Letter to the Editor

A Broader Definition of Occupancy: Comment on Hayes and Monfils

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Occupancy models are widely used to analyze presence–absence data for a variety of taxa while accounting for observation error (MacKenzie et al. 2002, 2006; Tyre et al. 2003; Royle and Dorazio 2008). Hayes and Monfils (2015) question their use for analyzing avian point count data based on purported violations of model assumptions incurred by avian mobility. Animal mobility is an important consideration, not just for occupancy models, but for a variety of population and habitat models (Boyce 2006, Royle et al. 2009, Manning and Goldberg 2010, Dormann et al. 2013, Renner et al. 2015). Nevertheless, we believe the ultimate conclusions of Hayes and Monfils are shortsighted mainly due to a narrow interpretation of occupancy. Rather than turn away from the use of occupancy models, we believe they remain an appropriate method for analyzing many data sets collected from avian point count surveys. Further, we suggest that there is value in having a broader and more nuanced interpretation of occupancy that incorporates the potential for animal movement.

Our disagreement with Hayes and Monfils stems from their incomplete examination of avian point count methods used in conjunction with occupancy modeling and their interpretations of occupancy model parameters. The authors dismiss single-survey methods that include supplemental information to estimate detection probability (e.g., distance sampling, double observer) as too cumbersome and not applicable to many historical data sets. Instead, they favor the basic occupancy model of MacKenzie et al. (2002), which requires repeat surveys across a season. Hayes and Monfils then suggest that in order to meet closure assumptions, the occupancy status of a site must remain constant between surveys within a season (i.e., the period within which closure is assumed; MacKenzie et al. 2002, 2006). They strictly equate occupancy status with whether or not ≥1 individuals are physically present within a prescribed survey plot during the entire season in which surveys are repeated. This view is best suited to analyses focused on sessile organisms, nests, burrows, or dens, which remain fixed for an entire season. For mobile animals, the implication of this view is that data must be collected instantaneously (during a snapshot) or else the survey plot must be large enough to encompass the animals’ movements during the season; otherwise, movement will cause changes in physical presence between surveys, thus violating the closure assumption and rendering useless any inference from occupancy models. Single-survey methods are arguably more appropriate for estimating occupancy during a snapshot in time and may fit Hayes and Monfils’ definition of occupancy. In fact, although they did not formally assess these methods, the authors suggest that analysis of single-survey data could improve occupancy estimates. In contrast, others offer a broader definition of occupancy: species presence at some point within a specified timeframe, the length of which depends on the question of interest (Tyre et al. 2003, MacKenzie and Royle 2005, Lele et al. 2013). For mobile animals, the probability of occupancy over an extended timeframe (i.e., probability of use in MacKenzie and Royle 2005) can be of equal or greater interest than that during a snapshot. For example, whether sites are occupied over the course of a breeding season (i.e., intersect the breeding range of ≥1 individuals) or even multiple seasons may be most relevant for identifying or characterizing important breeding habitats (Royle and Kéry 2007, White et al. 2013, Latif et al. 2015). Hayes and Monfils review studies that suggest alternate interpretations of the occupancy probability parameter but then ultimately brush off these distinctions: “We fail to see the distinction between physical occurrence and usage” (Hayes and Monfils 2015:1367). In fact, sampling affects interpretation of estimated parameters in virtually all efforts to quantify animal use of space and habitat. Whether one uses logistic regression, point-process, or occupancy models to analyze survey data, animal movement can result in individuals being observed at multiple sampling units, which changes the interpretation of the predicted parameter.

How one interprets occupancy probability affects the definition of truth and estimation bias in simulations. Based on their comparison of occupancy parameter estimates in their figures 6, 7, and 8 with purported truth, we infer that Hayes and Monfils equate truth with occupancy probabilities when animals are immobile. In fact, they repeatedly reference estimation bias but fail to clearly describe their definition of truth other than to claim “…a complete census of all possible sites [allowed] a direct evaluation of the bias and consistency of the estimators”.

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Following their implied definition of truth, Hayes and Monfils infer positive bias from the fact that occupancy estimates increase as organisms become mobile, which is typical for animals. The relationship between mobility and occupancy makes intuitive sense and is well studied (Chandler et al. 2011, Amundson et al. 2014, Ramsey et al. 2015) but only constitutes evidence of bias given the narrow definition of occupancy presented by Hayes and Monfils. With a broader definition, when home range size (i.e., mobility) increases, individuals actually occupy more space such that occupancy probabilities truly increase as reflected in the results reported by Hayes and Monfils. Conversely, detectability truly decreases with increasing mobility because individuals occupying more area are less likely to be present at any one site during a given survey. Low detectability can incur actual bias (MacKenzie et al. 2002, McKann et al. 2013, Hutchinson et al. 2015), so more surveys may be needed to ensure reliable estimation as the timeframe over which occupancy is estimated or subject mobility increase. With broader interpretation of model parameters, Hayes and Monfils would not have misconstrued the effects of movement on occupancy as bias and also might have offered useful insights for sampling design.

In addition to their narrow view of occupancy, Hayes and Monfils overgeneralize from simulations with limited relevance to the subject of interest: analysis of avian point count data. Hayes and Monfils simulate a scenario involving grid-based sampling whereby sites (i.e., cells) are juxtaposed with no spacing between them. Although grid-based sampling schemes are employed (Tipton et al. 2008, Ellis et al. 2014), Hayes and Monfils’ simulations do not emulate any specific study. Rather, they claim to simulate the generic case of “arbitrary plots in continuous habitat” (Efford and Dawson 2012:1). Although this concept is germane, the relevance of Hayes and Monfils’ simulations to avian point counts stops there. Ornithologists typically space point count stations some distance apart to reduce the possibility of a single individual occupying >1 station and to encourage some statistical independence among stations (Ralph et al. 1993, Dudley and Saab 2003). Without any spacing between sampled cells, movement induces much more spatial dependency among sampling units than would be expected for typical point count data. Spatially explicit models can leverage spatial dependency to improve spatial prediction (Chandler and Royle 2013, Ramsey et al. 2015), although such models may be unnecessary if desired inference is of the number of cells occupied. Regardless, point count data are unlikely to reflect the level of spatial dependency in occupancy reflected in Hayes and Monfils’ simulations and discussed at length in their paper.

A broader view of occupancy would be more useful for analyzing point count data, and targeted simulation work could inform ecological inference. Hayes and Monfils suggest that modeling options are currently limited, particularly when analyzing historical datasets that do not contain auxiliary data necessary to support models that account for movement (e.g., temporary emigration models; Chandler et al. 2011, Amundson et al. 2014, Ramsey et al. 2015). Developing biologically realistic models may be a worthwhile venture, but until such developments materialize for existing data, we suggest making the best use of available models. For example, when forced to use models incapable of explicitly accounting for movement (e.g., simple occupancy models, logistic regression, or point–process models), researchers should, nevertheless, acknowledge the potential effects of movement when interpreting model parameters. For example, although Hayes and Monfils strictly interpret detectability (\(\psi\)) as reflecting the observation process, we suggest detectability should be interpreted as the product of availability and perceptibility (Amundson et al. 2014) given any potential for within-season movement. Given their interests, Hayes and Monfils could have simulated marsh bird populations while explicitly representing parameters of interest (e.g., occupancy at the desired scale of inference), nuisance parameters (e.g., availability), and the observation process under attainable sampling schemes (e.g., perceptibility). Such simulations could have suggested how parameter estimates from simple models would likely reflect underlying processes (e.g., whether \(\psi = \text{occupancy} \times \text{availability}\) or \(\psi = \text{availability} \times \text{perceptibility}\) for a given sampling scheme). Additionally, simulations could be used to assess the feasibility of sampling to support more complex models that explicitly estimate parameters representing additional levels of information (Nichols et al. 2008, Chandler et al. 2011, Amundson et al. 2014). Such work could be extremely useful for studies of marsh birds given their intractability (Conway and Gibbs 2005, 2011). Although Hayes and Monfils discuss their results primarily in terms of bias relative to occupancy, their main concern may instead relate to how well the resulting estimates of occupancy reflect the underlying density of animals across the landscape being sampled. Indeed, estimating densities of animals across multiple visits requires closure to movement unless the models account explicitly for immigration and emigration (Amundson et al. 2014). The relationships between occupancy and abundance are the subject of much study and, as alluded to by Hayes and Monfils, depend on how sampling corresponds with spatial ecology of the species of interest (Joseph et al. 2006, Clare et al. 2015). Spatially explicit simulation tools and approaches capable of informing inference of abundance from occupancy patterns for specific systems are the subject of ongoing research (Ellis et al. 2014, 2015). We encourage researchers to think about the inferences they can make from available models by critically examining how model-based estimates reflect data and underlying ecological processes within spatial and temporal frames of interest.

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