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Effects of point-count duration on estimated detection probabilities and occupancy of breeding birds

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ABSTRACT. Increasingly, point-count data are used to estimate occupancy, the probability that a species is present at a given location; occupancy accounts for imperfect detection, the probability that a species is detected given that it is present. To our knowledge, effects of sampling duration on inferences from models of bird occupancy have not been evaluated. Our objective was to determine whether changing count duration from 5 to 8 min affected inferences about the occupancy of birds sampled in the Chesapeake Bay Lowlands (eastern United States) and the central and western Great Basin (western United States) in 2012 and 2013. We examined the proportion of species (two doves, one cuckoo, two swifts, five hummingbirds, 11 woodpeckers, and 122 passerines) for which estimates of detection probability were ≥ 0.3. For species with single-season detection probabilities ≥ 0.3, we compared occupancy estimates derived from 5- and 8-min counts. We also compared estimates for three species sampled annually for 5 yr in the central Great Basin. Detection probabilities based on both the 5- and 8-min counts were ≥ 0.3 for $40\% \pm 3\%$ of the species in an ecosystem. Extending the count duration from 5 to 8 min increased the detection probability to ≥ 0.3 for $5\% \pm 0.5\%$ of the species. We found no difference in occupancy estimates that were based on 5- versus 8-min counts for species sampled over two or five consecutive years. However, for 97% of species sampled over 2 yr, precision of occupancy estimates that were based on 8-min counts averaged $12\% \pm 2\%$ higher than those based on 5-min counts. We suggest that it may be worthwhile to conduct a pilot season to determine the number of locations and surveys needed to achieve detection probabilities that are sufficiently high to estimate occupancy for species of interest.

RESUMEN. **El efecto de la duración de conteo por puntos sobre las estimaciones de la probabilidad de detección y la ocupación de aves reproductoras**
Progresivamente se utilizan datos de conteo por puntos para estimar la ocupación, la probabilidad de que una especie esté presente en un lugar determinado; la determinación de la ocupación se incluye la detección imperfecta, la probabilidad de que una especie que está presente sea detectado. A nuestro conocimiento, no han sido evaluados los efectos de la duración del muestreo sobre las inferencias de los modelos de ocupación de aves. Nuestro objetivo fue determinar si el cambio de la duración del conteo, de 5 min a 8 min, afectó las inferencias sobre la ocupación de las aves tomadas en las tierras bajas de la bahía de Chesapeake (este de Estados Unidos) y en el centro y oeste de la Gran Cuenca (oeste de Estados Unidos) en 2012 y 2013. Examinamos la proporción de especies (dos palomas, un cuco, dos vencejos, cinco colibríes, 11 pájaros carpinteros y 122 paseriformes) para los cuales las estimaciones de probabilidad de detección fueron ≥ 0.3. Para las especies con probabilidades de detección de una sola estación ≥ 0.3, se compararon las estimaciones de ocupación derivadas de conteos de 5 min y 8 min. También comparamos las estimaciones de detección de tres especies que fueron muestreadas anualmente por cinco años en la Gran Cuenca Central. Las probabilidades de detección basadas en los recuentos de 5 min y 8 min fueron ≥ 0.3 para el $40\% \pm 3\%$ de las especies en el ecosistema. La extensión de la duración del recuento de 5 min a 8 min aumentó la probabilidad de detección a ≥ 0.3 para el $5\% \pm 0.5\%$ de las especies. No encontramos diferencias en las estimaciones de ocupación que fueron basados en conteos de 5 minutos contra 8 minutos para las especies muestreadas durante dos o cinco años consecutivos. Sin embargo, para el 97% de las especies muestreadas durante dos años, las estimaciones de precisión de ocupación basadas en conteos de 8 minutos fueron un 12% más altas que aquellas basadas en conteos de 5 minutos. Sugerimos que quizás valga la pena para realizar un estudio piloto para determinar el número de ubicaciones y encuestas necesarias para lograr probabilidades de detección suficientemente altas para estimar la ocupación de las especies de interés.

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Point-count surveys are the most common method of sampling birds (Rosenstock et al. 2002, Bart 2005, Buckland 2006), and many investigators have examined whether species- or community-level inferences derived from point counts are affected by sampling design (e.g., Ralph et al. 1993, 1995, Petit et al. 1995, Smith et al. 1995, Thompson and Schwalbach 1995, Bibby et al. 2000, Shiu and Lee 2003, Esquivel and Peris 2008, Cimprich 2009, Reidy et al. 2011). The temporal window for effectively sampling birds on a given day can be relatively short, sometimes less than 4 h, and breeding seasons are often limited to 5 to 8 weeks. Therefore, there are trade-offs among the number of point-count locations (hereafter, points; Buskirk and McDonald 1995) sampled, the geographic extent of sampling, and the duration of point-count surveys (hereafter, counts; Buskirk and McDonald 1995, Ralph et al. 1995, Vergara et al. 2010).

Estimates of detection probability and abundance generally increase as count duration increases, but there is considerable variation among species. For example, detection probabilities of 14 songbird species that breed in deciduous forests in the eastern United States increased from > 0.4 to > 0.9 when count duration increased from 5 to 20 min. However, detection probabilities of 57% of these species varied among years (Dawson et al. 1995). Similarly, detection probability increased as count duration increased from 3 to 6 to 10 min for six songbird species that breed in deciduous forests in the eastern United States (Buskirk and McDonald 1995). By contrast, mean abundance derived from 10-min counts was higher than that derived from 6-min counts for 15% of 13 species (Thompson et al. 2002). Other studies have revealed that the number of individuals detected increased as count duration increased regardless of either the period during the morning when 3-, 6-, or 10-min counts were conducted (Buskirk and McDonald 1995) or the time of year when 5-, 10-, 15-, or 20-min counts were conducted (Smith et al. 1998). In southwestern France, the abundance of 90% of 21 breeding species was greater when

based on 10-min rather than 5-min counts, and the abundance of all 21 species was greater when based on 20-min rather than 15-min counts (Bonthoux and Balent 2012). Estimates of the density of tropical species that were adjusted for imperfect detection were 13% greater when based on 10-min rather than 2-min counts (Lee and Marsden 2008).

Count models suggest that the effect of count duration on precision is equivocal. Precision based on the coefficient of variation (CV) was homogenous among 6-, 8-, and 10-min counts (Thompson et al. 2002), and precision based on the standard error (SE) was homogenous among 3-, 6-, and 10-min counts (Buskirk and McDonald 1995). However, Smith et al. (1998) found that SE-based precision decreased as count duration increased in 5-min increments from 5 to 20 min. Although many investigators have studied the effects of increasing count duration on inferences from models based on counts, how count duration might affect inferences from occupancy models is unclear (MacKenzie et al. 2002).

Occupancy models (MacKenzie et al. 2002) are frequently implemented to analyze point-count data (e.g., Betts et al. 2008, Saracco et al. 2011, Frey et al. 2012). Occupancy is defined as the probability that a species is present at a given location, and occupancy models account for imperfect detection (MacKenzie et al. 2002). Typically, occupancy models use data from repeated surveys at multiple locations to infer the proportion of locations or area occupied by a species and, optionally, the environmental attributes associated with occupancy. Assessments of trade-offs between the number of sampling locations and the number of surveys at each location have resulted in guidelines for sampling design (MacKenzie et al. 2002, 2006, MacKenzie and Royle 2005, Bailey et al. 2007). The effect of count duration on inferences from occupancy models, however, has received relatively little attention.

We examined the effect of 5- and 8-min count durations on inferences about detection probability and occupancy, and the precision

of occupancy estimates, during the breeding seasons of 2012 and 2013 in three ecosystems: the Chesapeake Bay Lowlands, central Great Basin, and western Great Basin. We conducted our study in multiple ecosystems to investigate potential geographical differences in inferences about detection and occupancy. To extend the comparison beyond 2 yr, we also examined whether estimates of occupancy differed from 2009 through 2013 for three species in the central Great Basin. Furthermore, we determined the percentage of species for which occupancy models converged, i.e., diagnostics indicated no problems with parameter estimation, and for which detection probabilities derived from both 5- and 8-min counts were ≥ 0.3. The 0.3 threshold was suggested as a reasonable means to minimize bias (i.e., deviation of estimated occupancy from the true occupancy value) in occupancy estimates (MacKenzie et al. 2002). We chose the 5-min count duration to be consistent with standard point-count protocols (Ralph et al. 1993, 1995, Matsuoka et al. 2014). We chose the 8-min duration because the results of a pilot survey in the Chesapeake Bay Lowlands revealed that ~94% of species were detected within 8 min (Leu, unpubl. data) and because 8 min was the maximum count duration at which no reduction in the number of points was necessary given logistic constraints and associated travel time between points in the central and western Great Basin. The geographic and temporal breadth of our analysis is novel, and our inferences are relevant to the design of surveys based on counts and estimates of species richness based on occupancy models (e.g., Iknayan et al. 2014).

METHODS

In the Chesapeake Bay Lowlands, our study area included the Virginia Peninsula between Toano and Hampton (Charles City, Henrico, James City, Newport News, Williamsburg, and York counties, Virginia) and the Middle Peninsula near West Point (King and Queen and King William counties, Virginia). Our central Great Basin study area included much of the adjacent Shoshone Mountains and Toiyabe, Toquima, and Monitor Ranges (Lander, Nye, and Eureka counties, Nevada). In the western Great Basin, our study area included the east slope of the Sierra Nevada and the adjacent Wassuk Range and Sweetwater Mountains (Mono County, California, and Mineral, Douglas, and Lyon counties, Nevada).

In the Chesapeake Bay Lowlands, we located points at random on public lands in upland coniferous and deciduous forests and riparian forests. The canopy of upland coniferous forests was dominated by loblolly pine (*Pinus taeda*) and, in early successional stands, by sweetgum (*Liquidambar styraciflua*) (Monette and Ware 1983, Weakley et al. 2012). Dominant canopy species in upland deciduous forests were American beech (*Fagus grandifolia*) and oaks (*Quercus* spp.). Loblolly pine, tulip poplar (*Liriodendron tulipifera*), and sweetgum were also present (Monette and Ware 1983, Weakley et al. 2012). The composition of the canopy in riparian forests depends on hydrology and soil drainage. Common species included red maple (*Acer rubrum*), birch (*Betula* spp.), black walnut (*Juglans nigra*), sweetgum, tulip poplar, water tupelo (*Nyssa aquatica*), black tupelo (*N. sylvatica*), sycamore (*Platanus occidentalis*), and oaks (Weakley et al. 2012). We sampled the same 131 points in both 2012 and 2013.

In the central and western Great Basin, we located points along the full elevational gradient of multiple canyons in each mountain range. We typically established two or three points per 100-m vertical gain in elevation. Points were positioned to sample the dominant land-cover types throughout the canyons, including woodlands dominated by single-leaf pinyon (*Pinus monophylla*) and juniper (*Juniperus osteosperma* and *J. occidentalis*), shrubsteppe dominated by sagebrush (*Artemisia* spp.), and riparian woodland dominated by deciduous trees, including aspen (*Populus tremuloides*), chokecherry (*Prunus virginiana*), and cottonwood (*Populus angustifolia* and *P. fremontii*), and deciduous shrubs, e.g., willow (*Salix* spp.) and Woods' rose (*Rosa woodsii*). In the central Great Basin, we sampled 296 points in 2012, including 49 points in four canyons in the Shoshone Mountains, 123 points in nine canyons in the Toiyabe Range, 59 points in six canyons in the Toquima Range, and 65 points in eight canyons in the Monitor Range. In 2013, we sampled 314 points, including the same 296 sampled in 2012 plus 18 additional points in two additional canyons in the Monitor

Range. In the western Great Basin, we sampled the same 158 points in both 2012 and 2013 with 79 points located in seven canyons in the Sierra Nevada, 23 points in two canyons in the Sweetwater Mountains, and 56 points in four canyons in the Wassuk Range.

Point-count surveys.   In all three ecosystems, we conducted 100-m, fixed-radius point counts during the peak breeding seasons (late May through June) of 2012 and 2013 between 15 min after sunrise and 10:00. Most point centers were > 350 m apart (mean = 406 ± 157 [SD] m), minimizing the probability that observer activity would cause birds to move among points. In the Chesapeake Bay Lowlands, point counts were surveyed by five and four observers in 2012 and 2013, respectively, with two observers conducting surveys in both years. In the central Great Basin, two different sets of four observers conducted surveys in 2012 and 2013. In the western Great Basin, the same two observers conducted surveys in both years. During each visit, we recorded all species detected by sound or sight, but here we focus on doves, cuckoos, swifts, hummingbirds, woodpeckers, and passerines because most observations of species in these orders were birds either perched or foraging within the points. We sampled each point three times per year to capture potential variation in phenology. We restricted sampling to mornings with no precipitation and low wind speed. We also noted whether detections occurred during the first 5 min or the last 3 min.

Occupancy estimates.   To estimate detection probabilities and occupancy, we used a hierarchical, single-season occupancy model that considered detection and occupancy processes separately (MacKenzie et al. 2006). The joint distribution of the observed detections and non-detections is conditioned on the latent, or unobserved, true occupancy state, and on the marginal distribution of the occupancy state variable. All models had the following general form:

$$Z_i \sim \text{Bernoulli}(\psi) \quad \text{for} \quad i = 1, 2, , M$$
$$Y_{ij}|Z_i \sim \text{Bernoulli}(Z_i P) \quad \text{for} \quad i = 1, 2, , J,$$

where the unobserved, true occupancy state of each species is Z_i, and ψ is the probability that any one of the M points is occupied by the species. The observed pattern of detections and non-detections, Y_{ij}, for a given species across the $j = 1, \ldots, J$ counts at the ith point therefore is conditional on the latent occupancy process with probability $Z_i P$, where P is the estimated detection probability of the species.

We modified the general form of the model to allow detection probability to vary among observers (Diefenbach et al. 2003, Alldredge et al. 2007a):

$$\text{logit}(P_k) = x^{\text{T}} \beta_k,$$

where the logit link function constrains the detection probability for each observer, k, to a value from zero to one. The transpose of the vector of observers is indicated by x^T, and β_k is a given observer's effect on detection probability.

We modeled single-season occupancy (MacKenzie et al. 2002) in 2012 and 2013 for species detected during 5-min counts (i.e., 8-min counts truncated at 5 min) and species detected during 8-min counts. We estimated occupancy for all species with a detection probability ≥ 0.3 for both 5- and 8-min counts in a given year and where the confidence intervals around the detection probability did not range from zero to one. We tested whether the occupancy estimates for each species were significantly different when based on 5- versus 8-min counts. We considered differences in occupancy between count durations to be statistically significant if the 95% confidence interval centered on the difference between the 5- and 8-min occupancy estimate did not include zero (Schenker and Gentleman 2001):

$$(\psi 5\text{min} - \psi 8\text{min}) \pm 1.96\sqrt{\text{SE5min}^2 + \text{SE8min}^2}$$

We report the percentage (mean ± SE) of species for which occupancy models converged and produced estimates (i.e., 95% confidence interval did not range from zero to one and other diagnostics did not indicate estimation problems), and for which detection probabilities based on both count durations were ≥ 0.3.

To examine whether inferences about occupancy over 2 yr were consistent over longer periods of time, we also fit single-season occupancy models to data from 2009–2013 for American Robins (*Turdus migratorius*), MacGillivray's Warblers (*Geothlypis tolmiei*), and Vesper Sparrows (*Pooecetes gramineus*) in the central Great Basin. These species collectively span gradients of land-cover associations, local rarity, and ease of identification. American Robins are primarily associated with riparian woodlands (Vanderhoff et al. 2016), MacGillivray's Warblers with shrub-dominated riparian thickets (Pitocchelli 2013), and Vesper Sparrows with sagebrush shrubsteppe (Jones and Cornely 2002). American Robins are widespread, easily recognized, and not likely to be confused with co-occurring species. MacGillivray's Warblers are fairly widespread, and can be confused with co-occurring species. Vesper Sparrows are relatively uncommon, difficult to detect, and can be confused with co-occurring species.

We examined difference in the precision of occupancy estimates based on 5- and 8-min counts. We defined precision as the coefficient of variation (CV), calculated as (SD[ψ]/ψ) 100. We conducted all analyses in package Unmarked (Fiske et al. 2015) in R (R Core Team 2014).

RESULTS

We detected 143 species across the three ecosystems, including two doves, one cuckoo, two swifts, five hummingbirds, 11 woodpeckers, and 122 passerines (Tables S1–S6). We detected 84 species in the western Great Basin (75 in 2012, 76 in 2013), 80 species in the central Great Basin (70 in 2012, 73 in 2013), and 62 species in the Chesapeake Bay Lowlands (58 in 2012, 59 in 2013; Table 1, Tables S1–S6). We detected nine species in all three ecosystems, including Mourning Doves, Hairy Woodpeckers, Northern Flickers, White-breasted Nuthatches, Blue-gray Gnatcatchers, American Robins, Chipping Sparrows, Brown-headed Cowbirds, and House Finches (scientific names are in Tables S1–S6).

Detection estimates. For 81 ± 3% (range = 73–92%) of species, models of detection probability based on both the 5- and 8-min counts converged. Neither the model based on the 5-min counts nor the model based on the 8-min counts converged for 14 ± 4% (range = 0–24%) of the species (Table 1). Irrespective of count duration, a higher percentage of models converged for species in the Chesapeake Bay Lowlands (91% in 2012, 92% in 2013) than for species in either the central Great Basin (73% in 2012, 78% in 2013) or western Great Basin (73% in 2012, 79% in 2013). For 4 ± 1% of species (range = 0–7%), extending the count duration from 5 to 8 min resulted in model convergence (Table 1).

Detection probabilities based on both the 5- and 8-min counts were ≥ 0.3 for 40 ± 3% of the species (range = 24–53%) and < 0.3 for 35 ± 1% of the species (range = 31–41%; Table 1). The percentage of species with detection probabilities ≥ 0.3 was higher in Chesapeake Bay Lowlands (53% in 2012, 47% in 2013) than in either the central Great Basin (24% in 2012, 36% in 2013) or western Great Basin (35% in 2012, 41% in 2013). Increasing count duration from 5 to 8 min increased the detection probability to ≥ 0.3 for 5 ± 0.5% of the species (range = 3–7%), but decreased the detection probability to < 0.3 for 2.0 ± 0.5% (range = 0–4%) of the species (Table 1).

Occupancy estimates. We estimated occupancy for 35 species (56% of those detected) in the Chesapeake Bay Lowlands (31 in 2012, 27 in 2013), 27 species (34% of those detected) in the central Great Basin (17 in 2012, 26 in 2013), and 37 species (44% of those detected) in the western Great Basin (26 in 2012, 31 in 2013) (Table 1). Occupancy estimates based on 5- and 8-min counts were not statistically different for any species (Figs. 1–3). Species with low naïve occupancy (percentage of points occupied, not accounting for imperfect detection) for which models did not converge included those with home ranges larger than the area of the points (~3 ha) (e.g., woodpeckers or corvids), those that rarely occur in the land-cover types we sampled (e.g., synanthropic and wetland species), and those that were rare in our study areas (Tables S1–S6).

Across ecosystems and years, point estimates of occupancy for 71 ± 4% of the species were 0.001–0.12 higher when based on 8-min rather than 5-min counts (Figs. 1–3). We found no difference in the point

Table 1. Total number of species detected in 2012 and 2013 in the Chesapeake Lowlands, central Great Basin, and western Great Basin, the number (percentage) of species for which models did or did not converge, and the number (percentage) of species for which detection probabilities (P) based on 5- and 8-min counts were either ≥ 0.3 or < 0.3 (MacKenzie et al. 2002). Percentages are based on the total number of species detected in a given year and ecosystem.

	Chesapeake Bay Lowlands		Central Great Basin		Western Great Basin	
	2012	2013	2012	2013	2012	2013
Number of species detected	58	59	70	73	75	76
Models based on 5- and 8-min counts converged	53 (91)	54 (92)	51 (73)	57 (78)	55 (73)	60 (79)
Models converged when based on 8-min but not 5-min counts	4 (7)	3 (5)	1 (1)	5 (7)	1 (1)	0 (0)
Models converged when based on 5-min but not 8-min counts	1 (2)	2 (3)	1 (1)	0 (0)	2 (3)	1 (1)
Neither model converged	0 (0)	0 (0)	17 (24)	11 (15)	17 (23)	15 (20)
$P \geq 0.3$ when based on 5- and 8-min counts	31 (53)	28 (47)[a]	17 (24)	26 (36)	26 (35)	31 (41)
$P \geq 0.3$ when based on 8-min but not 5-min counts	3 (5)	5 (8)	4 (6)	4 (5)	2 (3)	4 (5)
$P \geq 0.3$ when based on 5-min but not 8-min counts	1 (2)	1 (2)	2 (3)	3 (4)	1 (1)	0 (0)
$P < 0.3$ when based on 5- and 8-min counts	18 (31)	21 (36)	29 (41)	24 (33)	26 (35)	25 (33)

[a] We excluded Blue-gray Gnatcatchers because confidence intervals for occupancy ranged from zero to one.

estimates for $9 \pm 3\%$ of the species. By contrast, point estimates of occupancy for $19 \pm 5\%$ of the species were 0.001–0.32 higher when based on 5-min rather than 8-min counts (Figs. 1–3).

Occupancy estimates for American Robins, MacGillivray's Warblers, and Vesper Sparrows based on 5- and 8-min counts did not differ significantly within or among five consecutive years (Table 2). In addition, differences in estimates of occupancy based on 5- and 8-min counts were consistent (did not exceed 0.06) among years and species. The difference among years in occupancy based on 5- versus 8-min counts ranged from 0.05 (American Robin) to 0.08 (MacGillivray's Warbler).

The precision of occupancy estimates based on 8-min counts was higher than those for 5-min counts for 97% of species. Two exceptions to this pattern were occupancy estimates for Yellow-rumped Warblers (*Setophaga coronata*) in 2012 and 2013 and Spotted Towhees (*Pipilo maculatus*) in 2012 in the western Great Basin (Tables S7–S9).

Excluding these two species, precision increased by $12 \pm 2\%$ (range = 0–38%) when count duration increased from 5 to 8 min. Similarly, precision based on 8-min counts was higher than precision based on 5-min counts for American Robins and MacGillivray's Warblers from 2009 through 2013, and in three of 5 yr for Vesper Sparrows (Table S10). Precision increased by $18 \pm 4\%$ (range = 3–25%), $20 \pm 3\%$ (range = 9–27%), and $10 \pm 5\%$ (range = 0–29%) for American Robins, MacGillivray's Warblers, and Vesper Sparrows, respectively.

DISCUSSION

We found that occupancy estimates based on 5- and 8-min counts did not differ for species with detection probabilities ≥ 0.3. These results were consistent among three ecosystems and for both 2-yr and 5-yr temporal windows. This suggests that a modest extension of the recommended 5-min duration of standardized counts (Ralph et al. 1993, 1995, Matsuoka et al. 2014) is unlikely
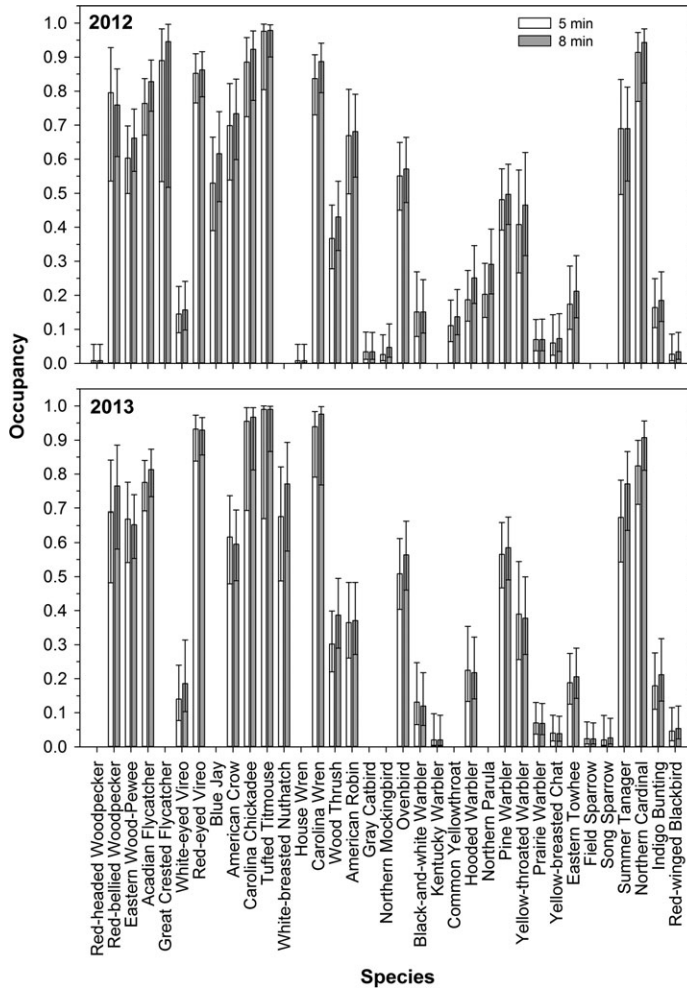
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Fig. 1. Occupancy estimate and lower and upper bounds of 95% confidence intervals for species of birds with detection probabilities ≥ 0.3 when based on either 5- or 8-min counts in the Chesapeake Bay Lowlands during 2012 and 2013. The two occupancy estimates did not differ significantly for any species.

to affect inferences based on occupancy models. However, we found that the precision (CV) of occupancy estimates for 97% of the species we examined increased by 12 ± 2% (range = 0–38%) when count duration increased from 5 to 8 min. This suggests a trade-off between count duration and precision and that a modest 3-min increase in count duration can provide more precise occupancy estimates.

Our study highlights the difficulty of modeling occupancy of rare species and species with large home ranges. We found that detection probabilities based on both the 5- and 8-

min counts were ≥ 0.3 for 40 ± 3% of the species in our study. In addition, extending count duration from 5 to 8 min increased detection probability to ≥ 0.3 for an average of 5 ± 0.5% of species. Similarly, detection probabilities of 14 species increased as sampling duration increased in 5-min increments from 5 to 20 min, but detection probabilities did not reach 1 for any species even when points were sampled for 20 min (Dawson et al. 1995). Although we sampled > 100 points in each ecosystem, three counts per point may not be sufficient to detect species with home ranges larger than the area of the
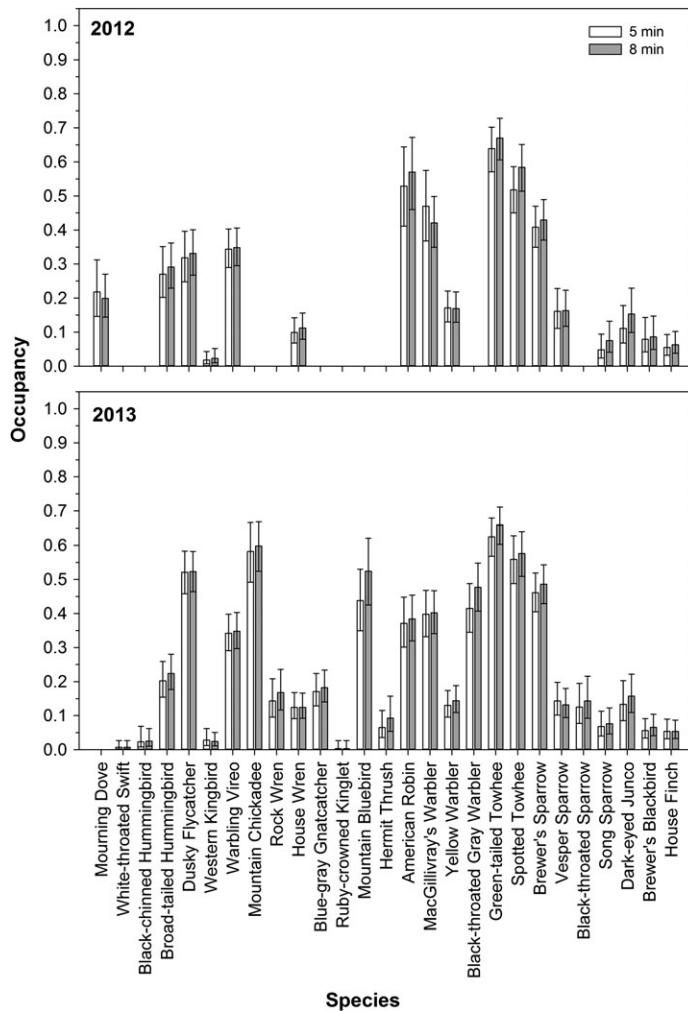
Fig. 2. Occupancy estimate and lower and upper bounds of 95% confidence intervals for species of birds with detection probabilities ≥ 0.3 when based on either 5- or 8-min counts in the central Great Basin during 2012 and 2013. The two occupancy estimates did not differ significantly for any species.

point or species with low abundances. As a general guideline, MacKenzie and Royle (2005) recommended increasing the number of counts rather than the number of points to maximize the precision of estimates for common species, and increasing the number of points rather than the number of counts to maximize precision for rare species. Increasing the number of counts from three to four might have increased the number of species for which we could have estimated occupancy. Simulations indicated that four counts were sufficient to sample species with detection probabilities of 0.4 and occupancy from

0.2–0.5, and species with detection probabilities of 0.5 and occupancy from 0.7–0.8 (MacKenzie and Royle 2005). Sampling constraints may limit the application of distance sampling to point-count data; 75–100 observations of each species are recommended to achieve robust density estimates (Buckland et al. 2001).

For 19 ± 5% of species in our study, estimates of occupancy based on 5-min counts were higher than those based on 8-min counts. This counterintuitive result reflects the manner in which occupancy is estimated. The naïve estimate of occupancy, ψ_{naive} (i.e.,
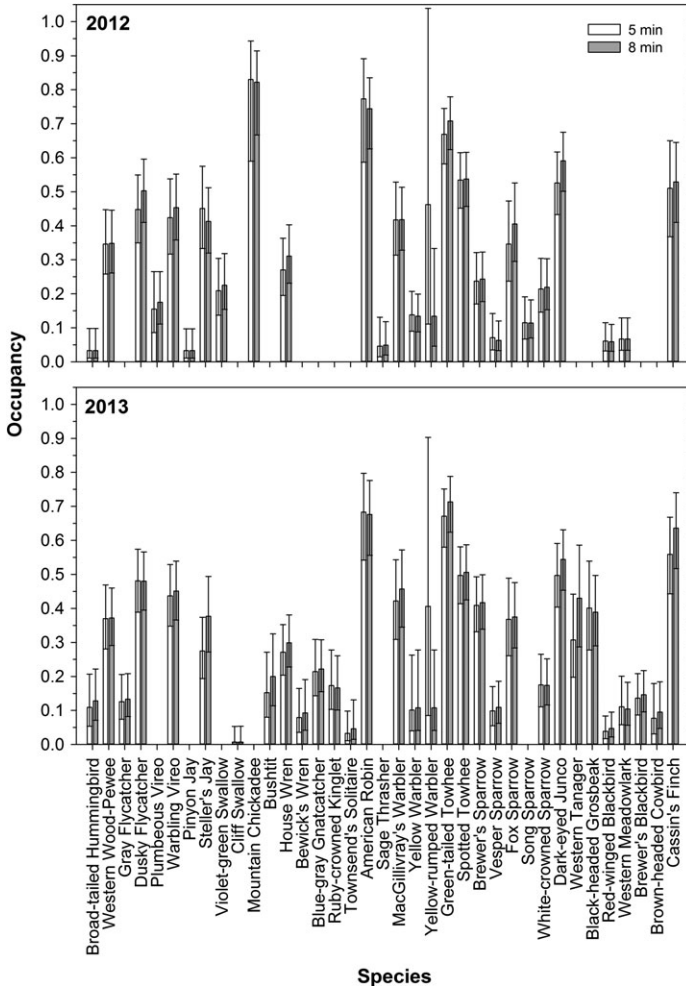
Fig. 3. Occupancy estimate and lower and upper bounds of 95% confidence intervals for species of birds with detection probabilities ≥ 0.3 when based on either 5- or 8-min counts in the western Great Basin during 2012 and 2013. The two occupancy estimates did not differ significantly for any species.

the proportion of sites at which the species was detected at least once), is adjusted as

$$\hat{\psi} = \frac{\psi_{naive}}{P^*},$$

where P^* is the probability of detecting the species at least once across j counts. When P is homogeneous across surveys, P^* is estimated as $1-(1-P)^j$, where j is the number of counts in a given year. When P is heterogeneous across surveys, P^* is estimated as $1-((1-P_1)(1-P_2)(1-P_3))$, where subscript 1–3 indexes the count (MacKenzie et al. 2006). Occupancy estimates based on 5-min counts can

be higher than those based on 8-min counts when naïve occupancy from 5- and 8-min counts are similar, but a species is detected on fewer of the 5-min counts than the 8-min counts. This is illustrated by occupancy estimates for American Robins in the western Great Basin in 2012. Naïve estimates of occupancy based on 5- and 8-min counts were 0.56 and 0.63, respectively. However, estimates of P^* based on 5- and 8-min counts were 0.72 and 0.84, respectively. Thus, the occupancy estimates derived from 5- and 8-min counts were 0.77 and 0.75, respectively. We suspect that these slight differences could affect estimates of species richness based on

Table 2. Occupancy estimates (Ψ), standard error (SE), and lower and upper bounds of 95% confidence intervals (LCI, UCI) for three species of birds detected during 5- and 8-min counts in the central Great Basin from 2009 to 2013. Means of the five occupancy estimates did not differ significantly for any species.

Species	Year	5 min				8 min			
		Ψ	SE	LCI	UCI	Ψ	SE	LCI	UCI
American Robin (*Turdus migratorius*)	2009	0.42	0.05	0.32	0.51	0.45	0.04	0.36	0.53
	2010	0.61	0.07	0.46	0.74	0.67	0.06	0.53	0.78
	2011	0.50	0.06	0.39	0.61	0.52	0.05	0.42	0.62
	2012	0.53	0.06	0.41	0.65	0.57	0.05	0.46	0.67
	2013	0.37	0.04	0.30	0.45	0.38	0.04	0.32	0.45
MacGillivray's Warbler (*Geothlypis tolmiei*)	2009	0.39	0.04	0.32	0.46	0.43	0.04	0.36	0.50
	2010	0.45	0.05	0.36	0.54	0.50	0.04	0.41	0.58
	2011	0.49	0.05	0.40	0.58	0.52	0.04	0.44	0.60
	2012	0.46	0.05	0.37	0.56	0.42	0.04	0.35	0.50
	2013	0.40	0.04	0.33	0.47	0.41	0.03	0.34	0.47
Vesper Sparrow (*Pooecetes gramineus*)	2009	0.15	0.04	0.09	0.24	0.21	0.04	0.14	0.31
	2010	0.28	0.06	0.18	0.41	0.28	0.05	0.19	0.39
	2011	0.15	0.03	0.11	0.21	0.16	0.03	0.12	0.22
	2012	0.16	0.03	0.11	0.23	0.16	0.03	0.11	0.22
	2013	0.14	0.02	0.10	0.20	0.14	0.02	0.10	0.19

occupancy models (Iknayan et al. 2014), especially because sample sizes were too small to estimate occupancy for a substantial proportion of the birds in our study.

Because most point-count protocols are not species-specific, but sample communities (Thompson 2002), we believe that evaluating whether the proposed number of points and counts is likely to yield a sufficient number of detections is worthwhile. The proportion of species for which we were able to derive robust estimates of occupancy on the basis of single-season models differed among ecosystems. Nevertheless, we could not estimate occupancy for between 47% and 76% of the species detected. A suggested method for estimating occupancy despite low detection probabilities is to make estimates at the level of functional groups rather than individual species. Analyses of functional groups take advantage of similarities in detection processes among common and rare species in a given functional group (Alldredge et al. 2007b, Dorazio et al. 2010). Alldredge et al. (2007b) found that multi-species analyses yielded more precise density estimates than single-species analyses. Occupancy has been estimated at the level of functional groups with methods such as multi-season hierarchical Bayesian models (Gelman and Hill 2007, Dorazio et al. 2010, Zipkin et al. 2010). Whether multi-species analyses on the basis of single-season occupancy models provide more precise occupancy estimates than single-species analyses remains unclear.

Hayes and Monfils (2015) suggested that point-count data are not well suited for occupancy modeling because the mobility of birds violates the assumption that the occupancy status of points does not change among counts (i.e., the closure assumption). Because the area of most points is smaller than the smallest home range of the species sampled, individuals regularly move in and out of the points (Rota et al. 2009). Simulations indicated that even slight movements resulted in detection probabilities that were lower than the true value and occupancy estimates that were higher than the true value (Hayes and Monfils 2015). Our results were consistent with the results of these simulations, with detection probabilities < 0.3 for species with large home ranges, such as woodpeckers. Ultimately, whether point-count data can be used to estimate occupancy hinges on the definition of use (i.e., open system) versus occupancy (i.e., closed system) (Latif et al. 2016).

Our finding that occupancy estimates based on 5- and 8-min counts did not differ significantly may not be transferable to study

designs that include fewer or more than three counts. On the basis of our results, we do not recommend conducting fewer than three counts because doing so will likely lead to inferences with low precision. MacKenzie and Royle (2005) found that two counts were sufficient to estimate occupancy if detection probability of a species was ≥ 0.6, which was the case for 12% ($N = 358$) of our single-season models, and four counts were sufficient if detection probability of a species was ≥ 0.4. Because 8-min counts improved precision of occupancy estimates for 97% of our species, and because estimates of species richness generally increase as count duration increases (Dawson et al. 1995, Drapeau et al. 1999), we recommend 8-min rather than 5-min counts. Ultimately, because we found that detection probabilities varied among species, we also recommend conducting a pilot year of surveys to identify species for which detection probabilities are sufficiently large to estimate occupancy precisely. The freeware GENPRES can be used to explore the optimal number of points and counts (Bailey et al. 2007).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Table S1. Detection probability (P), standard error (SE), and lower and upper bounds of 95% confidence intervals (LCI, UCI) for species detected in the Chesapeake Bay Lowlands in 2012 during 5- and 8-min point counts (100-m fixed radius). Blank cells indicate that the model did not converge for a given species. For species for which $P < 0.3$ in at least one count, P and variance estimates are highly uncertain.

Table S2. Detection probability (P), standard error (SE), and lower and upper bounds of 95% confidence intervals (LCI, UCI) for species detected in the Chesapeake Bay Lowlands in 2013 during 5- and 8-min point counts (100-m fixed radius). Blank cells indicate that the model did not converge for a given species. For species for which $P < 0.3$ in at least one count, P and variance estimates are highly uncertain.

Table S3. Detection probability (P), standard error (SE), and lower and upper bounds of 95% confidence intervals (LCI, UCI) for species detected in the central Great Basin in 2012 during 5- and 8-min point counts (100-m fixed radius). Blank cells indicate that the model did not converge for a given species. For species for which $P < 0.3$ in at least one count, P and variance estimates are highly uncertain.

Table S4. Detection probability (P), standard error (SE), and lower and upper bounds of 95% confidence intervals (LCI, UCI) for species detected in the central Great Basin in 2013 during 5- and 8-min point counts (100-m fixed-radius). Blank cells indicate that the model did not converge for a given species. For species for which $P < 0.3$ in at least one count, P and variance estimates are highly uncertain.

Table S5. Detection probability (P), standard error (SE), and lower and upper bounds of 95% confidence intervals (LCI, UCI) for species detected in the western Great Basin in 2012 during 5- and 8-min point counts (100-m fixed radius). Blank cells indicate that the model did not converge for a given species. For species for which $P < 0.3$ in at least one count, P and variance estimates are highly uncertain.

Table S6. Detection probability (P), standard error (SE), and lower and upper bounds of 95% confidence intervals (LCI, UCI) for species detected in the western Great Basin in 2013 during 5- and 8-min point counts (100-m fixed radius). Blank cells indicate that the model did not converge for a given species. For species for which $P < 0.3$ in at least one count, P and variance estimates are highly uncertain.

Table S7. Annual occupancy (ψ), standard error (SE), coefficient of variation (CV = SE $\sqrt{n}/\psi$), and percentage change in the CV (% Δ) when count duration increased from 5 to 8 min for species surveyed in the Chesapeake Bay Lowlands in 2012 and 2013 at 131 points (100-m fixed radius). A positive change in the CV indicates that the precision of occupancy estimates was higher when based on 8-min than 5-min counts. Only species with detection probabilities ≥ 0.3 are listed. Blank cells indicate that the model did not converge for a given species. Scientific names are in Supporting Information Table S1 and S2.

Table S8. Annual occupancy (ψ), standard error (SE), coefficient of variation (CV = SE $\sqrt{n}/\psi$), and percentage change in the CV (% Δ) when count duration increased from 5 to 8 min for species surveyed in the central Great Basin in 2012 and 2013 at 296 and 314 points (100-m fixed radius), respectively. A positive change (% Δ) in the CV indicates

that the precision of occupancy estimates was higher when based on 8-min than 5-min counts. Only species with detection probabilities ≥ 0.3 are listed. Blank cells indicate that the model did not converge for a given species. Scientific names are in Supporting Information Table S3 and S4

Table S9. Annual occupancy (ψ), standard error (SE), coefficient of variation (CV = SE $\sqrt{n}/\psi$), and percentage change in the CV (% Δ) when count duration increased from 5 to 8 min counts for species detected in the western Great Basin in 2012 and 2013 at 158 points (100-m fixed radius). A positive change in the CV indicates that the precision of occupancy estimates was higher when based on 8-min than to 5-min counts whereas a negative change indicates that the precision of occupancy estimates was higher when based on 5-min than 8-min

counts. Only species with detection probabilities ≥ 0.3 are listed. Blank cells indicate that the model did not converge for a given species. Scientific names are in Supporting Information Table S5 and S6.

Table S10. Annual occupancy (ψ), standard error (SE), coefficient of variation (CV = SE $\sqrt{n}/\psi$), and percentage change in the CV (% Δ) when count duration increased from 5 to 8 min for three species of birds detected in the central Great Basin from 2009–2013 at 300, 244, 295, 296, and 314 points (100-m fixed radius), respectively. A positive change in the CV indicates that the precision of occupancy estimates was higher when based on 8-min than 5-min counts. Scientific names are in Supporting Information Table S5 and S6.