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The use of photographic rates to estimate densities of cryptic mammals: response to Jennelle *et al.*

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Most species-specific conservation efforts require estimates of population size to establish priorities and to monitor management activities. Yet obtaining reliable estimates of animal populations is often difficult, especially given time and funding limitations experienced by many research programmes. Consequently, there is a great need for practical methods to provide indices of animal density. Ideally, accurate estimates of populations would be obtained through mark–recapture data collected from recognizable individuals over multiple censuses that cover the entire population range. Such data are rarely available, so conservation biologists have no alternative but to resort to analyses of less perfect data, ranging from permanent-point censuses from cameras through to transect data on sightings and spoor encounters. The importance of census and monitoring data makes the development, and validation, of new techniques a priority. Because we do not live in a perfect world, there is a need to develop methods that can give an estimate of population sizes. It would be naïve to assume that these will give hugely accurate estimates of population size, but these techniques can prove useful in identifying areas that are likely to benefit from conservation action.

Our previous paper (Carbone *et al.*, 2001) assessed a methodology that relied on using camera trapping rates to provide an index of animal density. We argued that such a technique could provide a useful index of animal abundance, especially for species that cannot be individually recognized from their markings, and for which mark–recapture techniques like the one presented in Karanth & Nichols (1998) would not be possible. We argued that camera trap rates should on average be correlated with animal abundance if animal movement with respect to the location of the camera traps was random. We used data from 19 camera trapping studies of tigers obtained from five countries, spanning the full range of densities of tigers found in the wild (Carbone *et al.*, 2001). We used a gas model to provide a comparison with the observed patterns in the data because these models have been used successfully in the past to predict rates of animal interaction (Lowen & Dunbar, 1994; Barrett & Lowen, 1998).

Jennelle, Runge & MacKenzie (this volume, pp. 119–120) argue that we have not adequately established the utility of using camera traps as an index of animal abundance and that, because of this, readers may opt for this simpler approach when more direct and rigorous methods are more appropriate. We appreciate the reasons for their concern, and agree that it should be stressed that rate based indices should only be used where more rigorous methods cannot be implemented. Indeed, it was because we were mindful of the dangers to which Jennelle *et al.* refer that we explicitly drew attention to two caveats in our paper: (1) where possible, the use of mark–recapture based estimates is preferable to rate based indices; (2) rate based methods must be calibrated against an independent measure of density. We disagree, however, with Jennelle *et al.* in their view that photographic rates are unlikely to provide a useful index for large mammal abundance and we take the opportunity here to clarify a number of issues and to argue for the potential usefulness of this technique in future.

The main focus of our paper was to use photographic trapping rates to provide indices of animal abundance

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for those species that are not individually recognizable from their markings. Carbone *et al.* (2001) used data on tiger camera trapping programmes from a wide range of different habitat types and tiger densities, and in these respects these data were ideal for testing our method. We were limited to estimates of population size based on the minimum number of individuals counted, but because resighting rates of the same individual were high (typically four or more times in a study) this suggested that our estimates of population size were robust. Indeed, in Karanth & Nichols (1998), the minimum number based estimate of the population size often fell within the confidence limits of the mark–recapture based estimates of population size (depending on the model used). Our results were consistent with the predictions of a random walk simulation and we feel this provides support for the finding that we have identified a real functional relationship, not just a statistical artefact. We acknowledge the potential problem on non-independence between camera trapping rate and tiger number. With carnivores, it is difficult to compare photo trapping rates with another fully independent measure of population size. To our knowledge, there are no published accounts to support our conclusions that camera trapping rates are correlated with animal densities in other species – a point queried by Jennelle *et al.* However, our analysis provides testable predictions to obtain a practical, cost-effective census technique. Recent evidence provides support for the potential usefulness of this technique. T. O'Brien & M. Kinnard (unpublished manuscript), for example, found that camera trapping rates of tiger prey species are significantly correlated with prey density estimates based on line transect counts. Line transect counts are regularly used to provide estimates of medium- to large-herbivore density and this technique has been used to estimate prey density in a recent tiger camera trapping study (Karanth & Nichols, 1998). We believe that it is practical to develop similar studies in other areas or indeed for other species in order to validate our approach. We also feel that a camera trap based index of abundance is likely to be at least as reliable as and arguably statistically more transparent than spoor count based indices, which are confounded by, for example, substrate and observer differences.

Jennelle *et al.* have calculated confidence intervals around our regression analysis and show that the margins of error for estimating tiger density using photo trapping rates are large. They then compare these confidence intervals against estimates using mark–recapture (Karanth & Nichols, 1998). Despite the large confidence limits, we believe there is considerable potential for using camera trapping rates to provide an index of the animal density. First, one needs to consider that Carbone *et al.* (2001) presented the first review of camera trapping data of its kind. Our data came from a range of independently organized studies relying on very different camera trapping methods. With our approach in mind, future researchers might be able to reduce margins of error by standardizing camera trapping techniques. In future, there may also be the potential to correct for habitat differences (e.g., trail density and habitat openness, etc.) as more data become available. Second, while Karanth & Nichols's (1998) estimates, using mark–recapture, certainly do have far lower estimates of error around the mean, their data were obtained from the same country, and from areas containing the highest densities of tigers found in the wild and based on a consistent method. Where tigers occur at very low densities, error estimates will tend to be much larger – the scatter in our data increases dramatically below a tiger density of 5/100km^2 – Karanth & Nichols's data were all obtained from tiger densities of 5/100km^2 or more. In this respect, we think the comparison made by Jennelle *et al.* is biased and, as a basis for criticizing our approach, overly harsh.

Considering the urgent need for reliable estimates of population size, we are surprised at the readiness with which Jennelle *et al.* dismiss our proposals. Although we developed the idea using tigers, we expect that the technique would be most effective for non-carnivore species. Carnivores occur at much lower densities than their prey. (Carnivore biomass is typically 1–3% of the biomass of their prey (Vezina, 1985). We might expect, therefore, populations of prey to be 33–100 times more abundant (following predator–prey size relationships found in Carbone *et al.* (1999).) If trapping rates were to increase correspondingly, we would expect, using linear calibration, that the predicted variation in the estimate would be far smaller.

When choosing methods for estimating animal abundance, biologists must be careful to weigh the pros and cons of different methods and to make appropriate choices based on the circumstances in which they are working. It is clear that the method we presented in Carbone *et al.* (2001) is not intended to replace mark–recapture based estimates – certainly we never suggested this. Indeed, for tigers and other forest-dwelling carnivores, mark–recapture using camera traps following Karanth & Nichols (1998) provides a very useful technique for estimating population size and other population parameters. Equally, it is clear that conventional mark–recapture techniques are not always workable, and the general principle that encounter rates (in this case with cameras) can provide reliable estimates of population size seems to us to be a helpful one. Clearly, the method proposed by Carbone *et al.* (2001) would be most easily implemented and explored in studies where camera trapping programmes are already in place, and for species that cannot be identified by their markings. We recognize that the method will require density calibration at representative sites, but would argue that this would be worthwhile and would increase the usefulness of camera trapping programmes. This technique could also be used in conjunction with camera trapping programmes on large carnivores to provide an index of prey populations in order to assess the suitability of carnivore habitats (e.g. Dinerstein *et al.* 1997).

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