

# Avoiding misleading messages: Population assessment using camera trapping is not a simple task

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Handling Editor: Jean-Michel Gaillard

## KEYWORD

*Alces alces*, Brownian, camera traps, home range, moose, population estimate, simulation

## 1 | INTRODUCTION

Researchers have striven for many decades to find better and better methods to estimate the size, or the density, of natural populations, and the development of camera traps (CT) has stimulated the research of new methods for population assessment (see Keuling et al., 2018 for a recent review). In a recent paper in the *Journal of Animal Ecology*, using CT to assess the size of natural populations, Campos-Candela et al. (2018), hereafter CC, claimed that 'the absolute density is given by the average number of animals counted per frame'. Ideally, the method proposed by CC is perfect for wildlife managers: easy to use and cheap. CC developed their approach according to a theoretical framework where animals are assumed to behave as particles of an 'ideal gas' (Hutchinson & Waser, 2007). Since such an assumption appears difficult to be respected or even reasonably approached in actual animals, CC correctly verified that such a result remains valid also when the animals behave in more realistic ways, specifically when they exhibit home range (HR) behaviour. Considering the potential relevance of this work to wildlife conservation and management, we have carefully read the paper and noted several problems in the method used to simulate the home ranges and CT detections.

In section 1, we show that the model of CC is unable to properly account for the actual behaviour of animals. Accordingly, we propose a different method of simulation which circumvents the problems found in CC's model. However, our main interest in this forum paper is not to discuss the best methods to be used to simulate home ranges but to verify whether the proposed method for population estimation can be reliable in practice. Taking the moose (*Alces alces*) (one of

the archetypes used by CC) as an example, in section 2 we replicate their numerical experiments using a more realistic set-up and rejected their conclusion that "the results....of the model demonstrate that density can be precisely and accurately estimated after an emphasized sampling effort" (our emphases). On the contrary, we found that the proposed method, albeit being asymptotically correct, does not provide appropriate density estimates under realistic survey designs (survey duration, number of cameras and their radius of detection, Rovero, Zimmermann, Berzi, & Meek, 2013).

Information about population size is necessary to improve our understanding of fundamental ecological processes such as density dependence, functional response, dispersal, epidemiology and so forth. For rare and endangered populations, correct information about their size is indispensable to estimate the extinction risk and may help to allocate the (usually scarce) resources for conservation where they are most needed. On the other hand, for invasive species, one needs to know whether eradication/control programmes have been successful, while for game species, the knowledge of population size can be useful to develop sustainable harvest programmes.

Estimation methods based on capture-mark-recapture (CMR) have been largely used and present many different ramifications including non-invasive genetics (Rodgers & Janečka, 2013) and removal methods (St. Clair, Dunton, & Giudice, 2013). Managers usually do not use CMR methods because animals have to be individually identified. This approach is, however, used routinely when animals are naturally recognizable, for example tigers or whales (Karanth & Nichols, 2017). Distance sampling, where detectability

is estimated by the distance of the animal from a reference point or transect, has been widely used to assess the population size of marine and terrestrial organisms (Buckland, et al., 2004). Since CT are cheap and easy to use, recently several methods have been proposed to estimate the population size of unmarked individuals such as Random Encounter Model (REM; Rowcliffe, Field, Turvey, & Carbone, 2008), point transects (Howe, Buckland, Després-Einspinner, & Kühl, 2017), REST model (Nakashima, Fukasawa, & Samejima, 2018), N-mixture models (Keever et al., 2017) and SECR models (Chandler and Royle, 2013). Available methods assume that the population to be assessed is demographically closed. In practice, this means to perform a snapshot survey, very short in relation to the demography of the species of interest so that deaths, births, immigration and emigration can be overlooked. For instance, for a large terrestrial mammal, it is reasonable that a survey can last, at most, 30 days in periods when the species is known to be not dispersing, migrating or reproducing, and mortality is low.

When evaluating the simulation results, it is fundamental to consider the coefficient of variation in the estimates, to understand the capacity of the method to perform trend detection (Gerrodette, 1987); accordingly, Skalski, Ryding, and Millsbaugh (2010) suggested that a coefficient of variation <0.2 (20%) is appropriate for sound management.

The main reason for this paper is that we believe that given the fundamental importance of population assessment in research and applications, scientists have to avoid statements which may cause an erroneous use of the statistical methodology and, as a consequence, to determine negative impacts on wildlife conservation and management.

## 2 | WEAK POINTS IN CC MODEL

Our criticism to the methodology used by CC in the simulations can be summarized in four points:

1. The derivation of the species-dependent parameters, at the base of their model is incorrect;
2. The rescaling of the detection radius has no reason and is highly misleading;
3. The time step used is too large to yield correct results;
4. For some of the archetypes proposed by CC, their model is inappropriate to the biology of the species.

The equation at the base of the CC model:

$$\frac{d\mathbf{X}}{dt} = -k(\mathbf{X} - \mathbf{X}_c) + \mathbf{R}, \quad (1)$$

describes the evolution of the position  $\mathbf{X}$  of a Brownian particle subjected to a noise  $\mathbf{R}$  in a quadratic potential, for example subjected to a restoring force such as a particle attached to a spring, where  $k$  represents the elastic constant and  $\mathbf{X}_c$  is the centre of the HR. The noise  $\mathbf{R}$

is Gaussian (white noise) with zero mean, zero covariance between the two dimensions (i.e. spatial coordinates) and the same variance ( $\epsilon\sqrt{\Delta t}$ ) in each spatial dimension. The HR radius depends on the two parameters of model 1,  $k$  and  $\epsilon$ , as:

$$\text{radius}_{\text{HR}} = C_1 \sqrt{\frac{\epsilon}{k}}, \quad (2)$$

where the constant  $C_1$  depends on how the HR radius is defined. To get sensible simulations for the species of interest (in our case the moose), we need to estimate  $k$  and  $\epsilon$  from actual data.

For estimating two parameters, we need two equations. One is given by the home range radius (which is usually known). For the second equation, CC used the animal velocity which can be estimated from GPS data. CC used the following equation:

$$\langle |V| \rangle = \frac{\sqrt{\epsilon(1 - e^{-2k\Delta t})}/k}{\Delta t}, \quad (3)$$

where  $\langle |V| \rangle$  is the velocity magnitude, and  $\Delta t$  is the time step. This is the critically wrong passage in CC, since in model 1 it is not possible to define a mean absolute velocity of the particle since the displacement scales as  $\sqrt{\Delta t}$  and in performing the limit:

$$v = \lim_{\Delta t \rightarrow 0} \frac{dx}{dt} \propto \lim_{\Delta t \rightarrow 0} \frac{\sqrt{\Delta t}}{\Delta t} = \infty. \quad (4)$$

For the moose, CC used a HR of 82 km<sup>2</sup> by McCauley et al. (2015) and the mean speed of 0.033 m/s from Vander Vennen et al. (2016), which is based on 1 hr fix sampling. As shown in Equation 3, the mean speed depends on  $\Delta t$ ,  $k$  and  $\epsilon$ , and to solve this equation, CC were obliged to fix arbitrarily the relation  $\Delta t = 0.1/k$ . Unfortunately, this approach yields a  $\Delta t$  of 10 hr, quite different from the actual time used for fix sampling by Vander Vennen et al. (2016). However, as seen in Equation 3, the movement model (Brownian motion) used by CC implies that the speed is dependent on  $\Delta t$ . If we compute back the speed at 1-hr intervals using the value found for 10 hr, we find that the animals move at the speed of 0.112 m/s instead of the true velocity of 0.033 m/s, almost four times faster, which is clearly wrong. In the case of moose, for which we have made the computation, this implies that the simulations of CC reduce very much the CV of the population estimates, simply because a larger number of animals walk through the cross section of the CT field since the animals move too fast. Note also that at least three of the other archetypes (*Camptostoma anomalum*, *Testudo graeca*, *Brachyramphus marmoratus*) are subjected to a similar error, while *Chaetodon baronessa* cannot be evaluated due to lack of data.

According to CC, the 'Invariant settings were preferred to facilitate the archetype comparisons. Accordingly, the radius of the circular area within which any animal is detected (camera radius) was defined in a way that, on average,  $m$  animals per frame are counted'. This approach makes any comparison with actual CT experiments impossible since only this length scale is rescaled and not all the other parameters, such as the distance between cameras or the HR size. For a detailed discussion of the topic, see Section S3 in

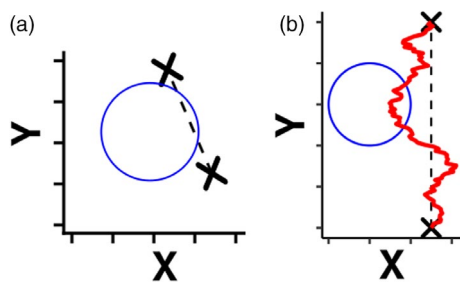
Supporting Information. In particular in the case of the moose, the camera detection radius was set to 630 m by CC; therefore, the huge HR radius of the moose is almost nine times the camera detection radius which is completely absurd. Told in another way, such a detection area needs an equivalent of 4,900 'true' CT with a detection radius of 9 m to be sampled.

CC is not mentioning explicitly the type of camera used (motion-triggered or time-lapse); however, from the discussion (p. 833), it appears that CC's method can be applied also to motion-triggered cameras, which are the most frequently used CT (Rovero et al., 2013). For motion-triggered cameras, the value of  $\Delta t \sim 10$  hr used by CC is probably too high to avoid round-off errors in the detection of the animals as sketched in Figure 1. Since in 10 hr, the average displacement is about 1.26 km, an animal can very easily cross the detection area without being recorded in the simulation, as shown in Figure 1a. Another source of error is represented by the tortuosity of the Brownian motion between two fixes as shown in Figure 1b. Indeed, it is possible that an animal whose fixes are outside the detection area may have crossed the detection area during the 10-hr interval. These errors can considerably reduce the efficiency of the CT-simulated survey, and one needs a very long survey duration to get reasonably high precision even with 10 cameras with 630 m detection radius as done by CC. We note also that this part of the description of the method of CC is quite unclear. This criticism is not applicable in case of the use of time-lapse CT. Usually, wildlife managers use motion-triggered cameras because this method is more informative than time-lapse sampling. However, there are monitoring methods that require time-lapse methods (Moeller et al., 2018).

Finally, for one of the archetypes used by CC, *Diomedea calonectris*, the motion of birds at large scales is not Brownian-like diffusive as supposed by CC model, but on the contrary Lévy-like super-diffusive (Abolaffio, Reynolds, Cecere, Paiva, & Focardi, 2018, and references therein).

### 3 | SIMULATION MODEL AND RESULTS

We propose a model where the equation of the velocity is the sum of three terms. The first one tends to bring the velocity of the animal



**FIGURE 1** We show the path followed by an animal in relation to the detection area (blue). Cross indicates the fix used by CC to determine whether the animal is detected by the CT. (a) The animal has crossed the detection area but it remained undetected. (b) Via linear interpolation, the animal has not crossed the detection area (broken line), but the actual path can have crossed it (red line)

close to the characteristic speed of the species  $V_a$ , the second one is an acceleration towards the centre of the HR and the third component is a random noise. The velocity yields the displacement  $\mathbf{X}$  of the animals:

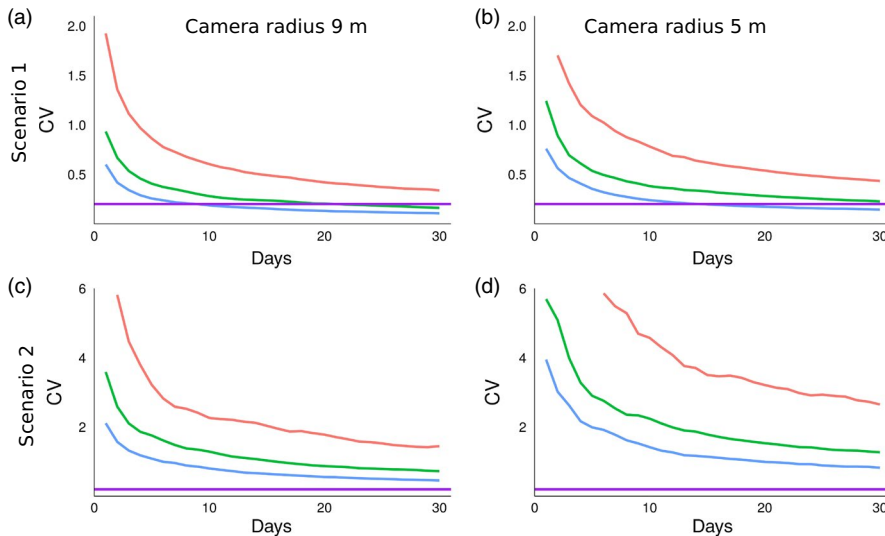
$$\mathbf{V}(t + \Delta t) = \mathbf{V}(t) \frac{V_a + (V(t) - V_a)e^{-\Delta t/\tau}}{V(t)} - K(\mathbf{X} - \mathbf{X}_c)\Delta t + \mathbf{R}, \quad (5)$$

$$\mathbf{X}(t + \Delta t) = \mathbf{X}(t) + \mathbf{V}(t)\Delta t, \quad (6)$$

where  $V(t)$  is the velocity magnitude of the animal at time  $t$  and  $\tau$  is the time-scale of the fluctuation on the magnitude of the velocity. In our model, the velocity, not the displacement, tends to be oriented towards the centre; note that  $K$  has dimension  $1/t^2$  while  $k$  (Equation 1) has dimension  $1/t$ . An instance of a simulated trajectory is shown in Figure S3.

According to a large body of literature, for short times the direction of movement, that is the angular component of  $\mathbf{V}(t)$  has a persistence (correlated random walk, Turchin, 1998), while for long times the trajectory resembles the one of the model 1. While CC's model assumed a complete independence of movement direction from step to step, more realistically, we assume that, in the short term, directions are correlated, that is animals perform a correlated random walk. More detailed explanations are reported in Section S1.

We define an arena of  $10 \times 10$  km with periodic boundary conditions. Inside this arena, we set a squared grid of equidistant cameras, from a minimum of 16 to a maximum of 100 samplers (i.e.  $4 \times 4$  to  $10 \times 10$ ), as commonly done in these kinds of studies. Here, we report only the scenario with  $8 \times 8$  cameras but in the Section S2.2, we report also the other cases. We simulated three different animal densities: low,  $0.1$  animals/ $\text{km}^2$ , normal,  $0.4/\text{km}^2$  (the same value used by CC), and high,  $1/\text{km}^2$ . The coordinates of the HR range centre are randomly assigned. Animals move according to Equation 5 and are recorded by cameras when the camera-animal distance is lower than the detection radius (we used a 'usual' detection radius, 5 m, and an 'optimistic' radius of 9 m). We performed two sets of simulations. In the first scenario, simulated moose maintain a constant speed as assumed by CC. However, to assume that the speed is constant during the day is clearly wrong in moose (and in any other animal) as shown, for instance, by Van Ballenberghe and Miquelle (1990) where active displacements take a short part of the daytime while the remaining time is allocated to resting/rumination and grazing. Thus, in the second scenario, we simulated a moose population with two possible behavioural modes: active and resting (which also include grazing). According to Van Ballenberghe and Miquelle (1990) movements take about 7% of the activity budget. We also assumed that in resting mode there is no movement. In a third scenario, we assume a more realistic 3-mode activity patterns where we differentiate among no movement, grazing and moving, respectively, 62.7%, 30.4% and 6.9% of the activity budget. Since this set of simulations have yielded very similar results to the one of scenario 2, the results are presented in Section S2.3. To be consistent, the velocity of the moose in scenarios 2 and 3 is calculated in order to



**FIGURE 2** The coefficient of variation (CV) is reported as a function of the duration of the monitoring programme for three different values of animal density (0.1, 0.4 and 1 animal/km<sup>2</sup>, red, green and blue, respectively) and two different CT radius and patterns of animal movement. In (a) and (b), the animal moves with constant speed and, in (c) and (d), the animal exhibits two different speeds. In (a) and (c), the camera radius is set to 9 m, while in (c) and (d) to 5 m. The horizontal purple line represents the prescribed CV threshold set to 0.2 (i.e. 20%)

have the same mean overall velocity as in scenario 1, calculated as a weighted mean.

The statistical estimator proposed by CC yields asymptotically unbiased estimates of population size (Figure 2). In case of constant animal speed and large detection radius of CT (Figure 2a), the estimate attains the prescribed CV threshold in less than 30 days at least for large and intermediate populations, while, unsurprisingly, for the lowest density value, the precision is too low to be acceptable. On the contrary, if we simulate animals characterized by two different activity patterns, we observe a rapid decay of the precision of the statistical estimator (Figure 2b). Even for the highest density populations, the result remains quite unsatisfactory. Since we know a priori that there are important differences in speed within each individual animal, we may conclude, with some degree of generality, that the method proposed by CC cannot represent a practical method for estimating the population size of moose. As one could expect, when the detection radius is lowered to a more realistic value (5 m), the system generally fails to provide acceptable estimates. We have also performed one numerical experiment with more realistic activity patterns including resting/ruminating, foraging and moving, but the results remain qualitatively the same (Section S2.3). Of course, we should not exclude that there can be situations characterized by a set of parameter values (density, HR radius, etc.) where the estimator proposed by CC can work appropriately, but wildlife managers should test, by simulation, if the situation of interest can be precisely surveyed by this method.

## 4 | DISCUSSION

The simulation model of CC was affected by errors which could improve but also deteriorate the efficiency of the proposed estimator. Such concerns obliged us to develop a simple but more consistent model to describe the behaviour of the animals in order to correctly evaluate the efficiency of the estimator proposed by CC.

We showed that under ideal condition (cf. Figure 2a) the estimator is able to correctly evaluate the population size under reasonable study conditions (high/medium density, large camera detection radius). However, the introduction of more realistic constraints (e.g. two or more different activity modes) led to a strong deterioration in the performance of the estimator. In other words, the method is scarcely robust to variations in parameter values.

We have to stress that under natural conditions, where there is an intrinsic and uncontrolled variability, one needs statistical methods robust to limited violations of the assumptions and characterized by a reduced propagation of uncertainty. If a statistical estimator is very sensitive to the details of the movement patterns, or to random fluctuations in parameter values, the system becomes practically useless, or it may request a complicated modelling study which is usually outside the skills of wildlife managers. Hayward and Laupacis (1993) made it clear that statistical robustness is fundamental to develop appropriate wildlife monitoring programmes.

Note that we have assumed that our samplers detect all animal in areas of 78.5 and 254.5 m<sup>2</sup>. In the second case, the resulting cross section of our monitoring design is quite optimistic since, in the field, the area where a CT has a certain detection probability is no larger than 4 m<sup>2</sup> (with a dependence on several parameters such as body mass, movement speed, etc., Nakashima et al., 2018); further, the shape of the camera field of view (FOV) is not circular but roughly triangular. If we should have used more realistic values for the FOV, we would have obtained worse CV values than the ones we reported in Figure 2; however, we used very conservative values because we wished to show that discouraging results were independent of the camera detection area. A basic problem of naive methods used to estimate the population size via camera trapping is that one has to assume a certain probability of detection, an assumption which, to be respected, reduces a lot the area covered. Howe et al. (2017) showed experimentally that in CT the detection probability gets <1 at distance around 6–7 m (for *Philantomba maxwelli*, a small antelope) and wildlife managers should take very seriously this limitation of CT.

To evaluate monitoring methods, it is important to keep in mind what are the practical constraints encountered in the field, which is not the case when CC used, for moose, a detection radius of 630.8 m, which yields a covered area of 1.28 km<sup>2</sup>, a surface which needs almost 5,000 CT to be sampled. The problem here it is that CT can be used in practice whether their number is limited because a huge amount of manpower is necessary to review the videos/pictures and to install/remove the CT from the field. In agreement with CC, in Section S2.2 we showed that good results can be obtained using hundreds or thousands of cameras but such numbers are outside any practical possibility of use.

The technical evolution of more and more efficient camera traps has stimulated the development of new methods of population assessment which is of the greatest interests for ecological research, conservation and management. The different methods proposed in literature are all correct in mathematical–statistical sense, when their assumptions are respected. However, this analysis of CC methods showed that this condition it is necessary but not sufficient given the limitation in the sampling effort and the sensibility to the violation of the assumptions, violations which for sure are present during a field survey. Now, we miss a comparative analysis of the different proposed methods in order to indicate to wildlife managers and practitioners the best method and its precision that can be used in different field conditions. With this paper, we hope to stimulate deeper insights on the matter.

## ACKNOWLEDGEMENTS

We thank Dr. J. Borysow for the correction of the manuscript and two anonymous referees for their suggestions and criticisms which much improved the manuscript. We thank Valentina Bellini for the CT photo.

## AUTHORS' CONTRIBUTIONS

M.A. designed the paper and provided all the calculation and simulations with inputs by S.F. M.A. and S.F. wrote the paper, and all authors contributed to the revision of the manuscript.

## DATA AVAILABILITY STATEMENT

This manuscript does not use data.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Abolaffio M, Focardi S, Santini G. Avoiding misleading messages: Population assessment using camera trapping is not a simple task. *J Anim Ecol*. 2019;88:2011–2016. <https://doi.org/10.1111/1365-2656.13085>