Running Head: Multiple surveys & bias in density estimation

BIAS IN THE ESTIMATION OF BIRD DENSITY AND RELATIVE ABUNDANCE WHEN THE CLOSURE ASSUMPTION OF MULTIPLE SURVEY APPROACHES IS VIOLATED: A SIMULATION STUDY

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ABSTRACT

Ornithologists are increasingly cognizant of the effect of detection error on abundance estimation and are using multiple visit surveys with occupancy and N-mixture models to account for detection error. These approaches assume the population of interest is closed. The effects of violating closure on density and relative differences between habitats are not fully appreciated. Closure might be violated during point count surveys for birds because of within-territory movement. A spatial simulation was used to generate data that would occur in a multiple visit survey if birds move within their territories between repeat visits. We varied bird density, territory size, and number of visits and studied how density estimates from various analytical techniques changed with bird movement. Large biases (up to 900% overestimation) in density estimates were observed using maximum occurrence, maximum count, occupancy, and N-mixture models. The relative abundance ratio between habitats was generally underestimated using the maximum or multiple visit approaches. Average presence and count were not biased as these metrics do not require closure. Importance of detection error in avian studies cannot be denied. However, given closure is likely violated in most point count applications due to bird movement, density estimates or even relative comparisons of bird abundance among habitats obtained by multiple visits must be checked for ecological plausibility. There is a clear need to develop metrics of bird abundance that do not rely on population closure but account for detection error.

Key Words: density estimation, point counts, N-mixture, occupancy, population estimation

MEASURING BIRD ABUNDANCE to understand the effects of environmental variation on populations is a fundamental aspect of ornithological research. Many sampling methods and statistical approaches have been developed to estimate the abundance of birds (Bibby et al. 2000). Despite many advances in sampling and analysis techniques, much ornithological research and monitoring continues to rely on comparisons of relative abundance over time or between habitats (Marsh and Trenham 2008). While such approaches have improved our qualitative understanding of environmental factors influencing bird populations they do not facilitate effective comparisons among studies. Ideally, ornithologists would report their results using a common metric, such as the density of birds per unit area, to allow direct comparisons among studies.

Estimating density of birds accurately is challenging. Spot-mapping is a methodology used to determine the number of birds in an area by mapping the territories of individuals in a known area. While relatively accurate (Paul and Roth 1983 but see Verner and Milne 1990), spot-mapping requires multiple visits to a site and is best done with banded individuals. The result is relatively few sites per study are done, limiting the scope of ecological investigations using this technique. To increase efficiency, many ornithologists have turned to point counts (Bibby et al. 2000). Point counts are stationary surveys where all birds heard or seen in a given area over a given unit of time are recorded. Point count assessments are rapid and efficient but can not estimate density directly. Statistical corrections are required to convert observed count information from point counts into density estimates. A diversity of statistical approaches has been developed to convert raw counts from point counts into density estimates with an explosion of techniques occurring in the last five years.

Two recent methods that are being widely used to estimate bird density based on point counts are occupancy and N-mixture models. Occupancy models attempt to estimate the true proportion of sites where a species occurs (MacKenzie et al. 2002). N-mixture models attempt to estimate the true number of individuals of a species present at a site (Royle 2004). Occupancy and N-mixture models estimate density by correcting the observed count data for detection error. Detection error is the probability that a species (occupancy) or an individual (N-mixture) is not observed at a site during a survey even though it was present. To account for detection error, many have suggested that multiple visits to the same site must be done (MacKenzie et al. 2002). During multiple visits, the status of a species (detected versus not-detected) or individuals (number of individuals present) is recorded for each visit. The rationale of multiple visit approaches is that at locations where the species or individuals are present, detection error will occasionally result in a species or individual not being detected during a visit despite being present during the period of observation. Assuming occupancy status or abundance does not change over the period of observation, differences in detection of a species at a site between visits is caused by detection error. The assumption that occupancy status or abundance does not change during the period between the first and the last survey is known as the closed population assumption. If the closed population assumption is met, the resulting estimate of occupancy rate or true count can be divided by the area sampled to derive a density estimate (MacKenzie et al. 2006). In general, density estimates derived by multiple-visit methods are higher than those generated by naïve models (Kery et al. 2005). However, for such estimates to be an accurate, it is essential that the closed population assumption is satisfied. How often this assumption is violated and the degree of bias introduced if the closure assumption is not met remains poorly understood.

Recently, Rota et al. (2009) suggested that the assumption of closure is not met for passerine birds surveyed using point counts. Using a robust occupancy estimation design where sampling consisted of secondary sampling periods nested within primary sampling periods they found the closure assumption was violated for 71 to 100% of the species evaluated in two datasets. Closure was found to be violated over periods ranging from 8 days to 3 weeks. They attributed these violations in the closure assumption mainly to local extinction and recolonization events whereby populations were open to demographic changes between primary survey periods.

We suggest that violation of the closed population assumption will occur at almost any temporal scale for passerine birds using standard point count methods. Our rationale is that the spatial scale of sampling of point counts is not concordant with the spatial scale of within-territory movement behavior of passerine birds. If birds defend small territories that are consistently within the bounds of the point count area then the assumption of population closure may be met for occupancy models as at least one individual will always be present in the sampling area. However, in N-mixture models where counts are used, individuals often have partial overlap between their territory and the point count sampling area (Fig. 1). How much bias this creates when estimating density is unclear. When an observer visits a point count site where a species or individual was previously detected but is not detected during a particular visit it could be due to detection error. However, it also could be due to the bird being in that part of the territory that is outside the sampling area. Strictly speaking such movement in the territory is a violation of the closed population assumption and could occur in virtually any time interval depending on within-territory movement rates of birds. Such behavior could dramatically influence estimates derived from multiple visit methods. Our objective was to study the effect of within-territory movement on estimates of density and relative abundance ratios derived from occupancy rate and N-mixture models. To isolate the effect of the closure assumption, we assumed that detection was perfect. In other words, if present within the sampling area when the observer was present the bird was always detected. We also studied the effect of movement on the more commonly used metrics of average or maximum counts. Although our study is motivated by ornithological studies, the results have implications for other ecological studies where density estimates are obtained using occupancy and N-mixture models and the species of interest is mobile.

METHODS

To test how violations of the closed population assumption might influence density estimates of passerine birds using multiple visits, we created a series of spatial simulations using Arcview 3.2 and program R (R Development Core Team 2009). We used Arcview to create a spatial map of territories based on a series of randomly generated hexagons on an island 9175 hectares in size. This established a known population of birds. We then overlaid 100 random point count sites onto this map and determined the area of overlap between the simulated territories and the point count site (Fig. 1). Point count areas were circular and 3 hectares in size (~ equivalent to a 100 metre fixed radius point count). Point count sites were randomly distributed on the island, and had a minimum distance of 300 meters between sites. Arcview 3.2 was then used to randomly select a certain number of territories to be occupied. A random number from a uniform distribution on (0 to 1) was used to determine whether the bird was present in the portion of his territory that was within the bounds of the point count sampling area at the time of the survey: if the random number was less than or equal to the observed proportion then the bird was present. If a bird was present in that portion of his territory that was within the point count area during the time the observer was present it was detected with probability one. If the bird was outside the 100 meter point count radius it was not recorded by the observer. We then drew another random number for each territory to decide where the bird was located during a 2nd visit to the same point count site. We did this to a maximum of 10 visits. This created a data set that was similar to what ornithologists obtain when using multiple visits to point count sites. These data were then analyzed using program R with the package “unmarked” (Fiske and Chandler 2010). The key assumption of our simulations was that birds sing at random locations within their territories. The location of the point count sites and the territories of the birds were fixed at the start of the simulation.

In our simulations, we varied 1) % of carrying capacity (% of all possible territories that were occupied); 2) ratio of territory size to point count area; and 3) number of visits to a site. Carrying capacity was modeled in 10% increments from 10 to 100%. The area of the point count was fixed at 3 hectares with territory size ranging from 0.5 to 5 hectares in increments of 0.5 hectares; a range we felt was typical of most passerine species (e.g. Bayne et al. 2005). Number of visits to the same point count site ranged from 1 to 10. Average presence was calculated as the average number of detections of a species per point count site over *K* visits, average count was the average number of individuals of a species detected over *K* visits, maximum presence was whether or not a species was detected over *K* visits, and maximum count was the highest count of individuals detected per point count site over *K* visits. All presence (i.e. probability of occurrence) and count estimates were divided by the area of the point count site (3 hectares) to derive a density estimate. For each scenario (i.e. when territory size was 1 hectare, 10 visits to each site occurred, and carrying capacity was 100%) we ran 300 simulations to derive median estimates of presence and count estimates for that scenario.

The resulting density estimates were multiplied by the area of the island to calculate an estimated population size. Bias in population size estimates was calculated as percentage bias from the actual population size using:

$$Bias = \left(\frac{Est.PS - Act.PS)}{Act.Ps} \right) * 100$$

While density and population estimation are the objective of some scientific studies, there is much more research evaluating how bird abundance changes in response to variation in vegetation or other habitat characteristics. To determine whether the relative difference in density was influenced by violations of closure, we created a series of scenarios where we estimated average presence, average count, maximum presence, maximum count, occupancy, and N-mixture estimates in two habitats. In these scenarios there were 100 point count sites in each habitat. The following scenarios were modeled: 1) in habitat A & B, individual birds have the same size territories but were at different densities; 2) in habitat A & B, there were the same number of individuals but they varied in territory size; and 3) in habitat A birds were abundant and had small territories but in habitat B they were less common and had larger territories. Simulations used 1 to 10 visits. The relative abundance ratio between habitats (hereafter RAR) was calculated as:

$$RAR = \frac{Density.\text{in } Habitat\ A}{Density.\text{in } Habitat\ B}$$

Habitat A was defined as the area where birds had the smallest territories.

RESULTS

Bias in population estimation — Fig. 2 shows the trends in median bias for occupancy estimates as compared to the bias in the average presence or maximum presence metrics. In general, occupancy estimates of density overestimated the size of the population relative to average presence and maximum presence. Average presence had relatively little bias. The bias that did exist for average presence was simply due to random placement of point count sites relative to the territories. If we had moved the point count sites randomly in our simulations the slight bias we observed would not have occurred. Average presence as a density estimator did not change with an increasing number of visits. Maximum presence and occupancy estimates generally converged to the same level of bias with more visits. However, the magnitude of the bias tended to increase with more visits. Occupancy estimates were more biased than maximum presence when the number of visits to a point count site was low. Bias was highest when birds had territories larger than the point count area. The bias also increased when birds were rare. Occupancy estimates underestimated population size when birds were abundant but had territories smaller than the point count area.

Fig. 3 shows the trends in median bias for N-mixture estimation compared to the bias in average count or maximum count. N-mixture estimates of density always overestimated the size of the population as compared to the average or maximum count. Again, the average count had relatively little bias and did not change with the number of visits. The bias for N-mixture estimates was higher than the bias in maximum counts up to 10 visits. Bias in maximum count estimates increased with more visits although it approached an asymptote in several scenarios. The direction of bias with increasing number of visits changed for N-mixture models depending on territory size and carrying capacity. When a species had a large or intermediate size territory (i.e. ≥ the size of the point count area) bias decreased with increasing visits although the bias always was severe (200 to 300% overestimation of population size). As territory size decreased or the species became rare the bias became less severe. Scenarios with small territories and/or low density showed an increasing bias with more visits. For the intermediate - abundant scenario (3 hectare territory and 90% carrying capacity) we simulated the predicted count from N-mixture models versus the maximum count for 100 visits. It took between 20 to 30 visits to have N-mixture estimates converge to the maximum count.

Bias in relative abundance between habitats. —To study the influence of within-territory movement on the estimation of RAR, we calculated estimates of density for 5 (large), 3 (intermediate), and 1(small) hectare territories with bird abundance at 90% carrying capacity in habitat A and 10% carrying capacity in habitat B. Actual RAR was defined as the actual population size in Habitat A divided by the actual population size in Habitat B. A RAR of 1 indicated an equal number of individuals in each habitat. Values > 1 indicated habitat A had more individuals while values < 1 indicated that habitat B had more individuals.

Fig. 4 shows the results of simulations where habitat A had 9 times as many birds as habitat B. When territories were large relative to the point count area, N-mixture models were the most biased estimators of RAR. For example, when birds had territories of 5 hectares and point count sites were visited 2 to 5 times, habitat A was estimated to have 20 to 25 times more birds than habitat B. In truth, habitat A had only 9 times more birds. With more visits this bias decreased. The maximum count typically underestimated RAR. With more visits, both maximum count and N-mixture estimates of RAR suggested habitat A had fewer birds relative to habitat B than was actually the case. In all cases, habitat A was identified as having more birds although the actual RAR was poorly estimated. The average count was a consistent estimator of RAR with increasing visits.

Fig. 4 also shows that occupancy, average presence, and maximum presence always underestimated RAR. The smaller the territory the less accurate presence/absence data was in estimating RAR. This is because such data does not take into account that multiple individuals are present at point count sites in habitat A. Average presence was a consistent estimator with increasing visits but was also biased. With more visits, both maximum presence and occupancy resulted in a decline in the RAR.

Fig. 5 shows three scenarios of how changes in territory size and density in two habitats might influence RAR. Fig. 5 (left column) shows birds increasing their territory size in habitat B but with the total land area used by the species the same as in habitat A. In habitat A there were more individuals but each individual had a smaller territory. In this scenario, we found N-mixture and maximum counts typically underestimated RAR. Average count was the best estimator of RAR and was consistent with increasing visits. Of particular concern in this scenario was the situation where birds had 1 hectare territories in habitat A and 3 hectare territories in habitat B. With < 4 visits, N-mixture models predicted that habitat B had more birds than habitat A. In truth, habitat A had three times as many birds as habitat B.

In our second scenario (Fig. 5 - middle column), we had an identical number of individuals in habitat A and B (1000 in each) but territory size varied between habitats. When territory sizes were greater than the point count area, estimates of RAR from all methods were reasonably close to the actual 1:1 ratio simulated. However, when territories in one habitat were smaller than the point count area, habitat A (habitat with smaller territories) was always viewed as having fewer birds than habitat B for all metrics.

In our final scenario (Fig. 5 - right column), birds in habitat A had higher density and smaller territories than birds in habitat B. N-mixture models were the least accurate estimators of RAR in this scenario although the change in RAR with more visits showed only minor declines relative to using the maximum count. In one scenario, habitat A had 27 times more birds than habitat B but N-mixture models and maximum count models suggested that there were only 12.5 times more birds in habitat A than B.

DISCUSSION

Our simulations suggest that using multiple visit methods to estimate density and relative abundance ratios for birds could be problematic if there is within-territory movement during the period when closure is assumed. It is well established that birds move throughout their territories during the period when observers conduct point counts (Bayne et al. 2005) but the extent to which this could bias estimates of density is under appreciated. As Fig. 1 shows, the variance in counts that ornithologists typically attribute to detection error could be caused by within-territory movements. It is unclear how much of the variation in counts is due to detection error and how much due to movement. We have followed the movements of 71 color-banded or radio-marked Ovenbirds (*Seiurus aurocapilla*) for one to five hours (Lankau and Bayne, unpublished data) and found that the mean time spent in one location is 5.4 minutes, the median 3 minutes, and the mode < 1 minute (Fig. 6). This suggests closure could be violated even if one used a five-minute point count with one-minute intervals to generate the multiple visits required for occupancy or N-mixture estimation. The practicality of recording bird point count information this rapidly in the field is also questionable.

The absolute magnitude of bias in density estimates generated by within-territory movement seems to be highly dependent on the ratio of the size of the territory to the point count area. Many ornithologists use small radius point counts (i.e. 50 meters) under the belief that they more accurately estimate the number of individuals present, mainly because different observers are more consistently able to estimate a 50 meter distance interval than larger distances (i.e. 100 meters). While this is true, the gain in accuracy of area sampled using a smaller point count radius will be swamped by the variation caused by movement (Thompson et al. 2002). Movement of birds over small point count areas is more likely to result in violations of the closure assumption, particularly for species with larger territories resulting in severe bias using multiple visit techniques.   The increase in bias caused by multiple visit methods due to movement also occurs when using maximum presence or maximum count. This occurs because the more visits to a single site, the more likely an observer will find individuals whose territories only partly overlap the sampling area. Based on our simulations, the maximum and multiple visits methods will not estimate density accurately for passerine birds under these behavioral assumptions.

If the closure assumption is met then occupancy rate and maximum presence (assuming only one individual per species is detected per site) as well as N-mixture count and maximum count should be unbiased estimators of density. Unlike average presence and average count, these approaches allow ornithologists to correct for detection error caused by differential singing rates, observer error, and possibly differences in detectability among habitats.   Rota et al. (2009) provide a test for closure over longer time intervals that can be used with birds, but it remains to be seen if this approach could be biased due to within-territory movement. Given the inability to test for closure at time intervals relevant to bird movement it seems premature to accept that multiple visit methods, even with primary and secondary sampling intervals, will provide accurate estimates of density for birds. Even when multiple visits can be done over a time interval where closure *might* be met (i.e. breaking a 5-minute point count into five 1-minute intervals) there is a concern that observations may not be independent. Riddle et al. (2010) found that independence of observations conducted over relatively short time intervals resulted in significant bias in occupancy and N-mixture estimates for three species of birds because observers tend to remember where and when they located an individual or species. Rota et al. (2009) suggest using a removal sampling protocol to reduce the independence problem whereby sampling is done for a species only until it is first detected up to a maximum number of surveys.

While possibly reducing the impact of dependence, this approach does not explicitly test for violations of the closure assumption caused by within-territory movement of birds.

At face value, our simulations suggest that average presence and average counts modeled using generalized linear models would provide better estimates of true density. This is true only if detection probability is one. Ornithologists are well aware of the fact that detection error is nearly always present in point counts. Our simulations purposely did not include all of the biological realities that influence the number of birds detected using point counts. Our goal was to demonstrate how important the assumption of closure is for density estimation not to identify the relative importance of closure versus detection error. The current push to account for detection error in ornithological studies is important but we feel it is critical to make sure that the assumptions behind such methods are reasonable and satisfied in practice. Ensuring that the occupancy rates and N-mixture count models generate plausible density estimates is crucial. Many papers that use multiple visit models emphasize model fitting rather than providing the estimates of density derived from the models (Joseph et al. 2009).

Recently we had a paper reviewed where we compared the average count versus N-mixture density estimate for the Dark-eyed Junco (*Junco hyemalis*) in relation to an experimental treatment. We found an average density of 0.25 birds per hectare in control and 0.38 birds per hectare in thinned stands based on a generalized linear mixed model (Bayne and Nielsen, in review). N-mixture models using various distributional forms (i.e. negative binomial, Poisson, zero-inflated Poisson) estimated 2.22 birds per hectare in controls and 3.67 birds per hectare in thinned stands, an almost ten-fold increase over raw counts. While we did not have spot-mapping density estimates for this species in our study area, it seemed the N-mixture estimates were not biologically plausible given that spot-mapping studies in other areas suggest a density of about 0.65 birds per hectare (Sperry et al. 2008). Despite our protests that some assumption underlying the N-mixture technique was violated, it was recommended that we only report the density estimates from N-mixture model because "detection error is a critical factor to account for in thinning studies". Modeling the factors influencing detection error seems to have become such a dominant issue to ornithologists that we seem willing to ignore the ecological plausibility of the resulting density estimates. From a conservation perspective, ornithologists should start considering the implications of using methods that, due to violations in assumptions, either underestimate (i.e. raw counts) or overestimate (i.e. multiple visits) bird density (Joseph et al. 2009).

For many scientific investigations, estimating absolute density is not critical. Thousands of studies have relied on comparisons of relative abundance between habitats to draw scientific inference. Proponents of multiple visit methods argue that biases in detectability among habitats (i.e. you can not hear birds as well in one habitat versus another) makes such inferences suspect (Kery et al. 2005). While we agree this should be a concern, there are several reasons why relative abundance ratios between habitats as estimated by multiple visits methods may also be biased. First, lower quality habitats typically have fewer individuals than high quality habitat. This can lead to greater violation of the closure assumption in the lower quality habitat than higher quality habitat as a smaller proportion of territories will be completely within the point count sampling area in the low quality habitat. The result is that detection error for occupancy and N-mixture estimates will be estimated to be higher in the low density habitat. However, in our simulations this error was purely due to movement not actual detection error. Higher detection error that is in fact due to violation of closure results in higher occupancy and N-mixture estimates in habitats with fewer birds, biasing estimates of the relative abundance ratio of birds in different habitats.

Birds in habitats with low conspecific density often have large territories than areas with many conspecifics. For example, Cooper et al. (2009) found the territory size of Prothonotary Warblers (*Protonotaria citrea*) increased by 50% after forest harvesting relative to controls while density decreased about the same amount. Whether such increases are caused by birds requiring more space to acquire resources or birds simply moving over larger areas because space is available due to fewer conspecifics is unclear. The end result of differential territory size between habitats is that the assumption of closure is violated to a different degree in each habitat. The consequence is relative abundance ratios between habitats, as estimated by multiple visits, decrease the perceived magnitude difference between “high and low” quality habitats. In certain circumstances we found that differences in territory size and density between habitats could in fact result in a reversal of relative abundance ratios between habitats using multiple visit approaches. In most scenarios that we evaluated, all approaches correctly identified the habitat where the species was more abundant but the actual magnitude of difference between habitats was incorrect when using multiple visit methods or the maximum. We argue metrics of relative abundance between habitats are misleading if they do not accurately estimate the correct relative abundance ratio (Krebs 1999).

Most studies correcting for detection error in point count data concentrate on factors that affect detection such as observers, habitat types, conditions at the time of survey etc. None of the simulations we have seen that test the effect of detection error on density estimates have incorporated movement of birds as well as factors influencing actual detection error. As we have illustrated, the movement of the birds is likely a crucial factor that affects the population closure assumption and resultant density estimates. It is important that ornithologists interpret their data in this context. Methods and metrics need to be developed that account for detection error but they also need to be robust against the violation of closure assumption.

ACKNOWLEDGMENTS

We would like to thank Stan Boutin, Steve Cumming, Monica Moreno, Jim Schieck, Fiona Schmiegelow, Samantha Song, and the Boreal Avian Modeling Project Technical committee for helpful discussions on the issue of detection error. Funding for this research was provided by the Alberta Biodiversity Monitoring Institute, Environment Canada, North American Migratory Bird Conservation Act, and Natural Sciences and Engineering Research Council.

LITERATURE CITED

Bayne, E.M., S. VanWilgenburg, S. Boutin, and K.A. Hobson. 2005. Modeling and field-testing of Ovenbird (*Seiurus aurocapillus*) responses to boreal forest dissection by energy sector development at multiple spatial scales. Landscape Ecology 20: 203-216.

Bayne, E.M. and B. Nielsen. 2010. Thinning of lodgepole pine (*Pinus contorta*) stands at two stages of succession: Short-term changes in forest birds. Wildlife Research – In Review.

Bibby, C.J., N.D. Burgess, D.A. Hill, and S.H. Mustoe. 2000. Bird census techniques, 2nd edition. Academic Press. London England.

Cooper, R.J., L.A. Wood, J.G Gannon, and R.R Wilson. 2009. Effect of timber harvest and other factors on a floodplain forest indicator species, the Prothonotary Warbler. Wetlands 29: 574-585.

Fiske, I. and R. Chandler. 2010. unmarked: Models for Data from Unmarked Animals. R package version 0.8-1/r555. http://R-Forge.R-project.org/projects/unmarked/

Joseph, L.N., C. Elkin, T.G. Martin, and H.P. Possingham. 2009. Modeling abundance using N-mixture models: The importance of considering ecological mechanisms. Ecological Applications 19:631-642.

Kery, M., J. A. Royle, and H. Schmid. 2005. Modeling avian abundance from replicated counts using binomial mixture models. Ecological Applications 15:1450–1461.

Krebs, C.J. 1999. Ecological Methodology – 2nd edition. Benjamin Cummings Press.

MacKenzie, D.I., J.D Nichols, J.A. Royle, K.H. Pollock, L.L. Bailey, and J.E. Hines. 2006. Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. Academic Press.

MacKenzie, D.I., J.D. Nichols, G.B. Lachman, and S. Droege. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83: 2248-2255.

Marsh, D.M., and P.C. Trenham. 2008. Current trends in plant and animal monitoring. Conservation Biology 22:647-655.

Paul, J.T. Jr. and R.R. Roth. 1983. Accuracy of a version of the spot-mapping census method. Journal of Field Ornithology 54:42-49.

R Development Core Team (2009). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Riddle, J.S., R.A. Mordecai, K.H. Pollock, and T.R. Simons. 2010. Effects of prior detections on estimates of detection probability, abundance, and occupancy. Auk 127: 94-99.

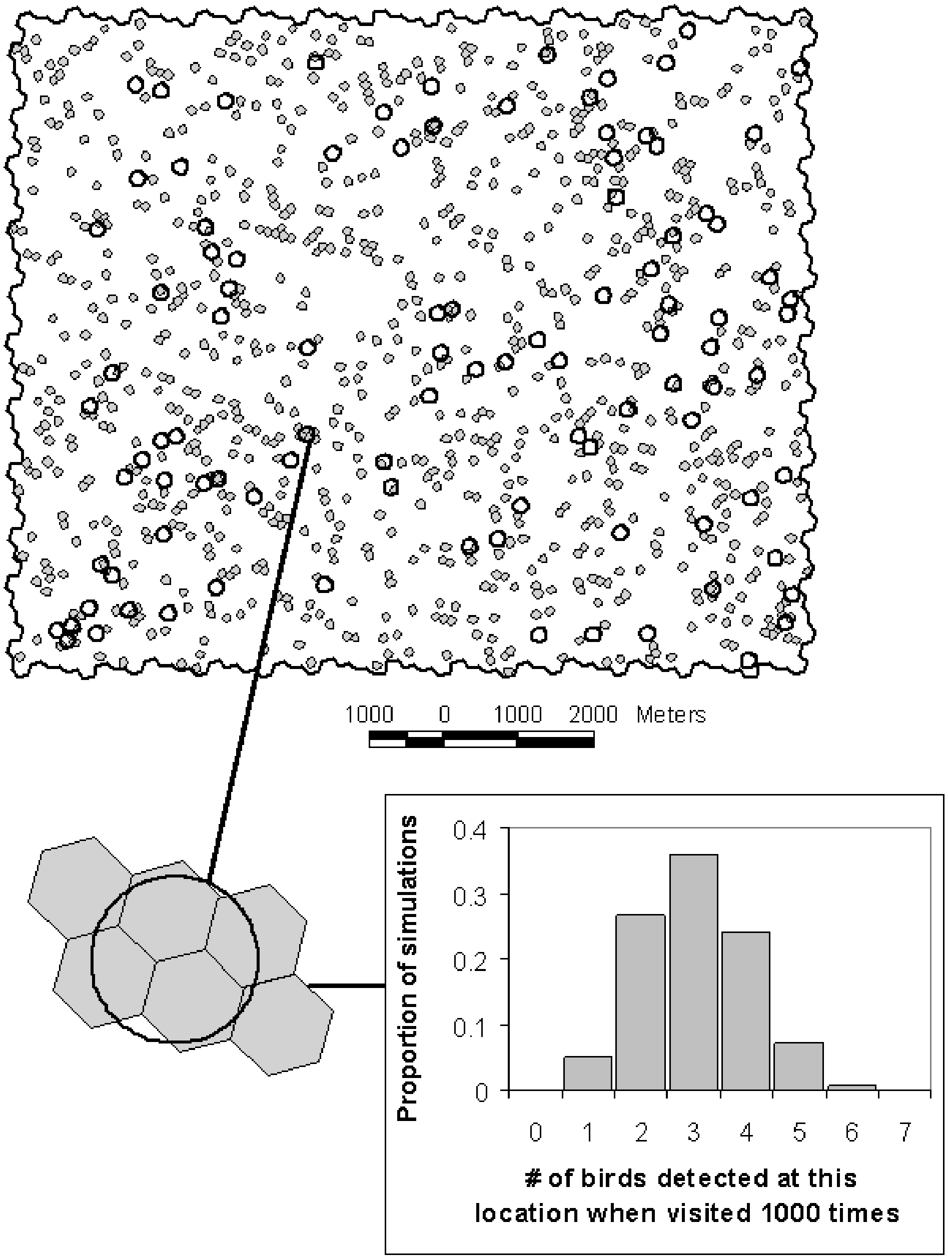
Rota, C.T., R.T. Fletcher Jr., R.M. Dorazio, and M.G. Betts. 2009. Occupancy estimation and the closure assumption. Journal of Applied Ecology 46: 1173-1181.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108–115.

Sperry, J.H., T.L. George, and S. Zack. 2008. Ecological factors affecting response of dark-eyed juncos to prescribed burning. Wilson Journal of Ornithology 120:131-138.

Thompson F.R., D.E. Burhans, and B. Root. 2002. Effect of point count protocol on bird abundance and variability estimates and power to detect trends. Journal of Field Ornithology 73: 141-150.

Verner, J. and K.A. Milne. 1990. Analyst and observer variability in density estimates from spot-mapping. Condor 92:313-325.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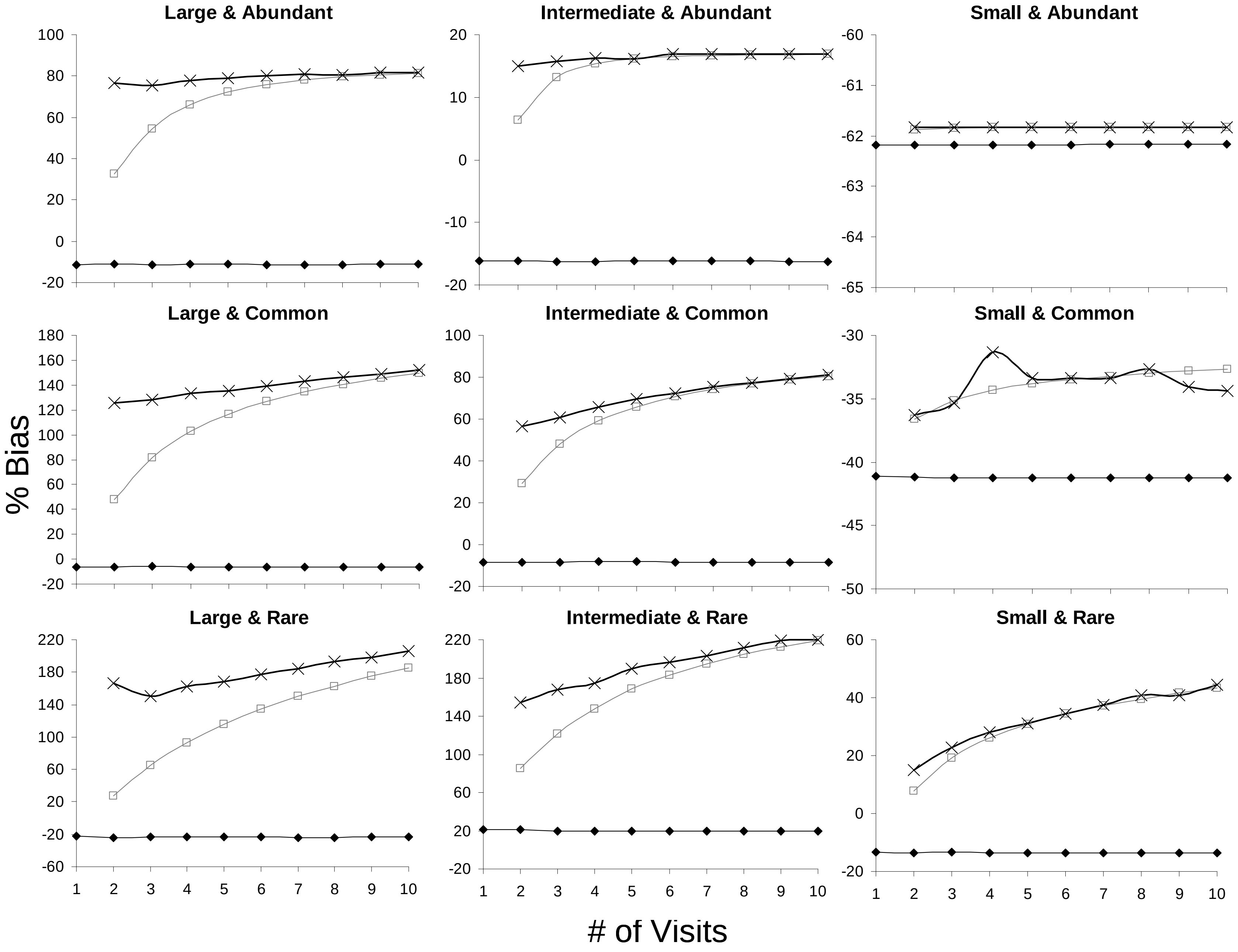
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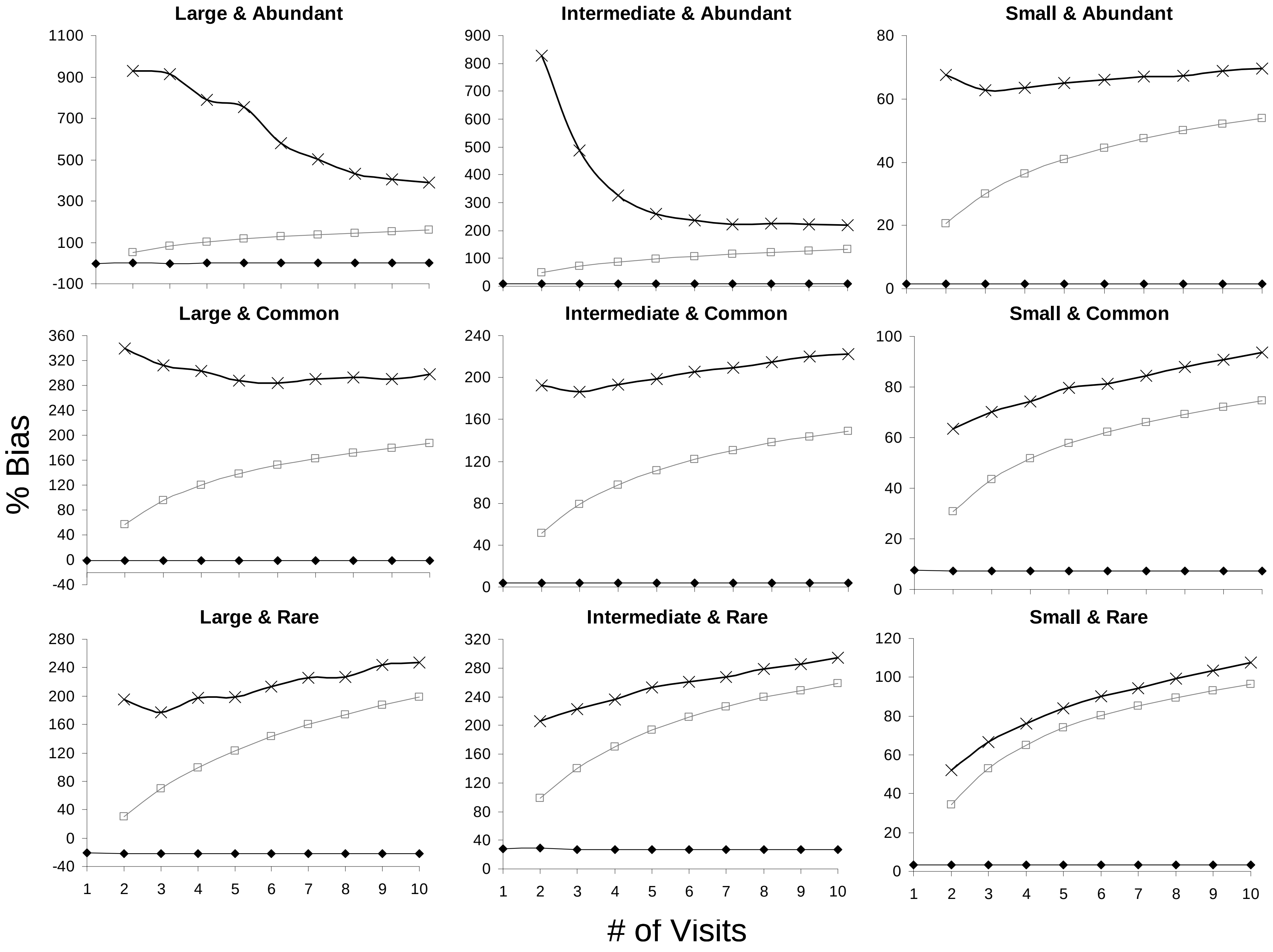
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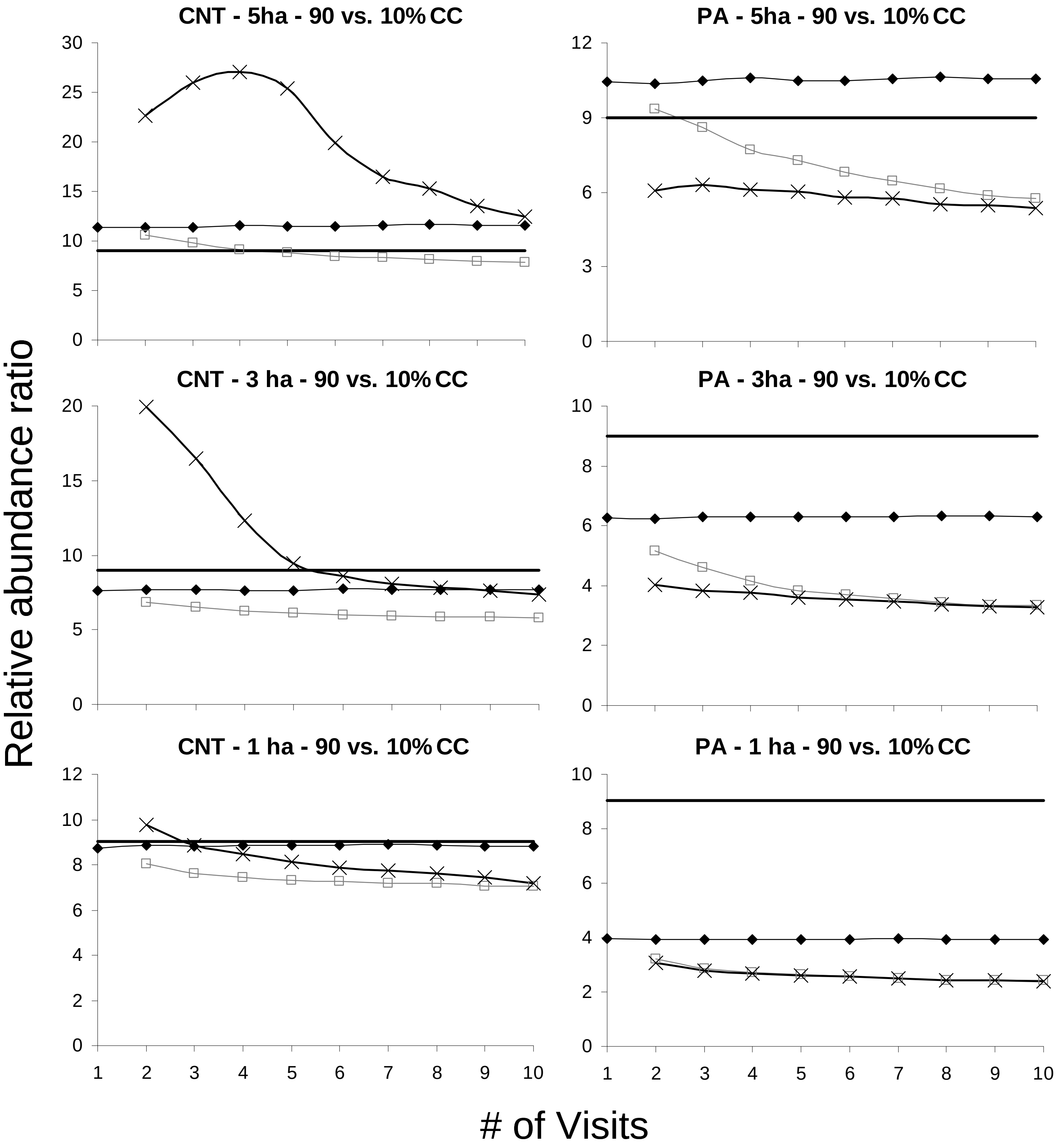
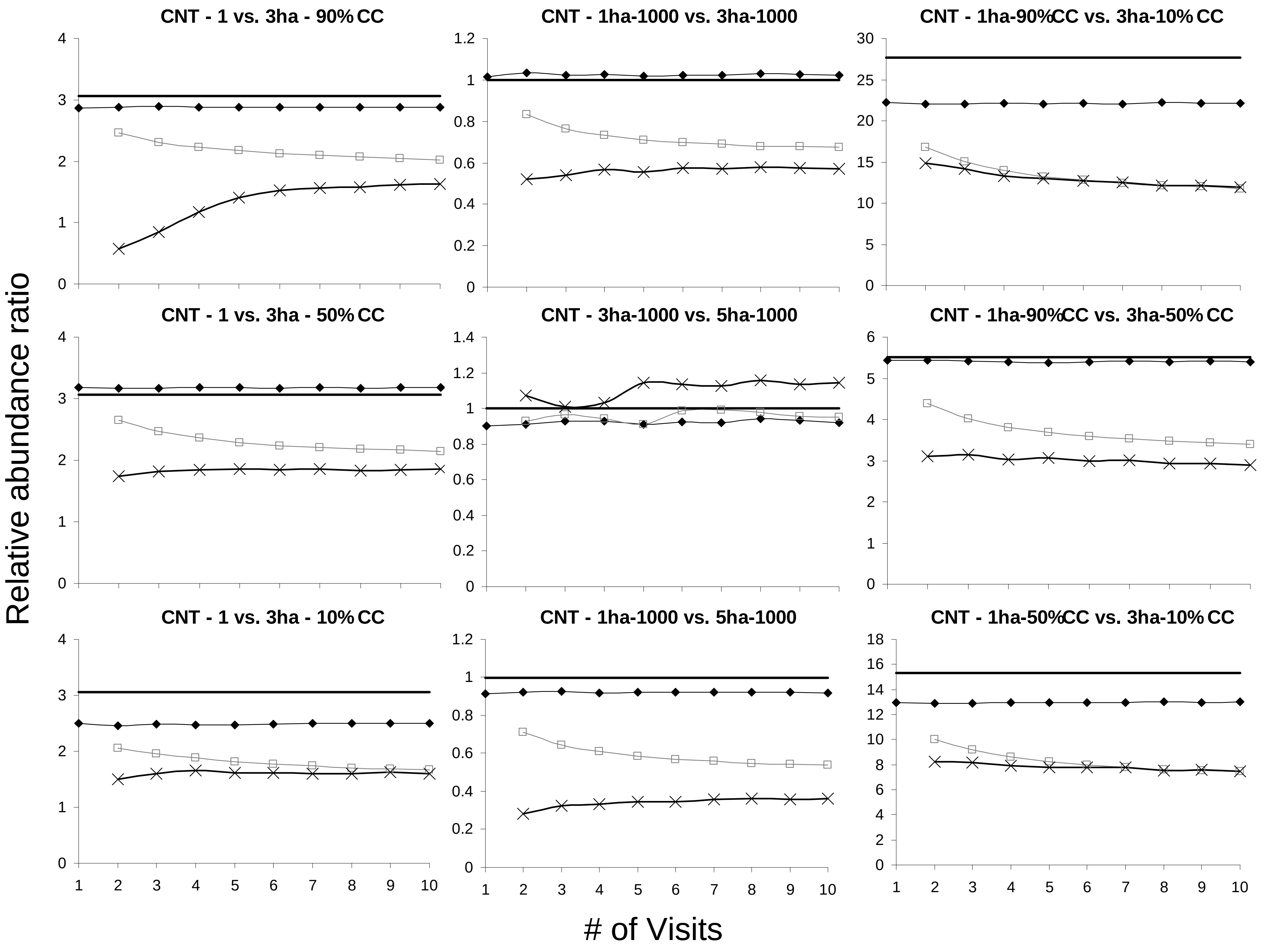
% Bias
# of Visits


CNT - 5ha - 90 vs. 10% CC
PA - 5ha - 90 vs. 10% CC
CNT - 3 ha - 90 vs. 10% CC
PA - 3ha - 90 vs. 10% CC
CNT - 1 ha - 90 vs. 10% CC
PA - 1 ha - 90 vs. 10% CC
0
5
10
15
20
25
30
0
3
6
9
12
0
5
10
15
20
0
2
4
6
8
10
0
2
4
6
8
10
12
0
2
4
6
8
10
1
2
3
4
5
6
7
8
9
10
1
2
3
4
5
6
7
8
9
10
Relative abundance ratio
# of Visits


CNT - 1 vs. 3ha - 90% CC
CNT - 1ha-1000 vs. 3ha-1000
CNT - 1ha-90%CC vs. 3ha-10% CC
CNT - 1 vs. 3ha - 50% CC
CNT - 3ha-1000 vs. 5ha-1000
CNT - 1ha-90%CC vs. 3ha-50% CC
CNT - 1 vs. 3ha - 10% CC
CNT - 1ha-1000 vs. 5ha-1000
CNT - 1ha-50%CC vs. 3ha-10% CC
0
1
2
3
4
0
0.2
0.4
0.6
0.8
1
1.2
1.4
0
5
10
15
20
25
30
0
1
2
3
4
5
6
0
2
4
6
8
10
12
14
16
18
1
2
3
4
5
6
7
8
9
10
Relative abundance ratio
# of Visits

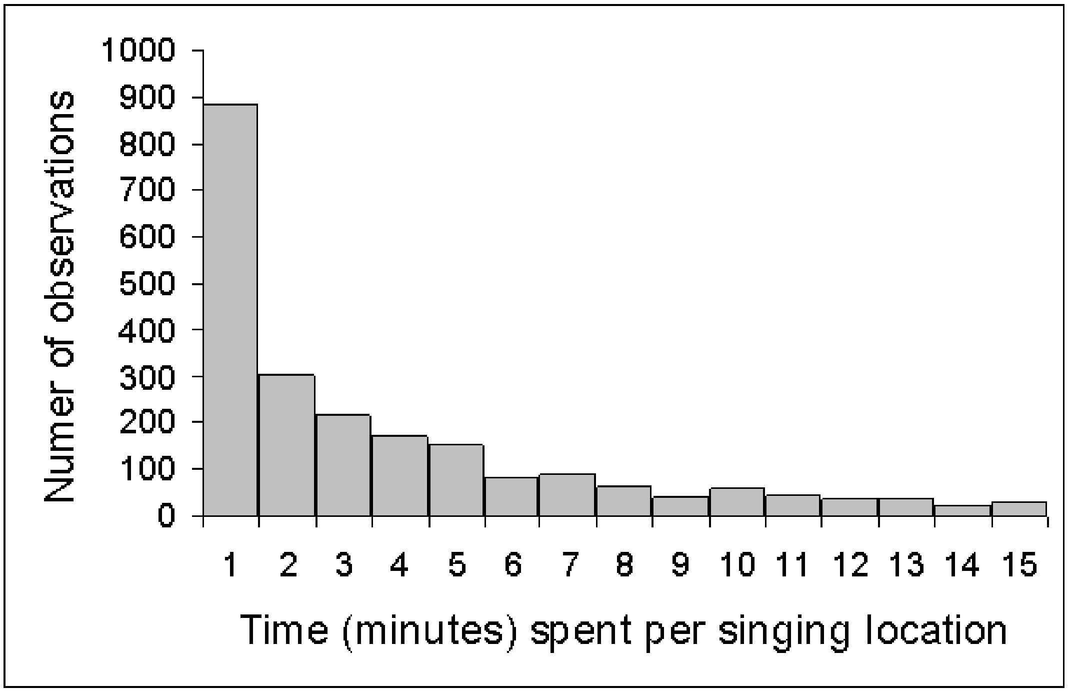

Numer of observations
1000
900
800
700
600
500
400
300
200
100
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Time (minutes) spent per singing location

FIG. 1. Example of a GIS simulation. Map shows bird population at 10% of carrying capacity with individual birds holding non-overlapping 1 hectare territories. Dark circles represent the locations of 100 randomly chosen point count sites. The insert shows a single point count site where multiple territories overlap the sampling area to a partial extent resulting in a violation of closure assumption. Histogram shows the distribution of count values you might expect from a point count site for this location if birds move randomly in their territories

FIG. 2. Median bias (percentage difference of estimated population size from actual population size) with increasing number of repeat visits to a site using detected – not detected data. Solid diamonds show bias when using average frequency of occurrence to calculate density, open squares show bias when using whether a species was detected during any visit, while crosses show bias using occupancy estimation. Results are shown for species with small (1), intermediate (3ha), and large (5ha) territories and for rare (10% of carrying capacity), common (50% of carrying capacity), and abundant species (90% of carrying capacity).

FIG. 3**.** Median bias (percentage difference of estimated population size from actual population size) with increasing number of repeat visits to a site using count data. Solid diamonds show bias when using average count to calculate density, open squares show bias when using maximum number of individuals detected during a visit, while crosses show bias using N-mixture estimation. Results are shown for species with small (1), intermediate (3ha), and large (5ha) territories and for rare (10% of carrying capacity), common (50% of carrying capacity), and abundant species (90% of carrying capacity).

FIG. 4. Relative abundance ratio (density in habitat A/ density in habitat B) for count (left column - CNT) and presence (right column -PA) data. Solid line indicates actual relative abundance ratio. Solid diamonds show relative abundance ratio based on average count or presence, open squares showing maximum presence or count, and crosses showing multiple visit methods. In each panel the territory size is constant but varies as a function of number of visits to a site and the difference density between two habitats (CC = carrying capacity).

FIG. 5**.** Relative abundance ratio (density in habitat A/ density in habitat B) for count data under various scenarios of density and territory size. Solid line indicates actual relative abundance ratio. Solid diamonds show relative abundance ratio based on average count, open squares using maximum count, and crosses N-mixture estimates. In the left column, the territory size of birds is larger in habitat B than A. The total population size is changed as a function of total carrying capacity with a constant relative abundance ratio of 3:1. The middle column has equal numbers of individuals in each habitat but different territory sizes. The right column shows scenarios with different densities of birds in each habitat and different territory sizes.

FIG. 6. Frequency distribution showing number of minutes male Ovenbirds spent singing in a single location based on following color-banded birds for a period of 1 to 5 hours.