National Quail Symposium Proceedings

Volume 7

Article 75

2012

Effect of Abundance and Survey Protocol on Estimates of Occupancy and Detection Probability for Northern Bobwhites

Andrew D. Crosby
Oklahoma State University

R. Dwayne Elmore
Oklahoma State University

Recommended Citation

Crosby, Andrew D. and Elmore, R. Dwayne (2012) "Effect of Abundance and Survey Protocol on Estimates of Occupancy and Detection Probability for Northern Bobwhites," *National Quail Symposium Proceedings*: Vol. 7 , Article 75.
Available at: http://trace.tennessee.edu/nqsp/vol7/iss1/75

EFFECT OF ABUNDANCE AND SURVEY PROTOCOL ON ESTIMATES OF OCCUPANCY AND DETECTION PROBABILITY FOR NORTHERN BOBWHITES

Andrew D. Crosby[1]
Department of Natural Resource Ecology and Management, Oklahoma State University, 008C Agriculture Hall, Stillwater, OK 74078, USA

R. Dwayne Elmore
Department of Natural Resource Ecology and Management, Oklahoma State University, 008C Agriculture Hall, Stillwater, OK 74078, USA

ABSTRACT

We compared estimates of occupancy of northern bobwhite (*Colinus virginianus*) between areas with relatively low and high abundance using single-survey and multiple-survey protocols, with and without accounting for detection probability, and investigated how time during the breeding season affected detection probability in Oklahoma, USA, in 2009–2011. Estimates of occupancy and detection probability increased as the number of survey occasions increased. Detection probability was significantly higher in the area of high abundance ($P \leq 0.001$), and increased as the breeding season advanced from mid-May to late July. Accounting for detection probability increased occupancy estimates by 31% in the low-abundance area but only 1.9% in the high abundance area when using 3 survey occasions per year. Managers using occupancy to detect changes in bobwhite populations should use ≥ 4 survey occasions per year to ensure accurate estimates of both occupancy and detection probability.

Citation: Crosby, A. D., and R. D. Elmore. 2012. Effect of abundance and survey protocol on estimates of occupancy and detection probability for northern bobwhites. Proceedings of the National Quail Symposium 7:127–133.

Key words: BBS, call counts, *Colinus virginianus*, detection probability, monitoring, occupancy, Oklahoma, PAO, population

INTRODUCTION

Many published reports of northern bobwhite population dynamics have relied on the number of calling males heard during spring and summer survey stops as their source of data (Cram et al. 2002, Lusk et al. 2002, Veech 2006, Twedt et al. 2007, Spinola and Gates 2008). This method, known as the call-count index, is an efficient way to index long-term trends in bobwhite populations over large areas (Church et al. 1993, Hansen and Guthery 2001), but may not be an accurate reflection of the state of the population in any given year or of short-term trends in abundance (Norton et al. 1961, Schwartz 1974, Hansen and Guthery 2001) due to a lack of a well-defined relationship between the number of calling males heard and bobwhite abundance. Additionally, many of these surveys are conducted only once per year and do not consider the probability of failing to detect bobwhites even when they are present (Veech 2006, Spinola and Gates 2008). The number of bobwhites heard during a given survey can vary substantially due to survey-specific factors such as time of year, time of day, cloud cover, temperature, and wind speed (Robel et al. 1969, Hansen and Guthery 2001), as well as simple random chance. Thus, given the deficiencies in using call counts as a short-term index of bobwhite abundance, it is useful to consider alternative variables in monitoring efforts directed at describing the current status and short-term trends in bobwhite populations. Proportion of area occupied, or occupancy, is commonly used in monitoring efforts for other species (Zielinski and Stauffer 1996, Trenham et al. 2003, Rhodes et al. 2006), and may offer an alternative.

Occupancy is defined as the proportion of the area or sample sites occupied by the species of interest (MacKenzie et al. 2006) and is often estimated from repeated or unrepeated presence-absence surveys. Traditional presence-absence surveys assume that when a species is not detected at a given site, it is absent from that site (MacKenzie and Royle 2005, MacKenzie et al. 2006) and the occupancy estimate is the proportion of sites where the species was detected. This method does not consider the possibility the species was present but not detected (a 'false absence') and, consequently, the occupancy estimate may be biased low if the species is rare and/or not easily detected (MacKenzie et al. 2002, MacKenzie et al. 2005). Theoretical advances over the last decade have addressed the issue of estimating occupancy when detection probabilities are < 1 (MacKenzie et al. 2002, MacKenzie 2005, MacKenzie et al. 2006). Methods that have been developed use repeat visits to survey sites to estimate the probability of detection of the target species with the goal of estimating the proportion of sites

---

[1] *E-mail: andrew.crosby@okstate.edu*

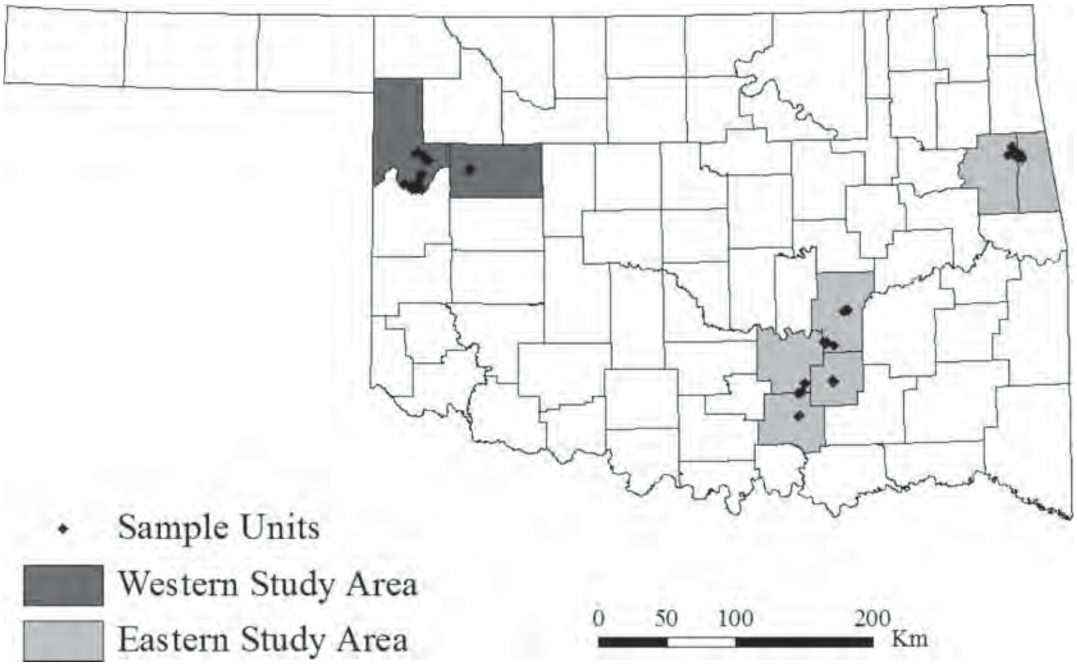

Fig. 1. Study areas and sample units where northern bobwhite surveys were conducted in Oklahoma, USA (2009–2011).

occupied knowing the species can be present yet not detected.

Estimates of bobwhite occupancy may change significantly based on the number of times survey sites are visited per season and whether or not detection probability is considered. Bobwhites, which are normally considered easy to detect, may also have significantly lower detection probabilities in areas where abundance is low as opposed to areas where it is high (Royle and Nichols 2003, Smith et al. 2007). Our objectives were to: (1) compare estimates of occupancy between areas with relatively low and high populations using single-survey and multiple-survey protocols, both with and without accounting for detection probability; and (2) investigate how time during the breeding season affects detection probability. We hypothesized that: (1) multiple surveys would result in significantly higher estimates of occupancy and detection probability than single surveys in both areas; (2) detection probability would be significantly higher in the high-population area; and (3) due to temporal differences in calling rates, a model that allowed detection probability to vary with time during the breeding season would perform better than a model where detection probability remained constant.

STUDY AREA

This study was conducted on properties enrolled in the Quail Habitat Restoration Initiative (QHRI) in Oklahoma, a program funded through the U. S. Department of Agriculture's Environmental Quality Incentives Program (EQIP) to provide cost-share incentives to private landowners for restoring or maintaining bobwhite habitat on their properties, and in control areas not enrolled in the program. We established 2 study areas for the purposes of this analysis that were analyzed separately: eastern and western. The eastern study area included portions of Adair, Cherokee, Hughes, Coal, Johnston, and Pontotoc counties in Oklahoma (Fig. 1). Properties consisted of 10 private ranches and 2 properties owned by The Nature Conservancy. These properties are characterized by a mosaic of tallgrass prairie and cross-timbers or central hardwoods forest. Dominant tree species are oaks (*Quercus* spp.) and hickories (*Carya* spp.), and the most prominent grasses include big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and Indiangrass (*Sorghastrum nutans*). Bobwhite populations within these properties and within the study area were relatively low with an average of 20 bobwhites heard per BBS route between 1966 and 2003 (Sauer et al. 2011) and little existing habitat on the private ranches under study.

The western study area included portions of Ellis and Dewey counties in Oklahoma (Fig. 1). Four private ranches and the Packsaddle State Wildlife Management Area, operated by the Oklahoma Department of Wildlife Conservation, were included in this study area. These properties are dominated by sand shinnery oak (*Quercus havardii*) and sand sage (*Artemisia filifolia*) plant communities. Dominant grasses are little bluestem and Indiangrass, and sand plum (*Prunus angustifolia*) is a common shrub. Bobwhite populations within these properties and in this study area were relatively more common than in the eastern study area with an average of 46 bobwhites heard per BBS route between 1966 and 2003 (Sauer et al. 2011), and large areas of habitat within the properties under study. We believe the differences in relative abundance as measured by the BBS were sufficient to test the impact abundance has on occupancy modeling while recognizing abundance varies greatly between years and the BBS is a coarse method of measuring absolute abundance.

METHODS

Bobwhite Surveys

We located 23 sample units in the eastern study area where habitat restoration was scheduled to occur and subjectively located 8 sample units in control areas, 2 that were closed-canopy forest and 6 that consisted of existing bobwhite habitat, for a total of 31 established sample units. This design was chosen as there was an ongoing bobwhite research project in the area that included treatments to create useable space for bobwhites. The necessity of specifically sampling restoration and maintenance areas precluded completely random placement of the sample units but, because our purpose was to census bobwhites within the sample units, rather than describe populations in the region, this was not considered detrimental to the analysis. We randomly located 1 to 4 sample units within pastures in the western study area where prescribed burning to maintain bobwhite habitat was scheduled to occur, for a total of 27 established sample units. We sampled 31 sample units in 2009 and 2010, and 29 sample units in 2011 in the eastern study area, and 27 sample units in 2009 and 2010, and 26 sample units in 2011 in the western study area. Differences in number of sample units between years were due to loss of access.

Each sample unit consisted of a 400-m radius circle where call counts were conducted from the center point (Stoddard 1931, Hansen and Guthery 2001). Center points of all sample units were $\geq$ 800 m apart, and sample units did not include agriculture or human development. We conducted call counts at each sample unit 3 times during the breeding season (mid-May–late Jul) at intervals of 2–3 weeks in 2009–2011, where all bobwhites seen or heard within 400 m of the sample unit center point during a 5-min period were recorded. We assumed the detection probability for bobwhites was $\geq$ 0.5, and used 3 surveys per season as recommended by MacKenzie and Royle (2005). Call counts were completed between 0.5 hr before and 4.5 hrs after sunrise; we did not sample when it was raining or when wind speeds exceeded 20 km/hr (Winter et al. 2005). We grouped sample units based on geographic proximity and surveyed one group per day, alternating the order in which both sample units and groups were surveyed to avoid detection bias due to time of day or time during the breeding season.

Occupancy Estimation and Survey-specific *p*

Our methods were similar to those used by Bailey et al. (2004) in an assessment of occupancy and detection probabilities for terrestrial salamanders in Great Smokey Mountains National Park, USA. We began with the assumption that probabilities of occupancy (ψ) and detection (p) were equal across times and sites, $\psi(.)$ $p(.)$. This constant model is not necessarily the most accurate representation of the system, but our objective was to compare the impacts of different sampling protocols on the parameters of interest; the inclusion of additional variables may have confounded our results (Bailey et al. 2004). Occupancy modeling is based on closed-population capture-recapture methods and assumes sample sites are closed to changes in occupancy status during the course of the surveys (MacKenzie et al. 2006). It is probable that individual bobwhites moved into or out of sample units during the sample period but, we assumed the limited breeding-season movements of bobwhites (Murphy and Baskett 1952, Fies et al. 2002, Townsend et al. 2003) would cause the occupancy status of sample units to remain constant during our survey periods despite some individual movements. The western study area represented a region where bobwhites were relatively common and the eastern study area represented a region where bobwhites were relatively uncommon for all statistical comparisons. We treated year as a random variable and combined data for all years.

We compared estimates of ψ and p using 3 different 'sampling protocols' reflecting different survey intensities (1-, 2-, or 3-surveys per season), and 2 different estimation procedures for ψ, separately for the eastern study area and the western study area. We randomly selected first 1 and then 2 of the survey occasions from each sampling unit in each year to represent the 1- and 2-survey protocols, respectively. All 3 sampling occasions combined were used to represent the 3-survey protocol. We first calculated the proportion of sample units where the species was observed, ψ(obs), which is a naïve estimate of occupancy that does not account for detection probability, using 1-, 2-, and 3-sampling occasions per year. We then estimated $\psi(.)$ and $p(.)$ from occupancy models accounting for detection probability using both 2 and 3 sampling occasions. Our estimate of the precision of $\psi(.)$ and $p(.)$ was the standard error of the estimate divided by the estimate, and precision was considered good if the result was < 0.3 (Bailey et al. 2004). We compared ψ(obs) between each protocol using McNemar's Chi-square test for paired samples (Conover 1999), and compared $p(.)$ between the 2 study areas using a Chi-square test on proportions. We considered all inferential tests with $P < 0.05$ to be significant.

The literature indicates calling rates change throughout the breeding season (Rosene 1957, Robel et al. 1969, Hansen and Guthery 2001); thus, we tested the hypothesis that a model that allowed detection probability to vary with time during the breeding season would perform better than a model where detection probability remained constant by modeling detection probability as a function of Julian day, $\psi(.)$ p(day), and comparing it to the model where detection probability was constant, $\psi(.)$ $p(.)$, using Akaike's Information Criterion (Anderson 2008). We interpreted a change in the AIC score (ΔAIC) of > 4 to indicate the first-ranked model was significantly better than the second-ranked model (Anderson 2008). Estimation of ψ and p, as well as AIC model selection, was done using Program PRESENCE (Version 4.0, http://www.mbr-pwrc.usgs.gov/software/presence.html). We conduct-

Table 1. Observed occupancy rates [ψ(obs)], estimates of occupancy [ψ(.)], and detection probability [*p*(.)] and their associated standard errors from occupancy models accounting for detection probability, using 1-, 2-, and 3-survey occasions per year for northern bobwhites in an area where populations were relatively low (Eastern) and an area where they were relatively high (Western) in Oklahoma, USA (2009–2011).

						Precision[b]		
	Area	ψ(obs)	ψ(.)	SE	*p*(.)	SE	ψ(.)	*p*(.)
One survey[a]	Eastern	0.075						
	Western	0.711						
Two surveys	Eastern	0.194	0.970	0.870	0.105	0.097	0.897	0.924
	Western	0.901	0.997	0.046	0.708	0.047	0.046	0.066
Three surveys	Eastern	0.226	0.296	0.066	0.396	0.082	0.223	0.207
	Western	0.938	0.956	0.028	0.732	0.032	0.029	0.044

[a] *p* cannot be estimated from only 1-survey occasion and only the (obs) values were calculated.

[b] Precision = [SE$_{estimate}$/estimate].

ed all other statistical analyses using Program R (R Version 2.13.1, http://cran.r-project.org).

RESULTS

We detected bobwhites on 96 of 174 sampling occasions at 58 individual sample units in 2009–2011. Twenty-one detections occurred in the eastern study area and 75 occurred in the western study area. The standard presence-absence analysis showed that ψ(obs) increased as survey intensity increased (Table 1). The McNemar's test showed statistically significant increases between 1-survey and 2- or 3-survey protocols, but not between 2- and 3-survey protocols for both areas. Bobwhites were less common in the eastern study area and ψ(obs) increased 201% between the 1- and 3-survey protocols ($P \leq 0.001$) but only increased 16.5% between the 2- and 3-survey protocols ($P = 0.248$). Bobwhites were more common in the western study area and there was an increase in ψ(obs) of 32% between the 1- and 3-survey protocols ($P \leq 0.001$), and an increase of 4% between the 2- and 3-survey protocols ($P = 0.480$).

Our estimate of ψ(.), when using the 3-survey protocol, was 31% higher than ψ(obs) in the eastern study area and 1.9% higher in the western study area. Estimates of p were significantly higher in the western than in the eastern study area ($P \leq 0.001$). The 2-survey protocols in the eastern study area had an estimated p of 0.105, resulting in an estimate of ψ that was extremely high relative to the 3-survey protocol with high standard error and low precision (Table 1). A slightly lower detection probability in the western study area using the 2-survey protocol resulted in a slightly higher estimate of ψ than when using the 3-survey protocol. Precision of the model estimates of both ψ and p were considered good with the SE$_{estimate}$/estimate ≤ 0.223, except in the case of the 2-survey protocol in the eastern study area (SE$_{estimate}$/estimate = 0.897).

Model comparison showed significant support for the model using Julian day as a survey-specific variable, ψ(.) p(day), over the constant model, ψ(.) p(.), (ΔAIC = 11.17). The plot of Julian day versus p increased in detection probability as the breeding season advanced (Fig. 2).

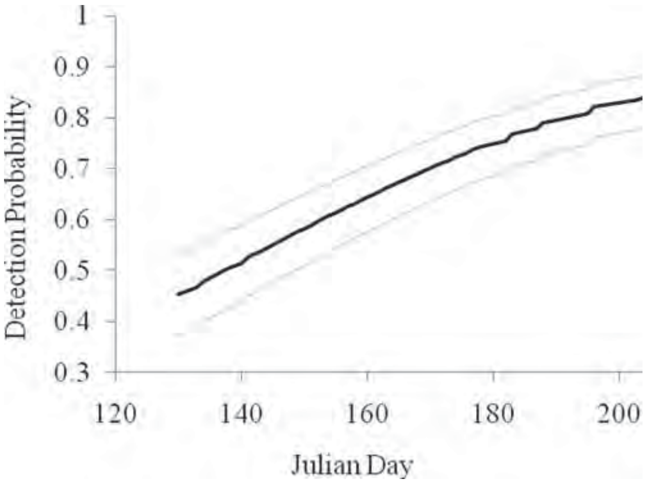

Fig. 2. Predicted detection probabilities (solid line) and standard errors (dotted lines) for northern bobwhite call-count surveys as a function of Julian day in Oklahoma, USA (2009–2011).

DISCUSSION

Survey protocols requiring > 1 sampling occasion per season are crucial to obtaining accurate estimates of bobwhite occupancy; estimates may be biased low if detection probability is not considered. Our results show estimates of occupancy and detection probability can change substantially based on bobwhite abundance and survey protocol, and indicate when surveys are done only once per year unreliable estimates of the state of the population can be expected in any given year. Accounting for detection probability in the analysis of occupancy data for bobwhites is particularly important in areas where abundance is relatively low, as in our eastern study area. As abundance and/or detection probability decreases, the number of sample sites or survey occasions required to obtain accurate estimates of occupancy increases (MacKenzie and Royle 2005).

The number of survey occasions per season can have a substantial influence on estimates of occupancy and detection probability (Bailey et al. 2004, MacKenzie and Royle 2005, Royle 2006). Our results suggest values of ψ(obs) based on only 1-survey occasion per season will significantly underestimate occupancy, and $<$ 3-survey occasions may not be adequate in areas where bobwhite abundance is relatively low even when detection probability is considered. The 2-survey protocol in our eastern study area had such a low detection probability that it resulted in an unrealistically high occupancy estimate. This is consistent with the findings of MacKenzie et al. (2002) and Bailey et al. (2004) who showed that detection probabilities < 0.15 can yield unreasonable estimates of occupancy.

Our results support the conclusions of Royle and Nichols (2003) and Smith et al. (2007) that local abundance may be the most important source of variation in detection probability between sample sites, study areas, or years. This is because the probability of detecting a single individual increases as local density increases (Bailey et al. 2004). Methods have been developed to estimate abundance from repeated presence/absence surveys by formalizing the relationship between detection probability and abundance (Royle and Nichols 2003), but the relationship between calling male bobwhites and breeding season abundance is still unknown. Thus, it is not possible at this time to relate detection probability to actual abundance. However, the significantly higher detection probability that we found in the western study area, where bobwhite abundance was higher, shows that estimates of detection probability may be good predictors of relative abundance.

Improving detection probability is important in increasing the reliability and utility of occupancy models (Royle 2006). Maximizing detection probability through survey design will maximize the variation between sample sites and provide the most information about differences between sites (Hansen and Guthery 2001). It is possible to increase the precision of estimates of detection probability through increasing the complexity of the models, but Royle (2006) showed it is better to address this issue with design-based approaches. Sampling during daily and seasonal peaks in calling activity as well as using an appropriate number of sampling occasions per year is most efficient when using summer call-counts for bobwhites (Robel et al. 1969, Hansen and Guthery 2001). Our goal was not to establish parameter estimates for maximizing detection probabilities, but our results agree with Hansen and Guthery (2001) in that detection probability increases throughout June and into late July and should be considered when designing studies. Our assumption that detection probability for bobwhites would be ≥ 0.5 was incorrect for the eastern study area. According to MacKenzie and Royle (2005), if detection probability is < 5, then >3 sampling occasions would be required to obtain accurate estimates of occupancy. Thus, sampling designs requiring ≥ 4 sampling occasions per season should be considered to ensure accurate estimates of occupancy as the status of abundance may be unknown and highly variable between years (i.e., abundance can fall quickly even in areas of suitable habitat due to climatic variation).

Our estimates of occupancy and detection probability between the eastern and western study areas are reflective of the relative differences in abundance between the 2 areas, but they can only be interpreted in terms of the collection of sample units in each area and should not be generalized to the regional level. It is possible, given the time interval between sampling occasions (2–3 weeks), the model assumption that sample units were closed to changes in occupancy over the course of the season was violated. It is certainly possible for individual bobwhites to move into and out of a 400-m sample unit, but our definition of occupancy reflected ongoing use by bobwhites. Thus, while it was likely the number of individuals changed during our sampling, it is unlikely occupancy status would change. Dispersing bobwhites could have colonized unoccupied sample units after sampling was begun, which would have affected our results by biasing our estimate of detection probability low (MacKenzie et al. 2006). This effect can be mitigated by allowing detection probability to vary with survey occasion (MacKenzie et al. 2006).

MANAGEMENT IMPLICATIONS

Monitoring programs that seek to establish the status of a population and detect spatial or temporal changes can use either of 3 variables: (1) abundance, (2) an index of abundance, and (3) occupancy (Hansen and Guthery 2001, Manley et al. 2004, MacKenzie et al. 2006, Johnson 2008). The choice of which variable to use depends on the system under study, specific objectives of the program, and resources available (Bailey et al. 2004, MacKenzie and Royle 2005, MacKenzie et al. 2006). Methods have been developed to obtain density estimates for bobwhites from autumn covey-call counts (DeMaso et al. 1992, Wellendorf et al. 2004, Riddle et al. 2008); however, these methods require considerably more time and expense than summer call-count surveys. The call-count index has been useful for monitoring long-term trends in abundance over large areas (Church et al. 1993, Twedt et al. 2007, Spinola and Gates 2008, Sauer et al. 2011), but violations of assumptions necessary for inference about annual trends in abundance make its reliability for short-term studies questionable (Hansen and Guthery 2001), and there is still disagreement as to what male call counts actually measure (Terhune et al. 2006). Occupancy is not a measure of abundance, but an estimate of the proportion of area occupied by the species of interest. It can be considered to be a crude surrogate for abundance (Bailey et al. 2004, MacKenzie et al. 2006), but it is a fundamentally different variable. The advantages of using occupancy modeling are that occupancy estimates are generally much less costly to obtain than abundance estimates (Manley et al. 2004), and occupancy is less sensitive to variability in detection probability than abundance estimates or indices of abundance (Bailey et al. 2004). The main disadvantages are that models are not reliable when detection probability is extremely low

(MacKenzie et al. 2002) nor are they useful when occupancy is ~1 (Perry et al. 2011).

Occupancy modeling offers a viable alternative to the call-count index for detecting changes in bobwhite populations both spatially and temporally, and may be particularly appropriate for detecting annual changes in areas where populations are low to moderate. That estimates of occupancy are less sensitive than abundance indices to factors affecting detection probability may make it a more stable variable when monitoring population changes over short time periods. When occupancy is ~1, as in our western study area, differences in detection probability may act as a surrogate for relative abundance although this possibility has not, to our knowledge, been explored and should be approached with caution because abundance is only one of the factors that affect detection probability (Anderson 2001). Sampling protocols must ensure that detection probabilities will be > 0.15 to provide accurate estimates of bobwhite occupancy when abundance is extremely low (Bailey et al. 2004).

ACKNOWLEDGMENTS

Funding was provided by the Pittman-Robertson Federal Aid to Wildlife Restoration Act under project W-161-R of the Oklahoma Department of Wildlife Conservation and Oklahoma State University with additional support of The Nature Conservancy's Weaver Grant Program, Oklahoma Ornithological Society, and Payne County Audubon Society. The project was administered through the Oklahoma Cooperative Fish and Wildlife Research Unit (Oklahoma Department of Wildlife Conservation, Oklahoma State University, U.S. Geological Survey, U. S. Fish and Wildlife Service, and the Wildlife Management Institute cooperating). We thank all of the landowners who allowed us to conduct research on their property, M. G. Sams and E. M. Bartholomew of the Oklahoma Department of Wildlife Conservation, D. M. Leslie of the Oklahoma Cooperative Fish and Wildlife Research Unit, and R. E. Will of the Oklahoma State University Department of Natural Resource Ecology and Management; R. J. Cervantes, Cody Griffin, C. E. Chappell, and Nathan Hillis for assistance in the field; and Mark Payton of the Oklahoma State University Department of Statistics for statistical consulting help.

LITERATURE CITED

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:1294–1297.

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York, USA.

Bailey, L. L., T. R. Simons, and K. H. Pollock. 2004. Estimating site occupancy and species detection probability parameters for terrestrial salamanders. Ecological Applications 14:692–702.

Church, K. E., J. R. Sauer, and S. Droege. 1993. Population trends of quails in North America. Proceedings of the National Quail Symposium 3:44–54.

Conover, W. J. 1999. Practical nonparametric statistics. John Wiley and Sons Inc., New York, USA.

Cram, D. S., R. E. Masters, F. S. Guthery, D. M. Engle, and W. G. Montague. 2002. Northern bobwhite population and habitat response to pine-grassland restoration. Journal of Wildlife Management 66:1031–1039.

DeMaso, S. J., F. S. Guthery, G. S. Spears, and S. M. Rice. 1992. Morning covey calls as an index of northern bobwhite density. Wildlife Society Bulletin 20:94–101.

Fies, M. L., K. M. Puckett, and B. Larson-Brogdon. 2002. Breeding season movements and dispersal of northern bobwhites in fragmented habitats of Virginia. Proceedings of the National Quail Symposium 5:173–179.

Hansen, H. M., and F. S. Guthery. 2001. Calling behavior of bobwhite males and the call-count index. Wildlife Society Bulletin 29:145–152.

Johnson, D. H. 2008. In defense of indices: the case of bird surveys. Journal of Wildlife Management 72:857–868.

Lusk, J. J., F. S. Guthery, R. R. George, M. J. Peterson, and S. J. DeMaso. 2002. Relative abundance of bobwhites in relation to weather and land use. Journal of Wildlife Management 66:1040–1051.

MacKenzie, D. I. 2005. Was it there? Dealing with imperfect detection for species presence/absence data. Australian and New Zealand Journal of Statistics 47:65–74.

MacKenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42:1105–1114.

MacKenzie, D. I., J. D. Nichols, N. Sutton, K. Kawanishi, and L. L. Bailey. 2005. Improving inferences in population studies of rare species that are detected imperfectly. Ecology 86:1101–1113.

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

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. Elsevier, San Diego, California, USA.

Manley, P. N., W. J. Zielinski, M. D. Schlesinger, and S. R. Mori. 2004. Evaluation of a multiple-species approach to monitoring species at the ecoregional scale. Ecological Applications 14:296–310.

Murphy, D. A., and T. S. Baskett. 1952. Bobwhite mobility in central Missouri. Journal of Wildlife Management 16:498–510.

Norton, H. W., T. G. Scott, W. R. Hanson, and W. D. Klimstra. 1961. Whistling-cock indices and bobwhite populations in autumn. Journal of Wildlife Management 25:398–403.

Perry, R. W., T. B. Wigley, M. A. Melchiors, R. E. Thill, P. A. Tappe, and D. A. Miller. 2011. Width of riparian buffer and structure of adjacent plantations influence occupancy of conservation priority birds. Biodiversity and Conservation 20:625–642.

Rhodes, J. R., A. J. Tyre, N. Jonzen, C. A. McAlpine, and H. P. Possingham. 2006. Optimizing presence-absence surveys for detecting population trends. Journal of Wildlife Management 70:8–18.

Riddle, J. D., C. E. Moorman, and K. H. Pollock. 2008. A comparison of methods for estimating northern bobwhite covey detection probabilities. Journal of Wildlife Management 72:1437–1442.

Robel, R. J., D. J. Dick, and G. F. Krause. 1969. Regression coefficients used to adjust bobwhite quail whistle count data. Journal of Wildlife Management 33:662–668.

Rosene Jr., W. 1957. A summer whistling cock count of bobwhite quail as an index to wintering populations. Journal of Wildlife Management 21:153–158.

Royle, J. A. 2006. Site occupancy models with heterogeneous detection probabilities. Biometrics 62:97–102.

Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84:777–790.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, and D. J. Ziolkowski Jr. 2011. The North American Breeding Bird Survey, results and analysis 1966–2009. Version 3.23.2011. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA. www.mbr-pwrc.usgs.gov/bbs/bbs.html

Schwartz, C. C. 1974. Analysis of survey data collected on bobwhite in Iowa. Journal of Wildlife Management 38:674–678.

Smith, J. B., J. A. Jenks, and R. W. Klaver. 2007. Evaluating detection probabilities for American marten in the Black Hills, South Dakota. Journal of Wildlife Management 71:2412–2416.

Spinola, R. M., and R. Gates. 2008. Population status and trends of northern bobwhite (*Colinus virginianus*) in Ohio: 1984–2004. Ohio Journal of Science 108:26–30.

Stoddard, H. L. 1931. The bobwhite quail: it's habits, preservation, and increase. Charles Scribner's Sons, New York, USA.

Terhune, T. M., R. G. Hamrick, D. C. Sisson, and H. L. Stribling. 2006. Summer male call index relative to nesting chronology and autumn density of northern bobwhite. Gamebird 2006: Quail VI and Perdix XII:54–64.

Townsend, D. E., D. M. Leslie Jr., R. L. Lochmiller, S. J. DeMaso, S. A. Cox, and A. D. Peoples. 2003. Fitness costs and benefits associated with dispersal in northern bobwhites (*Colinus virginianus*). American Midland Naturalist 150:73–82.

Trenham, P. C., W. D. Koenig, M. J. Mossman, S. L. Stark, and L. A. Jagger. 2003. Regional dynamics of wetland-breeding frogs and toads: turnover and synchrony. Ecological Applications 13:1522–1532.

Twedt, D. J., R. R. Wilson, and A. S. Keister. 2007. Spatial models of northern bobwhite populations for conservation planning. Journal of Wildlife Management 71:1808–1818.

Veech, J. A. 2006. Increasing and declining populations of northern bobwhites inhabit different types of landscapes. Journal of Wildlife Management 70:922–930.

Wellendorf, S. D., W. E. Palmer, and P. T. Bromley. 2004. Estimating calling rates of northern bobwhite coveys and measuring abundance. Journal of Wildlife Management 68:672–682.

Winter, M., D. H. Johnson, and J. A. Shaffer. 2005. Variability in vegetation effects on density and nesting success of grassland birds. Journal of Wildlife Management 69:185–197.

Zielinski, W. J., and H. B. Stauffer. 1996. Monitoring *Martes* populations in California: survey design and power analysis. Ecological Applications 6:1254–1267.