

LETTER TO THE EDITOR

## Making the best of a hard job: A response to Nakashima (2022)

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Nakashima (2022) commented on our paper Santini et al. (2022) recently published in this journal about the critical assessment of existing methods to estimate the abundance of unmarked animals using camera traps. The Author of the letter, while acknowledging the general value of the paper, raised a series of interesting elements for further discussion, pointing out presumed weaknesses in our approach. Most of these points touch important aspects of the estimation process and we are grateful to Y. Nakashima for raising them. In general, although in principle we agree with Nakashima (2022) on most of the points, it appears that the criticisms he raised originate from a misunderstanding of the aim of the paper. In particular, we aimed at comparing camera trapping-based methods to estimate population density without individual recognition, by applying available procedures on comparable simulation exercises. It was not our aim to attempt any further improvement of these procedures, and we used them as they would likely be applied by practitioners.

The knowledge of population density and abundance of wildlife species are fundamental for effective management and conservation of animal populations, particularly now when new diseases favored by climate change are appearing on the scene. This need has stimulated the development of a number of methodologies for population assessment. The recent technological improvement of camera traps, their decreasing cost and ease of use has induced researchers to develop camera trap-based methods to estimate population density for species without obvious visual patterns allowing individual identification (cf. Santini et al., 2022 and Nakashima, 2022). Yet, wildlife managers are confronted with the difficult choice of what method to use in relation to the population to survey (e.g., a population of a presumably rare species) and the specific context of investigation (e.g., the number of available camera traps). To help managers in their choice, our work proposes a systematic comparison of four of such methods via simulations under identical conditions and known population density. The four methods compared in the paper were applied as proposed by their developers, without attempting any further improvement, i.e. as they would likely be applied by practitioners. In order to develop

a fair comparison among methods we developed two models for animal movement to support simulations: (i) a simple model where animals move at constant speed (Santini et al., 2022, Fig. 2) and (ii) a more realistic model where animals alternate different movement patterns (Santini et al., 2022, Fig. 3). We showed that all models perform pretty well in simplified situations (case (i)), whilst bias and reduced precision emerge when movement complexity is introduced (case (ii)).

Nakashima (2022) has rightly pointed out four main potential weaknesses relating to potential limitations and biases of estimation methods used. We here address them in the order of presentation.

The first criticism refers to the way we applied the TTE (Moeller et al., 2018), and in particular how we defined the sampling period. In our study, we decided to use “the time necessary to cross the field-of-view at the maximum distance during movement”. According to Nakashima (2022), “this definition underestimates the number of sampling periods required for detection and overestimates the density”, although specific evidence to support this claim is not provided, nor suggestions for alternative approaches. We chose to follow this procedure as it is in line with Moeller et al. (2018) and Moeller and Lukacs (2021) which defined the duration of the sampling period as the “time needed for an animal to move across the camera viewshed”. Indeed, we stressed that a thorough sensitivity analysis of the variation of population density estimates in dependence on the definition of the sampling period is needed when applying this method, and in general for camera trapping-based methods. In particular we underlined that it is necessary to clarify how the sampling period shall depend on the relationship between an animal movement rate, and the camera viewshed (“exact relationship between movement rate and camera size”, Moeller et al., 2018).

The second criticism raised is that “evaluators should discuss the results carefully, particularly when they obtain unexpected results”, suggesting that we should have not limited our study to checking the agreement/disagreement with expected values but analyze in detail “. . . which estimation processes were distorted” (Nakashima, 2022). We agree that

this suggestion represents an interesting avenue of research for future evaluations. However, as already stated, the aim of Santini et al. (2022) is to provide a comparison of the performance of the different methods applied *as they have been proposed*, i.e. as practitioners are likely to apply them, leaving the detailed examination of the flaws and possible improvements to further investigation as it would not fit in a synthetic piece of work.

The third criticism from Nakashima (2022) states that “it is more constructive to compare models under identical conditions”, referring in particular to auxiliary data (e.g. animal movement speed) being differently used across models (i.e. only for REM and TTE). Although this is true in principle, Nakashima (2022) seems to have overlooked that we used auxiliary data also for REST, specifically to estimate the proportion of activity. This method requires an estimate of the proportion of activity, which normally can be estimated from the data, e.g. following the method developed by Rowcliffe, Kays, Kranstauber, Carbone, & Jansen, 2014. However, in our paper, we adopted the exact value used to simulate the data set, and in fact we clearly stated that “The activity proportion was known without errors”.

Nakashima (2022) also points out that “(…) the high precision of TTE is largely attributable to the authors’ unrealistic assumption that animal detection follows a Poisson process (and thus the time to event follows an exponential distribution)”. In accordance with our overall goal, we followed Moeller et al. (2018) without attempting any improvement. However, we agree with Nakashima (2022) that the violation of such assumption would be critical. Indeed, we recommend a preliminary check of the distribution of the time to event and the sensitivity of the method to violations of this central assumption.

In the fourth and final criticism, Nakashima (2022) states “(…) the evaluator should estimate density and its uncertainty using the most appropriate procedure. The authors estimated density and the confidence intervals for REM and AM by bootstrapping, for REST by MCMC samples in a Bayesian framework, and for TTE by maximum likelihood estimation and the Fisher information matrix.” We are sorry that our explanation of the method used to compute confidence limits was not clear enough. Indeed, for empirical surveys, precision should be evaluated using methods as the ones described above. Since the comparison between methods was based on simulations with the same number of replicates, we considered the central density value for the estimates and the simulation replicates to compute confidence intervals, instead.

The main goal of our paper was to stimulate discussion on camera trapping-based methods to estimate animal population density, which, if applied uncritically, may lead to biased results, with detrimental consequences for the management and conservation of wildlife. The fact that a debate is arising therefore goes in the desired direction. Indeed, most of the criticisms raised in Nakashima (2022) point at

important limitations of some of the proposed estimation methods, opening a stimulating debate towards future developments. The robustness of methods to violations of assumptions is a key element for evaluating their performance and the reliability of the output they return. This is an aspect too often poorly considered both in the field approach and evaluation of papers. Beyond the relative performance of the methods under the set of conditions we tested, i.e. their basic form as described in the literature, it is important to underline that improvements are possible and desirable, as comparisons like the one performed in Santini et al. (2022) or critical comments in Nakashima (2022) help identify important directions of research.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Giacomo Santini\*

Dipartimento di Biologia, Università degli Studi di Firenze,  
50019 Sesto Fiorentino, Italy  
E-mail address: giacomo.santini@unifi.it (G. Santini).

Milo Abolaffio

ISC-CNR, Sesto Fiorentino 50019, Italy

Federico Ossi

C3A - Centro Agricoltura Alimenti Ambiente, Università  
degli Studi di Trento, Via Edmund Mach, 1, 38010 San  
Michele all'Adige, TN, Italy

Barbara Franzetti

*Istituto Superiore per la Protezione e la Ricerca Ambientale,  
Via Vitaliano Brancati 48, 00147 Roma, Italy*

Francesca Cagnacci

*Biodiversity and Molecular Ecology Department, Animal  
Ecology Unit, Research and Innovation Centre, Fondazione  
Edmund Mach, 38010 San Michele all'Adige, Italy*

Stefano Focardi

*ISC-CNR, Sesto Fiorentino 50019, Italy  
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