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Estimating the abundance of rare and elusive carnivores from photographic-sampling data when the population size is very small

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Abstract Conservation and management agencies require accurate and precise estimates of abundance when considering the status of a species and the need for directed actions. Due to the proliferation of remote sampling cameras, there has been an increase in capture–recapture studies that estimate the abundance of rare and/or elusive species using closed capture–recapture estimators (C–R). However, data from these studies often do not meet necessary statistical assumptions. Common attributes of these data are (1) infrequent detections, (2) a small number of individuals detected, (3) long survey durations, and (4) variability in detection among individuals. We believe there is a need for guidance when analyzing this type of sparse data. We highlight statistical limitations of closed C–R estimators when data are sparse and suggest an alternative approach over the conventional use of the Jackknife estimator. Our approach aims to maximize the probability individuals are detected at least once over the entire sampling period, thus making the modeling of variability in the detection process irrelevant, estimating abundance accurately and precisely. We use simulations to demonstrate when using the unconditional-likelihood M_0 (constant detection probability) closed C–R estimator with profile-likelihood confidence intervals provides reliable results even when detection varies by individual. If each individual in the population is detected on average of at least 2.5 times, abundance estimates are accurate and precise. When studies sample the same species at multiple areas or at the same area over time, we suggest sharing detection information across datasets to increase precision when estimating abundance. The approach suggested here should be useful for monitoring small populations of species that are difficult to detect.

Keywords Camera traps · Capture–recapture · Heterogeneous detection · Small population

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Introduction

Management and conservation of wildlife requires reliable information on the population status of species. Knowledge of abundance is critical to assessing species status and essential for ecological research (e.g., predator–prey dynamics, species-habitat relationships). A common approach for estimating abundance is to collect data on detections of uniquely marked individuals that are (re)captured over two or more sampling occasions (t; usually days or weeks). Then closed capture–recapture (C–R) estimators (Borchers et al. 2002) can be fit to the data to estimate (1) the probability of detecting an individual on a given occasion ($\hat{p}$) and (2) abundance ($\hat{N}$).

The recent proliferation of remote sampling cameras (camera-traps) has led to a rapid increase of C–R studies estimating the abundance of medium to large carnivores (O'Connell et al. 2010; Foster and Harmsen 2012). Data common to these studies are often of low information quantity in that few unique individuals are detected (M_{t+1}) and then only a small number of times. Sparse data can generally be recognized when the capture-history has many zeroes. Characteristics of carnivore photographic C–R data were summarized in Harmsen et al. (2011) and Foster and Harmsen (2012). These data are typified by (1) infrequent detections [$\bar{\hat{p}} = 0.17$, SD($\hat{p}$) = 0.16, range($\hat{p}$) = 0.02−0.79], (2) a small number of individuals detected [$\bar{M}_{t+1} = 12.6$, SD(M_{t+1}) = 10.4, range(M_{t+1}) = 2−65] due to naturally low densities, (3) long survey durations (19–65 occasions), and (4) variability in detection among individuals (heterogeneity). Closed C–R estimators were developed to estimate abundance when animal populations are too large for a complete census or when individuals are difficult to detect. Total sampling duration is assumed to occur over a small snapshot in time, for example ≤10 days. As such, statistical assumptions of C–R estimators have not often been considered in the literature when sampling occasions are spread over long periods of time, which may be appropriate for long-lived species (Karanth and Nichols 2002). It was further assumed that a reasonably large number of individuals could be detected and that many, but not all individuals would be detected several times (White et al. 1982). Thus, the characteristics of common photographic-sampling data on rare carnivores do not match well with the type of data abundance estimation has previously considered.

We believe there is a need for guidance when estimating the abundance of low density, long-lived species, where heterogeneity is expected and sampling effort is protracted. These conditions limit the utility of traditional C–R estimators but these limitations are not clear in the literature. Clarification is especially important because carnivore C–R studies often target rare, poorly studied, and/or threatened species (Jackson et al. 2006; Gerber et al. 2012). To ensure appropriate conservation actions are implemented, estimating abundance precisely and accurately is critical. The uncertainty common to estimates from carnivore C–R data (Foster and Harmsen 2012) may mask the true and possibly critical status of a population, thus delaying conservation actions. For large carnivores where the population size is naturally low, an imprecise abundance estimate is especially problematic, as the uncertainty of only a few individuals is a significant proportion of the population.

Our objectives are four-fold. First, we discuss statistical limitations relevant to estimating abundance with closed C–R estimators when detection probability per occasion is

low and heterogeneous, sampling duration is long, and few individuals are detected but they are likely to be a large proportion of the total population (these elements are collectively referred to below as 'rare carnivore C–R data'). We also comment on appropriate measures of precision. Second, we suggest that when a population size is naturally small (e.g., <20 animals), p is small, and t is long enough such that most individuals in the population are detected, using C–R data in a confirmatory census framework is more appropriate than traditional modeling of the detection process to estimate abundance. This is in contrast to the usual approach of using the Jackknife estimator, which is inappropriate with sparse data (Burnham and Overton 1978; Harmsen et al. 2011; B. D. Gerber, unpublished data). We provide combinations of p and t useful in planning a C–R study to census a population. We then describe minimum frequencies of individual detections that will lead to informative estimates and confirm a complete or near-complete census for a small population size using an unconditional-likelihood closed C–R estimator with constant detection probability (referred as M_0 from here on; White et al. 1982). Third, using Monte Carlo simulations we demonstrate the reliability of estimating abundance with the M_0 and quantifying uncertainty with profile-likelihood confidence intervals (PLCI; Venzon and Moolgavkar 1988) when detection is heterogeneous. Fourth, we discuss sharing information on p to estimate abundance at multiple sampling areas or at the same area across different sampling sessions. We emphasize that the suggestions detailed below should only be applied to the specific type of data we describe above.

Statistical limitations

For statistical estimation of any parameter, ideal estimators are unbiased, precise, and produce nominal confidence interval coverage at the $(1 − \alpha)$ level (α = probability of a Type I error). Most commonly used C–R estimators of abundance rely on likelihood theory to estimate parameters. As such, they meet the characteristics of an ideal estimator, but under asymptotic properties of consistency, normality, and efficiency, which are generally not applicable when sample size is small. Thus, commonly used estimators are not guaranteed to 'do the right thing' given typical carnivore photographic-sampling data. White et al. (1982) make this point clear for C–R studies with a small number of sampling occasions, "… if $N < 100$ and $p < 0.3$, a good capture–recapture study probably cannot be done."

Precision and confidence interval coverage are especially problematic for sparse data. Log-based confidence intervals are most often used for abundance estimates as

they can be formulated to ensure that the lower bound is $\geq M_{t+1}$. However, log-based confidence intervals are known to perform poorly (i.e., they do not include the true parameter value as intended) with sparse data due to a poorly estimated variance–covariance matrix and bias in maximum-likelihood estimates (MLE; Hudson 1971; Donaldson and Schnabel 1987). An additional problem occurs when protracted sampling leads to a large proportion of the population being detected, even though per occasion p may be low. This situation constrains the lower bound of the abundance estimation to be $\geq M_{t+1}$ (except for conditional-likelihood estimators that derive $\hat{N}$ Huggins 1991), which in turn violates a condition required for large-sample likelihood inference to perform well: that the true parameter value is not on or near a boundary (e.g., it is not near 0 or 1, or in this case M_{t+1} and is therefore "unconstrained" of the parameter space). Under such constraints, estimates of the variance–covariance matrix are often poor (i.e., estimates of sampling variance may be 0 or exceedingly large). The boundary issue is compounded when sample size is small; a circumstance that often leads to "flat" likelihoods (as opposed to highly "peaked" likelihoods with large sample size) which makes it difficult to find a maximum and increases the chance that the MLE(s) are on or near a boundary.

Aside from boundary issues, sampling a large portion of the population can result in non-existent diagonal elements of the Fisher information matrix which can lead to poor estimates of sampling variation or preclude estimates entirely. For the special case where $M_{t+1} = \hat{N}$, the second-partial derivatives of the likelihood evaluated at the MLE(s) are guaranteed to not exist due to lack of curvature in the likelihood and thus there will be no standard estimate of $\text{Var}(\hat{N})$. Finally, when a large portion of the population is detected, the estimated number of animals that were never detected (f_0) goes to zero. This is problematic when using log-normal confidence intervals to characterize uncertainty, as is the standard practice in Programs CAPTURE (Rexstad and Burnham 1991) and MARK (White and Burnham 1999) because f_0 appears in the denominator of the confidence interval calculation. Thus, precise estimation of N using asymptotic theory, when most of the population is detected, or when sample size is small, is either not possible or is unlikely to be at the $(1 - \alpha)$ level using common interval estimators.

Characteristics of typical carnivore C–R data also make it difficult to address the ubiquitous issue of heterogeneous detection. Heterogeneity is often regarded as the most dominant form of variation in p for a variety of reasons, including effects of the sampling layout and its relationship to animal movement, natural variability among age classes or between sexes, and intrinsic-individual variation that may be

unmeasurable (Noyce et al. 2001; Harmsen et al. 2011; Royle et al. 2013). Failing to account for existing heterogeneity when many individuals in the population are not detected can result in negatively biased estimates of abundance, but adequately accounting for heterogeneity is difficult. With large samples, one can make use of conditional-likelihood closed models (Huggins 1991) and incorporate individual covariates (e.g., sex) to model heterogeneity. Alternatively, one could use mixture models that assume animals belong to 2 or more arbitrary groups having distinct capture probabilities (Pledger 2000). However, due to low information quantity in sparse data, very few parameters may be estimable, thus estimating multiple detection parameters to account for heterogeneity is often unrealistic. Despite the low quality of data, many carnivore C–R studies follow recommendations of foundational carnivore photographic-sampling work (Karanth and Nichols 1998, 2002) and estimate abundance using the Jackknife estimator (Foster and Harmsen 2012). However, the Jackknife estimator also relies on asymptotic and regularity conditions that are not met with small sample size and such estimates, especially those of precision should not be considered reliable (B. D. Gerber, unpublished data). Furthermore, when most of the population is detected, which may often be the case, as noted above, the Jackknife estimator is known to overestimate abundance (Chao and Huggins 2005). For endangered species, this may be of a larger detriment than underestimation.

Recommendations

Design studies to be complete or near-complete censuses

Due to the limitations associated with estimating abundance using rare carnivore C–R data, we suggest it is more appropriate to refocus the design of such studies to detect all (or almost all) individuals in the population and provide confidence of such. By doing so, we can reduce the number of relevant parameters that need to be estimated to achieve an accurate and precise abundance estimate. Given the long duration of many carnivore C–R sampling, even low p can result in detection of most animals in the population, albeit with each animal likely observed a small number of times relative to the total number of occasions. For example, if $p = 0.10$ and sampling occurs for 30 occasions (e.g., 30 days) the probability of detecting an individual at least once over the total sampling period would be $p^* = 1 - (1 - 0.10)^{30} = 0.958$. As such, when t gets large, even when p is very low, M_{t+1} converges to N and p^* can be interpreted as the fraction of the population seen over the entire sampling period. While sampling a large portion of

Fig. 1 Combinations of detection probability (*p*) and sampling occasions (*t*), where ≥95 % of the true population is detected (*black cells*) or not (*grey cells*)
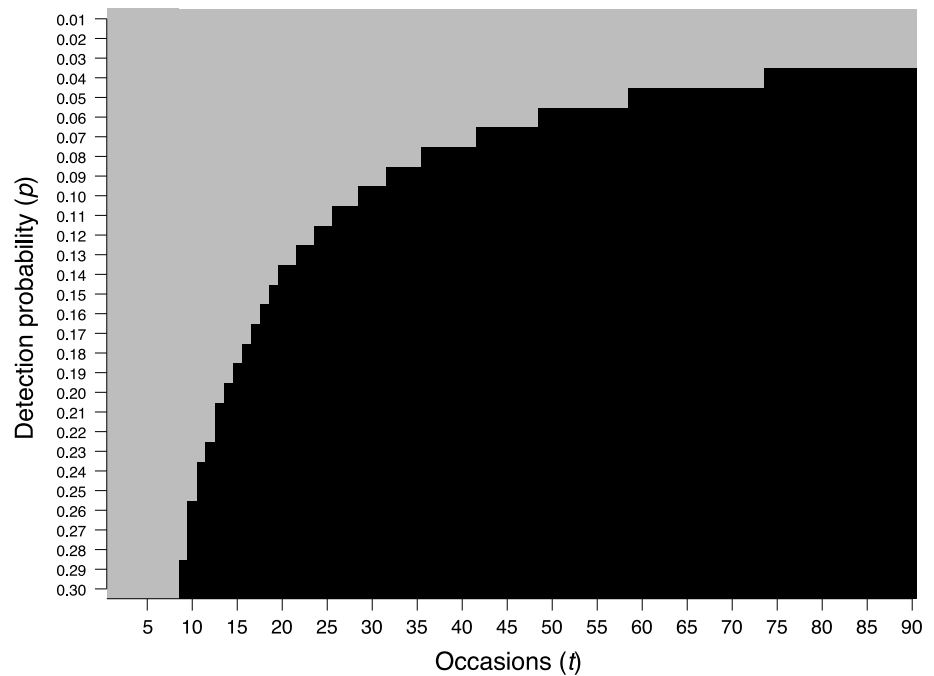
the population causes estimation issues as described above, the need for estimation is secondary for rare carnivore C–R data as most individuals will be detected given a long enough sample period.

Toward this end, we computed *p** for plausible combinations of low detection probability (*p* = 0.01 − 0.30) and protracted sampling (*t* = 1–90; Fig. 1) and identify combinations that result in a near-census (*p** ≥ 0.95), similar to White et al. (1982). Given anticipated values for *p,* researchers can assess the number of sampling occasions required for a census. For example, if *p* = 0.05, 60 occasions would be required to achieve a near-complete census. If pilot data are available and indicate heterogeneity in detection, then we recommend the use of the lowest possible or observed $\hat{p}$ in order to provide a conservative estimate of *t* required to obtain a near census. Note that when *p** is close to one, there is little room for variation in detection due to heterogeneity, time, or other factors and such modeling of this variation becomes irrelevant in estimating abundance (see simulation below). Although heterogeneity is expected in many carnivore C–R datasets, it should not be assumed that a statistical estimator that incorporates heterogeneity is inherently the most appropriate when the data are sparse. Below we demonstrate when a simpler model that estimates fewer parameters than any heterogeneity model will perform well with sparse data.

Sample to attain minimum capture frequencies that will lead to informative estimates

By 'thinking like an estimator' we can consider how many individual detections (capture frequencies) are required to

obtain reliable estimates of abundance. Using simulation we explored the relationship between capture frequencies and precision as a means for practitioners to discern when a study can be considered a near-census. Specifically, we started with an initial scenario of *t* = 20, *N* = 10, 9 animals were detected once each, and 1 individual was never detected. For subsequent simulations we added detections such that for the second scenario 1 individual was caught twice, others were caught once, and 1 individual was never detected. For the third scenario 2 individuals were captured twice, etc. We incremented the scenarios sequentially until all animals were detected three times each except for the 1 individual that was never detected. We estimated abundance for each of these nineteen scenarios by fitting M_0 and computing PLCI's. We recommend profile-likelihood confidence intervals as they have several advantages over log-based confidence intervals, which are most often used. First, PLCI do not rely on the assumption of asymptotic normality and usually provide estimates close to nominal levels even when sample size is small or estimation is on or near a boundary (Bates and Watts 1980). Even in the special case where $M_{t+1} = \hat{N}$, PLCI will still provide meaningful confidence bounds. Second, PLCI guarantee the lower bound will be greater than or equal to M_{t+1}. Lastly, profiling the likelihood to estimate confidence intervals directly uses the information in the data regarding the parameter estimate(s) and is based on a relatively robust distributional assumption of the asymptotic χ^2 distribution (Venzon and Moolgavkar 1988).

When each individual is only caught once, the point estimate was unreliable and the upper confidence interval
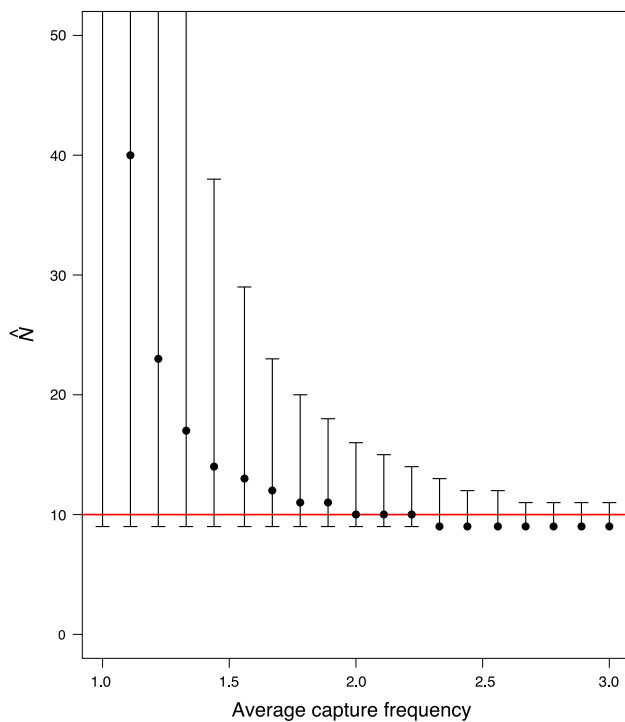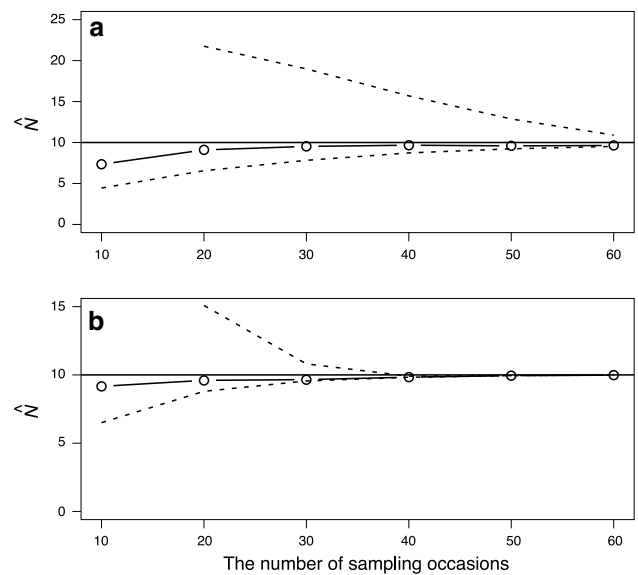
Fig. 2 Abundance estimates where nine individuals are detected a varying number of times using the M_0 (constant detection probability) unconditional-likelihood capture–recapture estimator and 95 % profile likelihood confidence intervals. The true population size is 10. The upper confidence interval is excessively large when the average capture frequency is <1.4 and is not presented

Fig. 3 Expected abundance estimate ($\hat{N}$) and 95 % profile likelihood confidence intervals from the M_0 (constant detection probability) unconditional-likelihood capture–recapture estimator with simulated heterogeneous capture–recapture data where the mean detection probability was **a** $\mu = 0.05$ or **b** 0.1 and $\sigma = 0.1$ over sampling occasions of 10–60. The upper confidence limit was often infinite when the sampling occasions were 10 and thus is not presented

was positive infinity. However, when most individuals in the population were captured two or more times, the point estimate was very close to N and the upper confidence interval was reasonable (Fig. 2). An average capture frequency of 2.5 or more resulted in a near-complete census. While we used $t = 20$ for this simulation, the number of sampling occasions is irrelevant to the general patterns in our results. If detection probability is low, more than 20 sampling occasions will be necessary to ensure most individuals are detected two or more times; however, the accuracy and precision will be similar to the patterns observed here.

Estimating abundance with heterogeneous detections

To investigate the reliability of using M_0 and associated 95 % PLCI under commonly observed heterogeneity in detection, we simulated poorly informative data as presented in the Electronic Supplementary Material (ESM). For all simulations, true population size (N) was 10 and $t = 10, 20, 30, 40, 50,$ and 60 occasions. We considered a generic form of heterogeneity where p_i is a logit-normal distribution for the ith individual using the combinations of $\mu = 0.05, 0.1$ and $\sigma = 0.1$ (Fig. S1 in ESM). Heterogeneity could be due to any number of reasons, such as the spatial arrangement of the

trapping layout. Our specific choice of variability (σ) in detection was chosen to functionally capture p's often observed in carnivore studies (Harmsen et al. 2011). For each individual i we randomly drew a single p_i from the specified distribution. We then created a t-occasion capture history for individual i by inserting a '1' or '0' for each occasion according to a Bernoulli process with probability p_i. For each combination of N and t, we simulated 1000 iterations and investigated empirical distributions, bias, and precision of $\hat{N}$.

We found that the bias was minimal for both $\mu = 0.05$ and $\mu = 0.1$ when $t \geq 20$ (Fig. 3; empirical distributions are presented in Fig. S2 in ESM). However, precision was relatively poor until $t \geq 30$ for $\mu = 0.1$ or $t \geq 50$ for $\mu = 0.05$. The upper 95 % PLCI was often infinite at $t = 10$ for both detection distributions. In general, when expected p^* was >0.6, this approach estimated abundance accurately and with reasonable precision. In other words, despite considerable heterogeneity in detection, this simple model estimated abundance well. The failure rate in estimating abundance for both scenarios was ≤ 5 % after $t = 30$ (Fig. S3 in ESM). Models that require estimation of additional parameters over M_0 will have worse precision, due to the limited information in the data.

Sharing information on p to estimate N

Sample sizes in many carnivore C–R studies are simply not large enough to use closed C–R estimators as they were

intended, modeling p to estimate N. This sentiment is stated plainly by White et al. (1982), "experiments in which M_{t+1} is on the order of 10 or 20 animals simply do not provide enough information for any procedure to perform well". However, in many studies, the target species is sampled at more than one area or across multiple sessions at the same area. While information regarding the detection process may be sparse with one dataset, information can be shared across datasets when estimating abundance for each area (White 2005). This can be accomplished by specifying an appropriate linear model for detection, as is possible in several software packages (e.g., Program MARK). Care must be taken to sample each area similarly such that sharing information about detection is reasonable. An information-theoretic approach (Burnham and Anderson 2002) can be used to evaluate whether sharing information is supported by the data. One simulation found this to be a useful approach when a population at a single sampling area was small ($N = 20$; Conn et al. 2006). When sample sizes of combined datasets are >20 individuals and sharing detection information is considered reasonable a priori, modeling the detection process in a shared framework is appropriate. This approach has the potential to allow for added model complexity to explain realistic variation in detection, better identify appropriate models through model selection, and likely produce more reliable abundance estimates (Boulanger et al. 2002; Bowden et al. 2003; White 2005). In other words, sharing information may release an analysis from the bounds of poor data and allow additional parameters to be estimated. Although, when most animals are detected, sharing information may not be particularly useful, as point estimates will be similar, regardless of variation in detection.

Discussion

We emphasize again that the approach described here should only be considered for the unique data typical of photographic-sampling: (1) infrequent detections, (2) a small number of individuals detected, (3) long survey durations, and (4) variability in detection among individuals. With better data, more sophisticated approaches are warranted. Given the type of data described here, the goal of carnivore C–R studies of low density populations should be to make modeling the detection process irrelevant by maximizing $p*$ and detecting all or almost all of the population. Even with heterogeneous detection among individuals, as long as $p* \geq 0.6$, the M_0 estimator with PLCIs can be used to accurately estimate abundance and quantify uncertainty. When a species is sampled multiple times at an area or at multiple areas using the same methodology, we encourage researchers to combine these data and determine whether information about the detection process can be shared.

M_0 and PLCIs can be computed by many software programs, including Program MARK (White and Burnham 1999), Program DENSITY (Efford et al. 2004), or through the R programming language in packages RMark (Laake 2013) and secr (Efford 2011). Since PLCI's require parameters are in a likelihood framework, they cannot be used with conditional-likelihood models or with the Jack-knife estimator.

We recommend that C–R studies of very small populations consider capture frequencies as sampling proceeds and provide such frequencies in publications, so readers can (1) examine how often individuals are detected and qualitatively assess the likelihood of a census, (2) determine how reliable estimates are likely to be, and (3) consider the degree of heterogeneity and whether it is important in the estimation of abundance. This will allow reviewers to examine when a heterogeneity model may or may not be useful.

Results shown here suggest that detecting most of the population two or three times will provide minimal expected bias and acceptable levels of precision that will be useful to conservation and management agencies. A common suggestion in photographic-sampling studies to achieve appropriate frequencies of detection is to ensure multiple camera sites are within each potential home range of individuals within the study area (Karanth and Nichols 2002). However, this may be impractical due to restrictions on the number of cameras available. An alternative design is to move cameras during sampling to maximize the chance of placing multiple cameras within each individual's home range, thereby increasing an individual's probability of being detected at least once. A goal of every study should be to ensure no individual in the population has a zero probability of detection; one way to do this is to move cameras. When animals have zero probability of detection due to the sampling technique or layout, estimating their numbers is equivalent to asking the question, how many invisible animals are there? There is of course no statistical solution to mitigate this bias.

To maximize $p*$ and reduce potential bias of "invisible" individuals by moving cameras, one could use a block design where a grid of cameras placed close together is moved jointly to survey a larger area in total (Karanth and Nichols 2002). Alternatively, each camera site could be independently moved within the survey area after a given criterion is met. For example, when a camera site detects individuals at least twice within a given time frame (e.g., one month), it would be advantageous to move the site in an attempt to increase the detection of others not observed yet. After detecting the same individual three times, there is little benefit in further detections. Lastly, if photographs

cannot be reviewed and individuals identified within the sampling period, camera sites could be deployed throughout the study area for a set time period (e.g., one month) and then all simultaneously redeployed within the same area for the same amount of time.

In this paper, we have assumed that the closure assumption of C–R models is met, such that there are no geographic or demographic changes in the population during sampling. While we have demonstrated the usefulness of protracted sampling to maximize p^*, which makes modeling detection irrelevant and thus helps overcome the issues of small sample size to estimate abundance accurately and precisely, we do not encourage researchers to do so at the cost of violating this assumption. Because carnivores are typically long-lived (relative to the study period) it has been common to assume populations are closed to permanent demographic changes over a period of a month or even more (Karanth and Nichols 2002). However, a consequence of a long sampling duration is that highly mobile animals may temporarily move on and off of the study area. Minor temporary emigration (e.g., absence from the study area on only a few occasions) over a long sampling duration may be inconsequential (although it does depress p and induce heterogeneity). However, considerable movement in and out of the study area will introduce bias to estimating abundance and/or necessitate a redefinition of the population inference to the super population of animals that could have used the area over the course of sampling (Kendall 1999).

Recently, much focus has been on the use of spatially-explicit C–R models to estimate animal density and/or abundance (Efford and Fewster 2013; Royle et al. 2013). However, to do so requires estimation of more parameters (i.e., a spatial component), which generally requires better data than considered here and an additional set of assumptions (Efford and Fewster 2013; Ivan et al. 2013). Given the estimation challenges we've noted here with sparse data, estimating additional parameters to obtain density estimates is seemingly unrealistic without ancillary information (e.g., more data or prior information). We suggest that if the goal is to monitor a small population in a relatively well defined area in which N is expected to be less than 20 individuals and p is expected to be ≤ 0.1, a confirmatory census approach as outlined here may be reasonable. It's interesting to note that simulations using spatially-explicit models found that when the population size is much larger than considered in this paper, the M_0 model performs well (low bias and high precision) when the detection process is assumed to follow a strict circular bivariate Gaussian kernel and even when the sampling occurs over patchy habitat, as long as the suitable habitat of the target animal is appropriately covered (Efford and Fewster 2013). In these simulations, the Jackknife estimator was found to be unreliable.

Throughout we have focused on carnivore photographic-sampling studies, but our suggestions pertain more generally when the population is very small and most individuals in the population are detected. For instance, when the sampling methodology is highly efficient, such as when scat dogs are used to collect DNA (Wasser et al. 2004) most of the individuals may be detected and p^* may be near one. Also, estimating species richness may result in sample sizes on the order of those discussed here (Walther and Morand 1998).

Lastly, researchers should always keep ecology in mind when estimating abundance. C–R estimators and the mathematics that underlie them are ignorant of biology—that piece will always be the responsibility of the investigator.

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