



EFFECTS OF PRIOR DETECTIONS ON ESTIMATES OF DETECTION PROBABILITY, ABUNDANCE, AND OCCUPANCY

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ABSTRACT.—Survey methods that account for detection probability often require repeated detections of individual birds or repeated visits to a site to conduct counts or collect presence–absence data. Initial encounters with individual species or individuals of a species could influence detection probabilities for subsequent encounters. For example, observers may be more likely to redetect a species or individual once they are aware of the presence of that species or individual at a particular site. Not accounting for these effects could result in biased estimators of detection probability, abundance, and occupancy. We tested for effects of prior detections in three data sets that differed dramatically by species, geographic location, and method of counting birds. We found strong support (AIC weights from 83% to 100%) for models that allowed for the effects of prior detections. These models produced estimates of detection probability, abundance, and occupancy that differed substantially from those produced by models that ignored the effects of prior detections. We discuss the consequences of the effects of prior detections on estimation for several sampling methods and provide recommendations for avoiding these effects through survey design or by modeling them when they cannot be avoided. *Received 27 January 2009, accepted 13 July 2009.*

Key words: abundance, detection probability, MARK, occupancy, PRESENCE, presence–absence, repeated counts, time-of-detection.

Efectos de Detecciones Previas sobre Estimados de Probabilidad de Detección, Abundancia y Ocupación

RESUMEN.—Los métodos de muestreo que explican la probabilidad de detección usualmente requieren detecciones repetidas de aves individuales o visitas repetidas a un sitio para realizar conteos o recolectar datos de presencia-ausencia. Los encuentros iniciales con especies individuales o individuos de una especie podrían influenciar las probabilidades de detección de encuentros subsiguientes. Por ejemplo, los observadores pueden tener una mayor probabilidad de detectar repetidamente una especie o un individuo una vez que están conscientes de la presencia de esta especie o individuo en un sitio en particular. No considerar estos efectos podría conducir a estimadores sesgados de la probabilidad de detección, abundancia y ocupación. Evaluamos los efectos de detecciones previas en tres bases de datos que difirieron dramáticamente en las especies, localización geográfica y método de conteo de las aves. Encontramos una fuerte evidencia (pesos del criterio de información de Akaike de 83% a 100%) a favor de modelos que permitieron incorporar los efectos de detecciones previas. Estos modelos produjeron estimados de la probabilidad de detección, abundancia y ocupación que difirieron substancialmente de aquellos producidos por los modelos que ignoraron los efectos de las detecciones previas. Discutimos las consecuencias de los efectos de las detecciones previas para varios métodos de muestreo y brindamos recomendaciones para evitar estos efectos a través del diseño de los muestreos o mediante su modelado cuando no pueden ser evitados.

HUMAN BEHAVIOR IS influenced strongly by expectation of a specific result (e.g., Bargh et al. 1996, Lee et al. 2006). This is particularly problematic in surveys involving repeated detections of individuals or species at survey locations. After detecting an individual

or species at a survey location, an observer is likely to have increased expectations of detecting that individual or species again at the same location. This increased expectation may result in an increased probability of redetection compared with the probability

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of first detection, which could adversely affect estimates of abundance (N) and occupancy (ψ) if the models do not account for it.

It is now widely acknowledged that wildlife species or individuals of species are not always detected when present at a survey location (Williams et al. 2002, MacKenzie et al. 2006, Royle and Dorazio 2008). Therefore, not accounting for detection probability (p) can lead to underestimation of abundance and of the proportion of sites occupied by a target species (occupancy). Many methods of incorporating detection probability rely on repeated detections of individuals or species in the same survey location to estimate abundance—for example, time-of-detection (Allredge et al. 2007), repeated counts (Royle 2004), or occupancy (e.g., single-season occupancy models; MacKenzie et al. 2006). However, many practitioners may not consider the possibility that the initial detection of an individual or species at a survey location will influence the probability of detecting that individual or species at a later time. Not accounting for the influence of these prior detections may adversely affect estimates of abundance and occupancy. For example, consider a repeated presence–absence survey in which a site is visited 2 times by 1 observer to survey Northern Bobwhite (*Colinus virginianus*), with only 3 days between site visits. On the first visit, an individual is detected. On the second visit, the observer may have a higher probability of detecting Northern Bobwhites because he or she already knows that the site is occupied and expects to detect the species again. This increase in the probability of redetection could result in substantial underestimation of occupancy. In the case of the time-of-detection method, consider a point-count survey for Eastern Towhees (*Pipilo erythrophthalmus*) in which each point count lasts 6 min and is divided into four 1.5-min intervals. If an observer first hears an Eastern Towhee in the second interval, they may focus their attention on this individual and be more likely to hear it in the 2 subsequent intervals. This increase in the probability of redetection is analogous to a “trap-happy” response or behavioral effect in traditional capture–recapture methods and is known to result in underestimation of abundance unless it is accounted for in the model (Williams et al. 2002). Traditionally, behavioral effects in capture–recapture methods are considered to be inherent to the animals that are being captured (i.e., it is the animal that responds to the trap). However, we generally use the term to refer to the observer’s response to the animal. For this reason, we adopt the term “observer-based behavioral effects” to distinguish our use of the term from the more traditional use. Note that in the repeated presence–absence example, the observer-based behavioral effect occurs at the species-level, but in the time-of-detection example, the observer-based behavioral effect occurs at the level of individual birds.

Here, we provide evidence of observer-based behavioral effects in three data sets that differ substantially by species, geographic location, and sampling method. To our knowledge, this is the first demonstration that prior detections affect estimates of occupancy or abundance based on repeated count and presence–absence data. Additionally, we provide methods for testing species-level effects of prior detection in the program PRESENCE (see Acknowledgments).

METHODS

Example data.—The first data set we consider is from a landscape-scale survey of Northern Bobwhite in eastern North Carolina.

Data were collected by the same 2 observers on 24 farms using the time-of-detection method with 10-min point counts divided into four 2.5-min intervals. Detailed descriptions of the survey methods and sites are provided in Riddle (2007) and Riddle et al. (2008b).

The second data set we consider is the Northern Spotted Owl (*Strix occidentalis caurina*) data set available as part of PRESENCE and described in Franklin et al. (1996) and MacKenzie et al. (2003). Observers visited 55 sites in northern California up to 8 times each year, but we restricted our analysis to data from 1997 for simplicity.

The final data set is from a range-wide survey of the eastern population of Painted Bunting (*Passerina ciris*). Observers visited 852 sites up to 3 times. During each 5-min visit, observers recorded each individual encountered within a 75-m radius. The same observer conducted all counts at a particular site. Repeated visits to a site occurred either on separate days or during the same day but were separated by at least 6 h. A detailed description of survey methods can be found online (see Acknowledgments).

Analysis.—The Northern Bobwhite data were analyzed in the program MARK using the “Huggins closed captures” option (Huggins 1989, 1991; White and Burnham 1999). We considered the following three models for our purposes here: $M_{b(\text{tod})}$ (observer-based behavioral effect at the individual level), $M_{t(\text{tod})}$ (time effect), and $M_{0(\text{tod})}$ (constant detection probability). Note the “(tod)” component of the subscript, which indicates that these models are from time-of-detection data.

The Northern Spotted Owl data were analyzed in PRESENCE using the “single-season occupancy” option. To test for species-level observer-based behavioral effects, we used a simple indicator variable as a sampling covariate to indicate whether 1 or more individuals had been detected previously, as recommended by MacKenzie et al. (2004). For example, the site history 0, 0, 1, 1, 1 for the Northern Spotted Owl occupancy data would have sampling covariates 0, 0, 0, 1, 1 to indicate that prior exposure had not occurred on visits 1–3 but had occurred by visits 4 and 5 because the species was initially detected on visit 3. We considered the following 3 models for this data set: $M_{b(\text{occ})}$ (observer-based behavioral effect at the species level), $M_{t(\text{occ})}$, and $M_{0(\text{occ})}$. Note the “(occ)” component of these subscripts, which indicates that these models are from the repeated occupancy surveys.

The Painted Bunting data were analyzed in PRESENCE using the “Royle biometrics” option (Royle 2004). Again, we used a simple indicator variable as a sampling covariate to indicate prior detection of 1 or more individuals. For example, the site history 1, 2, 0 for Painted Buntings would have sampling covariates 0, 1, 1 to indicate that prior exposure had not occurred on visit 1 (not possible) but had occurred for all subsequent visits because the species was initially detected on the first visit. We considered the following three models for this data set: $M_{b(\text{rc})}$ (observer-based behavioral effect at the species level), $M_{t(\text{rc})}$, and $M_{0(\text{rc})}$. Note the “(rc)” component of the subscript, which indicates that these models are from the repeated-counts data set.

Our rationale for including an M_0 and M_b model in each model set was to provide a comparison of models that assumed constant detection probability (M_0) with those that allow subsequent detection probabilities to differ from initial detection probabilities (M_b). The inclusion of an M_t model in each model set was

TABLE 1. Model-selection results for Northern Bobwhite, Northern Spotted Owl, and Painted Bunting data sets.

Data set	Model	AIC	Δ AIC	AIC weight	Model likelihood	Number of parameters	Deviance
Northern Bobwhite	$M_{b(\text{tod})}$	2,493.50	0.00	1.000	1.000	2	2,489.50
	$M_{t(\text{tod})}$	2,519.33	25.83	0.000	0.000	4	2,511.33
	$M_{0(\text{tod})}$	2,523.95	30.45	0.000	0.000	1	2,521.95
Northern Spotted Owl	$M_{b(\text{occ})}$	281.16	0.00	0.9754	1.000	3	275.16
	$M_{0(\text{occ})}$	289.31	8.15	0.0166	0.0170	2	285.31
	$M_{t(\text{occ})}$	290.76	9.60	0.0008	0.0082	9	272.76
Painted Bunting	$M_{b(\text{rc})}$	2,623.99	0.00	0.8338	1.0000	3	2,617.99
	$M_{0(\text{rc})}$	2,627.65	3.66	0.1337	0.1604	2	2,623.65
	$M_{t(\text{rc})}$	2,630.48	6.49	0.0325	0.039	4	2,622.48

to ensure that M_b models were detecting a systematic increase in redetection probability and not just an increase in overall detection probability over the course of each survey. Again, we emphasize that the M_b model for the Northern Bobwhite data set represents an increase in the redetection probability for individual animals, but the M_b models for the Northern Spotted Owl and Painted Bunting data sets represent an increase in the redetection probability at the species level. For all model sets, we used Akaike's information criterion (AIC) for model selection and inference (Burnham and Anderson 2002).

RESULTS

Model $M_{b(\text{tod})}$ was the top model for the Northern Bobwhite time-of-detection models, with 100% of the AIC weight (Table 1). Estimates of N and p are provided in Table 2. $M_{b(\text{occ})}$ was the top model for Northern Spotted Owl occupancy models, with >97% of AIC weight (Table 1). Estimates of ψ and p for all Northern Spotted Owl models are provided in Table 3. $M_{b(\text{rc})}$ was the top model for Painted Bunting abundance models, with 83% of the AIC weight (Table 1). Estimates of N and p for all Painted Bunting models are provided in Table 4.

Probability of subsequent detections increased in all data sets after an initial detection. In other words, the M_b models took the form of a trap-happy response in every case. The probability of detection increased by 47% from 0.45 to 0.66 for Northern Bobwhite. The probability of detection increased by 68% from 0.41 to 0.69 for Northern Spotted Owl. The probability of detection increased by 29% from 0.31 to 0.40 for Painted Bunting. M_0 models that did not account for observer-based behavioral effects had detection probability estimates of 0.59, 0.59, and 0.4 for Northern Bobwhite, Northern Spotted Owl, and Painted Bunting, respectively.

DISCUSSION

There was strong support for a prior detection effect on detection probability in all data sets. As expected, the probability of redetection increased after an initial detection. The strong evidence of this pattern in three surveys with different methodologies, geographic locations, and target species suggests that this pattern may be common in surveys that use individual detection or site histories.

Consequences in time-of-detection surveys.—In time-of-detection surveys, the consequences of not accounting for individual-level observer-based behavioral effects when they occur (i.e., not using an M_b model when observer-based behavioral effects are present) depend on whether the probability of redetection is higher or lower than the probability of initial detection. When the probability of redetection is higher than initial detection (as in our Northern Bobwhite example), abundance is underestimated. For example, the abundance estimate for Northern Bobwhite was ~7.3% lower in the $M_{0(\text{tod})}$ model than in the $M_{b(\text{tod})}$ model. Again, this is analogous to a trap-happy response in classic M_b capture-recapture models, except that in this example it is the observer (trap) that is responding to the organism. It is also possible for the probability of redetection to be lower than initial detection (e.g., an observer may ignore or tune out an individual after an initial encounter). This is analogous to a “trap-shy” response and would result in overestimated abundance (Williams et al. 2002). However, we expect that this scenario is much less common than that of elevated redetection probabilities. For example, in a preliminary analysis of detection histories from 12 Breeding Bird Survey (BBS) routes in North Carolina collected by 6 observers using the time-of-detection method, we found strong evidence of elevated redetection probabilities for 9 of 10 focal species, including American Robin (*Turdus migratorius*), Carolina Wren

TABLE 2. Estimates (\pm SE) of abundance (N) and detection probability (p) for Northern Bobwhite models.

Model	\hat{N}	\hat{p}					
		Initial	Subsequent	Interval 1	Interval 2	Interval 3	Interval 4
$M_{b(\text{tod})}$	287.84 \pm 9.29	0.45 \pm 0.04	0.66 \pm 0.02	NA	NA	NA	NA
$M_{t(\text{tod})}$	268.09 \pm 2.95	NA	NA	0.51 \pm 0.03	0.64 \pm 0.03	0.62 \pm 0.03	0.61 \pm 0.03
$M_{0(\text{tod})}$	268.33 \pm 3.00	0.59 \pm 0.02	NA	NA	NA	NA	NA

TABLE 3. Site-level estimates (\pm SE) of occupancy (Ψ) and detection probability (p) for Northern Spotted Owl models.

Model	$\hat{\Psi}$	\hat{p}										
		Initial	Subsequent	Visit 1	Visit 2	Visit 3	Visit 4	Visit 5	Visit 6	Visit 7	Visit 8	
$M_{b(occ)}$	0.66 ± 0.08	0.41 ± 0.08	0.69 ± 0.11	NA	NA							
$M_{0(occ)}$	0.62 ± 0.07	0.59 ± 0.04	NA	NA								
$M_{t(occ)}$	0.63 ± 0.07	NA	NA	0.40 ± 0.08	0.58 ± 0.09	0.58 ± 0.09	0.57 ± 0.11	0.73 ± 0.10	0.80 ± 0.10	0.57 ± 0.19	1.00 ± 0.00	

(*Thryothorus ludovicianus*), Common Yellowthroat (*Geothlypis trichas*), Eastern Towhee, Eastern Bluebird (*Sialia sialis*), Indigo Bunting (*Passerina cyanea*), Northern Mockingbird (*Mimus polyglottos*), Northern Cardinal (*Cardinalis cardinalis*), and Red-eyed Vireo (*Vireo olivaceus*) (J. D. Riddle et al. unpubl. data).

When repeated samples are closely spaced, as time intervals in time-of-detection surveys are, other behavioral patterns (e.g., singing bouts) could also contribute to increased redetection probabilities. Depending on the length and frequency of the behavior, recurring behaviors could appear to be observer-based behavioral effects. However, we believe that in most cases, the observer-based behavioral effects are a more pervasive sampling issue. For example, the 9 aforementioned species from our BBS work do not have identical vocalization patterns, yet there is substantial support for $M_{b(tod)}$ models for each species. Regardless of the relative contribution of observer-based behavioral effects and recurring behaviors (if present), when behavioral effects are present, the $M_{b(tod)}$ model we present is the most appropriate way to obtain estimates of abundance.

Consequences in repeated presence-absence surveys.—Estimates of occupancy will be artificially low for models that use presence-absence data to estimate occupancy and do not account for positive behavioral effects (either observer-based or traditional) when they occur. For example, the estimate of occupancy for Northern Spotted Owl was 6.5% lower in the $M_{0(occ)}$ model than in the $M_{b(occ)}$ model. In occupancy models that use presence-absence data, the probability that a site is occupied but the species is never detected is calculated on the basis of detections at occupied sites. If there is a higher detection probability for redetections, the overall probability of detection from those occupied sites will be greater than the probability of detection at occupied sites where the species is never detected. This will result in an artificially low estimate of the probability that no individuals are detected at an occupied site.

Consequences in repeated-count surveys.—Unlike occupancy models, which estimate the probability of detecting a species (i.e., at least 1 individual of that species), repeated-count models estimate the probability of detecting an individual. Therefore, counts

at every site are corrected for the expected number of unobserved individuals. The consequences of ignoring effects of prior detection on repeated counts are complex. In our Painted Bunting example, the estimate of abundance was 14.5% lower in the $M_{0(rc)}$ model than in the $M_{b(rc)}$ model. However, preliminary simulations suggest that when there is an increased probability of redetection, the amount and direction of under- or overestimation in abundance from repeated-count models depends on initial detection probability and site-specific abundance (R. S. Mordecai unpubl. data).

Species versus individual effects in repeated simple counts and presence-absence surveys.—With respect to repeated counts and presence-absence surveys, we have focused here on species-level effects of prior detections. However, individual-level effects of prior detections, like those observed in the Northern Bobwhite example, may occur when repeated visits are closely spaced in time. Species-level effects occur when an observer is more likely to detect a species because they expect the species to occur at a site. Individual-level effects occur when an observer is more likely to detect an individual because they already know its general location. For example, imagine a 5-min survey that is split into 5 back-to-back 1-min counts. Once an observer detects an individual in a specific location during the first minute, the observer will expect to detect that individual again in the same general location.

Individual effects also could result in substantial under- or overestimation of occupancy and abundance from occupancy models. Furthermore, strong support for species-effects models may actually represent an individual effect. The identity of individuals is typically not known in occupancy models, and without information on individual identity there is no way to separate species effects from individual effects. Separating species and individual effects is not essential for presence-absence data, because the approach described here essentially specifies a removal-based occupancy model (e.g., Mordecai et al. 2009) because data collected after the first detection of a species at a site are not used to estimate occupancy. However, individual effects are particularly problematic for repeated-count data because our proposed approach to account for species effects does not remove the influence induced

TABLE 4. Site-level estimates (\pm SE) of abundance (N) and detection probability (p) for Painted Bunting models.

Model	\hat{N}	\hat{p}				
		Initial	Subsequent	Visit 1	Visit 2	Visit 3
$M_{b(rc)}$	0.63 ± 0.07	0.31 ± 0.04	0.40 ± 0.07	NA	NA	NA
$M_{0(rc)}$	0.55 ± 0.04	0.40 ± 0.2	NA	NA	NA	NA
$M_{t(rc)}$	0.55 ± 0.04	NA	NA	0.38 ± 0.03	0.38 ± 0.04	0.41 ± 0.04

by individual effects. In repeated-count models, all data are used to estimate abundance. Our approach assumes that once a species is detected at a site, the detection probability changes in the same way for all individuals. If prior knowledge of an individual's location results in artificially high detection-probability estimates, abundance estimates will be artificially low. We are currently investigating the utility of removal-based repeated-count models in removing potential individual effects in these circumstances.

Situations where the effect of prior detection could be particularly problematic.—The strongest individual-level effects of prior detection are most likely in time-of-detection surveys with low to moderate numbers of individuals, because observers will likely have difficulty in tracking individuals at survey locations with high densities of target species. Note that the latter situation also violates an important assumption of the time-of-detection method, that individual animals are tracked accurately. Stronger individual effects also are expected in environments where individual animals are located and tracked easily. For example, Alldredge et al. (2007) found less support for M_b models for species sampled in heavily forested environments.

The strongest species-level effects for repeated counts will occur when the same observer repeatedly visits the same sites during a given year or season to collect count data for a small number of rare species. Observers will expect common species to be present at many sites; therefore, a previous detection will likely have a small effect on the expectation of redetection. By contrast, observers will expect rare species at only a limited number of sites, and a prior detection could greatly influence their expectation of redetection. Note that for many other reasons, rare species are often promoted as prime candidates for sampling with presence-absence methods (Pollock 2006). However, we want to emphasize again that observer-based behavioral effects are relatively easy to account for (regardless of whether they occur at the species or individual level) with presence-absence methods, whereas observer-based behavioral effects at the individual level are potentially more problematic when repeated counts are used.

Species effects also can occur across multiple years when the same observer repeatedly surveys a site. For example, in the BBS, the same observers typically visit the same sites for many years. During their first year surveying a site, observers often detect fewer birds than in subsequent years (Kendall et al. 1996). This could be caused by a species-level observer-based behavioral effect resulting from an observer's lack of knowledge about the bird species typically present along their route during the first year of sampling.

In repeated counts or presence-absence surveys, we would expect the strongest individual effects to occur when visits are closely spaced in time. Shorter periods between repeated counts or presence-absence surveys could result in both a higher probability that the organism is in the same general location as the previous visit and a higher probability that the observer remembers that location. In the most extreme case, where surveys are back to back, an individual could begin vocalizing or visibly moving at the end of the first survey and continue into the beginning of the second survey.

Survey-design recommendations.—There may be few practical survey-design recommendations that will reduce the effects of prior detections for time-of-detection surveys. This is especially true given that the very situations in which time-of-detection methods

may be most effective (environments where individuals can easily be tracked and survey locations with low to moderate densities of each target species) are precisely the situations in which observer-based behavioral effects may be most pronounced. Given the pervasiveness of observer-based behavioral effects in time-of-detection data sets, practitioners may be tempted to always use removal methods (e.g., Farnsworth et al. 2002). We would caution against this because there are unique situations when M_b models are not favored (e.g., Riddle et al. 2008a). Using time-of-removal surveys instead of time-of-detection surveys when observer-based behavioral effects are not present will result in less efficient estimates of detection probability and abundance (Alldredge et al. 2007). Fortunately, individual-level observer-based behavioral effects can be detected and dealt with easily via established M_b models using tools like MARK. In addition, time-of-detection data can always be analyzed as time-of-removal data.

Tradeoffs exist among the number of repeated counts or presence-absence surveys necessary for desired statistical power, the level of independence between sites due to spacing, and closure or constant occupancy rates during a sampling season when using repeated presence-absence methods. Certain aspects of these tradeoffs will depend on the species under investigation and available resources. However, there are some general recommendations that practitioners should follow to avoid the effects of prior detections of species on repeated-count or presence-absence data.

Ideally, practitioners should avoid protocols in which the same observer revisits the same survey locations. This is especially important when the number of total survey locations is small (i.e., fewer sites will likely make any prior detections easier to remember). Instead, observer assignments should be randomized or rotated, when possible, such that each observer visits a site only once. Note that rotating observers has the added benefit of reducing observer-induced heterogeneity among sites (MacKenzie and Royle 2005). In some studies, it also may be possible to reduce observer expectations by renaming sampling locations or providing different approach notes for subsequent visits. In addition to the steps described above, researchers should take precautions to limit the transfer of information on species occupancy at each site to reduce species-level effects of prior detection. When alternating observers, each observer should avoid discussing the results of specific visits with others who may perform subsequent visits to the same site.

If logistical constraints require observers to revisit the same sites, it may be helpful to increase the amount of time that elapses between visits. Although the optimal time between visits will vary by species behavior (e.g., vocalization and movement rates) and sampling logistics, the goal should be to ensure that observers are not biased by knowledge of the previous locations of individuals. Fortunately, when species-level effects cannot be avoided via survey design, they can at least be dealt with according to the methods we have demonstrated here.

Future work.—One reviewer commented that the evidence we found of observer-based behavioral effects in multiple species sampled with multiple techniques was only circumstantial and that true experiments would be necessary to provide direct proof that prior detections can result in increased probabilities of redetection. Although such experiments would be difficult with real bird populations, demonstrating purely observer-based behavior effects would be relatively simple with a field-based system for

simulating bird populations (e.g., Simons et al. 2007). In a simulated system in which birds are singing at a constant rate, any increase in redetection probabilities would be attributable to observed-based behavioral effects.

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