

Response to Abolaffio et al. (2019): Avoiding misleading messages

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1 | INTRODUCTION

Evaluating absolute population density is an extremely complex task that requires strengthening the links between theorists and empiricists. Both, Campos-Candela, Palmer, Balle, and Alós (2018) and Abolaffio, Forcadi, and Santini (2019), contributed to this challenge from the theoretical side; the first one by demonstrating a theoretical postulate to estimate absolute densities from camera counts; the second one by exploring the proposed method for a specific species (the moose, *Alces alces*). Note, however, that the undifferentiated use of *model*, *method* and *simulation* terms in Abolaffio et al. (2019), when addressing concerns exclusively about our simulation procedure or the applicability of the method for a particular case, may be misleading.

Concerning the camera-based *method*, our key contribution is that, for the case of animals whose movement leads to a stationary spatial pattern, absolute animal density can be properly estimated from the average number of animals counted per frame whenever a number of assumptions are met. The underlying *model* to this method states that, for a given camera, the number of animals' counts per frame is given by a Poisson distribution with mean equals to the product of the true animal density, the detection area of the camera and the probability of detection. Essentially, our model is equivalent to determine the distribution of the space occupation in time, which is a question that has been

largely discussed from the probabilistic perspective (Godrèche & Luck, 2001). The only strict condition for this *model* to apply is that animal density must be stationary within the scale of the sampled space and time. When focusing on moving animals, such a stationary property meets for animals displaying home range (HR) behaviour, which is a widespread movement type leading to the establishment of a bounded space-use area (Börger, Dalziel, & Fryxell, 2008; Burt, 1943). In these cases, the stationary condition should apply to the density of HR centres. The model was theoretically derived in Campos-Candela et al. (2018) but provided that it may be counter-intuitive, we also performed a number of *simulations* emulating a camera sampling program for demonstrating that animal density (i.e., number of HR centres per area unit) can be properly recovered by averaging the counts by frame.

In our extensive simulation analysis, a number of simplifications were stated (we refer the readership to the original work in Campos-Candela et al. (2018) for further details) because the objective was to demonstrate the generality of the model performance. Accordingly, our reported simulation results should be interpreted as a general guidance and not as species-specific recommendations. Likewise, the work by Abolaffio et al. (2019) should be considered an improved simulation exercise that takes into account several species specificities but, even so, it may still leave behind some other hidden particularities of the system. Therefore, even after improving simulations, a pilot study is required to properly evaluate the applicability of the

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method when confronted with the real cases of study and decide whether the use of cameras is feasible or may complement other methods (e.g., mark-and-recapture, animal tracking, environmental DNA).

We explicitly emphasized this point when claiming that '[...] notwithstanding the comprehensiveness of the method proposed here, a call of caution is necessary regarding the potential drawbacks [...]', for instance identifying technological limitations such as the feasible operational time. Therefore, [...], 'it is strongly recommended to complete a pilot study (i.e., case-specific simulation experiments), including both species specificities and case-related constraints (e.g., budget available or technological limitations of the cameras), to assess whether the optimal settings are fulfilling or not the objectives in terms of expected accuracy and precision'. In line with this recommendation, a nice example of such pilot study has been recently published by Follana-Berná et al. (2019), for the specific case of a coastal marine fish species using remote underwater video cameras when compared with other conventional methods for marine fauna. Additionally, they accounted for detection probabilities smaller than one (i.e., adapting our model to the cases in which assumption (i) in Campos-Candela et al., 2018 does not meet).

Accordingly, we did not recommend an uncritical, cursory use of the proposed method in Campos-Candela et al. (2018) by wildlife managers and practitioners. Instead, we proposed a specific protocol to evaluate the feasibility of our theoretical approach and its usefulness for any given case in the 'real world'. Therefore, the statement in Abolaffio et al. (2019): 'Ideally, the method proposed by CC is perfect for wildlife managers: easy to use and cheap' constitutes itself a deceiving message out of its original context. Their claim, quoted here: '[...] the proposed statistical method [...] is not recommended for the use by wildlife managers and practitioners', is exaggerated and misleading in itself. In fact, the improved simulation work developed in Abolaffio et al. (2019), which considers speed in a more mechanistic way and includes variability in the movement patterns, is framed in the explicit recommendations given in our previous work.

2 | COMMITMENT SOLUTIONS IN SIMULATION PROCEDURES: REPLYING TO CRITICISMS 1, 2 AND 3

In Campos-Candela et al. (2018), we selected a few (six) archetypes with the aim of covering a wide range of space-use strategies. In spite that the parameters selected for simulating the movement of each archetype were inspired in the values of HR size, animal density, movement speed and body mass for different species from the literature; they were not aimed to be species-specific. Instead, they were pretended to be general (i.e., archetypes), as the main purpose for simulations was to demonstrate that the proposed method is potentially useful for a wide range of species. However, potential applicability is always necessary but not sufficient condition because

species specificities, violation of the model assumptions and/or technical or logistic limitations may constraint the optimal sampling settings.

In response to criticism (1), features for the implemented simulations were dictated by mathematical convenience in order to avoid extremely large computing times. In sake of simplicity and generality, we decided to use the simplest version of a biased random walk model (BRW; Codling, Plank, Benhamou, & Interface, 2008) as a mathematical approximation for movement to make inference about density estimates. BRW results from combining an elastic drift (k) that pulls the animal towards the HR centre, and a stochastic component (Alós, Palmer, Balle, & Arlinghaus, 2016). The resulting space use will be characterized by a stationary probability density function with independence on the nature of the stochastic term (Dubkov & Spagnolo, 2007), and that will emerge when the stochastic part is either Gaussian (Codling et al., 2008; Godrèche & Luck, 2001) or, for example, a Lévy-like diffusive term (Bartumeus, 2007). In the BRW model used, when the drift force equals 0, the movement reduces to a random walk diffusion model (Codling et al., 2008). Equalling the stochastic term to 0, as Abolaffio et al. (2019) discussed, will lead to a linear trajectory towards the HR centre, where the animal will remain forever, which is not biologically meaningful. In any case, a BRW with a Gaussian stochastic component is the simplest choice for simulating animal trajectories but any other movement model meeting the requirement of stationary criteria should be considered when addressing the particularities of a given species.

In response to criticism (2), fixing the mean number of counts per camera was a criterion for getting some invariance and thus for facilitating the comparison between archetypes. In this way, any potential effect of density itself is not confounded with the effects of HR size and/or exploration rate.

In our simulations, the continuous movement trajectory was approximated as a series of discrete time steps, Δt , that may affect some properties of the movement pattern (Codling & Hill, 2005; Hill & Häder, 1997). In agreement with the criticism (3) in Abolaffio et al. (2019), as a consequence of the discretization for the BRW model in Campos-Candela et al. (2018), the estimated speed depends on Δt . In general, speed spread increases and tends to be underestimated when Δt increases (Codling & Hill, 2005; Hill & Häder, 1997; Rosser, Fletcher, Maini, & Baker, 2013). Then, when simulating specific-species animal movement, setting a small Δt is advisable. However, given that animal movement is an inherently autocorrelated process in space and time (Fleming et al., 2015), counting animals at each tiny Δt may result in statistically dependent samples. Typically, temporal autocorrelation diminishes as observations are made farther apart in time; but autocorrelation in movement data often persist over long-time periods (Fleming et al., 2015). The optimal solution for the simulation settings would be to move the animals with a tiny Δt but to count the animals at a longer time period. The compromise solution we adopted was to set the product $k * \Delta t$ small enough (i.e., 0.1), which still ensured a reasonable discretization of the movement path while speeding up the iterative process in simulations. Besides, and more important, this commitment decision was not affecting

the main purpose of simulations: to obtain snapshots of the system while minimizing autocorrelation.

3 | THE FEASIBILITY OF THE METHOD IN THE 'REAL WORLD': REPLYING TO CRITICISM 4

As stated above, the estimated sampling effort inferred from our simulations is only an approximation. When dealing for specific-species cases, many variables may modulate the actual effort needed for achieving a desired precision for density estimates. For example, the larger the area surveyed by the camera is, the smaller the number of frames/cameras needed for achieving a target precision will be. However, the pixels density imposes an obvious limit, which in addition will be species-dependent because, for a given pixel density, a larger area could be covered by larger-sized animals. Similarly, the larger the number of cameras is, the better the precision will be. However, the total number of cameras needed for a target precision can be out of the available budget for certain cases.

For two of the explored archetypes, the terrestrial mammal-based and the terrestrial reptile-based archetypes, the optimal sampling settings to recover stationary density of the HR centres with a target level of precision implied large sampling times along with big camera areas. Particularly, for the case of the terrestrial mammal-based archetype, when using 10 cameras with an area of detection of 630 m, the estimated sampling effort was of 11 days for a target level of precision of 0.2 (i.e., five frames analysed by camera); and 645 days for a target level of precision of 0.05 (i.e., 300 frames analysed by camera). In both cases, frames were 2 days apart one from other to avoid autocorrelation. Interestingly, results from the terrestrial mammal-based archetype are not so far when evaluating the case of moose with a more detailed movement model by Abolaffio et al. (2019).

Abolaffio et al. (2019) explored our method from different perspectives and simulated scenarios as realistic as possible for a particular species case. Camera trapping (CT) radius was set to 5 or 9 m and variable movement speed (with two behavioural states) was considered. From the results shown, to reach a target level of precision of 0.2 may require around 1,250 or 2,500 cameras, respectively, sampling during 30 days (no information on the number of frames sampled by camera nor the time between frames to control for autocorrelation is provided). Therefore, both simulation strategies agreed in that the target precision level can be reached within 30 days either by increasing the camera radius (i.e., low number of cameras with wide range of detection; Campos-Candela et al., 2018) or by increasing the number of cameras (i.e., with shorter detection radius; Abolaffio et al., 2019). These observations actually demonstrate that the underlying dynamic system is ergodic.

In any case, the results from Abolaffio et al. (2019) corroborate the usefulness of our model, as they outlined in different parts of the text: 'The statistical estimator proposed by CC yields asymptotically unbiased estimates of population size [...]. In case of constant animal

speed and large detection radius of CT [...], the estimate attains the prescribed CV threshold in less than 30 days at least for large and intermediate populations, while, [...], for the lowest density value, the precision is too low to be acceptable'. Certainly, some combination of sampling settings (either bigger area or a larger number of cameras) may be unreasonable, especially when camera trapping has limited distance of detection (Rovero, Zimmermann, Berzi, & Meek, 2013). In this line, Abolaffio et al. (2019) pointed out that '[...] such a detection area needs an equivalent of 4,900 "true" CT with a detection radius of 9 m to be sampled', something 'completely absurd'.

However...why should it be considered 'absurd'? We agree that at a first glance, and with the settings stated by Abolaffio et al. (2019), this sampling effort is discouraging but to consider it as a 'completely absurd' solution overlooks the real opportunities existing nowadays to make it more reliable than impossible. We believe that this statement may be short-sighted and unambitious.

4 | CONCLUSION: WALKING INTO THE FUTURE TO OVERCOME CRITICISM 4

In the last years, animal ecology is experiencing a revolution in imaging, camera technology and related technologies (e.g., remote control), which can provide automatically images covering big areas with enough resolution to identify the target species for long-term periods. For example, images taken from the air (Groom, Stjernholm, Due, Fleetwood, & Krag, 2013; Martin et al., 2012; Williams, Hooten, Womble, & Bower, 2017) will benefit from the use of drones (UAS; Lejeune et al. 2013; Hodgson, Kelly, & Peel, 2013; Linchant, Lisein, Semeki, Lejeune, & Vermeulen, 2015; or UAVs; Groom et al., 2013), or particular vertical take-off and landing aircraft versions (VTOL; Goebel et al., 2015); whose relatively low cost is an additional attribute that makes these devices appealing for wildlife census applications (Goebel et al., 2015; Hodgson et al., 2018). Besides, the use of gigapixel snapshots discussed in Brady et al. (2012) and very high spatial resolution satellite image-data for wildlife counts (Barber-Meyer, Kooyman, & Ponganis, 2007; Laidre & Heide-Jørgensen, 2011; Rozhnov, Yachmennikova, & Dobrynin, 2014) offer novel panoramic windows for sampling very large areas.

In addition to that, remote camera sampling based on time-lapse cameras (Flynn et al., 2018) and camera trapping continue to be excellent tools in systems that cannot be sampled from the height-top (e.g., dense forest and underwater systems). The smaller field of vision entails increasing sampling times and/or the number of cameras (to increase the sampled area). Nowadays, applications of remote cameras to biodiversity conservation are quickly progressing; expanding and improving in quality for diverse management applications (see Burton et al., 2015 for a review in the use of camera trapping; and Steenweg et al., 2017 for a review of the opportunities of remote-camera sampling at global scale). There is a global potential of remote cameras as a standardized monitoring platform for terrestrial vertebrate biodiversity, which will allow for expanding from individual, localized camera studies to

coordinated regional and global camera networks (Steenweg et al., 2017). At this point, we can list several examples of sampling platforms collecting data from fixed cameras during long periods that can benefit from using our model: the Snapshot Wisconsin project (<https://www.zooniverse.org/projects/zooniverse/snaps-hot-wisconsin>), the Snapshot Serengeti project (www.snapshotserengeti.org), the NEPTUNE Canada network (Matabos et al., 2014) or the Sub-eye Underwater Observatory in Mallorca (<https://imedea.uib-csic.es/sites/sub-eye/home/>). For more examples of coordinated networks for remote sampling, see Steenweg et al. (2017). Overall, the list of projects engaging the collection of data from remote cameras is long and increasing, in both terrestrial (Steenweg et al., 2017) and aquatic systems (Aguzzi et al., 2013, 2015; Matabos et al., 2015), and brings the hope of making estimates of absolute abundances much more realistic and unbiased.

Animal population studies will benefit from moving to such larger scales, not only on the technological side but also in terms of collaborative networks, smartphone applications and citizen science (Swanson et al., 2015; Willi et al., 2019), where theoretical and empirical perspectives must converge and play together. Abolaffio et al. (2019) pointed out that they would need an equivalent of 4,900 cameras to estimate abundance in their species case study. Around 300,000 participants (cameras) have submitted around 300 million bird pictures to the citizen science programme 'eBird' since 2002 (<https://ebird.org/home>). Obviously, it is not comparable for the case of the moose (but see Swanson et al., 2015); however, it offers an idea of the potential working frame for methods like the one developed in Campos-Candela et al. (2018). Moreover, to efficiently exploit the increasing resources from digital imagery, there is a need for an urgent shift from manually counting animals by human experts, which is certainly expensive, to automatic methods (Hodgson et al., 2018), where machine learning offers a big window of opportunities for extracting information (Tabak et al., 2019).

These opportunities altogether will provide a huge amount of data in the next future that will require proper statistical approaches to estimate abundance. In such a context, the main contribution in Campos-Candela et al. (2018): for the case of animals whose movement leads to a stationary spatial pattern, absolute animal density can be properly estimated by the average number counts per frame whenever assumptions for the model meet; can provide the basis for the further assessment of wildlife by using camera sampling. We must continue to strive to accommodate our proposed model to the particularities of the study system and overcome its potential drawbacks (e.g., Follana-Berná et al., 2019). However, we really feel that the debate should not only focus on the applicability of the proposed method in Campos-Candela et al. (2018) for some species and case studies; but on the opportunities that it offers in the nearest future for wildlife assessment to many scientists and managers. Overall, this task requires strengthening the links between theorists, empiricists and engineers, but perhaps it would provide one of the most exciting fields for modern ecology in light of the increasing and unprecedented amount of ecological data.

AUTHORS' CONTRIBUTIONS

All authors contributed critically to the drafts and gave final approval for publication of this Forum response.

DATA AVAILABILITY STATEMENT

Data associated with this manuscript are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.m605m> (Campos-Candela, Palmer, Balle, & Alós, 2017).

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