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ARE POINT COUNTS OF BOREAL SONGBIRDS RELIABLE PROXIES FOR MORE INTENSIVE ABUNDANCE ESTIMATORS?

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ABSTRACT.—Point counts are often used to provide information on abundance of songbirds. If data from point counts are to be compared in space or time, however, any bias in the estimate should be consistent and linearly related to the true abundance. Several studies have suggested that this assumption may be violated for songbirds. Here, we used double sampling to test whether point counts are linearly related to true abundance, as estimated from spot mapping, for 12 songbird species in the boreal mixed-wood forest of northern Alberta, Canada. We found that total abundance of birds across several point-count stations was positively correlated with the number of territories and confirmed that point counts were linearly related to spot-mapping abundance for the species tested. However, large sampling errors masked this relationship at the scale of a single point-count station (100-m fixed-radius plot). Double-sampling models that accounted for differences in abundance between spot-mapping grids using random effects improved prediction for most species. We found no year effect on detectability. Maximum abundance over point-count rounds was a more sensitive index of abundance than mean abundance and tended to produce better-fitting models. Point-count abundance was more closely related to true abundance in species with relatively small territories, or those with large spatial or temporal variation in density. Our results further suggest that point-count abundance may be proportional to the total length of territorial boundaries in the plot rather than the total fraction of territories in the plot. Our analysis suggests that point counts provide a reasonable index of abundance, even though individual point-count stations are not consistently effective in estimating the density of territorial individuals. *Received 13 September 2004, accepted 26 July 2005.*

Key words: boreal forest, detectability, point count, sampling error, spatial variation, spot mapping, territory size.

Est-ce que les Points D'Écoute de Passereaux Boréaux Constituent une Méthode Fiable pour L'Obtention D'Estimateurs D'Abondance Plus Avancés?

RÉSUMÉ.—Les points d'écoute sont souvent utilisés pour fournir de l'information sur l'abondance des passereaux. Néanmoins, si les données de points d'écoute doivent être comparées dans l'espace et le temps, quelque soit le biais dans les estimés,

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ce biais devrait correspondre et être linéairement corrélé à la vraie abondance. Plusieurs études ont suggéré que cette prémisse pourrait être violée dans le cas des passereaux. Dans cette étude, nous avons utilisé du double échantillonnage pour tester si les points d'écoute sont linéairement corrélés à la vraie abondance, comme estimé par "spot mapping", pour 12 espèces de passereaux de la forêt boréale du nord de l'Alberta, Canada. Nous avons trouvé que l'abondance totale des oiseaux à travers plusieurs stations de points d'écoute était positivement corrélée avec le nombre de territoires, ce qui confirme que les points d'écoute sont linéairement corrélés aux abondances issues du "spot mapping" pour les espèces testées. Néanmoins, des erreurs d'échantillonnage importantes ont masqué cette relation à l'échelle de la station de point d'écoute (parcelle avec un rayon de 100 m fixe). Les modèles à double échantillonnage qui sont entrés dans les différences d'abondance entre les quadrillages de "spot mapping" qui utilisaient des effets aléatoires ont amélioré les prédictions pour la plupart des espèces. Nous n'avons trouvé aucun effet de l'année sur la détection. L'abondance maximale, issue des sessions de points d'écoute, était un index beaucoup plus fin que l'abondance moyenne et tendait à produire des modèles avec un meilleur ajustement. L'abondance issue des points d'écoute était mieux corrélée à la vraie abondance pour les espèces possédant des territoires relativement petits, ou les espèces avec de grandes variations spatiales et temporelles dans la densité. Nos résultats indiquent également que l'abondance par point d'écoute pourrait être proportionnelle à la longueur totale des limites de territoires dans la parcelle plutôt que la fraction totale des territoires dans la parcelle. Nos analyses suggèrent que les points d'écoute fournissent un index d'abondance intéressant, même si les stations individuelles de points d'écoute ne sont pas toujours efficaces dans l'estimation des densités d'individus territoriaux.

SONGBIRD ABUNDANCE CAN be estimated using many techniques, which vary in the effort and cost required and the resolution and accuracy of the data obtained. Detailed studies of avian demography, using techniques such as mist netting or nest searching, provide fairly accurate estimates of population size and other demographic parameters, but are expensive and limited to small spatial extents (Ralph et al. 1993). Techniques such as point or transect counts greatly increase the area that can be surveyed but provide information only on relative abundances between sites or habitats (Ralph et al. 1993, Rosenstock et al. 2002). In most circumstances, the actual proportion of individuals detected is unimportant so long as no systematic errors influence the observed patterns. It is not clear, however, whether point counts are sufficiently reliable to be used in place of more intensive estimates of population abundance. In particular, the reliability of point counts has not been sufficiently examined in four areas: (1) whether population density influences the proportion of individuals detected in point counts, such that point-count abundance is not a linear function of true density; (2) whether spatial or temporal variability in density influences detectability; (3) whether mean or maximum point-count abundances are equally reliable in estimating true abundance; and (4) whether the detectability of a species depends on its territory size.

Thompson (2002) divided variation in estimates of abundance into spatiotemporal variation (often the component of interest to the researcher), bias (systematic under- or overcounting), and random variation. If abundance estimates derived from point counts are to be compared, the associated bias must be consistent in time and space (i.e. the number of individuals observed must be linearly related to the true abundance; Link and Nichols 1994, Johnson 1995, Pollock et al. 2002, Rosenstock et al. 2002, Thompson 2002). This assumption may be violated for songbirds. Typically, the vast majority of individuals observed during a point-count survey are detected aurally (Gibbs and Wenny 1993, Rosenstock et al. 2002); therefore, changes in song output and environmental variables influencing observer efficiency can significantly affect detectability (Mackowicz 1977, Bart and Shoultz 1984, Verner 1985, Gibbs and Wenny

1993, Schieck 1997, Rosenstock et al. 2002). Researchers typically design their surveys to minimize these effects—for example, by limiting them to nonrainy, calm days and by rotating observers. However, population density may positively affect song rate and proportion of males singing (Mönkkönen and Aspi 1997), and unpaired males in marginal habitat (thus, at low densities) generally sing more frequently than paired males in populations at higher local densities (Gibbs and Wenny 1993). This could introduce bias into any index of abundance based on aural detections.

The bias of a sample depends on the dispersion pattern (spatial variability) within the sampling unit, which is unbiased only when individuals are evenly distributed (Mönkkönen and Aspi 1997). Given that dispersion patterns change with density, because less favorable habitats are more likely to be occupied only at high population densities (Mönkkönen and Aspi 1997, Chamberlain and Fuller 1999), bias of point-count surveys may depend on population density. A "good" index of abundance will measure a constant proportion of the true abundance over all population densities (Link and Nichols 1994, Johnson 1995, Pollock et al. 2002, Rosenstock et al. 2002, Thompson 2002). However, few indices have been evaluated in this context.

Finally, the probability of detecting an individual is reduced when only a fraction of its territory is sampled. The area surveyed around fixed-radius point-count stations is smaller than the territory size of some songbirds. Hence, abundance estimates from point counts would be more likely to be related to true abundance for species with smaller territories in surveys conducted at small spatial scales (i.e. the scale of the point-count station).

Our study addressed these concerns for 12 bird species breeding in the boreal mixed-wood forests of western Canada using a double-sampling technique (Bart and Earnst 2002). We compared estimates of abundance from an intensive survey method, spot mapping, with estimates of abundance from point-count surveys. We compared 108 point-count stations on 21 spot-mapping grids, a relatively large number of plots for a study of this type. True abundance was then predicted from the point counts by fitting a linear model (Eberhardt and Simmons 1987, Thompson 1992, Johnson 1995). Although spot mapping does not always count all individuals (Gibbs and Wenny 1993), it is considered a better approximation of a true census of birds (Verner 1985). We also compared models with mean and maximum point-count abundance observed over multiple survey rounds during a breeding season to determine which was more closely related to spot-mapping abundance.

Many studies (e.g. Emlen 1971, Franzreb 1976, Frochot et al. 1977, Svensson 1981, Szaro and Jankle 1982, Cyr et al. 1995, Howell et al. 2004) have compared data from point-count or line-transect surveys at the scale of a spot-mapping grid (typically 10–20 ha in forest; Bibby et al. 1992). However, consistency at the scale of a spot-mapping grid does not necessarily hold at finer spatial scales. Thus, another focus was to compare the two measures of abundance at the scale of a point-count station. We are unaware of any other study comparing these two indices in this context. Finally, we determined whether territory size influenced the accuracy of point-count estimates.

Methods

Study area and sampling design.—This study used a subset of data from the Calling Lake fragmentation study (Schmiegelow et al. 1997, Schmiegelow and Hannon 1999), located in north-central Alberta, Canada (55°N, 113°W; Fig. 1). The study area encompassed ~14,000 ha of boreal mixed-wood forest, dominated by 80–130 year-old aspen (*Populus tremuloides*) stands. Some white spruce (*Picea glauca*) and black spruce (*P. mariana*) were also present. For the present study, we used 108 stations that were surveyed using point counts and spot mapping from 1993 through 1996 (Fig. 1).

Point-count stations were 100-m-radius plots located 200 m apart on a grid (Schmiegelow et al. 1997). Birds were surveyed at each station for 5 min, five times each breeding season (every 10 days from the third week of May through late June). The first survey period was ignored here because most migrants were not yet breeding. More details on the sampling methods are available in Schmiegelow et al. (1997).

Point-count and spot-mapping surveys (F. Schmiegelow and M.-A. Villard unpubl. data) were conducted separately, so the observations were considered independent. Twenty-one spot-mapping grids of three sizes were used: 10 ha (6

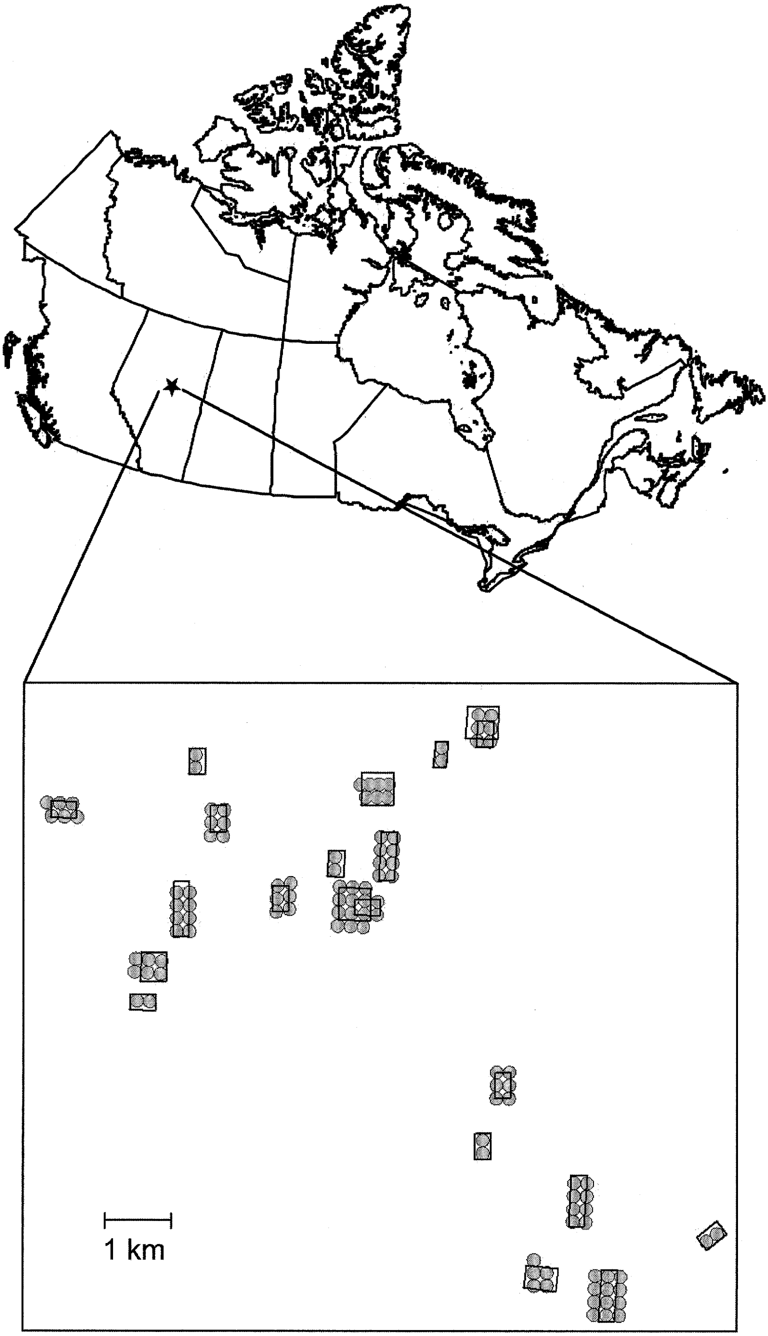

FIG. 1. Location of the Calling Lake fragmentation study in north-central Alberta. Also shown are point-count stations (circles) surveyed with spot mapping and locations of spot-mapping grids (rectangles).

grids), 20 ha (12 grids), and 25 ha (3 grids). Each spot-mapping grid contained some fraction of 2–12 point-count stations. Spot mapping started at dawn and finished within 5 h. The observer walked through the grid at a pace of approximately 15–17 min per 400 m of transect. Eight rounds of spot mapping were conducted during the breeding season (between the last week of May and the first week of July). Territories were delineated following Bibby et al. (1992) and the International Bird Census Committee (1969) using data from all rounds of spot mapping. As recommended (Bibby et al. 1992), at least two detections a minimum of 10 days apart were required to delineate a territory. However, most territories were drawn on the basis of more than two detections. Only birds with delineated territories were included in analyses. Different subsets of the spot-mapping grids were surveyed each year, though some grids were surveyed for up to four years.

Data.—We focused on 12 species that were relatively abundant in the surveyed plots: Least Flycatcher (*Empidonax minimus*), Red-eyed Vireo (*Vireo olivaceus*), Black-capped Chickadee (*Poecile atricapillus*), Red-breasted Nuthatch (*Sitta canadensis*), Yellow-rumped Warbler (*Dendroica coronata*), Black-throated Green Warbler (*D. virens*), Ovenbird (*Seiurus aurocapilla*), Connecticut Warbler (*Oporornis agilis*), Mourning Warbler (*O. philadelphia*), Western Tanager (*Piranga ludoviciana*), White-throated Sparrow (*Zonotrichia albicollis*), and Rose-breasted Grosbeak (*Pheucticus ludovicianus*). Independent estimates of territory sizes were obtained from the Birds of North America series, because data on territory sizes were not available for our study area (Morse 1993, Pitochelli 1993, Smith 1993, Briskie 1994, Falls and Kopachena 1994, Van Horn and Donovan 1994, Pitochelli et al. 1997, Hunt and Flaspohler 1998, Ghalambor and Martin 1999, Hudon 1999, Cimprich et al. 2000, Wyatt and Francis 2002). If a range of territory sizes was given, the midpoint of the range was used for statistical analyses.

In calculating point-count abundance in a single round, we counted each individual seen or heard singing or calling as a single individual, unless a pair or family group was observed (which we counted as two adults). Individuals observed flying over or through the plot were not counted. Two indices of abundance for each species were then derived from these point-count data: mean number of individuals counted at each station in rounds two through five, and maximum number of individuals counted at each station in any of rounds two through five. We also used two definitions of "true" abundance: (1) number of individuals with at least half their spot-mapped territory intersecting an individual point-count station, and (2) number of individuals with any fraction of their estimated territory within the point-count station.

Statistical analyses.—We fit linear double-sampling models and then examined the residuals to confirm that these models were truly linear. We used a log transformation of the indices to linearize them, because the response was a count that we modeled using Poisson regression. Using this transformation with estimated abundances could introduce bias, so we used an unbiased jack-knife estimator rather than simple transformed indices (Mooney and Duval 1993; see Toms 2004 for further details). Because the study was not designed to compare estimates from spot-mapping and point-count surveys, spot-mapping grids did not neatly coincide with point-count stations, except in a few instances. Instead, point-count stations intersected the spot-mapping grid to different extents, depending on the sample plot. Therefore, point-count observations were multiplied by the proportion of the station within the spot-mapping grid (range: 1–100%, mean ± SD: 57.8 ± 34.4%).

Several double-sampling models were evaluated. The simplest model assumed that the relationship between point-count abundance and number of territories did not depend on the spatial location of the spot-mapping grid or on the year. The other models included random intercepts associated with spot-mapping grid or year: point-count stations were grouped in space or time, and all stations within the group were assumed to have the same double-sampling relationship. Essentially, this technique modeled abundances at individual point-count stations as deviations from the spot-mapping grid or year averages. We plotted point-count abundance against spot-mapping abundance separately for each spot-mapping observer and experimental treatment (i.e. control, fragment, riparian). No differences were observed (J. D. Toms unpubl. data), so any bias introduced by these variables was assumed to be negligible.

All models were fit to the data as generalized linear mixed models using the NLMIXED procedure of SAS, version 8.2 (SAS Institute, Cary, North Carolina). Unfortunately, limitations of the model meant that we had to assume that the indices were measured without error, even though we knew this was not the case. This probably resulted in an underestimate of the slope parameter (Davies and Hutton 1975). Furthermore, models incorporating both space and time as main effects could not be fit using NLMIXED. Akaike weights (derived from AIC values) were used to determine the relative merits of each model. These are a measure of the weight of evidence that a given model is the best in the set evaluated (Anderson et al. 2000).

Finally, we tested the prediction that species with smaller territories would have a stronger correlation between estimates from the two survey techniques by examining whether model fit was influenced by territory size. Vonesh and Chinchilli (1997) suggest the use of a model concordance coefficient (r_c) as a measure of model fit. The values of r_c can range from –1 to 1: a perfect model fit corresponds to $r_c = 1$, and a significant lack of fit corresponds to $r_c \leq 0$. Thus our prediction was supported if territory size was negatively correlated with r_c. Spearman rank correlations were used to test this prediction.

RESULTS

The number of territories observed from spot mapping was plotted against the jack-knife estimates of point-count abundance (Fig. 2; see Toms 2004 for additional plots). Most species showed, at best, a weak relationship between the number of territories and the point-count indices at the scale of a point-count station. Least Flycatcher was the only species with a moderately strong linear relationship. For most species (except those with large territories), this relationship was stronger when we compared equivalent statistics calculated at the spot-mapping grid scale (i.e. summing across stations within a grid; Fig. 3). This suggested that sampling variation of some sort was obscuring the underlying relationship, and that estimators incorporating the effects of space or time would be useful if some of the sampling error was attributable to pseudoreplication or other spatial or temporal effects. In fact, Akaike weights clearly indicated that models incorporating spatial location through a random effect of spot-mapping grid were better for most species than fixed models or models incorporating time through a random effect of year (Table 1). Residual plots showed no evidence of nonlinearity (e.g. Fig. 4), so linear models were appropriate.

Using abundance from maximum point counts generally produced better model fits as measured by r_c (Table 1) and had model slopes that were closer to one (Table 2) than when using mean abundance as a response variable. As predicted, there was a significant negative correlation between territory size and model fit when the number of individuals with at least half their spot-mapped territory intersecting an individual point-count station was used as the response (as measured by r_c; $\rho = -0.61$, $P = 0.04$ for maximum point-count; $\rho = -0.62$, $P = 0.04$ for mean point-count). However, this did not occur when the number of individuals with any fraction of their estimated territory within the point-count station was used as the response (as measured by r_c; $\rho = -0.41$, $P = 0.17$ for maximum point count; $\rho = -0.46$, $P = 0.12$ for mean point count). In general, models using the number of individuals with any fraction of their estimated territory within the point-count station as the response variable fit much better than models using the number of individuals with at least half their spot-mapped territory intersecting an individual point-count station (as measured by r_c; Table 1) and often had slopes that were closer to one (Table 2).

DISCUSSION

Our results suggest that point counts are indeed a reasonable proxy for more intensive measures of true songbird abundance (e.g. spot mapping), particularly for species with relatively small territories or for systems with high spatial or temporal variability. As with others (Svensson 1981, Cyr et al. 1995, Howell et al. 2004), we found total abundance across several point-count stations to be positively correlated with the number of territories. However, we also found this to be true at the scale of a single, 100-m-radius point-count station (3.1 ha); abundance estimates from both maximum and mean point counts were linearly related to the number of territorial individuals (though only weakly). We found that maximum point-count abundance was preferable to mean point-count

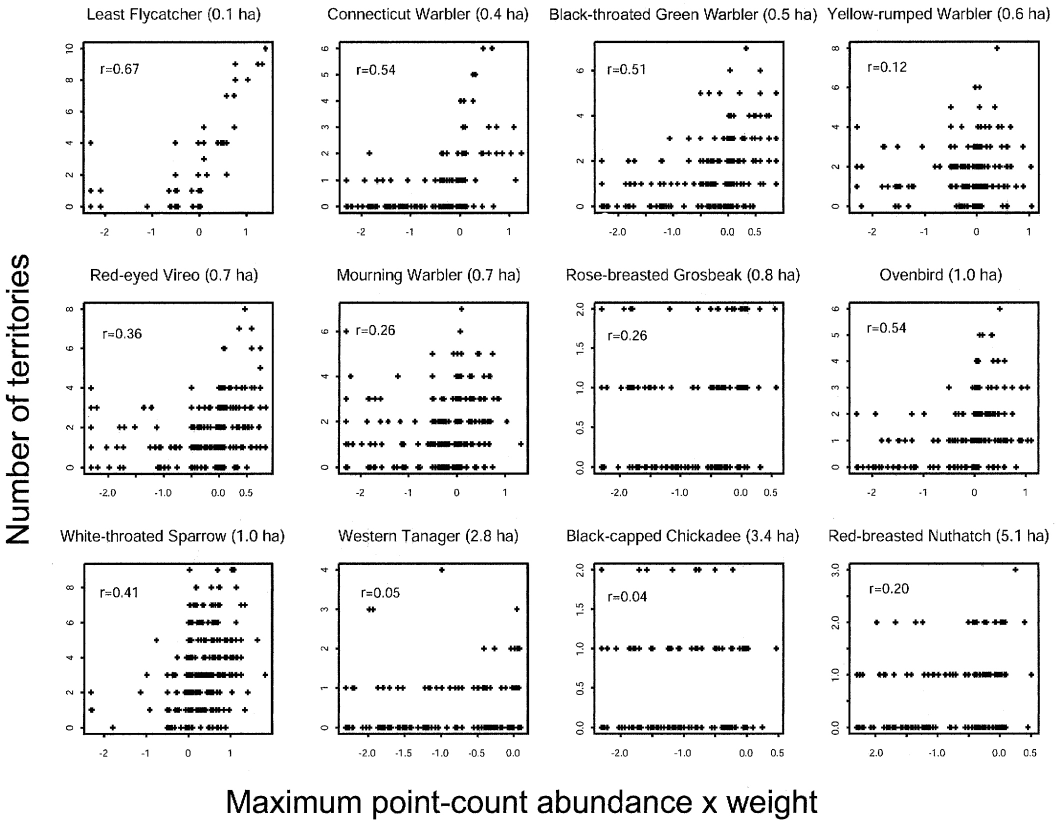

Fig. 2. Relationship is weak (mean Spearman rank correlation, $r = 0.33$) between the number of territories from spot-mapping and maximum point-count abundance (jack-knife estimator multiplied by sampling weights, the proportion of point-count station overlapping spot-mapping grid) at the scale of a 100-m-radius point-count station. Order of plots follows territory sizes of species (given in parentheses). Plots of mean point-count abundance are similar (Toms 2004).

abundance, because it produced better model fits and model slopes closer to one (Tables 1 and 2).

Individual point-count stations may not reflect the density of territorial individuals, because they also detect nonterritorial individuals ("floaters") and individuals moving outside their territorial boundaries (Granholm 1983, Verner 1985). Here, models that included effects of spatial location were better than models that ignored such effects (i.e. fits were improved when abundances at individual point-count stations were modeled as deviations from grid averages by including a random effect of spot-mapping grid). Extraterritorial movement of individuals within a spot-mapping grid may explain this result. However, the relative efficiency of each survey technique might vary for many other reasons: differences in observer efficiency (though the point-count survey rotated observers to reduce this possibility; Bibby et al. 1992), differences in vegetation (e.g. shrubby plots may be more difficult to survey than more open areas; Mackowicz 1977, Schieck 1997), or even local differences in bird communities (e.g. species with loud songs could reduce the likelihood of hearing a quiet species). Models with random effects of year were not supported by the data, which indicates that detectability did not significantly differ across the four years of the study.

A sensitive index of abundance should have a model slope near one, so that changes in true abundance are closely reflected in changes in the index. Slopes that are quite different from one can be problematic, because changes in

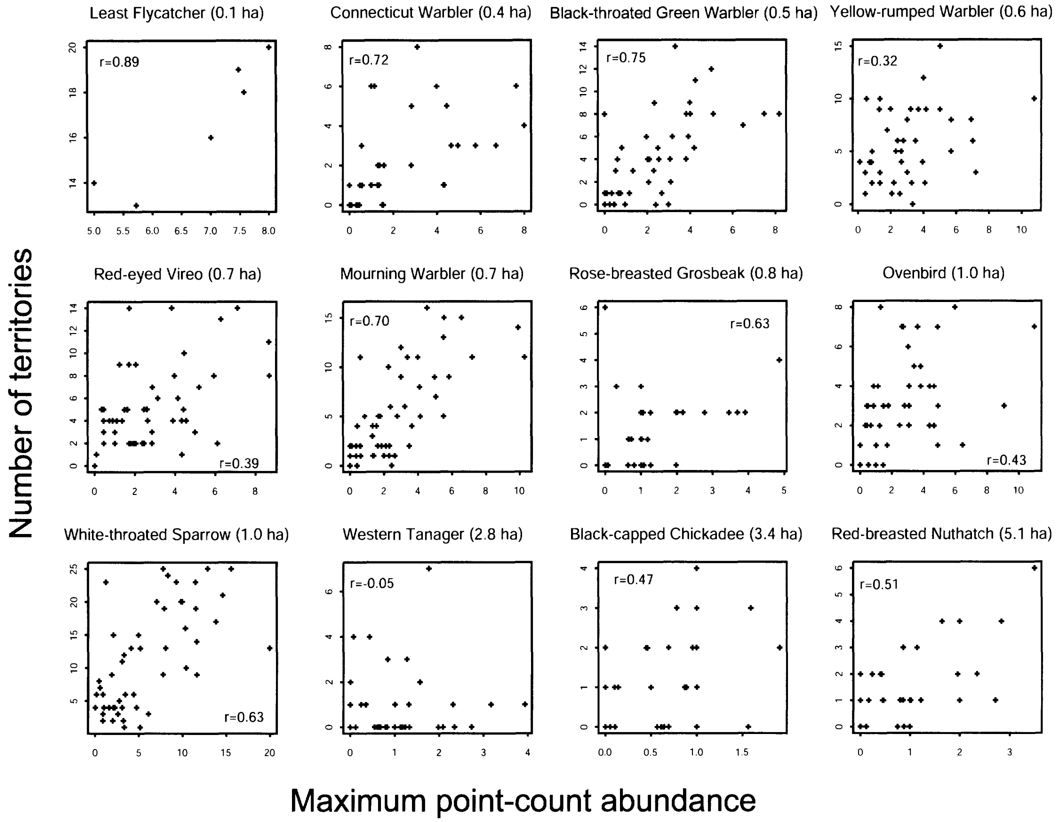

Fig. 3. Relationship is stronger (mean Spearman rank correlation, $r = 0.54$) between the number of territories from spot-mapping and maximum point-count abundance (summed over all stations within that grid) at the scale of a spot-mapping grid, even before adjusting for differences in abundance between grids. Order of plots follows territory sizes of species (given in parentheses). Plots of mean point-count abundance are similar (Toms 2004).

the index are not indicative of the true changes in abundance. In our study, maximum point-counts were a more sensitive index of abundance and tended to produce better model fit than mean point-counts, regardless of the definition of territorial individuals used. However, all models had only poor to moderate fits (even though our study included 21 spot-mapping grids). Moreover, the double-sampling models for most species we examined did not have slope parameters significantly different from zero, which indicates that the linear relationship between point-count abundance and spot-mapping abundance at the point-count-station scale was weak. In part, this may be attributable to an underestimation of the slope parameter caused by measurement error in the point-count abundance indices (Davies and Hutton 1975). Because some error is unavoidable, the usefulness of individual point-count stations is likely to be low compared with that of multiple point-count stations. The differences in slopes observed between species may reflect behavioral differences; for example, both sexes of Least Flycatcher are known to sing, and singing rates are believed to be very high (averaging 49 songs min^{-1}; Briskie 1994). This may explain why their estimated slope was very high (Table 2).

Interestingly, models defining the number of territorial individuals as the number of territories overlapping the point-count station to any extent fit much better than models defining the number of territorial individuals as those with at least half their spot-mapped territory intersecting an individual point-count station. This indicates that even individuals with small portions

TABLE 1. In most cases, models predicting spot-mapping abundance with point-count abundance performed better when they included a random effect of spot-mapping grid (space random, 42 of 48) than when including no random effects (no random, 6 of 48) or a random effect of year (time random, 0 of 48). Models using the number of individuals with at least half their spot-mapped territory intersecting an individual point-count station (>50%) as a response had stronger model fits (r_c, 23 of 24) than models using the number of territories overlapping the point-count station to any extent (>0%). Point-count abundance was measured as the mean or maximum number of individuals observed over four survey rounds. Akaike weights represent the probability that a given model is the best in the set tested. The best-fitting model is in bold; a perfect model fit corresponds to $r_c = 1$, and a significant lack of fit corresponds to $r_c \leq 0$.

			No random		Space random		Time random	
Species	Response	Point count index	Akaike weight	r_c	Akaike weight	r_c	Akaike weight	r_c
Least Flycatcher	≥50%	Maximum	**0.53**	**0.80**	0.28	0.80	0.19	0.80
	≥50%	Mean	0.13	0.66	**0.82**	**0.73**	0.05	0.66
	>0%	Maximum	**0.52**	**0.80**	0.29	0.80	0.19	0.80
	>0%	Mean	0.10	0.65	**0.86**	**0.69**	0.04	0.65
Red-eyed Vireo	≥50%	Maximum	0.00	0.02	**1.00**	**0.20**	0.00	0.02
	≥50%	Mean	0.00	0.02	**1.00**	**0.21**	0.00	0.02
	>0%	Maximum	0.00	0.15	**1.00**	**0.44**	0.00	0.15
	>0%	Mean	0.00	0.14	**1.00**	**0.43**	0.00	0.14
Black-capped Chickadee	≥50%	Maximum	**0.54**	**0.01**	0.26	0.05	0.20	0.01
	≥50%	Mean	**0.54**	**0.01**	0.26	0.04	0.20	0.01
	>0%	Maximum	0.09	0.01	**0.78**	**0.18**	0.14	0.07
	>0%	Mean	0.09	0.00	**0.77**	**0.17**	0.14	0.07
Red-breasted Nuthatch	≥50%	Maximum	0.15	0.02	**0.76**	**0.16**	0.08	0.06
	≥50%	Mean	0.16	0.01	**0.72**	**0.15**	0.12	0.06
	>0%	Maximum	0.00	0.13	**0.89**	**0.47**	0.11	0.31
	>0%	Mean	0.00	0.08	**0.69**	**0.44**	0.31	0.30
Yellow-rumped Warbler	≥50%	Maximum	0.12	0.01	**0.58**	**0.13**	0.30	0.09
	≥50%	Mean	0.13	0.01	**0.56**	**0.12**	0.31	0.08
	>0%	Maximum	0.00	0.02	**0.93**	**0.46**	0.07	0.28
	>0%	Mean	0.00	0.01	**0.94**	**0.46**	0.06	0.28
Black-throated Green Warbler	≥50%	Maximum	0.03	0.19	**0.94**	**0.32**	0.03	0.22
	≥50%	Mean	0.00	0.12	**1.00**	**0.30**	0.00	0.14
	>0%	Maximum	0.00	0.35	**1.00**	**0.62**	0.00	0.43
	>0%	Mean	0.00	0.23	**1.00**	**0.60**	0.00	0.33

Table 1. Continued.

Species	Response	Point count index	No random		Space random		Time random	
			Akaike weight	r_c	Akaike weight	r_c	Akaike weight	r_c
Ovenbird	≥50%	Maximum	**0.58**	**0.09**	0.21	0.09	0.21	0.09
	≥50%	Mean	**0.58**	**0.07**	0.21	0.09	0.21	0.07
	>0%	Maximum	0.00	0.32	**1.00**	**0.58**	0.00	0.38
	>0%	Mean	0.00	0.36	**1.00**	**0.59**	0.00	0.42
Connecticut Warbler	≥50%	Maximum	0.00	0.07	**1.00**	**0.27**	0.00	0.09
	≥50%	Mean	0.00	0.03	**1.00**	**0.27**	0.00	0.05
	>0%	Maximum	0.00	0.43	**1.00**	**0.65**	0.00	0.46
	>0%	Mean	0.00	0.41	**1.00**	**0.65**	0.00	0.43
Mourning Warbler	≥50%	Maximum	0.33	0.01	**0.55**	**0.07**	0.12	0.01
	≥50%	Mean	0.30	0.00	**0.60**	**0.07**	0.11	0.00
	>0%	Maximum	0.00	0.08	**1.00**	**0.41**	0.00	0.14
	>0%	Mean	0.00	0.02	**1.00**	**0.40**	0.00	0.09
Western Tanager	≥50%	Maximum	0.22	0.00	**0.60**	**0.14**	0.17	0.05
	≥50%	Mean	0.22	0.00	**0.60**	**0.14**	0.17	0.05
	>0%	Maximum	0.00	0.00	**1.00**	**0.65**	0.00	0.14
	>0%	Mean	0.00	0.00	**1.00**	**0.65**	0.00	0.14
White-throated Sparrow	≥50%	Maximum	0.00	0.01	**1.00**	**0.23**	0.00	0.01
	≥50%	Mean	0.00	0.01	**1.00**	**0.22**	0.00	0.01
	>0%	Maximum	0.00	0.21	**1.00**	**0.60**	0.00	0.30
	>0%	Mean	0.00	0.16	**1.00**	**0.59**	0.00	0.28
Rose-breasted Grosbeak	≥50%	Maximum	0.02	0.01	**0.93**	**0.24**	0.04	0.08
	≥50%	Mean	0.02	0.00	**0.93**	**0.23**	0.05	0.07
	>0%	Maximum	0.00	0.08	**1.00**	**0.57**	0.00	0.31
	>0%	Mean	0.00	0.04	**1.00**	**0.57**	0.00	0.29

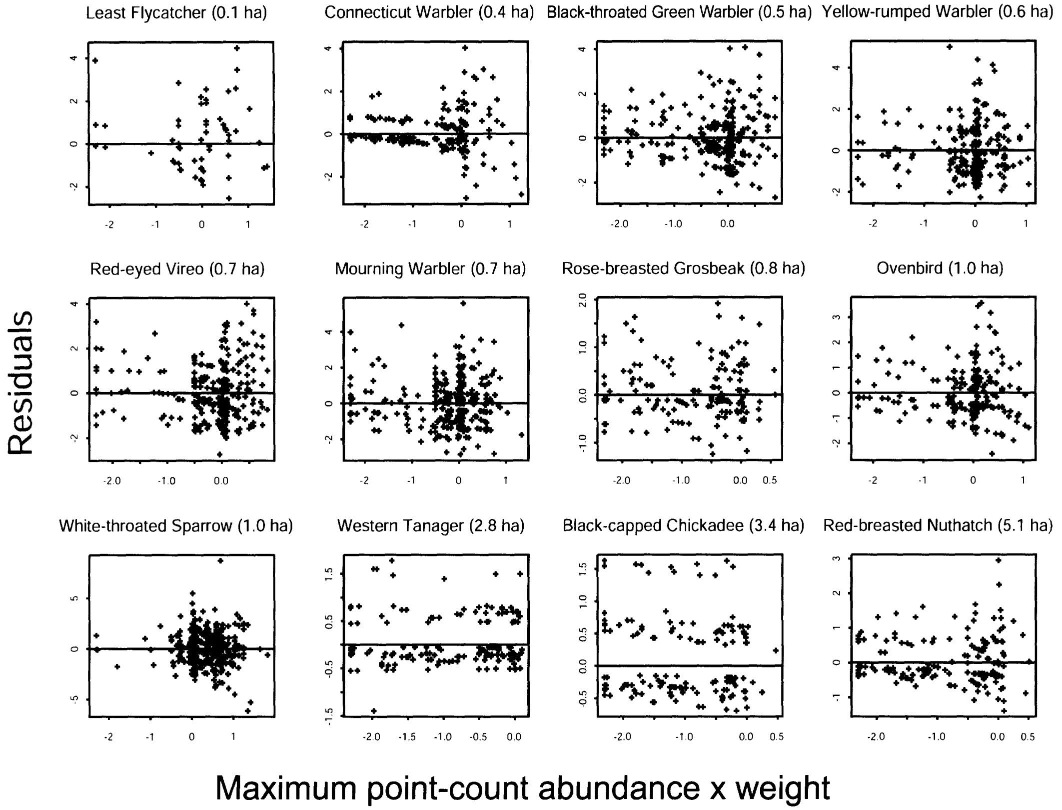

Fig. 4. Residuals from the best-fitting model of number of territories overlapping the point-count station to any extent (see Table 1) indicate that linear models are appropriate (residuals are evenly distributed). Order of plots follows territory sizes of species (given in parentheses). Similar results are obtained with other models.

of their territories falling within a point-count station are detected in the point counts. This is likely attributable, in part, to the use of four point-count surveys per breeding season. We would expect that individuals with only a small portion of their territory falling within a point-count station would be much less likely to be detected during any single point-count survey. It is also possible that this result is an artifact of poor distance estimation, if all observers conducting the point counts consistently recorded individuals within a larger radius despite careful training. However, it is more likely a result of songbird behavior: males often sing more at the edge of their territory than in the center (e.g. Hudon 1999, Cimprich et al. 2000). Because most registrations in point counts are of singing males (93% at Calling Lake, Schmiegelow et al. 1997; see also Gibbs and Wenny 1993, Rosenstock et al. 2002), point-count abundance may be proportional to the total length of territorial boundaries in the plot rather than to the total fraction of territory areas within the plot. Thus, species with proportionally less of their boundary in the point-count station (i.e. species with large territories) would not be as effectively surveyed using point counts. In fact, we found that model fits were negatively correlated with territory size when the response was the number of individuals with at least half their spot-mapped territory intersecting an individual point-count station, but not when the response was the number of territories overlapping the point-count station to any extent. Species with small territories were more likely to have >50% of their territory within the spot-mapping plot, resulting in a higher degree of similarity in the two estimates of territorial individuals.

In the present study, spot mapping was presumed to be an unbiased, precise measure of

Table 2. Maximum point counts seem to be a more sensitive index of abundance than mean point counts (15 of 24 slopes closer to 1.0: the slope of a perfect model). Moreover, point-count abundance is more closely related (16 of 24 slopes closer to 1.0) to the number of territories overlapping the point-count station to any extent (>0%) than to the number of individuals with at least half their spot-mapped territory intersecting an individual point-count station (>50%). Point-count abundance was measured as the mean or maximum number of individuals observed over four survey rounds. Models tested included no random effects (fixed), a random effect of spot-mapping grid (space), or a random effect of year (time).

Species	Response	Point count index	Best model	Intercept Estimate ± SE	Slope Estimate ± SE	Random effect Estimate ± SE
Least Flycatcher	≥50%	Maximum	Fixed	–0.10 ± 0.13	1.46 ± 0.17	–
	≥50%	Mean	Space	0.45 ± 0.22	1.28 ± 0.18	0.33 ± 0.18
	>0%	Maximum	Fixed	0.63 ± 0.09	1.24 ± 0.12	–
	>0%	Mean	Space	1.09 ± 0.17	1.09 ± 0.13	0.26 ± 0.14
Red-eyed Vireo	≥50%	Maximum	Space	–0.41 ± 0.13	0.17 ± 0.11	0.39 ± 0.10
	≥50%	Mean	Space	–0.35 ± 0.14	0.19 ± 0.12	0.39 ± 0.10
	>0%	Maximum	Space	0.62 ± 0.10	0.29 ± 0.08	0.34 ± 0.08
	>0%	Mean	Space	0.70 ± 0.10	0.30 ± 0.08	0.34 ± 0.08
Black-capped Chickadee	≥50%	Maximum	Fixed	–1.57 ± 0.27	0.26 ± 0.22	–
	≥50%	Mean	Fixed	–1.56 ± 0.30	0.24 ± 0.23	–
	>0%	Maximum	Space	–0.87 ± 0.23	0.15 ± 0.14	0.51 ± 0.20
	>0%	Mean	Space	–0.90 ± 0.25	0.12 ± 0.16	0.51 ± 0.20
Red-breasted Nuthatch	≥50%	Maximum	Space	–1.22 ± 0.25	0.34 ± 0.17	0.58 ± 0.22
	≥50%	Mean	Space	–0.51 ± 0.25	0.44 ± 0.15	0.71 ± 0.19
	>0%	Maximum	Space	–0.29 ± 0.21	0.51 ± 0.12	0.65 ± 0.17
	>0%	Mean	Space	–0.23 ± 0.23	0.50 ± 0.14	0.67 ± 0.18
Yellow-rumped Warbler	≥50%	Maximum	Space	–0.16 ± 0.10	–0.13 ± 0.11	0.26 ± 0.09
	≥50%	Mean	Space	–0.18 ± 0.11	–0.09 ± 0.12	0.26 ± 0.09
	>0%	Maximum	Space	0.74 ± 0.11	0.13 ± 0.08	0.41 ± 0.09
	>0%	Mean	Space	0.78 ± 0.11	0.13 ± 0.09	0.41 ± 0.09
Black-throated Green Warbler	≥50%	Maximum	Space	–0.55 ± 0.17	0.58 ± 0.13	0.44 ± 0.16
	≥50%	Mean	Space	–0.51 ± 0.20	0.48 ± 0.13	0.55 ± 0.18
	>0%	Maximum	Space	0.05 ± 0.23	0.42 ± 0.08	0.85 ± 0.22
	>0%	Mean	Space	0.09 ± 0.26	0.38 ± 0.09	0.94 ± 0.23

TABLE 2. Continued.

Species	Response	Point count index	Best model	Intercept Estimate ± SE	Slope Estimate ± SE	Random effect Estimate ± SE
Ovenbird	≥50%	Maximum	Fixed	–0.43 ± 0.08	0.40 ± 0.12	–
	≥50%	Mean	Fixed	–0.34 ± 0.09	0.38 ± 0.13	–
	>0%	Maximum	Space	0.29 ± 0.16	0.42 ± 0.12	0.57 ± 0.15
	>0%	Mean	Space	0.41 ± 0.15	0.51 ± 0.13	0.55 ± 0.14
Connecticut Warbler	≥50%	Maximum	Space	–1.18 ± 0.29	0.28 ± 0.15	0.82 ± 0.25
	≥50%	Mean	Space	–0.64 ± 0.35	0.74 ± 0.19	1.06 ± 0.31
	>0%	Maximum	Space	–0.39 ± 0.26	0.64 ± 0.15	0.80 ± 0.24
	>0%	Mean	Space	–0.31 ± 0.29	0.62 ± 0.17	0.88 ± 0.25
Mourning Warbler	≥50%	Maximum	Space	–0.28 ± 0.10	0.08 ± 0.09	0.22 ± 0.10
	≥50%	Mean	Space	–0.30 ± 0.11	0.02 ± 0.10	0.23 ± 0.10
	>0%	Maximum	Space	0.53 ± 0.14	0.15 ± 0.06	0.52 ± 0.12
	>0%	Mean	Space	0.53 ± 0.15	0.08 ± 0.07	0.55 ± 0.13
Western Tanager	≥50%	Maximum	Space	–1.97 ± 0.34	0.02 ± 0.22	0.68 ± 0.29
	≥50%	Mean	Space	–1.95 ± 0.37	0.04 ± 0.24	0.68 ± 0.29
	>0%	Maximum	Space	–1.38 ± 0.35	–0.03 ± 0.14	0.13 ± 0.28
	>0%	Mean	Space	–1.43 ± 0.37	–0.07 ± 0.17	1.13 ± 0.28
White-throated Sparrow	≥50%	Maximum	Space	0.22 ± 0.12	0.21 ± 0.10	0.39 ± 0.10
	≥50%	Mean	Space	0.28 ± 0.11	0.17 ± 0.11	0.39 ± 0.10
	>0%	Maximum	Space	1.10 ± 0.12	0.30 ± 0.07	0.46 ± 0.09
	>0%	Mean	Space	1.18 ± 0.11	0.27 ± 0.08	0.46 ± 0.09
Rose-breasted Grosbeak	≥50%	Maximum	Space	–2.41 ± 0.50	0.26 ± 0.24	1.08 ± 0.42
	≥50%	Mean	Space	2.59 ± 0.55	0.04 ± 0.26	1.10 ± 0.42
	>0%	Maximum	Space	–0.92 ± 0.35	0.17 ± 0.12	1.09 ± 0.31
	>0%	Mean	Space	–0.90 ± 0.36	0.17 ± 0.13	1.12 ± 0.31

true abundance. However, spot mapping also relies on aural detections for delineating territory boundaries and can be subject to sampling or observer error (Verner 1985, Verner and Milne 1990). Even if the number of territories is correctly determined by spot mapping, their locations are often slightly offset from territories obtained by following color-banded individuals (Enemar et al. 1979, Tiainen and Bastian 1983). If consistent errors were made in estimating territory locations or sizes, it would affect the degree of overlap between spot-mapped territories and point-count abundance and influence the slopes of the double-sampling models.

Our results suggest that for the species we evaluated, except for Least Flycatcher, point counts are associated with significant sampling errors at the scale of a 100-m-radius plot. Correlations between point counts and spot mapping are known to be stronger in species with substantial spatial or temporal variations in abundance (Svensson 1981, DeSante 1986), possibly because sampling variance then forms a smaller proportion of the total variance. At Calling Lake, Least Flycatcher territories tended to be found in groups in limited sections of the spot-mapping grids (i.e. they were spatially clustered, as also found by Sherry and Holmes 1985, Perry and Andersen 2003), which may have contributed to their stronger relationship at the scale of point-count stations. They also have the smallest territory of the species studied, and species with smaller territories had a stronger relationship between point-count and spot-mapping abundance. In general, point-count abundance was more closely related to spot-mapping abundance at the scale of a spot-mapping grid. However, large errors occurred even at this scale for species with larger territories (e.g. Rose-breasted Grosbeak, Western Tanager).

Results from four other studies that have been conducted at the scale of an individual point-count station are mixed (DeSante 1981, 1986; Tarvin et al. 1998; Jones et al. 2000). Fixed-radius and variable-radius point counts were linearly correlated with the density of breeding pairs of Blue Jays (*Cyanocitta cristata*; Tarvin et al. 1998) and Cerulean Warblers (*D. cerulea*; Jones et al. 2000), and significant linear correlations were found between variable-radius point-count abundance and spot mapping for five of eight species in California scrubland (DeSante 1981). However, even with an inflated sample size because of pseudoreplication, only 7 of 19 species surveyed in Californian subalpine forests showed significant positive correlations (DeSante 1986). Each of the species showing linear correlations in these studies had relatively small territories or showed evidence of spatial clustering. The evidence to date thus suggests that individual point-count stations are not consistently effective in estimating the density of territorial individuals, especially for species with larger territories and low temporal and spatial variability.

In conclusion, our results indicate that point-count abundance is linearly related to the number of territorial individuals for the 12 species examined. Thus, to answer our opening question, there is no evidence that population density affects detectability of songbirds during point counts. Maximum point counts were a better index than mean point counts for the species examined. However, both indices appear to have large sampling errors, particularly for species with larger territories. Although individual point-count stations seem to detect a constant proportion of the number of territorial individuals, this assumption should be validated in other studies. Therefore, the use of isolated point-count stations in monitoring schemes is not recommended, unless they have previously been shown to be a valid index for a given species.

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