and tapirs (Table 1). Many of the species studied with camera traps are wide-ranging and occur at low densities. This is in contrast to the development of conventional C–R theory, which was based largely on species that occur at high densities with relatively small ranges.

In camera-trap studies, populations are sampled (rather than enumerated) not because they are too large to count every individual, but because the target species are elusive.

Because many of the species of interest occur at low numbers, relatively small sample sizes and low capture probabilities are inevitable; however, this is no justification for applying an inappropriate method of population estimation. A plethora of population models exist. Most often, camera-trap studies estimate abundance using conventional C–R models (Table 1); although mark–resight methods have also been used (e.g., Fuller et al. 2001, Watts et al. 2008) and more recently, spatially explicit capture–recapture (SECR) models are becoming popular (e.g., Royle et al. 2009a, Royle and Gardner 2011). Conventional C–R estimators have been developed for all classes of closed population models described by Otis et al. (1978), in which capture probability is constant (M_0), or varies between individuals (M_h), within individuals (M_b), or through time (M_t), or any combination thereof (for a summary review see Chao and Huggins 2005).

Because C–R methods are widely used within the camera-trap literature, and the results may be used to make management decisions and drive policy, it is prudent to discuss some of the problems associated with the application of these methods to the study of elusive, low density, or wide-ranging species. We ask whether this tool is sometimes misused in field studies, because of the inability to identify individuals, biased sampling regimes, failure to sample large enough areas, failure to accurately estimate the effective sampling area, and application of conventional C–R population models to inadequate samples of individuals.

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Table 1. Published studies using camera-trap data for capture–recapture abundance estimation

Family	Number of studies	Species	Study ^a
Felidae	38	<i>Panthera tigris</i> (14), <i>Leopardus pardalis</i> (8), <i>Panthera onca</i> (7), <i>Puma concolor</i> (4), <i>Panthera pardus</i> (2), <i>Panthera uncia</i> (2), <i>Lynx rufus</i> (1), <i>Leopardus geoffroyi</i> (1)	1–38
Canidae	3	<i>Chrysocyon brachyurus</i> , <i>Canis latrans</i> , <i>Vulpes vulpes</i>	39–41
Ursidae	1	<i>Tremarctos ornatus</i>	42
Hyaenidae	1	<i>Hyaena hyaena</i>	43
Procyonidae	1	<i>Procyon cancrivorus</i>	44
Tapiridae	2	<i>Tapirus terrestris</i> (2)	45–46
Dasypodidae	1	<i>Priodontes maximus</i>	47

^a Tiger: ¹Karanth (1995), ²Karanth and Nichols (1998), ³O'Brien et al. (2003), ⁴Kawanishi and Sunquist (2004), ⁵Karanth et al. (2004a), ⁶Karanth et al. (2004b), ⁷Johnson et al. (2006), ⁸Lynam et al. (2007), ⁹Simcharoen et al. (2007), ¹⁰Linkie et al. (2008), ¹¹Harihar et al. (2009), ¹²Lynam et al. (2009), ¹³Rayan and Mohamad (2009), ¹⁴Wang and Macdonald (2009). Ocelot: ¹⁵Trolle and Kéry (2003), ¹⁶Maffei et al. (2005), ¹⁷Trolle and Kéry (2005), ¹⁸Haines et al. (2006), ¹⁹Di Bitetti et al. (2006), ²⁰Dillon and Kelly (2007), ²¹Di Bitetti et al. (2008), ²²Dillon and Kelly (2008). Jaguar: ²³Wallace et al. (2003), ²⁴Silver et al. (2004), ²⁵Maffei et al. (2004), ²⁶Cullen et al. (2005), ²⁷Soisalo and Cavalcanti (2006), ²⁸Salom-Pérez et al. (2007), ²⁹Paviolo et al. (2008). Puma: ³⁰Kelly et al. (2008), ³¹Paviolo et al. (2009), ³²Mazzolli (2010), ³³Negrões et al. (2010). Leopard: ³⁴Balme et al. (2009), ³⁵Wang and Macdonald (2009). Snow leopard: ³⁵Jackson et al. (2006), ³⁶McCarthy et al. (2008). Bobcats: ³⁷Heilbrun et al. (2006). Geoffrey's cat: ³⁸Cuellar et al. (2006). Canid: ³⁹Trolle et al. (2007), ⁴⁰Larrucea et al. (2007), ⁴¹Sarmiento et al. (2009). Other: ⁴²Ríos-Uzeda et al. (2007), ⁴³Harihar et al. (2010), ⁴⁴Arispe et al. (2008), ⁴⁵Noss et al. (2003), ⁴⁶Trolle et al. (2008), ⁴⁷Noss and Rumiz (2004).

INDIVIDUAL IDENTIFICATION

The utility of C-R methods using camera traps relies on individual recognition of members of the study population. For large felids such as tigers (*Panthera tigris*) or jaguars (*Panthera onca*), the pelt pattern is unique between individuals and used to identify each member of the sample (Karanth 1995, Silver et al. 2004). Recently, researchers have started using camera-trap data to estimate abundance of species that lack individually identifiable natural markers. Individuals are identified from phenotypic and environment-induced characteristics that are not necessarily found on all individuals within the population. For example, pumas (*Puma concolor*) and tapirs (*Tapirus terrestris*) have been identified by scars, parasites, torn ears, toenail markings or color, tail length and tail kinks, and dark or light body markings (Noss et al. 2003, Kelly et al. 2008, Trolle et al. 2008, Mazzolli 2010). This is acceptable in studies in which all individuals within the sample have a unique marker, but this is unlikely when samples are sufficiently large for reliable abundance estimation via C-R methods. The difficulty of identifying individuals that lack obvious natural markings increases with sample size (e.g., pumas, Harmsen 2006; Andean bears [*Tremarctos ornatus*], Ríos-Uzeda et al. 2007). When definitive identifications cannot be made, researchers sometimes assume that the unknowns are the same individual previously photographed at that location (e.g., Noss et al. 2003); an assumption that is only valid if the target species defends exclusive territories. Alternatively, they exclude the photos completely (e.g., Mazzolli 2010). At a minimum, authors should clearly report the proportion (or number) of photographs that were unidentifiable (e.g., Trolle et al. 2008) and explain whether or how they included them in the abundance estimate.

The misidentification of known individuals as new individuals, and the resultant overestimation of abundance, has led to the development of a framework to model such error in closed population estimates (Yoshizaki et al. 2009).

The new estimators performed well if capture probability was >0.2 (Yoshizaki et al. 2009); however, most published studies report smaller capture probabilities. Currently, the framework allows only for bias corrections when known individuals are misidentified as a new individual in a subsequent occasion, not when different individuals are identified as the same individual, which may be common in camera-trap studies of species that lack unique natural marks (e.g., Oliveira-Santos et al., 2010).

Assigning identities for C-R analysis requires reliable unique markers to be visible in every photograph, and they must have sufficient variation at the population level to allow individual identification. The use of phenotypic features such as white tail patches in pumas (e.g., Kelly et al. 2008) could be validated using data from captive individuals, museum specimens or hunted pelts to test whether inter-individual variation is sufficient to distinguish between individuals. The use of features such as overall condition, musculature, body shape and carriage, and tail carriage (e.g., coyotes [*Canis latrans*], Larrucea et al. 2007; pumas, Kelly et al. 2008, Mazzolli 2010; maned wolf [*Chrysocyon brachyurus*], Trolle et al. 2007) should not be used exclusively as these subjective characteristics will vary with the distance and angle from camera and flash, light and weather conditions, and with the health, behavior, and feeding history of the animal (Fig. 1). Negrões et al. (2010) identified puma individuals using permanent physical features, which may not have been unique (e.g., tail tip coloration), in combination with features that could change through time, such as scars and dermal parasites. By monitoring changes in the time-variable parameters from 1 photograph to the next, in chronological order, they recognized individuals that would otherwise have been incorrectly identified from the time-stable features alone.

Two studies have assessed inter-observer reliability in assigning individual identities to species that lack unique natural markings (pumas: Kelly et al. 2008, tapirs: Oliveira-

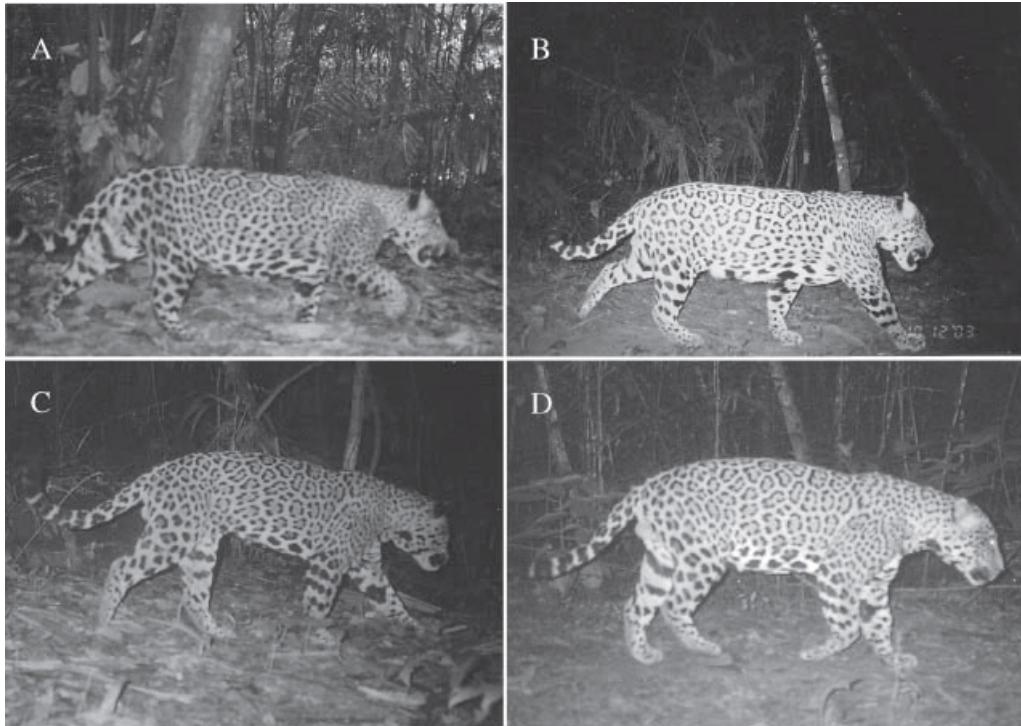


Figure 1. Camera-trap photographs of different jaguars with similar body shapes (A and B), and the same jaguar with a different body shape (C and D). In the absence of unique identifiers (individual spot pattern), it would not be possible to assign correct individual identifications to these cats.

Santos et al., 2010). Oliveira-Santos et al. (2010) asked researchers to identify camera-trap photographs from a closed tapir population of known size ($n = 8$). The number of individuals reported by observers ranged from 4 to 14. Kelly et al. (2008) demonstrated that variation between observers resulted in density estimates that differed by >100% between observers. They recommended that at least 2 investigators independently identify the photos, and that observer bias is evaluated and monitored. Researchers conducting C-R abundance estimates of species that lack natural markings must clearly indicate how they deal with the ambiguous photographs, stating how many captures are unidentifiable (e.g., Noss et al. 2003), report the inter-observer variation in identification (e.g., Paviolo et al. 2009), and report the level of inter-observer agreement or disagreement to assess the level of confidence in the results (e.g., Kelly et al. 2008, Harihar et al. 2010). They must provide enough information for adequate replication, avoid presenting only exemplary photographs, and perhaps include photos or descriptions of the unique features of the individuals (e.g., Trolle et al. 2007). Density estimates may not differ significantly between investigators because of low precision, rather than similar means (e.g., Kelly et al. 2008). Non-significant differences between means with large confidence intervals may indicate that the method is not reliable.

As an alternative to C-R analysis, Carbone et al. (2001) argued that photographic capture rates (photo captures per unit time) could be used as an index of density for species that cannot be individually identified. However, this requires describing and calibrating the relationship between capture rate and density, and measuring the precision of the calibra-

tion (Jenelle et al. 2002). Clearly, capture rate can vary independent of density; for example, Noss et al. (2003) found that the photo capture rate of tapirs increased during the wet season although density estimates remained constant across the seasons. Furthermore, when using capture rate only, one cannot distinguish between many individuals with few recaptures versus few individuals with many recaptures (Trolle et al. 2008).

Rowcliffe et al. (2008) developed a method for density estimation without the need for individual recognition. By modeling the process of contact between animals and cameras, density is estimated from the trapping rate, the speed of movement of the target species, and the distance and angle at which the camera sensor detects the animal. The model performed well in field tests with some species, but not others. The model assumes that animals move randomly and independently of one another, and that cameras are placed randomly. Given these assumptions, the method may not be appropriate for highly territorial or social species, or for elusive forest species that move along trails, such as jaguars and tigers, commonly the focal species of camera-trap studies (Table 1).

An alternative and more robust approach to dealing with unmarked animals in the sample is to use mark-resight estimators, which estimate abundance using the frequency of marked and unmarked individuals (e.g., Bartmann et al. 1987, Minta and Mangel 1989, Arnason et al. 1991, Bowden and Kufeld 1995, McClintock et al. 2009). Unlike C-R methods, mark-resight does not require that all animals in the sample are marked; therefore, abundance estimation is possible when only some of the study animals

have unique identifiers. The mark-resight approach has been largely overlooked in the camera-trap literature outside the United States. This may be because the methods traditionally require that the number of marked animals is known, and so a sample of the population must be captured and marked (e.g., tags, collars) prior to camera trapping (e.g., Mace et al. 1994, Grogan and Lindzey 1999, Sweitzer et al. 2000, Fuller et al. 2001, Matthews et al. 2008). Researchers who use camera traps generally do so because the method is non-invasive, and cheaper and more practical than live trapping, particularly for low density, wide-ranging, or elusive species; thus a physical capture and marking phase prior to camera-trapping is not a realistic option. Watts et al. (2008) applied mark-resight methods to camera-trap data of Florida Key deer (*Odocoileus virginianus clavium*) without physically capturing and marking deer. They divided the camera survey into a “mark” period, in which they used natural identifiers present on a subset of the deer to identify individuals, and a “resight” period, during which time they noted the number of photographs of “marked” and “unmarked” animals. Because camera traps monitor continuously, marked and unmarked individuals may be photographed multiple times through the survey period; therefore mark-resight methods are only appropriate for use with camera-trap data if they allow sampling with replacement (i.e., a given individual may be counted more than once). McClintock et al. (2009) developed the (zero-truncated) Poisson log-normal estimator ([Z]PNE) which allows sampling with replacement. It also allows the number of marked individuals to be unknown; therefore, it can be used with camera-trap data without the need for an initial marking phase (as long as some of the sampled animals can be uniquely identified). The (Z)PNE is freely available in the program MARK (White and Burnham 1999, McClintock 2011) and is potentially a more robust alternative to C-R methods when not all photographed animals can be assigned identities. However, misidentification of individuals due to the use of subjective natural markers will remain equally problematic for mark-resight as for C-R methods; all marked individuals must be recognizable throughout the sampling period, and photos of too poor quality cannot be used. Mark-resight methods are potentially a useful tool for density estimation from camera-trap data (e.g., Jordan et al. 2011); but, like all methods, they are not assumption-free and so are also vulnerable to misuse.

SAMPLE SIZE AND CAPTURE PROBABILITY

A challenge for many field biologists wanting to estimate density lies in obtaining data of suitable quality: sufficient sample size and high enough capture probability to select the most appropriate model. Ideally the precision and bias should be evaluated using simulated trapping data of low density populations that reflect the sample sizes and capture probabilities common in camera trapping (e.g., Ivan 2011). Sample sizes of 10–20 individuals may be too small for reliable estimates using C-R closed population models (Otis et al. 1978, White et al. 1982). In 47 published camera-trap

studies that estimated abundance using C-R methods (Table 1), the sample size was reported for 122 of 125 datasets (45 studies). Mean sample size was 12.6 individuals (SD = 10.4, $n = 122$), ranging from 2 to 65. For the subset of studies focusing on large cats (tigers, jaguars, pumas, leopards, and snow leopards), mean sample size was 10.2 (SD = 6.6, $n = 68$), ranging from 2 to 31. Linkie et al. (2008) noted that increased sample size decreased the coefficient of variation (CV) of the abundance estimates in 5 published studies of tiger density; estimates based on 10–15 individuals were more precise than those based on smaller samples. Of the studies reviewed here (Table 1), the abundance estimate and standard error were reported for 114 of 125 datasets (41 studies). The CV ranged from 0.2% to 175%, and low sample sizes were associated with low precision (Fig. 2; Spearman correlation between sample size and CV: $\rho = -0.438$, $P < 0.001$, $n = 114$). The CV exceeded 20% for samples with fewer than 17 individuals (see also Linkie et al. 2008). Estimates with such low precision will be of limited use for wildlife management such as monitoring population trends through time or for between-site comparisons.

Rather than estimate abundance from exceptionally small samples (e.g., tigers: $n = 2$, Lynam et al. 2009; jaguars: $n = 4$, Wallace et al. 2003; and ocelots: $n = 3$, Haines et al. 2006), some researchers simply report the minimum number alive as a conservative best guess (e.g., Lynam et al. 2007). This may be useful if researchers are investigating whether a threatened species exists at some minimal level in an area. For surveys with small samples, we recommend that researchers investigate further whether the low capture probability is an artifact of low detection probability at the assigned camera locations or truly represents low abundance of the target species within the study area. This can be achieved by investing efforts in alternative methods of assessing relative abundance such as sign surveys for comparison

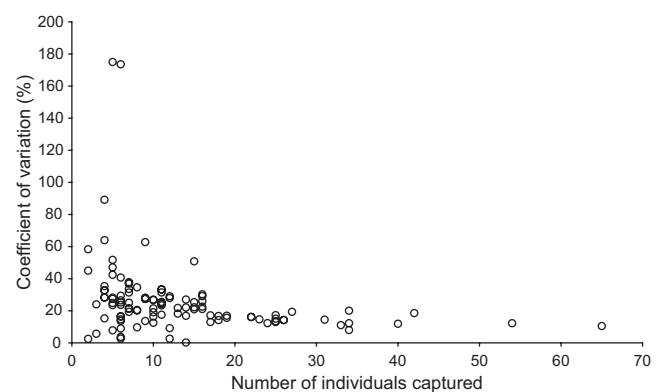


Figure 2. Decline in the coefficient of variation of C-R abundance estimates with increasing sample size (number of individuals captured during sampling period). Coefficient of variation is calculated as $SE[\hat{N}]/\hat{N} \times 100$. Abundance estimates (\hat{N}) and standard errors ($SE[\hat{N}]$) are from 41 published studies containing 114 independent C-R abundance estimates. Where studies estimated abundance multiple times with the same dataset (e.g., using different model estimators), we have selected only 1 abundance estimate for inclusion in the scatter plot. Data are from the following studies listed in Table 1: references 1–7, 9–22, 24, 26–30, 32–36, 38–41, and 43–47.

with the photographic capture rates (e.g., Paviolo et al. 2008), or by increasing trap effort (trap density and sampling duration; see Wegge et al. 2004).

Low capture probabilities make it difficult to select an appropriate estimator. Many published C-R abundance estimates based on camera-trap data are derived from the M_h jackknife closed-population estimator (Burnham and Overton 1978), which assumes heterogeneous capture probabilities of individuals. Heterogeneous capture probabilities are expected because of a combination of biological and sampling biases such as sex, social status, age, and trap location, so the M_h jackknife estimator is often selected a priori. It tends to be more robust than other model estimators, but if nearly all individuals are captured, it may overestimate abundance (Chao and Huggins 2005); this situation is unlikely given the low capture probability of many target species reported in the literature.

The M_h jackknife estimator will underestimate abundance at capture probabilities less than approximately 0.05 (White et al. 1982). Of the 47 studies reviewed in this study (Table 1), the estimated capture probability (\hat{p}) was reported for 88 of 125 abundance estimates (32 studies). Across the 32 studies, the mean \hat{p} used for abundance estimation was 0.17 (SD = 0.16), ranging from 0.02 to 0.79. For the subset of studies focusing on large cats, mean \hat{p} was 0.13 (SD = 0.09, $n = 56$ datasets), ranging from 0.02 to 0.42.

Simulations have shown that high levels of heterogeneity (extreme variation between individuals in capture probability) in small populations ($N = 50$) can reduce the reliability of the M_h jack-knife abundance estimate (Harmsen et al. 2010a). Highly heterogeneous capture probabilities may occur because of a range of biological and sampling biases. In addition, if the study population is not geographically closed, some individuals may be captured only once because they are transient individuals rather than residents, and it may not be possible to identify them as such. Inclusion of transients decreases capture probability and inflates estimates of density (e.g., Larrucea et al. 2007). Few published studies report on levels of observable heterogeneity; of the 47 studies reviewed here (Table 1), 20 provided some information but only 11 presented sufficient data, in the form of capture histories or capture frequencies, for the reader to assess levels of heterogeneity. We recommend that studies using the M_h jackknife estimator present the capture histories or a frequency distribution of captures, especially if the sample size is small.

Heterogeneous capture probability is also a problem for mark-resight studies. Traditionally these methods assumed equal capture (sighting) probability between the marked and unmarked sample (see Krebs 1999). The (Z)PNE incorporates heterogeneous sighting probability, but still assumes independent and identically distributed sighting probabilities for the marked and unmarked individuals (McClintock et al. 2009, McClintock and White 2010). This assumption is valid if the marked animals are a random sample from the population. Studies which employ an initial live capture and tagging phase prior to camera-trapping should therefore strive to capture a random sample of individuals. This

may be difficult to ensure if using baits or lures, or for species in which 1 sex is more likely to enter a live trap. Similarly, in studies that do not livetrapping, researchers must use a natural marker that is randomly distributed throughout the population. Some natural markers may not be appropriate if they are associated with a certain sex, social status or a particular behavioral trait, for example, scars and wounds may be more common on aggressive or dominant individuals who may also have a greater sightability than other individuals.

Camera traps sample continuously, therefore researchers divide the data into discrete trapping occasions for C-R analysis, usually 24-hr periods. This can lead to the so-called midnight problem (Jordan et al. 2011) in which an individual photographed a few minutes either side of the cut-off time (e.g., midnight) will be counted as 2 encounters, whereas the same individual photographed twice during the middle of the day would be counted as a single encounter. Individuals that are most active around the arbitrary cut-off time will have a positively biased capture probability compared to individuals that are more active at other times of the day. Mark-resight estimators that sample with replacement do not have this problem. For C-R analysis, solutions may include extending the occasion length or enforcing a criterion such that repeat captures are only classed as separate encounters if the captures are temporally spaced by up to 1 occasion length.

For low density, wide-ranging species, defining the occasion length as 24 hr often results in zero-heavy capture histories. Some studies define occasion length as >24 hr (e.g., Kawanishi and Sunquist 2004, Heilbrun et al. 2006, Dillon and Kelly 2007, Kelly et al. 2008). Extending the occasion length (e.g., pooling 7 consecutive 24-hr periods into a single week-long occasion) may eliminate more zeros than ones from the capture histories, and increase the probability of capture on any given occasion. Pooling occasions will reduce the number of captures, potentially making it more difficult to select an appropriate model. If the number of captures is low during a survey, some researchers choose to extend the sampling period in order to obtain sufficient captures for analysis, for example, several studies sampled for 6–14 months (Karanth 1995, Kawanishi and Sunquist 2004, Haines et al. 2006, Simcharoen et al. 2007, Mazzolli 2010). Depending on the target species, surveying for such extended periods may violate the assumption of demographic closure. Testing for demographic closure may not be powerful with small sample sizes (e.g., Kawanishi and Sunquist 2004), and closure tests may not distinguish between a behavioral response and an open population (e.g., Soisalo and Cavalcanti 2006). In the absence of suitable closure tests, a survey period of 2–3 months has been suggested as appropriate for big cats (Karanth and Nichols 1998, Silver et al. 2004).

CAMERA LOCATION AND SPACING

On the large-scale, cameras should be distributed according to model assumptions; whereas at the local-scale their locations are usually chosen to maximize capture probability (Carbone et al. 2001). Regular arrays of traps, which maximize the ratio of study area to its perimeter, are preferable for

conventional C-R methods using ad hoc density estimation. Increasing the surface area to perimeter ratio will reduce the edge effect caused by the overlap of home ranges of the study animals outside the study area. However, given a large survey area, camera distribution will often be a compromise between optimal study design and practical constraints.

Trap spacing and location choice are both important. Dillon and Kelly (2007) recommend that camera spacing should seek to maximize capture probability by including at least 2 traps per average home range. Traps which are spaced too widely may fail to detect individuals if they occupy home ranges that fall between trap locations, breaking the assumption of conventional C-R models that the probability of capture of every individual is greater than zero. Thus, a balance should be found between maximizing survey area (e.g., Maffei and Noss 2008) and optimizing trap spacing (e.g., Dillon and Kelly 2007). The extent to which gaps influence the reliability of density estimates is likely to depend on the spatial features of the survey grid and the ranging behavior of the target species. Wegge et al. (2004) sub-sampled survey data to determine the influence of reduced trap density on estimates of tiger abundance. They found that increasing the trap spacing above 1 km underestimated tiger abundance.

Failure of camera traps results in variable trap effort, and is equivalent to temporary gaps in the survey design. Trap failure has many causes (e.g., theft, vandalism, climatic conditions, animal damage, loss of power, etc.; Foster 2008). We therefore assume that it is common, yet levels of camera-trap failure are rarely reported in published studies. Simulations by Foster (2008) to assess the robustness of the M_h jackknife estimator to trap failure showed that trap failure could result in underestimation or overestimation of the abundance. Unless variation in trap effort is incorporated as a covariate, studies using conventional C-R models should report the level of trap failure during the survey period.

Subtle changes in the choice of trap location can have significant impact on the capture probability of the target species (e.g., Harmsen 2006). Several studies have detected differences in capture rate associated with certain habitat features at the point location of the camera trap, in particular, variation in capture rate with road and trail characteristics such as width, age, and substrate (e.g., Maffei et al. 2004, Di Bitetti et al. 2006, Dillon and Kelly 2007, Harmsen et al. 2010b, Foster et al. 2010). To improve precision of abundance estimates, researchers frequently select trap locations which will optimize capture probability. Selecting camera location to optimize capture probability may result in non-random, biased placement. Therefore care should be taken when extrapolating the resultant density estimates to larger areas where habitat may be of lesser quality (see the Study Area Section).

Sampling will be biased if the camera locations are only optimal for a subset of the sampled population. For example, Larrucea et al. (2007) documented spatial variation in capture probability of coyotes dependent on their social status and age; also, male biases in capture probability are often observed in studies of big cats (e.g., Silver et al. 2004) and

may be partially attributed to researchers preferentially placing cameras on trails systems which are dominated by males (e.g., Foster et al. 2010). Conducting a survey in which the capture probability of a subset of the population is very low (even if it is not zero) is not advisable because extreme heterogeneity of capture probability between individuals decreases the reliability of the abundance estimate (e.g., Harmsen et al. 2010a). Sampling biases arising from spatial variation in capture probability could be minimized by stratifying the study area and randomizing camera location within each stratum. This approach may not be logistically possible in some environments, and may be impractical for strata in which camera traps are inefficient, for example, sampling off-trail for forest-dwelling big cats. If sample sizes are large enough, 1 option may be to model capture probability as a function of the habitat at the camera location, and age, sex, or social status (if these characteristics can be observed).

Camera traps record any animal that passes, not just the target species, giving rise to huge datasets. Within the camera-trap literature there is a temptation to use the same survey to estimate the abundance of multiple species within the study area. For example, surveys designed to study wide-ranging species such as jaguars have been used to estimate densities of tapirs, giant armadillos, and small cat species (Noss et al. 2003, Maffei et al. 2004, Noss and Rumiz, 2004). Using the same database is cost efficient and can reveal interactions between sympatric species (e.g., Harmsen et al. 2009, Foster et al. 2010). However, using the same survey design for multiple species may produce imprecise density estimates because the optimal trap location, spacing, and minimum survey area for 1 species may not be optimal for another species. Also, it may be inappropriate to compare photographic capture rates between species within the same survey as measure of relative abundance, particularly in trail-based surveys (Harmsen et al. 2010b). Inter-specific variation in capture rate may reflect a difference in abundance or detection probability between the species (or a combination of both). Density estimates of similar species from the same survey may be valid if sufficient information is known about their ranging behaviors and if the survey is designed with this in mind; for example, a survey originally designed to study jaguars (Maffei et al. 2004) has been used to estimate puma density (Kelly et al. 2008) assuming similar ranging behavior in both species.

STUDY AREA

The study of wide-ranging species requires camera traps spaced over a large area but is often constrained by the costs and logistics of camera trapping. Various studies have reported that small survey areas give inflated density estimates (e.g., Cuellar et al. 2006, Jackson et al. 2006, Dillon and Kelly 2007, Foster 2008, Maffei and Noss 2008). This positive bias may arise because:

1. Individuals move farther than the maximum distance between traps. Consequently, the proxies for home range diameter derived from the camera data underestimate the true home range and the effective trapping area.

2. Individual ranges may overlap in relatively small areas despite maintaining exclusive ranges elsewhere, particularly if traps are located near a favored resource; for example, the high densities reported for jaguars in the Belizean forest (Silver et al. 2004, Harmsen 2006) may be an artifact of preferentially locating traps along logging roads favored by jaguars as easy travel routes through the dense forest. Extrapolating this density to areas without logging roads may be unreliable. Arguments in favor of sampling on roads to maximize capture probability (e.g., pumas, Negrões et al. 2010) must be balanced against how the resulting density estimates are extrapolated to the surrounding area.
3. Small survey areas may fail to sample all available habitat types. For example, Jackson et al. (2006) reported snow leopard density estimates decreased by half in a subsequent year when they increased the study area and sampled more habitat types.

Changing the size of a study area between repeated surveys is not a problem as long as it remains large enough for unbiased estimates. If the size of the study area is changed from 1 survey to the next and is consistently too small, then the degree of bias in the estimates will vary with survey size. In this case, unbiased inferences about population trends are not possible. Some published studies do not recognize the positive bias of a small survey area on their density estimates (e.g., Trolle et al. 2007). Maffei et al. (2004) extrapolated jaguar densities from 3 study sites (49–130 km²) to the entire Bolivian Gran Chaco, an area of 34,400 km², and concluded that the Chaco supports a viable jaguar population. Soisalo and Cavalcanti (2006) demonstrated the consequences of extrapolation, showing that overestimation of the jaguar density by 5 individuals per 100 km² would overestimate the population by 7,000 individuals across the entire Pantanal (140,000 km²).

For wide-ranging species, it is perhaps misleading to survey an area <100 km² and then report densities per 100 km², and yet this is frequently seen in the literature (e.g., Karanth 1995, Noss et al. 2003, Cuellar et al. 2006, Ríos-Uzeda et al. 2007, Arispe et al. 2008). Small area correction factors are sometimes used to correct for inflated density estimates from insufficient survey areas. Correction factors require knowledge of the home range size of the study animals, and make assumptions about their shape and distribution (Krebs 1999). Correction factors are therefore difficult to justify and validate, especially if extrapolating to other species (e.g., Kelly et al. 2008, Mazzolli 2010).

Simulations by Bondrup-Nielsen (1983) suggest that edge effects are minimized if the study area is at least 16 times the average home range size of the target species. This would be impractical for wide-ranging species such as jaguars, potentially requiring survey areas in excess of 2,000 km². Maffei and Noss (2008) discuss the appropriate minimum survey area relative to the home range of the target species, using empirical camera-trap and telemetry data of ocelots (their study and Dillon 2005), tapirs (Noss et al. 2003), and jaguars (Soisalo and Cavalcanti 2006). If home ranges are known for the site, they recommend that the survey area should cover at

least 4 times the average home range. Many studies do not have the funds to combine telemetry with camera trapping and estimated home range size may not be known for the target species at the study site. In this case, Maffei and Noss (2008) recommend surveying the largest area possible and sub-sampling the data to evaluate the threshold area above which the density estimate stabilizes. Large-scale camera-trap studies are expensive and can be logistically difficult to maintain. However, a few such studies could be used to guide camera-trap studies of the same species in similar environmental conditions elsewhere.

If cameras are limited, survey areas can be maximized by moving cameras within the sampling period and combining data from the sampled sub-areas (e.g., Karanth and Nichols 1998, O'Brien et al. 2003, Trolle and Kéry 2005, Di Bitetti et al. 2006, Soisalo and Cavalcanti 2006). Most of these studies sequentially sample adjacent trapping grids which are then combined, ignoring spatial and temporal variation such that the first day of each sampling block forms the same trapping occasion (e.g., Soisalo and Cavalcanti 2006). This will potentially induce individual and temporal heterogeneity within and across sampling occasions, depending on the size and configuration of home ranges relative to the block design. This technique should be validated with simulations or sub-samples of large empirical datasets. Di Bitetti et al. (2006) used an alternative approach in which the entire area was surveyed throughout the sampling period with traps at half density. The traps were shifted to new locations within the same area half-way through the sampling period. Compared to the adjacent block method, this method maybe considered superior since it reduces the confounding effect of space and time. In any case, it is important to clearly describe the study design so that it is repeatable.

If resources are limited, using single-camera stations instead of double-camera stations is an option to increase the survey area. Camera-trap studies using natural identifiers such as pelt pattern usually deploy 2 cameras at each station to photograph both flanks of the target species for definitive individual identification. Using only one camera per station effectively doubles the area that can be surveyed but increases the risk of trap failure and variable trap effort. Because left and right flanks cannot be identified as the same or different individuals, the analysis must be limited to 1 side only. Although it decreases the capture probability, this method has been used for density estimation (Karanth 1995, O'Brien et al. 2003). Digital cameras with rapid fire or video capability can take multiple photos with a single camera during a single capture event. Some researchers use lures or baits in front of the camera traps to increase detection probability of target species (e.g., Gimán et al. 2007, Watts et al. 2008, Thorn et al. 2009). Lures or baits may aid individual identification by increasing the chance of photographing both flanks with a single digital camera while the individual investigates the lure. However, lures and baits may also increase the individual, behavioral, and temporal heterogeneity in capture probability if individuals are differentially attracted or repelled by lures or exhibit different levels of habituation through time.

EFFECTIVE TRAPPING AREA

Unless the sampled population is truly geographically closed, individuals at the edge of the study area will live partially outside the study area. If the study area is small compared to the average home range, the effective trapping (or sampling) area (ETA) exceeds the study area and density calculated from the area bounded by the outer most traps will overestimate the true density. To estimate density in a geographically open population, the home range of the species should be negligible compared to the study area (White et al. 1982). This is impossible for most wide-ranging species. A few studies have defined the study area as the area bounded by a minimum convex polygon of the traps or the boundary of a park or reserve (e.g., tigers, Carbone et al. 2001; jaguars, Cullen et al. 2005; bobcat, Heilbrun et al. 2006). Using reserve area as the study area is only acceptable if the members of the population do not move beyond the park boundaries. Traditionally a buffer of width W is added to the study area, representing the additional area used by the captured individuals outside of the trapping grid. Merging a circular buffer (radius W) around each camera location gives a more realistic estimate of ETA than would be achieved by simply adding a buffer strip to the outer perimeter of the minimum convex polygon formed by the trapping grid (see Balme et al. 2009). The buffer radius (W) is based on movement data of the study animals; for example, Dice (1938) proposed using half the diameter of the animal's home range. If telemetry data are available from the target population, W may be based on the average home range size. In the rare situation that telemetry data are collected simultaneously with camera-trap data, it is possible to estimate the proportion of each animal on the trapping grid and correct the estimate accordingly (Ivan 2011). In the absence of telemetry data, various ad hoc approaches are used based on the distances between captures; for example, half of the maximum distance moved between captures averaged over all individuals ($0.5 \times$ mean maximum distance moved [MMDM]; Wilson and Anderson 1985), half of the asymptotic trap-revealed range length (Jett and Nichols 1987), or the absolute maximum distance moved (Kawanishi and Sunquist 2004). Wilson and Anderson (1985) showed that using $0.5 \times$ MMDM to estimate the ETA produced density estimates that were less positively biased than those based on the study area alone. However, because W is a function of the specific trap spacing, it is truncated at the edge of the study area (Wilson and Anderson 1985, Efford 2004) thus the ETA will be underestimated and the density overestimated (Efford et al. 2005). Although a buffer width of $0.5 \times$ MMDM performed well in simulation studies, Wilson and Anderson's (1985) simulations were based on densities of 25 individuals/ha and 100 individuals/ha (total populations of 100 and 400 animals, respectively), which far exceed the natural densities of species commonly targeted by camera-trap studies. Even so, camera-trap studies have almost universally adopted the use of $W = 0.5 \times$ MMDM of individuals captured at multiple camera stations, following the Karanth and Nichols' (1998) protocol.

Differences in home range radius between the sexes can lead to heterogeneous capture probabilities; the wider ranging sex has a greater probability of being detected. Thus, estimates of W derived from the trapping data will be biased towards the sex with the greater capture probability. For such species, it may be appropriate to estimate density separately for males and females, if samples sizes are adequate (e.g., Foster 2008). This allows a more appropriate ETA to be applied to the abundance estimate of each sex for samples in which 1 sex dominates the estimate of W , and removes extreme heterogeneity in capture probability thereby increasing the precision of the abundance estimate. Wallace et al. (2003) used the most conservative estimate of jaguar home range available in the literature (female: 10 km²) to estimate ETA for both sexes, an approach that will most likely overestimate the true jaguar density.

Derivation of W from trapping data requires the recapture of multiple individuals at multiple locations. Some studies have used as few as 2 individuals to calculate W because of the inability to capture >2 individuals at multiple stations (e.g., Trolle and Kéry 2003, Cuellar et al. 2006, Lynam et al. 2009). Accurate quantification of the ETA is unlikely from such small samples; and failure to capture the multiple individuals at multiple locations indicates that the stations are spaced too widely or are in sub-optimal locations.

Maffei and Noss (2008) emphasized that validation of MMDM as a proxy for home range diameter requires simultaneous telemetry and camera trapping. Several studies have validated MMDM in this manner with differing results. Home range diameter derived from camera traps and from telemetry agreed in a study of jaguars in Costa Rica (Salom-Pérez et al. 2007) and tapirs in Bolivia (Noss et al. 2003); however, camera-trap data underestimated home range diameter for jaguars in the Pantanal (Soisalo and Cavalcanti 2006), and ocelots in Belize (Dillon 2005) and in Bolivia if sample areas were small (Maffei and Noss 2008). This variation should be of no surprise. The relationship between a proxy of home range derived from camera-trap data will be a function of the spatial configuration of the traps in the particular study and the ranging behavior of the individuals sampled. Furthermore, measuring home range size from telemetry data may be as variable as the camera-trap data, depending on the method used, the season, and the sex of the study animal. Therefore, the suggestion that estimates of MMDM can be calibrated using telemetry and extrapolated to other studies (Soisalo and Cavalcanti 2006) needs further investigation.

Trolle and Kéry (2005) suggested the use of the MMDM over $0.5 \times$ MMDM for ad hoc density estimation from camera-trap data. This has no theoretical basis and seems to be driven by the similarity between MMDM (rather than $0.5 \times$ MMDM) and the home range radius derived from telemetry data at single sites (e.g., Soisalo and Cavalcanti 2006, Dillon and Kelly 2008). For lack of a suitable estimate of home range radius, researchers often report densities based on $0.5 \times$ MMDM and MMDM, as well as a number of other home range statistics derived from trap data or, when available, telemetry from the study area or elsewhere

(e.g., Johnson et al. 2006, Soisalo and Cavalcanti 2006, Ríos-Uzeda et al. 2007, Paviolo et al. 2008, Balme et al. 2009). In some studies, the density estimates may more than double and even triple, with buffers of width $0.5 \times$ MMDM versus MMDM (e.g., Trolle et al. 2007, Di Bitetti et al. 2008, Paviolo et al. 2009). A halving of density with doubling of the buffer width indicates that the buffer comprises a significant proportion of the ETA. It is almost entirely a theoretical construct with a comparatively small study area.

Parmenter et al. (2003) evaluated the use of $W = 0.5 \times$ MMDM versus MMDM in the density estimation of enclosed rodent populations of known size. Although they found that MMDM performed better than $0.5 \times$ MMDM, they cautioned against its use for density estimation in small mammal live-trapping studies because of the many theoretical assumptions required, most of which also apply to camera-trap studies of large mammals. Instead, they recommended the use of ranging data from telemetry for accurate estimation of W . Similar recommendations have been made by researchers who have combined telemetry and camera-trapping to estimate density; for example, Balme et al. (2009) tested the accuracy of different methods against a known population of leopards, and found that telemetry was most appropriate for defining the ETA.

The method used to estimate W and the ETA can profoundly influence the density estimate (e.g., Soisalo and Cavalcanti 2006, Balme et al. 2009), indicating that these conventional ad hoc methods for estimating density and ETA are not robust. The present trend to report multiple estimates based on a range of different values of W does not solve the problem of whether or how we can accurately estimate the ETA from camera-trap data. Maffei and Noss' (2008) suggestion to survey larger areas with camera traps, and then sub-sample the data to identify the threshold at which MMDM and density stabilize is valid, but rarely practical for the study of wide-ranging species.

The calculation of the ETA through the addition of a buffer derived from the trapping grid data is clearly not optimal for density estimation, particularly for studies with low sample size and a small study area relative to the home range of the target species, as is common in camera-trap studies of large, wide-ranging carnivores. Use of this method for such species should be supported by an evaluation of its precision and accuracy using simulated datasets. Spatially explicit capture–recapture methods (SECR), which are based on a spatial model of the detection (capture) process (e.g., Efford 2004, Borchers and Efford 2008, Royle et al. 2009b), show promise as they do not require the intermediate step of estimating the ETA, and formally link the encounter location to the home range (Royle and Gardner 2011). Ivan (2011) compared the relative performance of MMDM and SECR methods using simulations. He found that SECR performed better under most of the test conditions, although MMDM performed better when home ranges were highly asymmetric or elongated.

SPATIALLY EXPLICIT CAPTURE–RECAPTURE MODELS

Spatially explicit capture–recapture models combine information about the capture locations of individuals with their capture probability at point locations, to estimate density (Efford 2004; Borchers and Efford 2008; Efford et al. 2009a, b; Royle et al. 2009a, b). This is in contrast to conventional C-R or mark-resight methods, which estimate abundance, and do not assume that capture probability depends on trap location. The various SECR methods combine a state model (the distribution of activity centers of individuals) and an observation model (the spatial detection function) to estimate density using inverse prediction, maximum likelihood, or Bayesian methods (e.g., Efford 2004, Borchers and Efford 2008, Royle et al. 2009a).

The assumptions of SECR models vary between models, depending on the approach used and the incorporation of covariates, but in general it is assumed that 1) the population is demographically closed (although an open-population SECR model has recently been developed; Gardner et al. 2010), 2) individuals have independent activity centers (although under- or overdispersion can be modeled with spatial covariates), 3) the locations of the activity centers are fixed during the survey period, 4) the probability of detection of an individual at a camera trap declines with distance of its activity center from the trap (described by 1 of a choice of several functions (e.g., half-normal, exponential, hazard-rate), and 5) each capture is an independent event.

The core models account for variation in capture probability arising from the distribution of individuals relative to the traps (i.e., the number and locations of traps within each animal's home range), with or without the inclusion of spatial covariates such as habitat (Efford et al. 2009a, Royle et al. 2009b). Other sources of individual heterogeneity may be incorporated via mixture models (Borchers and Efford 2008); however, modeling variation in capture probability due to intrinsic factors (e.g., sex, social status, age) will be constrained by sample size (e.g., Royle et al. 2009b) and the ability to define and select appropriate covariates. The movement or removal of traps between occasions, and the death of known individuals, can also be incorporated into the models (e.g., Borchers and Efford 2008). This will be particularly useful for surveys which have suffered trap failure, have to move traps during the survey period to sample a sufficiently large area, or suffer human-induced mortality of the target species during the survey period, such as the illegal hunting of big cats outside protected areas (e.g., Foster 2008).

The assumption of independent activity centers is perhaps not realistic for territorial carnivores, often the focal species of camera-trap studies. Territorial carnivores do not occupy independent home ranges but may be attracted to mates (overdispersion) or avoid competitors (underdispersion; e.g., Sunquist and Sunquist 2002). Nor do they necessarily have a single activity center; for example, they may exploit 1 area of their range intensively before moving on to the next patch (e.g., Rabinowitz and Nottingham 1986) or they may

patrol borders intensively (e.g., Smith et al. 1989). Although current SECR theory requires that activity centers are randomly (independently) distributed, the theory of Borchers and Efford (2008) allows the density of these activity centers to vary across the landscape (i.e., as an inhomogeneous Poisson process) according to covariates. This can sometimes adequately model a dependent distribution, although we may expect it to be more robust to overdispersion (clustering, attraction between animals) than underdispersion (avoidance, territoriality). Software that implements spatially varying density is under development (D. Borchers, Centre for Research into Ecological and Environmental Modeling, personal communication). Also, the 'secr' package in R (secr: R Version 2.0.0, <http://cran.r-project.org>, accessed 20 Jan 2011) includes a variety of detection functions, among them an annular normal detection function that accommodates animals more likely to be captured far from their activity center than near it (Efford 2010). These models should be tested with empirical data or simulations that reflect the complicated dynamics of territorial carnivores; in particular, how robust the models are to under- or overdispersion.

Density may not be the end goal of camera-trap studies. In some situations, an abundance estimate may be preferred (e.g., for monitoring population trends in a given area). Density estimators from SECR methods allow for this; abundance within any portion of the study area can be obtained by integration, whether density is constant or varies across the landscape. If an estimate of the number of individuals using the grid is required, researchers can count how many individual location surfaces overlap with the defined area.

The estimation of the density of activity centers within the study area using SECR models requires multiple camera-trap locations within an average home range area of an individual. Traditionally C-R studies space cameras as a single station within a single (smallest) home range unit (e.g., Silver et al. 2004), and the resulting sample sizes and capture probabilities are often low. Efford et al. (2009a) recommend at least 20 recaptures for a precise estimate. Thus, SECR models do not remove the problems associated with the analysis of, and inference from, sparse datasets. This can only be achieved through sufficient resources and logistical support being made available to sample sufficient locations over a large enough area.

As the development of SECR models is relatively recent, the current literature focuses more on the mathematical formulations and less on the limitations of the models when applied to field data, or the robustness to assumption violation. As with C-R and mark-resight methods, it is important that field biologists understand the assumptions and limitations before applying SECR models to their data. Too often, the limitations of ad hoc density estimation have been ignored because of the logistical constraints of running large-scale camera surveys. In order for field biologists to make good use of these emerging SECR models, they need to know the requirements for reliable estimation: 1) the minimum sampling effort (i.e., the number of camera sta-

tions per average home range); 2) the camera density required to adequately sample an individual at a range of distances from its theoretical activity center; and 3) the minimum sample size (number of individuals) and (re)capture probability. Such information will help field biologists in the design of their studies and hopefully prevent situations in which models are fitted to poor quality data, as has been observed in the application of conventional C-R models to camera-trap data. Simulation studies, such as that by Ivan (2011), should be conducted to further investigate the effects of study design on the performance of SECR estimators before implementing large-scale field studies.

MANAGEMENT IMPLICATIONS

For studies that estimate population density from camera-trap data using conventional C-R models, we urge reviewers to demand greater transparency of the study design and quality of the data. Of the 47 studies reviewed here (Table 1), only 8 described the sampling design sufficiently by reporting all of the following: size of study area; number of stations; spacing between stations or station density; sampling period; sampling design (e.g., use of spatial or temporal blocks); method of estimating effective trapping area (e.g., size of buffer width); size of effective trapping area; and objective method of identifying individuals. Authors should clearly report on the camera density and spacing and, if used, the design of spatio-temporal blocks. They should also report on the trap effort, the level of trap failure, and whether this failure was accounted for in the population model. They should clearly state the survey period, and occasion length used for analysis. The results should include the number of individuals, number of recaptures, sex ratio (if possible), and degree of heterogeneity by indicating how many individuals had 1, 2, 3 ... n captures. Ideally, the capture histories and trap locations would be presented, although we appreciate that researchers may prefer not to publish raw data in the public domain. They should list the assumptions of the models that were fitted to the data, or refer to a source that states these assumptions, and indicate whether these assumptions were violated, and if so, the likely consequences for the interpretation of the resulting density estimate. In addition, for species that lack natural unique markings, authors using C-R in preference to mark-resight methods should indicate how many captures were unidentifiable and report the levels of inter-observer variation, agreement and disagreement. The use of SECR models with camera-trap data is still in its infancy, but we recommend a similar level of transparency in reporting. For studies using ad hoc density estimation; for example, those that do not have sufficient sample size for SECR analysis, we recommend using telemetry data of the target species to inform about the effective trapping area.

We urge field biologists to plan their camera surveys carefully in order to collect data of high quality that are suitable for analysis. Logistical difficulties and/or lack of sufficient resources are not valid excuses for fitting inappropriate models to inadequate datasets. We encourage field biologists to carefully review the range of available estimators when

designing their camera surveys so they can consider the assumptions and limitations. It is clear that large study areas are required to sufficiently sample populations of wide-ranging and/or low density species. If this is the goal, then adequate resources and support should be sourced before embarking on the study. Funding bodies should appreciate that these studies are necessarily large-scale to ensure that they achieve the goal of reliable density estimation. As camera traps become smaller, more reliable, and cheaper, it will become more feasible to run larger surveys within reasonable budgets.

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