



Letter to the Editor

Clarifying Assumptions Behind the Estimation of Animal Density From Camera Trap Rates

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Foster and Harmsen (2012) presented a useful review of density estimation from camera trap data, concluding with an important call for increased rigor and transparency in study design. Although most of their review focuses on mark-recapture and mark-resight analyses, they also briefly critique a recent effort to estimate density of species that cannot be recognized individually, the random encounter model (REM; Rowcliffe et al. 2008). Here, we explain that this critique follows from a misrepresentation of sources of bias in the REM.

First, Foster and Harmsen (2012) state that the REM assumes that animals move randomly and independently of one another. This assumption was mathematically convenient to derive a formula linking density with trap rate (Rowcliffe et al. 2008). However, Hutchinson and Waser (2007) demonstrated analytically that violations of this assumption do not bias expected contact rates as a function of density, and Rowcliffe et al. (2008) provided empirical evidence that field results are also unbiased in practice. Thus, the REM is not sensitive to nonrandom or non-independent movement of animals.

Second, Foster and Harmsen (2012) state that the REM assumes that cameras are placed randomly, which is overly restrictive. The key requirement for camera placement in density estimation using the REM is that parts of the landscape that are either used preferentially (e.g., trails for some species) or avoided by animals (e.g., trails for some species) are sampled in proportion to their coverage in the landscape. In essence, this is the fundamental requirement of any sampling strategy (such as distance sampling)—that it should be representative of the study area. In practice, this means that REM requires that animals are neither lured to the camera by bait (which would artificially raise encounter rate), nor avoid the cameras out of fear (which would artificially lower encounter rate). The REM also requires that cameras not be set only at sites thought to have high animal traffic (e.g., trails or underpasses). A variety of camera place-

ment strategies meet this requirement, including stratified random designs (Kays et al. 2011) or placing cameras systematically at regular intervals (e.g., Ahumada et al. 2011), as well as full randomization. These study designs will occasionally result in a camera trap sampling a trail, but only in proportion to trail density in the landscape. If trail use is of particular interest to a study, a stratified design could be used to sample both on and off trails.

Thus, the central assumption of the REM is not that animals move randomly, but that they move randomly with respect to cameras. In this light, we find no reason to suppose that the REM is fundamentally unsuitable for either territorial species or those that use trails. In practice, the REM may nonetheless be unsuitable for species with a strong tendency to use rare landscape features, particularly when that species is itself rare. In this case, the non-directed sampling design required by the REM will likely yield too few records to be of any use, and directed or baited placements with mark-recapture or mark-resight methods may indeed be preferable. However, this is a sampling efficiency issue, not one of bias due to violated assumptions.

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