

Should scientists be required to use a model-based solution to adjust for possible distance-based detectability bias?

RICHARD L. HUTTO¹

Division of Biological Sciences, University of Montana, 32 Campus Drive # 4824, Missoula, MT 59812 USA

Abstract. The most popular method used to gain an understanding of population trends or of differences in bird abundance among land condition categories is to use information derived from point counts. Unfortunately, various factors can affect one's ability to detect birds, and those factors need to be controlled or accounted for so that any difference in one's index among time periods or locations is an accurate reflection of differences in bird abundance and not differences in detectability. Avian ecologists could use appropriately sized fixed-area surveys to minimize the chance that they might be deceived by distance-based detectability bias, but the current method of choice is to use a modeling approach that allows one to account for distance-based bias by modeling the effects of distance on detectability or occupancy. I challenge the idea that modeling is the best approach to account for distance-based effects on the detectability of birds because the most important distance-based modeling assumptions can never be met. The use of a fixed-area survey method to generate an index of abundance is the simplest way to control for distance-based detectability bias and should not be universally condemned or be the basis for outright rejection in the publication process.

Key words: *detectability; distance; index; inference; occupancy; point count.*

INTRODUCTION

Numerous factors can affect one's ability to detect a bird that is within detection range, and differences in detectability among treatment categories or time periods can introduce a detectability bias if not controlled. These include factors such as the effective area surveyed, time of day, time of season, time of year, wind conditions, rain conditions, humidity, temperature, cloud cover, noise levels, clothing color, observer skill, observer behavior, and vegetation structure, among others (e.g., Ralph and Scott 1981). If the value of any potential source of bias is not equal among categories being compared (e.g., among vegetation types) or not controlled after the fact through statistical means, then there is a strong chance that any difference in bird abundance might be due to a difference in detectability and not to a difference in vegetation type or whatever variable constitutes the comparison of interest.

One potential source of detectability bias that has taken center stage in bird survey work is distance from an

observer because, at some point, detectability must decline with increasing distance. Therefore, if the distance profiles (a plot of the way detectability declines with distance) differ among treatment categories, then different numbers of birds will be recorded not because abundances differ, but because different effective areas are surveyed. Emlen (1971) struggled with this potential problem of reporting results derived from the use of unlimited-width transects, and he used first principles to design a variable-width transect method (the Emlen method) to deal with the fact that detectability drops off with distance from an observer, and it does so at different distances for different species. Emlen proposed an elegant solution where one can account for differences in detectability among species (or among land conditions for any one species) by creating a histogram of the distances of all species-specific bird detections from the transect line. He then argued that the inflection point on that detection profile (where detectability drops off most rapidly) probably represents a reasonable distance within which one can safely assume that detectability is near perfect and across which there are no net gains or losses in numbers of detections due to bird movement before detection. That is, the net numbers of additions due to the movement of birds toward the observer and bird losses

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¹E-mail: hutto@mso.umt.edu

due the movement of birds away from the observer before detection are zero at that distance. Beyond that distance, losses due to imperfect detection (beyond the baseline level of detection) begin to accrue, and one should not include those detections in density calculations. Thus, the density of each species is calculated separately, using an effective area that depends on a species' detectability. This modification of the fixed-width transect was thought to solve its most seriously violated assumption (that the proportion of actually occurring individuals detected within a fixed distance from the observer is the same for all species or all conditions for any one species), and it caught on like wildfire. One can use the effective area to estimate the number of birds per unit area (bird density) surrounding an observer. Alternatively, one can simply use presence-absence information to generate an index of abundance for a particular fixed width (for line transects) or fixed radius (for point counts) within which detectability is assumed to be equal across all categories of comparison. In this paper, I refer to these as traditional fixed-area approaches that one might use to deal with potential distance-based detectability bias.

By the early 1990s, computer power led to the evolution of sophisticated modeling approaches to obtain an objective estimate of the effective area within which a sample of bird detections is obtained from transect or point-count data (Buckland et al. 2001, Thomas et al. 2002, 2010, Buckland 2006). Using a model-based approach, one can now automate curve fitting and can (theoretically) control for additional covariates (e.g., observer, habitat type, time of day, time of season, etc.) that are known to affect detectability of birds (MacKenzie et al. 2006). For example, given adequate sample sizes, it is possible to use multiple covariate distance sampling (MCDS) modeling (Thomas et al. 2010) to account for the effects of distance covariates. The calculation of occupancy through the use of program PRESENCE (MacKenzie et al. 2006) provides a theoretically elegant solution because all sources of detectability bias at a point can be assessed simultaneously by repeating visits to a point and determining just how detectable a species is at that point or at a series of points within a particular treatment category. The theoretical underpinnings behind these modeling approaches may be elegant but, unfortunately, the necessary assumptions associated with each are unlikely to be met.

I argue here that the traditional method of using a reasonably limited, fixed-radius survey to generate index values (naive occupancy rates) using only those detections that occur within an empirically based fixed-radius survey area appropriate for one's target species may still be the best way to deal with potential distance-based detectability bias. Fixed-radius surveys should not be universally condemned and should certainly not be the basis for rejecting a study outright, a practice that is now commonplace. In the words of Brian McGill (2013), the calculation of detection probabilities has become the sine qua non of publishing in many journals. The prospect that journals are censoring sound science is bad enough, but even worse is the prospect that

the modeling requirement is misguided. Requiring everyone to adjust their data through the use of models that, although elegant, never meet their inherent assumptions is an undesirable development in science. There are two issues that I would like to bring into sharp focus in this commentary. The first is that modeling approaches designed to deal with distance-based detectability problems are fraught with insurmountable problems; the second is that distance-based detectability bias can probably be controlled satisfactorily through the use of fixed-radius surveys when a distance cutoff is set by knowledge of where one can assume uniformly high bird detectability rates.

MODELING IS UNLIKELY TO GENERATE RELIABLE DENSITY OR OCCUPANCY ESTIMATES

Numerous practical problems and unmet assumptions associated with the model-based methods commonly used to address the potential distance-based detectability problem should shake one's trust that those numbers necessarily represent accurate estimates of density or accurate estimates of occurrence probabilities. More than a decade ago, Hutto and Young (2002) discussed why the assumptions associated with modeling distance-based detectability are necessarily violated and why they preferred to control for that source of potential detectability bias through the use of data drawn from within a fixed and reasonably limited radius (see also Ellingson and Lukacs 2003, Hutto and Young 2003). Others (e.g., Engeman 2003, Johnson 2008) also concluded that it is possible to obtain reliable index values through careful research design. Given the current state of affairs, it may be time to reiterate the fact that there are insurmountable weaknesses associated with model-based approaches and that alternative methods to deal with potential detectability bias probably work quite well.

Seasoned field biologists are intimately familiar with what humans can be expected to do reliably in the field, and they will be the first to tell you that many of the assumptions associated with distance sampling (Thomas et al. 2010) are untenable. Unfortunately, the modeling approach has prevailed, perhaps because models appear to yield definitive results. Consequently, many are quick to apply modeling methods blindly rather than making an informed choice about whether a distance-controlled research design might be a better way to address the potential distance bias. Below, I outline the most significant assumption violations and significant practical problems associated with modeling detectability through the use of distance sampling (Thomas et al. 2010) or occupancy modeling (MacKenzie et al. 2006).

ASSUMPTION VIOLATIONS AND PRACTICAL PROBLEMS ASSOCIATED WITH DISTANCE SAMPLING

Not all objects at a point can be detected with certainty. Anyone with field experience knows that, on rare occasions, the assumption of perfect detectability at a survey

point is clearly violated; we are sometimes surprised by the presence of birds underfoot or overhead, or by birds that flush only after we move upon completion of a count. I readily admit, however, that this is a reasonable assumption because it is probably extremely rare that birders miss nearby birds in most vegetation types.

Birds move frequently. The assumption that birds are stationary is always in violation...always. We cannot relax this assumption. Birds are alive and they have behavior. Some move toward the observer after a count has begun but before they are detected (causing overestimates of abundance), some move away without being detected during a count (causing underestimates). Indeed, most are detected at a point that is very different from where they were at the beginning of the count. Anyone who believes that birds do not move from outside to within detection range during a count is mistaken. Birds move both independently of, and in direct response to, observers. The very common doughnut shape of bird detection rates surrounding a point (e.g., Fig. 2b in Thomas et al. 2010) most certainly results from bird movement after arrival of an observer but before detection and is a clear violation of the assumption that birds do not move away from or toward the observer before they are detected.

Measurements are inexact. About 90% of all bird detections are based on sound alone, and distances to bird sounds are notoriously difficult to estimate accurately. Despite their widespread use, laser range finders cannot fix the problem of not knowing where a bird is located. Experienced observers are constantly surprised by the magnitude of errors in both distance and direction after a bird that was heard suddenly becomes visible. Distances can be no more accurately estimated using a fixed-radius method, of course, but at least the problem is minimized when location errors are restricted to the relatively few birds detected near a single fixed-radius distance.

The number of individuals of any one species detected from a single point in space is impossible to determine precisely. Anyone with field experience knows that birds move nearly constantly, and that even experienced observers standing at the same point rarely agree on numbers of individual birds surrounding the point. For this reason alone, one should be very suspicious of density calculations based on numbers of individuals detected at a point. This is true for both fixed-area and distance sampling approaches; density calculations cannot be trusted if it is clear that observers cannot agree on whether multiple detections result from the same bird flitting from one location to another or whether they result from the presence of different individual birds. The use of a 5- to 10-min survey time window also guarantees an accumulation of birds from outside to within detection range during the count, and that can also complicate density estimation. Presence-absence data are far more consistent among observers who record detections from the same point, and the proportion of points on which a bird species is detected is perfectly adequate for addressing most questions that require estimates of relative abundance.

Sample sizes (numbers of points with detections) for most species (especially when one eliminates non-independent, repeat visits to points) are ridiculously small, and modeled curves are fantasies, at best. If you throw out the species for which detections are too few to create a reliable detectability profile, the number of species for which you can generate a reliable density estimate is tiny indeed, very few species generate the 60–80 detections required (Buckland et al. 2001) to estimate density reliably. Rather than forcing modeled curves through sparse datasets, it is probably much safer to use the detection profile as a guide for selecting a suitable fixed-distance within which detectability can be assumed to be uniformly high across all conditions being compared.

A decrease in number of bird detections with increasing distance from an observer is often a result of habitat heterogeneity rather than distance per se. As an extreme example, consider the nature of data that might be collected along a narrow riparian strip; the more riparian-dependent species are never detected beyond 20 m, but one would be wrong to conclude from their detectability profile that they are not very detectable. Distance sampling will generate density estimates that are way too high as a result, while relative abundance based on fixed-radius data will not be affected because the fixed radius will lie inside that apparent decline. Uniform vegetation conditions must lie within the range of detectability of a given species for its detectability profile to be meaningful, but that is rarely the case. Tiny habitat patches (e.g., riparian vegetation or any easily recognized heterogeneity in forest cover where patches of vegetation exist) will always influence detection distances, and detectability profiles for each species will always be biased by such habitat heterogeneity.

Curve-fitting is usually conducted using data obtained from repeat visits to the same point; in such cases, distance estimates are not independent because they are the result of recording the same birds in the same locations repeatedly. The detection profile of a relatively rare species may be less a reflection of how detectable the species is than a reflection of where a song post was located relative to a point where it was repeatedly detected. This is not a fault of modeling per se, but my experience suggests that practitioners frequently combine distance estimates from repeat visits during analysis, and that is a clear violation of the assumption of independence.

For what is supposedly an objective process, program DISTANCE requires significant and entirely subjective choices when curve fitting, and no two people are likely to generate the same density estimate given the same data (Welsh et al. 2013). A user is free to choose any combination of key function (uniform, half-normal, hazard-rate, and negative exponential) and series expansion (cosine, simple polynomial, and hermite polynomial) elements. Thus, even though this step is entirely automated these days, it is probably safe to say that most users can neither explain nor justify the particular curve-fitting choice they make.

Finally, there is a fundamental problem associated with one of the most common uses of adjusted, variable-distance,

point-count data: uncovering bird-habitat relationships. Because the spatial scale of important habitat heterogeneity for most bird species falls well within 100 m from any point, birds detected beyond a distance as close as 50 m frequently have little relationship with land conditions recorded at a survey point (Fig. 1). That means the inclusion of more distant detections in habitat or niche modeling will tend to obscure rather than expose important habitat associations that occur at fine spatial scales. Weighting detections by distance from the observer does not eliminate this problem; it merely lessens the strength of a relationship that simply does not exist. If one wants to learn something about habitat relationships, there is no substitute for recording habitat conditions at or very near a target bird. Vegetation conditions recorded at a survey point are unused by most of the bird species detected in a

variable-radius count. Index values emerging from well-designed, fixed-radius methods yield results that are almost certainly superior to variable-distance methods if one wishes to gain insight into bird-habitat relationships.

ASSUMPTION VIOLATIONS AND PRACTICAL PROBLEMS ASSOCIATED WITH OCCUPANCY MODELING

One cannot separate the probability of occupancy (availability, Ψ) from the probability of detection (detection given availability, P), which has been parameterized through repeated sampling in time or space. As Amundson et al. (2014) note, if one cannot distinguish a bird's availability from its perceptibility then one cannot know its detectability. Model-based practitioners use repeat visits or subsets of a 10-min count as sample

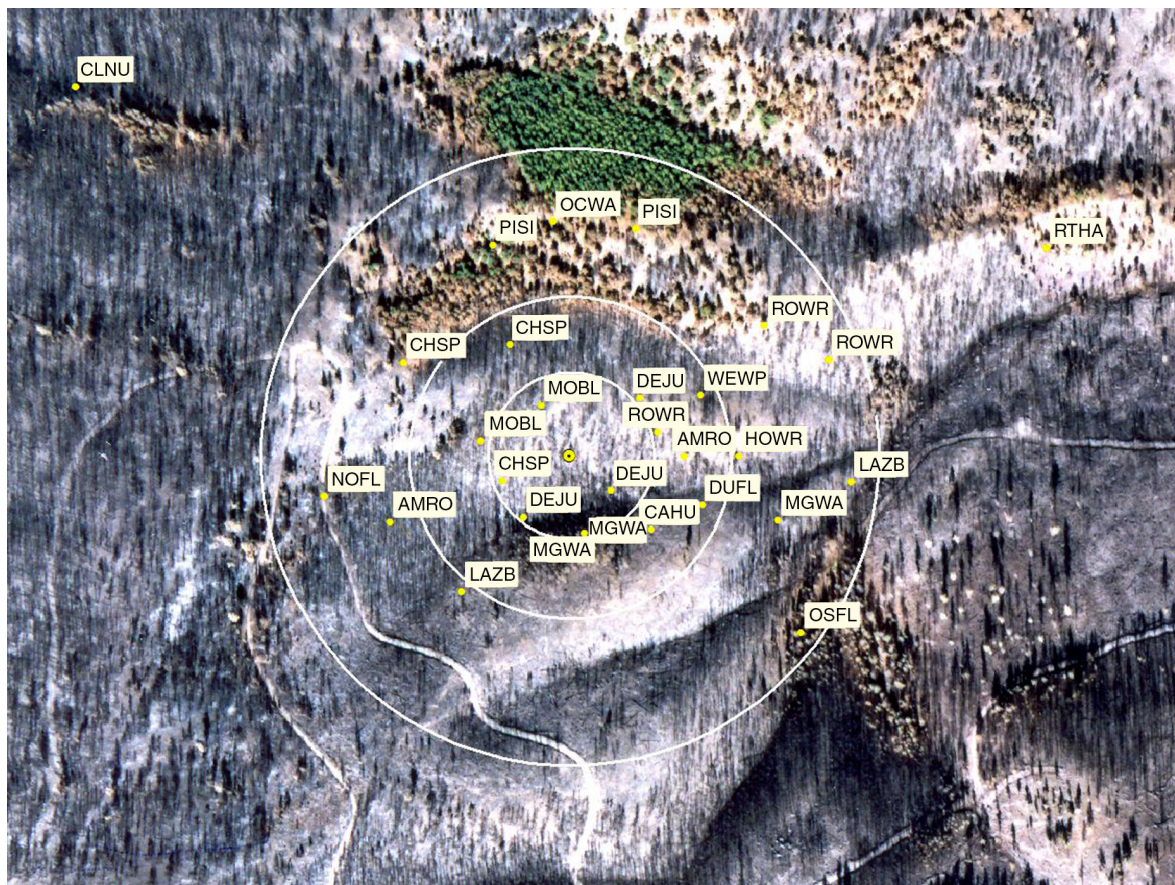


FIG. 1. Aerial view of the locations of birds detected from a single point in the 2003 Black Mountain fire near Missoula, Montana, USA. Circles represent approximate 50 m, 100 m, and 200 m radii surrounding the survey point. Note that the only species using severely burned forest conditions immediately surrounding the point (within about 50 m) were Mountain Bluebird (MOBL, *Sialia currucoides*), Chipping Sparrow (CHSP, *Spizella passerina*), and Dark-eyed Junco (DEJU, *Junco hyemalis*). The MacGillivray's Warblers (MGWA, *Geothlypis tolmiei*) were clearly using the riparian draw and had little to do with the open, burned forest conditions otherwise. In a similar vein, the Olive-sided Flycatcher (OSFL, *Contopus cooperi*), Red-tailed Hawk (RTHA, *Buteo jamaicensis*), Orange-crowned Warbler (OCWA, *Oreothlypis celata*), and Clark's Nutcracker (CLNU, *Nucifraga columbiana*) were clearly using distant elements of the forest that would not have been included in typical habitat relationships models built from density or occupancy models incorporating all bird detections. Other species depicted include American Robin (AMRO, *Turdus migratorius*), Calliope Hummingbird (CAHU, *Selasphorus calliope*), Dusky Flycatcher (DUFL, *Empidonax oberholseri*), House Wren (HOWR, *Troglodytes aedon*), Lazuli Bunting (LAZB, *Passerina amoena*), Northern Flicker (NOFL, *Colaptes auratus*), Pine Siskin (PISI, *Spinus pinus*), Rock Wren (ROWR, *Salpinctes obsoletus*) and Western Wood-Pewee (WEWP, *Contopus sordidulus*).

periods in an attempt to tease apart two kinds of zeroes: one when a bird is present during a survey but is undetected (a false absence) and the other when a resident bird is truly absent during a survey. Unfortunately, repeat visits to a point do not allow one to distinguish whether a bird was present but undetected or whether it was truly absent during some of the counts. In addition, by repeating visits across an entire season (the most common design in bird survey work) one clearly violates the assumption of closure to changes in the state of occupancy because not all bird species are present throughout the typical sample season (Hayes and Monfils 2015). Similarly, time period subsets of a single 10-min point count are not even close to being independent samples, where the probability of detection in one period is independent of the probability in another, as required by occupancy modeling.

An unfortunate consequence of occupancy modeling is that one must assume that absences during a subset of repeat visits or sample time periods result from birds that were, at times, present but missed. If the birds were not actually present during the count, that useful information gets thrown away by adjusting numbers under the assumption that they were present but missed. One of the most powerful measures of habitat suitability is actually reflected well in naïve detectability because it is probably safe to assume that a point where a bird is frequently detected is a much better place to be than a point where a bird is rarely detected. One retains that information with naïve occupancy data but throws it away by using adjustments that assume the bird was there all the time but undetected during some visits.

Occupancy modeling requires repeat visits to points to obtain both density and occupancy estimates, and those repeat visits are bought at a significant cost in terms of generality of results because a reallocation of effort could have provided two, three, or even five times more independent treatment samples. There will always a trade-off between breadth and depth in sampling, and there is no correct method, so requiring one to sacrifice generality is unwise.

Because occupancy modeling favors shorter count durations and requires repeat visits to a point, the relatively recent emergence of this modeling approach to account for imperfect detection has also interfered with our ability to maintain common standards in field methods and with the integrity of long-term monitoring efforts that were established decades ago (Matsuoka et al. 2014).

A FIXED-AREA DESIGN MAY BE THE BEST WAY TO DEAL WITH THE POTENTIAL PROBLEM OF DISTANCE-BASED DETECTABILITY BIAS

Nobody has ever argued that distance and numerous other factors do not pose potential problems when the land conditions or time periods being compared differ in bird detectability because of those factors. Nor has anyone ever argued that model-based solutions to the detectability problem lack a strong theoretical underpinning and mathematical elegance. What a number of us have argued

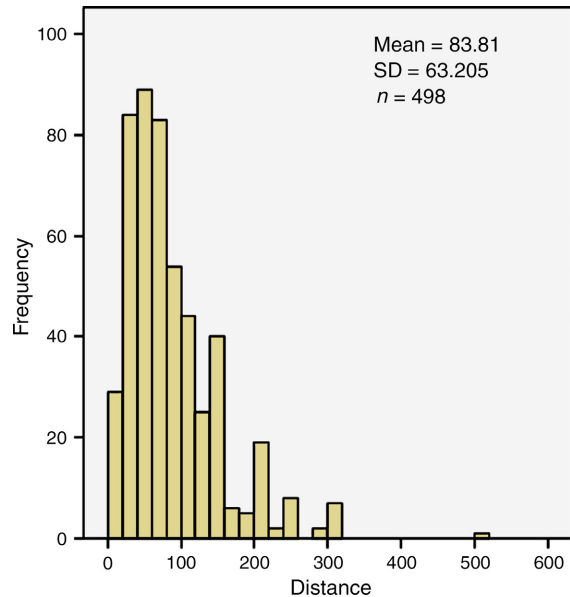


FIG. 2. Histogram showing numbers of Black-backed Woodpecker detections at different distances from the observer. Data were drawn from the author's point-count database. Any fixed radius inside the inflection point of about 100 m and beyond 40 m ought to provide a reasonable presence-absence index of bird abundance.

elsewhere (Hutto and Young 2002, 2003, Engeman 2003, Johnson 2008), and what I am arguing here, is that all of this potential bias cannot be eliminated with certainty through modeling because too many critical assumptions cannot be met and because sample sizes will always prevent us from being able to build reliable models for more than a handful of species or account for more than a few of the most common factors that can affect detectability. Modeling distance-based detectability is risky at best; we simply cannot model ourselves out of the potential problem of distance-based sampling bias.

By restricting data collection to within a reasonably limited radius around survey points, a researcher will lose some data, but at the same time will also largely eliminate the chance of distance-based detectability bias. For example, a histogram of the distance-based detectability profile for the Black-backed Woodpecker (*Picoides arcticus*) based on 498 detections shows that most birds are detected within 200 m and that detections fall off rapidly beyond 80–100 m (Fig. 2). By plotting occurrence rate vs. fire severity using a fixed radius of between 50 and 100 m (between the peak and the inflection point on the detection profile), it is quite clear that the species occurs predominantly in more severely burned forest patches (Fig. 3). Data drawn from within a smaller 20 m radius become sparse not only because the survey area is very small but because birds were present but moved away from the observer before detection, so sample size artifacts are likely to have affected the resulting distribution pattern. Data drawn from an unlimited radius probably also yield a less reliable distribution pattern not only because of differences in

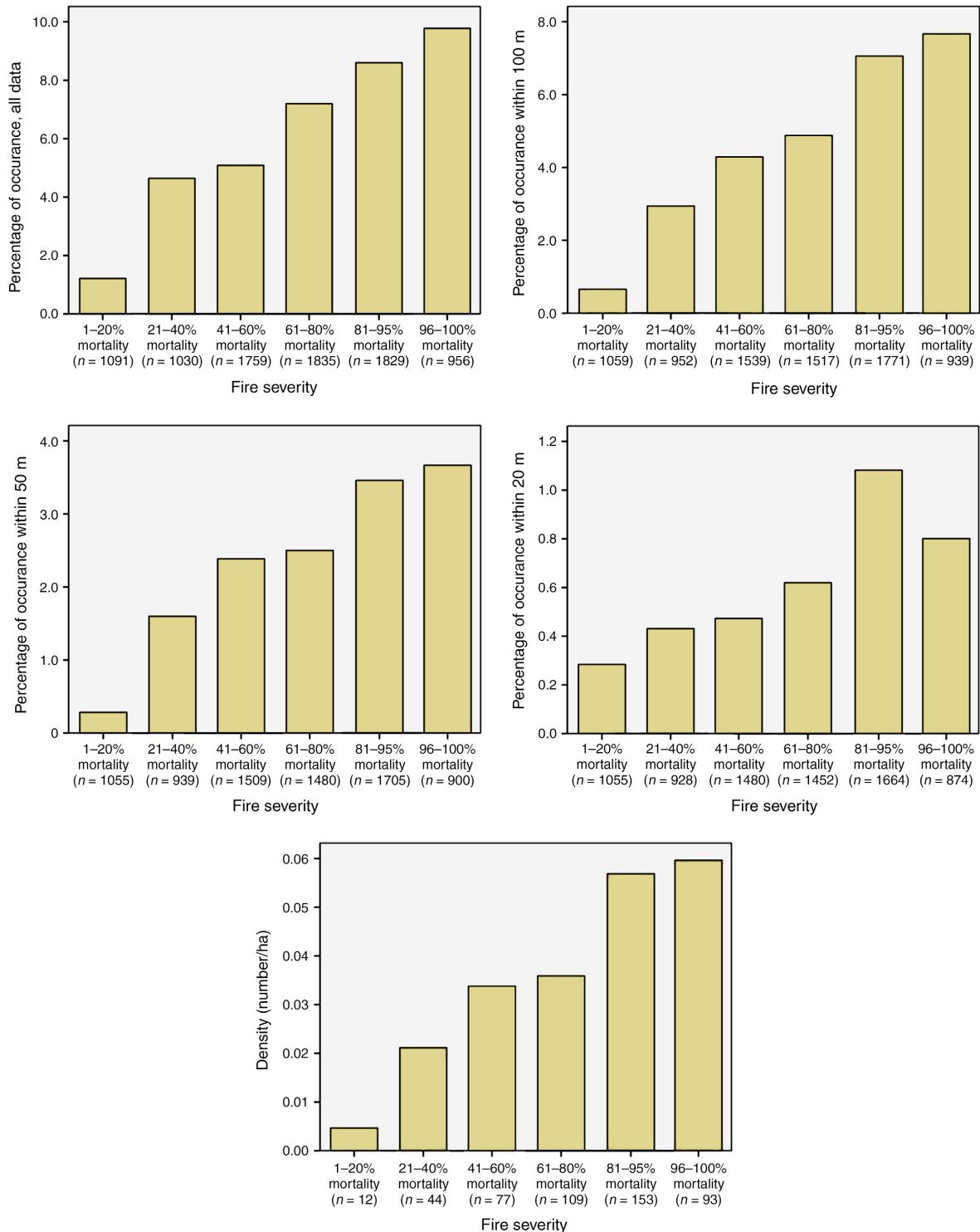


FIG. 3. The proportion of Black-backed Woodpeckers detected on different fixed-radius counts in each of several categories of fire severity, as measured by percentage of tree mortality within the count area surrounding the survey point. Note that the distribution pattern is very consistent using data from between 50 and 100 m, and that the pattern is nearly identical to that obtained by estimating density using program DISTANCE (using a half-normal/cosine model, 50-m data bins, and truncating the largest 2% of the distance values). The unlimited-radius data and 20-m-radius data probably suffer from errors in categorization and sample size bias, respectively.

detectability among severity categories but, more importantly, because of the inappropriate assignment of birds to severity categories (more distant birds frequently occur in environmental conditions that differ from the condition at or near the survey point). Given an appropriate 50–100 m fixed radius, the overall pattern is clearly no different from the pattern obtained by calculating density through the use of program DISTANCE (Fig. 3). Playback experiments provide additional evidence that one can adequately control for distance-based detectability bias by restricting data to those collected within a limited radius surrounding survey points. Playbacks draw nearby birds into view and most certainly increase detectability to near perfect levels. Results from playbacks conducted at more than 3,000 points positioned in forest patches that burned at four different severities confirm that the pattern of occurrence in more severely burned forest patches is a result of birds being more abundant, not simply more detectable, within a limited area around survey points (Hutto 2008). Others have also reported greater occurrence rates in more severely burned forest patches (e.g., Koivula and Schmiegelow 2007, Russell et al. 2007, Dudley et al. 2012). Thus, naïve occupancy within a fixed radius appears adequate to understand patterns of habitat use by the woodpecker.

To this day, there is no evidence that people who design their studies to simultaneously minimize many potential sources of bias and then work with data collected from within a reasonably limited radius have ever been deceived or misled by their results. That would, of course, include virtually all biologists who have helped us understand nature before model-based approaches to control for detectability bias were available. There have been studies comparing results derived from fixed-radius and distance-sampling methods (e.g., Norvell et al. 2003), but one cannot draw conclusions about the efficacy of one method by using results from the other as the basis of truth. Even doing so, results from the two methods were strikingly similar when the fixed radius (50 m) was beyond the distance of maximum detectability but still within the distance where detectability begins to drop precipitously. Note that 25 m lies inside the detectability profile peak (see Fig. 2 in Norvell et al. 2003), so a 25 m radius failed to produce results that were in agreement with those derived from use of the more appropriate 50 m or 100 m fixed radii or from distance sampling methods (see Fig. 4 in Norvell et al. 2003).

The only way one can judge the accuracy of results derived from indices of abundance and modeled densities (or occupancy rates) is to calculate bird density from the precise mapping of territories of marked birds and use that as a basis of comparison. That kind of comparison has been conducted only rarely, however, because the logistics needed to generate an accurate map (while not interfering with point-count results derived from the same area) are daunting. Published results using this approach (e.g., Gill 1980, Greene and Pryde 2012, Newell et al. 2013) show inconsistent results, which is not surprising given nearly infinite variation in the way each method is implemented. Nonetheless, there is most often general agreement in bird

occurrence patterns derived from territory mapping, appropriately selected fixed radius, and distance sampling methods. Perhaps we have become obsessed with trying to fix a detectability problem that is adequately handled through traditional research design methods. Indeed, even though one's analytical method is likely to affect conclusions requiring estimates of density or actual population size, the choice of method is unlikely to affect results involving comparisons of relative abundances among habitats or treatment categories (Reidy et al. 2011), which constitute the vast majority of bird survey needs.

CONCLUSION

The most commonly employed methods of controlling for distance-based detectability bias while modeling bird density (number per unit area) or occupancy (the proportion of sites occupied during counts) are not without problems. Specifically, assumptions that accompany the derivation of most distance-based density estimates are so clearly violated that one must question the accuracy of such estimates. The naïve probability of bird occurrence derived from carefully designed data collection scheme and from a carefully chosen fixed radius probably constitutes a satisfactory index to bird abundance and should be recognized as a suitable solution to the potential problem of distance-based detectability bias. Consider the Black-backed Woodpecker again. The probability of detecting this species within a limited radius surrounding survey points is some 20 times greater in burned forests than in any other major vegetation type or condition in the Northern Rockies (Hutto 2008). The naïve probabilities drawn from a limited and fixed area probably reflect relative abundances quite well and are unlikely to have created a misleading distribution pattern. It is far more likely that this statistically significant pattern reflects something biologically real. Whether the actual difference in abundance is a twentieth or a thirtieth or a tenth matters little: the difference is greater than that expected due to chance and is a difference that is in no way a product of some kind of detectability bias. Given a research design that includes use of limited distances, observer training, rotation of observers among sites, use of restricted times of day, restricted weather conditions, restricted times of season, etc., it would be foolish to think that the overall pattern is the result of observers having missed birds where fewer were detected. A little logic is all one needs to know that if one controls for known sources of detectability bias through reasonable design adjustments and restricts analyses to the data collected within a limited distance, the naïve probability of detection almost certainly reflects relative abundance. This woodpecker example and additional examples presented in other published studies (e.g., Reidy et al. 2011, Newell et al. 2013) suggest as much.

Modeling to account for a small subset of factors known to affect detectability does not necessarily eliminate the potential detectability problem nor does it stand as the only, or necessarily the best, way to deal with the potential

problem. The most important thing a researcher can do is use some common sense up front when designing a bird survey so that he or she is unlikely to be fooled by those potential problems. As Engeman (2003) emphasized a decade ago, after-the-fact modeling solutions will never be as strong as solutions based on before-the-fact research design. At some point, biological intuition gained through extensive field experience has to maintain a strong voice in ecology because such experience is much more likely to serve as a valuable check on results than is experience with model building alone. Indeed, only solid field experience can lead one to appreciate just how badly violated most of these modeling assumptions are and just how careful we have to be when interpreting results from these modeling efforts.

Reviewers and editors should not be so quick to condemn the use of fixed-radius count data; well-designed studies yield reliable indices that can be used to expose patterns of bird occurrence, population trends, and bird–habitat relationships. It is possible that we are using model-based approaches to cure a detectability bias disease that, in the words of Johnson (2008), “...may be little or no better than the original ailment.” What editors should be insisting on is the production of tables that include what observers measure reliably in the field (e.g., naïve occupancy or the proportion of points on which a species was detected within a meaningful fixed radius) and not just modeled density estimates and model parameters emerging from a process fraught with assumption violations. Common sense and biological insight really ought to prevail over what has become a frighteningly blind application of model-based solutions to the potential detectability problem.

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DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.46tp6>