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Research Papers

Land Cover Sampling Biases Associated with Roadside Bird Surveys

Biais d'échantillonnage des types de milieux associés aux dénombrements d'oiseaux nicheurs le long des routes

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ABSTRACT. Roadside surveys such as the Breeding Bird Survey (BBS) are widely used to assess the relative abundance of bird populations. The accuracy of roadside surveys depends on the extent to which surveys from roads represent the entire region under study. We quantified roadside land cover sampling bias in Tennessee, USA, by comparing land cover proportions near roads to proportions of the surrounding region. Roadside surveys gave a biased estimate of patterns across the region because some land cover types were over- or underrepresented near roads. These biases changed over time, introducing varying levels of distortion into the data. We constructed simulated population trends for five bird species of management interest based on these measured roadside sampling biases and on field data on bird abundance. These simulations indicated that roadside surveys may give overly negative assessments of the population trends of early successional birds and of synanthropic birds, but not of late-successional birds. Because roadside surveys are the primary source of avian population trend information in North America, we conclude that these surveys should be corrected for roadside land cover sampling bias. In addition, current recommendations about the need to create more early successional habitat for birds may need reassessment in the light of the undersampling of this habitat by roads.

RÉSUMÉ. Les programmes de dénombrement d'oiseaux tels que le Recensement des oiseaux nicheurs sont fréquemment utilisés pour estimer l'abondance relative des populations d'oiseaux. La précision des dénombrements effectués le long des routes dépend de la réprésentativité des types de milieux échantillonnés par rapport à leur proportion relative dans la région. Nous avons quantifié le biais existant dans l'échantillonnage des milieux situés en bordure de routes au Tennessee, É-U, en comparant les proportions représentées par chacun de ces types de milieux près des routes vs dans l'ensemble de la région. L'échantillonnage en bordure de routes a résulté en un échantillon biaisé des patrons à l'échelle de la région : certains types de milieux étaient sous-représentés ou sur-représentés près des routes. Les biais changeaient dans le temps, ce qui introduit un degré variable de distorsion dans les données. À l'aide de ces données sur le biais d'échantillonnage le long des routes et de données sur l'abondance d'oiseaux, nous avons simulé les fluctuations de populations de cinq espèces d'un intérêt particulier pour l'aménagement. Ces simulations ont indiqué que les dénombrements le long des routes peuvent résulter en une impression faussement négative des tendances des populations des espèces de début de succession et des espèces synanthropiques, tandis que les résultats sont fiables pour les espèces de fin de succession. Puisque les dénombrements effectués le long des routes constituent la principale source d'information sur les tendances des populations d'oiseaux en Amérique du Nord, nous concluons que ces dénombrements devraient être corrigés pour les biais identifiés dans la représentativité des types de milieux échantillonnés. De plus, les recommandations actuelles au sujet de la création d'habitat de début de succession devront être réévaluées en fonction du sous-échantillonnage de ce type d'habitat le long des routes.

Key Words: *Breeding Bird Survey; early successional; industrial forestry; point count; population estimate.*

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INTRODUCTION

Effective conservation or management of any species requires that reliable information be available about the population trends of the species in question (Bart et al. 2004*a*, Sauer et al. 2005*b*). This information is usually obtained by sampling a population over time and then estimating overall population trends from these samples. Thus, the reliability of any conclusions about population trends depends critically on the quality of the sampling methods used to estimate these trends (Link and Sauer 1998). Sampling methods that introduce biases could result in over- or underestimates of population size. These potential biases are particularly problematic if the extent of the bias changes over time, introducing variable levels of distortion into the data. Temporal variation in bias could produce spurious trends or mask true trends and would make correcting for the bias more challenging. Bird surveys have used a variety of sampling schemes to quantify populations. These range from counting nests in seabird colonies, to counting migrating raptors, to conducting playback surveys for owls (Bird Studies Canada 2004). Each method has its own associated set of biases. Bart (2005) reviews these survey methods and concludes that the correction of bias is essential for the reliable use of survey results.

The Breeding Bird Survey (BBS) is a survey of North American bird populations that has been conducted along approximately 3000 40 km long routes since 1966 (Sauer et al. 2005*a*, K. Pardieck *personal communication;* the exact number of routes surveyed varies from year to year). BBS results are widely used to make conservation plans and to assess the status of the North American avifauna. Interpretations of the BBS form the basis of federal, state, and local policies and influence conservation funding decisions (Robbins et al. 1989, Sauer and Droege 1990, Peterjohn and Sauer 1994, Brown et al. 1995, Villard et al. 1995, Curnutt et al. 1996, Flather and Sauer 1996, Sauer et al. 1996, Koenig 1998, Brawn et al. 2001, Rich et al. 2004). Recently, for example, BBS data have been used to suggest that early-successional bird species in North America are experiencing problematic population declines, and recommendations have been made to intensively manage and create new early-successional habitat to benefit these species (Brawn et al. 2001, Hunter et al. 2001, DeGraaf and Yamasaki 2003, Dettmers 2003, Litvaitis 2003, Oehler 2003).

The BBS is subject to a variety of biases that must be accounted for to ensure reliable results (O’Connor et al. 2000, Bart et al. 2004*a*, Sauer et al. 2005*b*). Recent studies evaluating the use of BBS data underscore the need for quantitative assessment of these biases (O’Connor et al. 2000, Bart et al. 2004*a*, Sauer et al. 2005*b*, Thogmartin et al. 2006). Past studies have documented biases that affect the BBS in four categories: differences in observer detection rates, bias caused by analytical methods, differences between on- and off-road point counts, and differences in land cover sampling (Table 1).

Three studies have analyzed how well the land cover proportions sampled by roadside surveys represent the land cover proportions of the region under study (Bart et al. 1995, Keller and Scallan 1999, Betts et al. 2007). This bias is critical to the reliability of the BBS and other roadside bird surveys such as the Northern Region Landbird Monitoring Program and the American Woodcock singing-ground survey (Bird Studies Canada 2004). If roads are disproportionately more common in some land cover types than in others, then roadside surveys may provide a biased estimate of overall population levels. If the distribution of land cover types in relation to roads changes over time, then these biases could produce spurious or variably distorted population trends.

Both Bart et al. (1995) and Keller and Scallan (1999) compared land cover near roads to land cover away from roads. At 27 locations in western Ohio that were not actual BBS routes, Bart et al. (1995) used aerial photographs to compare forest cover at three levels from roads: 0–140 m from roads, 140–280 m from roads, and in the surrounding 21 km² region; they found very low bias in estimates of land cover change (< 1%) along roads compared to away from roads, although there was significantly less forest cover near roads than in the surrounding region. Keller and Scallan (1999) used aerial photographs to compare land cover types within 200 m of BBS routes to land cover on a strip of land located 200–1600 m away from BBS routes in Maryland (n = 28 routes) and Ohio (n = 25 routes). They found that land cover changes near routes generally also occurred away from routes, although significantly more urban cover occurred along BBS routes than in the surrounding landscape along Maryland routes, but not along Ohio routes (Keller and Scallan 1999). These studies provide a preliminary assessment of potential roadside sampling land cover biases. However, because they do not

Table 1. Summary of the main findings of previous studies of bias in the North American Breeding Bird Survey (BBS).

Author and year	Focus of study	Main findings
Faanes and Bystrak 1981	Differences in hearing ability and observer expertise	In general, well-trained observers are comparable in their ability, whereas observers that are inadequately trained in bird identification provide significantly different BBS results than do qualified observers
Scott and Ramsey 1981	Effects of multiple species on accurate detection	Observers that recorded fewer species counted more individuals than did observers that recorded all species in the same area
Bart and Schoultz 1984	Effects of multiple individuals on accurate detection	In bird song simulations, as the number of singing birds increased from one to four, the proportion of individuals recorded declined by up to 50%
Emlen and DeJong 1992	Differences in hearing ability	Comparisons of audiograms of people’s hearing to spectograms of birdsong demonstrate that older people have large deficiencies in hearing and thus older surveyors provide incomplete and biased information to the BBS
Link and Sauer 1994	Analytical methods bias and survey design	The usual method of BBS population trend analysis (i.e., taking the logarithm of bird counts in a regression analysis) works well for abundant species, but not for uncommon species; a new estimating equation makes trend estimates of uncommon species more accurate
Sauer et al. 1994	Change in observer skill over time	Failure to recognize changes in observer skill over time results in overly optimistic estimates of bird populations
Bart et al. 1995	Representativeness of roadside habitat	There was very low bias in estimates of habitat change (< 1%) along roads compared to away from roads, although there was significantly less forest cover near roads than in the surrounding region
Hanowski and Niemi 1995	Differential bird incidence along roads	On average, on-road point counts recorded 2.5 more species and 3.5 more individuals than did nearby off-road point counts; 20 species were more abundant on roads, whereas five species were more abundant off-road
Hutto et al. 1995	Differential bird incidence along roads	Very few species were recorded at only on- or off-road point counts, but the mean species richness at a given point count was significantly greater at on-road points
Keller and Fuller 1995	Differential bird incidence along roads	On-road point counts recorded more edge species, but not lower numbers of interior forest species than did off-road point counts; more individuals and species were recorded at on-road counts because of the higher number of edge species
Rotenberry and Knick 1995	Differential bird incidence along roads	In shrubsteppe and grassland, only one species was differentially abundant at either on- or off-road points, suggesting that roads do not create as significant a habitat discontinuity in grassland habitats as in forested habitats
James et al. 1996	Change in observer skill over time	Nonlinear regressions are ideal for BBS trend analysis because they require few assumptions about a population curve through time, they produce population estimates for which the statistical significance can be tested, and they allow the inclusion of bias covariates in the analysis
Kendall et al. 1996	Change in observer skill over time	Failure to recognize changes in observer skill over time results in overly optimistic estimates of bird populations
Link and Sauer 1998	Analytical methods bias and survey design	Bias, such as differences in BBS observers, is inevitable in surveys and must be taken into account to ensure credible results; an effective way to account for BBS bias is to include it as a covariate in the trend analysis
Keller and Scallan 1999	Representativeness of roadside habitat	Land cover changes near BBS routes generally also occurred away from routes, although significantly more urban cover occurred along routes than in the surrounding landscape in Maryland, but not in Ohio

(con'd)

Bart et al. 2003	Analytical methods bias and survey design	A linear model of population trend analysis that is design based, not model based, shows very little bias, unlike, at least in some cases, the estimating equation approach
Bart et al. 2004*a*	Analytical methods bias and survey design	Current bias in the BBS is 0.008%; if the number of routes is increased to 5106 (i.e., by 40%), the bias will be decreased to 0.003%
Bart et al. 2004*b*	Analytical methods: reply to Sauer et al. (2004)	Observer effects can be accounted for before performing the trend estimation analysis; sometimes it is unnecessary to account for observer effects, and including these effects may even result in greater bias
Lawler and O'Connor 2004	Sampling bias of large-scale environments	High elevations and arid regions are underrepresented by the BBS, whereas northeastern deciduous forest is overrepresented; however, when the area of comparison is narrowed to BBS-defined physiogeographic regions and U.S. states, the differences are smaller
Sauer et al. 2004	Analytical methods: critique of Bart et al. (2003)	Bart et al. (2003)'s design-based analysis does not control for factors that influence bird detection such as observer effects; the analysis consequently incurs significant bias in trend estimation
Bart et al. 2005	Analytical methods bias and survey design	Increasing the number of BBS routes in the Pacific Northwest region of the U.S. and Canada would increase the number of species covered and decrease bias
Sauer et al. 2005*b*	Analytical methods: critique of Bart et al. (2004*a*)	Bart et al.'s (2004*a*) analysis has three flaws: their view of the uses of BBS data is overly simplistic, their model incorporates poorly supported bias estimates and is therefore statistically weak, and their trend analysis is flawed for several reasons
Francis et al. 2005	Analytical methods: reply to Sauer et al. (2005*a*)	The authors acknowledge that the BBS should meet multiple objectives, but they reaffirm that estimating bird population trends is of fundamental importance; the authors reiterate that efforts to reduce bias, to recognize that all bias cannot be eliminated, and to increase the number of routes would positively influence the BBS
Betts et al. 2007	Representativeness of roadside habitat	The roadside land cover sampling bias of the BBS may prevent the detection of population changes in forest-based bird species
Harris and Haskell *results herein*	Representativeness of roadside habitat	Roadside surveys in Tennessee give a biased representation of land cover in the region; these biases change over time and distort simulated bird population trends

compare roadsides to the entire surrounding region, it is not clear to what extent the results are dependent on the subsample of nonroad land cover that they analyze. In addition, these studies do not quantify how bird population trends might be affected by roadside sampling. Because bird species differ in their land cover preferences, the sampling of species that live in land cover types that are over- or undersampled by roads will be differentially affected by roadside land cover sampling bias.

Betts et al. (2007) studied the question of roadside sampling bias by relating land cover change to population trends of one forest-dwelling bird species, the Blackburnian Warbler (*Dendroica fucsa*), in New Brunswick. They used aerial photographs to compare the extent of mature forest within 150 m of BBS routes to forest cover in surrounding 1° blocks of latitude and longitude from 1974 to 2001. Betts et al. (2007) found that forest loss was more rapid in the blocks than along BBS routes from 1974 to 1985 and that forest loss was equally rapid in the comparisons from 1985 to 2001. They also found that the Blackburnian Warbler showed a decline corresponding to the loss of mature forest from 1985 to 2001, but not from 1974 to 1985 (Betts et al. 2007). These results suggest that the decline in the bird species from 1974 to 1985 was underestimated by the BBS because of the survey's roadside land cover sampling bias. Betts et al. (2007) demonstrated how roadside bias can affect estimates of the population trend of one mature-forest species. They did not, however, examine how these biases might relate to other species or land cover types.

We analyzed land cover on the southern Cumberland Plateau, Tennessee, and in the state of Tennessee, USA, to quantify roadside bias in the sampling of land cover. We tested the following predictions: (1) roadside surveys on the Cumberland Plateau and BBS routes in Tennessee give a biased estimate of land cover across the entire landscape, (2) the extent of these biases changes from year to year based on temporal changes in the distribution of land cover over the landscape, and (3) these biases influence the magnitude or direction of simulated bird population trends. Our study differs from previous work in that: we quantified how representative roadside samples compare to the entire region, we analyzed these patterns in all of the prominent land cover types of the region, and we analyzed the effects of the bias on simulated bird population estimates and trends for five bird species of conservation importance.

METHODS

We analyzed land cover along roads and away from roads on the southern Cumberland Plateau in eastern Tennessee, USA, using both fine- and coarse-resolution land cover databases. The Cumberland Plateau is a sandstone plateau that extends from Alabama to Kentucky and averages 600 m in elevation. Oak (*Quercus* spp.)-hickory (*Carya* spp.) forests dominate the region, with interspersed areas of pine plantations and townships; McGrath et al. (2004) and Haskell et al. (2006) provide detailed descriptions of the sampling area on the plateau. The fine-resolution land cover database contained vector (i.e., geographical information stored as digital polygons) land cover information for a seven-county area of the surface of the southern Cumberland Plateau that was derived from aerial photographs (1:24,000 scale) for 1980, 1990, 1997, 2000 (Evans et al. 2002, McGrath et al. 2004), and 2003 (J. Evans *unpublished data*). Every block of land cover that fell into the six categories listed below was digitized by hand from aerial imagery, regardless of the size of the land cover block. The overall accuracy based on ground-truthing of the vector layer was 80.6%, whereas the accuracy was > 90% for all pine plantations and 85% for mature native forest (Evans et al. 2002). This layer divided land cover into the following six categories (Table 2): mature native forest, thinned native forest, early-stage pine plantation, middle-stage pine plantation, mature pine plantation, and residential/rural. The coarse-resolution raster, i.e., geographical information stored as pixels, database was derived from LandSat Thematic Mapper satellite imagery (30-m pixel size; Tennessee Spatial Data Server 2005); the average accuracy of the raster layer at the per-patch level was 81% and at the per-pixel level was 62% (United States Geological Survey 2007). The raster layer divided land cover into 11 categories (Table 2): upland deciduous forest, upland mixed forest, upland coniferous forest, urban/developed, pasture/grassland, row crop, nonvegetated (e.g., barren land, strip mine, rock quarry), open water, forested wetland, nonforested wetland, and undefined (satellite image obstructed by clouds). The undefined class represented 0.007% of the landscape and was omitted from the analysis.

We created buffers of 50, 200, and 400 m around roads on the southern Cumberland Plateau for all named public roads (United States Census Bureau 2001). These distances represent the range of distances from which birds can be heard from Breeding Bird Survey (BBS) points and span most of the range previously used to estimate bird populations from BBS data (Rosenberg and Blancher 2005). In addition to analyzing land cover near roads, we used the coarse-resolution database to compare land cover near the actual BBS routes in Tennessee ($n = 50$) to the land cover proportions of the entire state (United States Geological Survey 2002). We studied how well the BBS samples land cover types at the state level for two reasons: conservation planning is often undertaken at the state level (e.g., Association of Fish and Wildlife Agencies 2007); and the BBS reports its findings by state, as well as by U.S. Fish and Wildlife Service multistate regions and physiogeographic provinces. Three of the BBS routes that we analyzed (i.e., Soddy 82030, McFarland 82035, and Walland 82039) are now no longer surveyed. Digitizing errors in the BBS database added artificial route length to two routes (i.e., Cades Cove 82904 and Newfound Gap 82903). We deleted these artificial segments before making the buffers. The BBS routes were all along roads in the named public roads database described above.

For all analyses, we measured the bias in land cover proportions near roads by calculating percentage of over- or underrepresentation of land cover near roads.

Table 2. Definitions of land cover categories in the fine-resolution vector data set, and correspondence between the land cover categories in the fine- and coarse-resolution data sets.

Vector layer category	Definition of vector layer category	LandSat raster category
Mature native forest	Deciduous forest at least 40 yr old with 70–100% intact forest canopy Oak (*Quercus* spp.)-hickory (*Carya* spp.) forest predominates Understory of immature trees, blueberry (*Vaccinium* spp.), greenbriar (*Smilax* spp.), and sassafras (*Sassafras albidum*).	Upland deciduous forest and Upland mixed forest
Thinned native forest	Mature forest at least 40 yr old with 30–90% of the canopy removed Has not been subjected to burning, herbicides, or bulldozing Portions are considered early successional	Upland deciduous forest
Early-stage pine plantation	Loblolly pine (*Pinus taeda*) plantation with seedlings < 0.5 m in height Ground has been bared by one or more site preparation techniques: burning, herbicides, and/or bulldozing No other visible plants or only sparse growth of ragweed (*Ambrosia* spp.) and grasses Is considered early successional	Nonvegetated
Middle-stage pine plantation	Loblolly pine 0.5–2 m in height Open canopy Dense grasses, forbs, and *Rubus* spp. between pines Is considered early successional	Upland coniferous forest
Mature pine plantation	Closed canopy of loblolly pine > 2 m in height Sparse understory of sassafras, maple (*Acer* spp.), and blueberry	Upland coniferous forest
Residential/rural	Ranges from suburban (e.g., strip malls, housing developments), through exurban, to rural (i.e., farmhouses scattered in a mixture of pasture and woodland)	Urban/developed, Pasture/grassland, and Row crop
n/a†	Composed < 1% of the study area and was not included as a land cover	Forested wetland
n/a†	Composed < 1% of the study area and was not included as a land cover	Nonforested wetland
Reservoir	Composed < 1% of the study area and was not included as a land cover	Open water and Undefined (i.e., satellite image obstructed by clouds)

†Not applicable.

$$Bias_{x,y,z} = 100\,(P_{x,y,z} - P_{T,x,z})\,P_{T,x,z}^{-1} \qquad (1)$$

where $Bias_{x,y,z}$ is the percent bias in land cover *x* for buffer width *y* in year *z*; $P_{x,y,z}$ is the proportion of land cover *x* in buffer width *y* in year *z*; and $P_{T,x,z}$ is the proportion of land cover *x* in year *z* over the entire region. Positive values indicate overrepresentation of a land cover in buffers along roads; negative values indicate underrepresentation.

Roadside surveys have been used to estimate the absolute population sizes of birds (Rich et al. 2004) and trends in bird populations over time (e.g., Robbins et al. 1989). Both of these estimates may be biased if surveys from roads do not representatively sample the entire landscape. Exactly how the estimates are affected depends on: the magnitude of the mis-sampling of land cover by roadside buffers, whether and how this misrepresentation changes over time, and how land cover proportions on the whole landscape change over time relative to those in roadside buffers. To explore how these factors might affect estimates of bird population sizes and trends, we modeled estimates of bird populations using five bird species. Four of the five species were the four top-ranked “species of continental importance” in the North American Landbird Conservation Plan (Rich et al. 2004); their field abundance in our study region was at least 0.1 birds detected per hectare in Haskell et al.’s (2006) analysis. These four species were Prairie Warbler (*Dendroica discolor*), Kentucky Warbler (*Oporornis formosus*), Eastern Towhee (*Pipilo erythrophthalmus*), and Wood Thrush (*Hylocichla mustelina*). These species are not only of high conservation interest, but they span a range of land cover preferences and therefore illustrate how roadside biases may affect surveys of species with different ecological requirements. The fifth species was European Starling (*Sturnus vulgaris*), a synanthropic (positively associated with human settlements) exotic species that has negative effects on some native species and is thus of management interest (Cabe 1993). The simulated relative densities in each land cover type for these five species (Table 3) correspond to field estimates in this study area made from point counts (n = 503) conducted during the breeding season (Haskell et al. 2006) and analyzed using both a fixed-radius (50 m radius) estimate and a distance-sampling estimate. All counts were made by the same observer. The estimates used in this simulation were based on fixed-radius counts. The model was designed to provide general information about how roadside bias may affect estimates of bird populations. The model did not aim to provide information about actual historical population trends of birds in the region. Rather, we used simulated populations of these species as a modeling exercise and deliberately held constant all other factors that might affect bird populations to examine only the effects of changing roadside bias and land cover.

In the simulation, the modeled population estimate of each species in each year for the whole landscape was the population density of the simulated species (Table 3) in each land cover multiplied by the number of hectares of each land cover for that year.

$$S_{s,z} = \sum_{x} D_{s,x}\, A_{x,z} \qquad (2)$$

where $S_{s,z}$ is the simulated number of individuals in the entire region for species *s* in year *z*; $D_{s,x}$ is the density of species *s* in land cover *x*; and $A_{x,z}$ is the area of land cover *x* in year *z*. The modeled population estimate of each bird species in each year for the simulations using buffers of 50, 200, and 400 m width is the estimated mean population density of the species in each land cover type multiplied by the number of hectares of each land cover class indicated by surveys limited to within the buffer widths.

$$S_{s,y,z} = \sum_{x} (D_{s,x}\; T\, A_{x,y,z}\; B_{y,z}^{-1}) \qquad (3)$$

where $S_{s,y,z}$ is the simulated number of individuals in the study region for species *s* in year *z*, estimated for buffer of width *y*; $D_{s,x}$ is the density of species *s* in land cover *x*; *T* is the total area of the study region; $A_{x,y,z}$ is the area of land cover *x* within buffer of width *y* in year *z*; and $B_{y,z}$ is the total area within buffer of width *y* in year *z*. Therefore, the simulation allows the comparison of simulated populations across the whole landscape with the populations that would be revealed by roadside surveys. This provides a demonstration of the potential effects of roadside land cover sampling bias on bird population estimates.

Table 3. Densities of five avian species of management interest in each land cover category used in the simulation (individuals/ha).

Land cover	Species				
	Eastern Towhee (*Pipilo erythrophthalmus*)	European Starling (*Sturnus vulgaris*)	Kentucky Warbler (*Oporornis formosus*)	Prairie Warbler (*Dendroica discolor*)	Wood Thrush (*Hylocichla mustelina*)
Mature native forest	0.01	0	0.12	0	0.27
Residential/rural	0.19	2.60	0.04	0.04	0.23
Early-stage pine plantation	0.20	0	0	0.35	0
Middle-stage pine plantation	0.59	0	0	1.77	0
Mature pine plantation	0.05	0	0.07	0.09	0.02
Thinned native forest	0.68	0	0.04	0.84	0.25

Note: Densities were estimated from point count data from Haskell et al. (2006). Based on distance sampling methods (Haskell et al. 2006), the 95% confidence intervals for density estimates of birds in early-, middle-, and late-stage pine plantation, mature native forest, residential/rural areas, and thinned native forests are 17.8, 13.4, 21.6, 12.8, 6.9, and 14.5% of the estimated value, respectively. However, in the simulation, it is the proportion of the relative abundance in each habitat category, not the absolute value, that determines the extent of the roadside sampling bias.

We calculated simulated population trends using linear regression of population size against time, after checking normal probability plots. Because we analyzed data points from one region, not from multiple routes, our regression approach was simpler than linear route regression based on estimating equations (Link and Sauer 1994) and the locally weighted least squares method that uses nonlinear regression (James et al. 1996).

RESULTS

For all land cover types, roadsides provided a biased estimate of the actual land cover of the region. In general, this bias was higher for narrower buffers (Tables 4 and 5). In the fine-resolution land cover analysis for the southern Cumberland Plateau, residential/rural areas were oversampled by roads by up to 266%, mature native forest was undersampled by up to 25%, and pine plantations were undersampled by up to 80% (Table 4). In the coarse-resolution analysis, urban/developed, row crop, and pasture/grassland were overrepresented by roads by up to 866%, 55%, and 168%, respectively (Table 5). These land cover types are equivalent to the residential/rural land cover category in the fine-resolution data set. Upland deciduous forest and upland coniferous forest were underrepresented by up to 41% and 44%, respectively; on the southern Cumberland Plateau upland coniferous forest is mostly pine plantation, whereas upland deciduous forest is mature native oak-hickory forest (Table 2).

The extent of these biases changed over time because of large-scale changes in the distribution of land cover. The percentage misrepresentation of

Table 4. Percentage over- (positive values) or underrepresentation (negative values) of land cover in roadside buffers of three widths along roads on the southern Cumberland Plateau, Tennessee, compared to the land cover of the surrounding region for fine-resolution land cover data.

Buffer width	Land cover	1980	1990	1997	2000	2003
400 m	Mature native forest	–3.47	–6.11	–9.3	–6.29	–6.44
	Residential/rural	64.24	96.28	76.04	71.75	60.22
	Early-stage pine plantation	–44.1	–31.21	–28.64	–42.89	–39.17
	Middle-stage pine plantation	–17.17	–80.23	–54.4	–43.78	–40.55
	Mature pine plantation	–30.78	–36.75	–36.75	–35.34	–35.45
	Thinned native forest	–4.32	–0.55	–2.48	–18.09	–23.26
200 m	Mature native forest	–9.01	–16.75	–16.32	–13.21	–14.08
	Residential/rural	129.4	188.7	117.4	112.2	92.85
	Early-stage pine plantation	–56.24	–36.9	–41.28	–50.98	–44.59
	Middle-stage pine plantation	–23.44	–78.13	–65.19	–51.78	–49.6
	Mature pine plantation	–49.19	–44.87	–46.01	–43.03	–42.98
	Thinned native forest	1.52	2.94	2.23	–23.68	–30.48
50 m	Mature native forest	–17.5	–25.41	–25.41	–22.22	–25.09
	Residential/rural	223.5	265.7	171.4	164.9	137.4
	Early-stage pine plantation	–59.9	–25.8	–44.21	–50.89	–48.98
	Middle-stage pine plantation	–24.18	–55.39	–72.88	–62.61	–54.93
	Mature pine plantation	–54.18	–53.0	–52.9	–52.39	–54.01
	Thinned native forest	–18.86	–16.08	–18.11	–38.76	–42.54

Note: The percent cover of each land cover category in entire surrounding region (i.e., the surface of the southern Cumberland Plateau, Tennessee) in 2003 was: mature native forest, 59.3%; residential/rural, 19.0%; early-stage pine plantation, 5.5%; middle-stage pine plantation, 4.8%; mature pine plantation, 6.6%; thinned native forest, 4.8%. The proportion of the region covered by each of the three buffers was: 400-m buffer, 0.39; 200-m buffer, 0.23; 50-m buffer, 0.06. The total area of land cover analyzed was 248,500 ha.

Table 5. Percentage over- (positive values) or underrepresentation (negative values) of land cover in roadside buffers of three widths compared to the land cover of the surrounding region for coarse-resolution land cover data.

	Buffer width (m)		
Land cover category†	400	200	50
Roads on southern Cumberland Plateau‡			
Nonforested wetland (< 1.0%)	–0.05	–7.06	–65.77
Forested wetland (0%)	n/a§	n/a	n/a
Pasture/grassland (18.3%)	62.97	102.1	167.9
Row crop (1.3%)	44.19	55.02	54.58
Upland deciduous forest (69.8%)	–14.23	–24.33	–40.99
Upland mixed forest (1.6%)	–3.89	4.02	20.56
Upland coniferous forest (7.5%)	–25.82	–31.85	–44.26
Urban/developed (< 1.0%)	126.9	288.1	866.1
Nonvegetated (1.0%)	–31.58	–33.8	–39.39
Breeding Bird Survey routes in Tennessee¦			
Nonforested wetland (< 1.0%)	–65.44	–66.62	–75.52
Forested wetland (3.0%)	–55.66	–59.54	–62.47
Pasture/grassland (37.3%)	9.33	20.42	34.17
Row crop (5.8%)	18.11	21.66	22.92
Upland deciduous forest (40.6%)	–13.67	–22.66	–31.84
Upland mixed forest (4.5%)	19.9	19.01	10.64
Upland coniferous forest (3.6%)	5.71	–0.31	–16.02
Urban/developed (1.9%)	15.53	37.24	68.98
Non-vegetated (< 1.0%)	–57.63	–70.22	–77.05

† The proportion of the entire surrounding region covered by each of the three buffers for the statewide analysis was: 400-m buffer, 0.009; 200-m buffer, 0.007; 50-m buffer 0.002. The total area of land cover analyzed (i.e., the state of Tennessee) was 10,905,576 ha.
‡The percent cover of the land cover category in the entire surrounding region in 1990 is given in parentheses.
§Not applicable.
¦The percent cover of the land cover category in Tennessee is given in parentheses.

residential/rural areas changed by as much as 128% over time. Mature native forest bias changed by as much as 8% and pine plantation bias changed by as much as 63% over time (Table 4).

In general, the same land cover types that were overrepresented in the analyses of the Cumberland Plateau were overrepresented around Tennessee Breeding Bird Survey (BBS) routes and land cover types that were underrepresented in the plateau analyses were underrepresented around BBS routes (Table 5). Urban/developed areas around BBS routes were overrepresented by up to 69%, and row crop and pasture/grassland were overrepresented by up to 23% and up to 34%, respectively. Upland deciduous forest was underrepresented by up to 32%. Upland coniferous forest was either overrepresented or underrepresented, depending on the buffer width. This upland coniferous forest consists of pine plantations in some regions of Tennessee (e.g., on the Cumberland Plateau) and natural coniferous forest in others (e.g., high elevations in the Smoky Mountains).

The extent to which these biases affected estimates of population sizes and population trends differed by species. When we simulated populations of birds on the southern Cumberland Plateau by combining our measurements of roadside bias with simulated data on bird densities in different land cover types within the study area, we found that both estimates of population size and estimates of population trends differed if the estimates were made for roadside buffers compared to the surrounding region.

Roadside surveys overestimated the population size of European Starling by several times (range of overestimate: 60.2–265.7%; Table 6). The overestimate was most severe for 50-m buffers, but even for 400-m buffers, the overestimate ranged from 60.2 to 96.3% depending on the year. The magnitude of the bias decreased over time for all three buffer widths as the extent of overestimation of residential areas declined (Table 4). The population sizes of Eastern Towhee and Wood Thrush were also generally overestimated, but to a lesser degree than for European Starling: up to 65.7% for Eastern Towhee and up to 6.5% for Wood Thrush. The magnitude of the overestimate for Eastern Towhee declined through time and turned into a slight underestimate for the 400-m buffer in 2003, whereas the magnitude of the overestimate increased through time for Wood Thrush. The population sizes of Kentucky Warbler and Prairie Warbler were both underestimated by roadside surveys (Table 6). The magnitude of this underestimate increased through time for Prairie Warbler, but decreased for Kentucky Warbler. The underestimate was more severe for Prairie Warbler (range: –11.8 to –41.8%) than for Kentucky Warbler (range: –2.1 to –15.8%).

For simulated estimates of population trends (i.e., changes in population size through time), roadside surveys gave biased results for all species (Table 7). These differences were statistically significant in four of five species. The population increases of Eastern Towhee, European Starling, and Prairie Warbler were underestimated by roadside surveys by 1.20–1.87, 1.03–2.02, and 1.69–3.17 times, respectively. The population decline of Wood Thrush was underestimated (i.e., estimated to be less negative) by roadside surveys by 1.43–1.65 times, whereas the decline of Kentucky Warbler was very slightly exaggerated (i.e., estimated to be more negative) by roadside surveys.

DISCUSSION

Roadside land cover sampling biases

Our data indicate that roadside surveys in the study area sampled land cover types in different proportions than they occurred in the surrounding region (Tables 4 and 5). This pattern was not limited to roads on the southern Cumberland Plateau; land cover types were misrepresented in similar ways by Breeding Bird Survey (BBS) routes across Tennessee. The magnitude of these biases was substantial. The BBS in Tennessee, for example, undersampled upland deciduous forest, the largest land cover in the state, by nearly one-third and oversampled urban/developed areas by two-thirds based on 50-m buffers around roads.

The biases that we measured were qualitatively similar in the fine- and coarse-grained analyses that we conducted in the same region. This suggests that coarse-grained data such as the publicly available interpretations of LandSat Thematic Mapper satellite data (United States Geological Survey 2006) may be sufficient to detect, quantify, and possibly correct biases in roadside sampling. We caution, however, that analyses are needed from other regions before this conclusion can be

Table 6. Percentage overestimate (positive values) or underestimate (negative values) of the total population sizes of five avian species of management interest by estimates made in roadside buffers in five years.

		Species				
Buffer width	Year	Eastern Towhee (*Pipilo erythrophthalmus*)	European Starling (*Sturnus vulgaris*)	Kentucky Warbler (*Oporornis formosus*)	Prairie Warbler (*Dendroica discolor*)	Wood Thrush (*Hylocichla mustelina*)
50 m	1980	36.7	223.5	–10.7	–15.8	1.7
	1990	65.7	265.7	–15.8	–18.4	2.5
	1997	45.7	171.4	–15.1	–24.5	3.5
	2000	15.9	164.9	–12.3	–38.4	5.0
	2003	9.9	137.4	–12.6	–41.8	6.5
200 m	1980	22.1	129.4	–5.5	–11.8	2.3
	1990	44.3	188.7	–10.3	–25.6	3.2
	1997	33.3	117.4	–9.8	–17.5	3.7
	2000	9.3	112.2	–7.2	–30.4	5.0
	2003	2.1	92.9	–6.5	–37.0	6.4
400 m	1980	7.3	64.2	–2.1	–11.7	1.8
	1990	15.3	96.3	–3.9	–32.2	3.6
	1997	18.8	76.0	–5.8	–17.5	3.3
	2000	2.4	71.8	–3.3	–26.0	4.6
	2003	–2.7	60.2	–2.4	–30.9	5.9

generalized. LandSat data are generally broken into a few broad thematic categories that, in some regions, may obscure important land cover differences. For example, on the southern Cumberland Plateau, the upland deciduous forest land cover category is composed of native vegetation and the upland coniferous forest is mostly composed of exotic pine plantations (Table 2). However, in other areas, these categories may combine native forest and exotic plantations, land cover types that are likely to have very different bird communities. In addition, publicly available raster land cover data may contain significant sources of error (Thogmartin et al. 2004, United States Geological Survey 2007). The quantification of roadside bias will be most effective when biases for different land cover types can be teased apart using accurate fine-resolution land cover data.

Because the fine-resolution land cover data for the southern Cumberland Plateau extended over several years, we were able to estimate the extent of temporal changes in roadside sampling bias. Such temporal analyses were not possible for the coarse-resolution databases that covered just 1 yr. On the southern Cumberland Plateau, we found that the extent of roadside biases changed over time because of large-scale changes in the distribution of land

Table 7. Slope of the simulated population against time (% population change/yr) for five avian species of management interest based on roadside surveys and on the entire study region. Positive values indicate increasing populations; negative values indicate decreasing populations.

	Species				
Source of estimate	Eastern Towhee (*Pipilo erythrophthalmus*)	European Starling (*Sturnus vulgaris*)	Kentucky Warbler (*Oporornis formosus*)	Prairie Warbler (*Dendroica discolor*)	Wood Thrush (*Hylocichla mustelina*)
Land cover proportions on the entire landscape	3.21 (1.15)†	5.08 (1.08)	–0.71 (0.21)	3.36 (2.37)	–0.43 (0.09)
Land cover proportions within 50-m buffers	1.72 (0.41)*	2.51 (0.31)***	–0.76 (0.11)***	1.06 (1.44)	–0.26 (0.05)**
Land cover proportions within 200-m buffers	2.06 (0.52)	3.47 (0.43)***	–0.74 (0.09)**	1.46 (1.63)	–0.30 (0.06)**
Land cover proportions within 400-m buffers	2.68 (0.91)	4.92 (0.54)***	–0.75 (0.14)	1.99 (1.96)	–0.30 (0.07)**

†The numbers in parentheses are the standard deviations of the regression coefficients, expressed as % change/yr relative to the simulated starting population in 1980.
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$ for the slope of the regression for the entire landscape (first row) vs. that for the buffer (last three rows).

cover (Table 4). Two large-scale processes appear to drive these trends. First, extensive areas of native forest were cleared for pine plantations during the time period covered by our study (Evans et al. 2002, McGrath et al. 2004). These conversions of land cover occurred, on average, away from roads, but the exact distance from roads of new forest clearings varied over time, creating varying levels of undersampling by roads. Second, low-density housing development sprawled out from existing towns, converting native forest into residential areas (Evans et al. 2002, McGrath et al. 2004) and making native forest proportionally less common near roads at the end of the study period than at the start. In addition, the decrease in the percentage of oversampling of residential areas by roads suggests that the new residential areas were less intensely permeated by roads than were older townships.

Effects on estimates of bird populations

The magnitude of the biases that we report seem large, but their effects on surveys of bird populations cannot be immediately inferred from the examination of data on land cover bias (Tables 4 and 5). To examine how these biases might affect estimates of bird population sizes and population trends, we combined our measurements of roadside bias with simulated data on bird densities in different land cover types within the study area. These simulations held all other variables constant to examine the effects of roadside bias only. We found that roadside bias influenced both estimates of population size and estimates of population trends, but that the extent of this influence differed with the land cover preferences of the species under simulation. Before discussing the simulation results, we emphasize that this simulation provides modeled information about the potential effects of changing roadside bias and land cover and does not provide information about actual historical population trends of birds in the study region.

For estimates of population size (Table 6), we found that simulated European Starling was overestimated by 60.2–265.7%, depending on the year and buffer size used along roads. Thus, the biases that we found in roadside surveys (Tables 4 and 5) can potentially have substantial effects on the conclusions of bird surveys. The population sizes of Eastern Towhee and Wood Thrush were also overestimated by roadside surveys, although by a lesser degree than for European Starling. For European Starling and Eastern Towhee, the magnitude of the overestimate decreased through time, but for Wood Thrush the magnitude increased. The differences in these trends through time are caused by the different land cover preferences of the species: the overestimate of European Starling and Eastern Towhee is strongly influenced by declining oversampling of residential/rural areas, whereas Wood Thrush population estimates are affected by mature native forest, thinned native forest, and residential/rural areas, which are land cover types that showed conflicting trends of oversampling through time (Table 4). In contrast, the population sizes of Prairie Warbler and Kentucky Warbler were underestimated by roadside surveys (Table 6). The magnitude of the underestimate for Kentucky Warbler fluctuated through time, but the estimate for Prairie Warbler increased in magnitude because of the increasing underestimation of this species' preferred land cover types: thinned native forest and middle-stage pine plantations.

Not only are overall population estimates biased, but the changing magnitude of these biases distorts estimates of population trends. Our simulations found that these distortions vary considerably according to the land cover preferences of the species in question (Table 7). We found that roadside surveys significantly underestimated the population increase of European Starling by up to 2.57% per year depending on the buffer width. This misrepresentation was caused by the high but declining overpresentation of residential land cover types along roadsides in the study area.

Because of the shrinking area of mature native forest in the study region, the two late-successional species, i.e., Wood Thrush and Kentucky Warbler, both had simulated population declines. For Wood Thrush, these declines were significantly underestimated by nearly one-half by simulated roadside surveys. Roadside surveys slightly but significantly exaggerated the decline for Kentucky Warbler by 0.05% per year (Table 7). The differences between the degree of bias for these two species was caused by the different habitat preferences for immature forest habitat (e.g., residential areas and pine plantations) used in the simulation (Table 3).

Because large areas of native forest were converted to pine plantations during the study period, the simulated populations of both Prairie Warbler and Eastern Towhee increased by > 3% per year across the 23 yr of the study period. However, roadside surveys indicated a much smaller yearly population increase, especially for narrower buffers. The magnitude of the underestimate differed between the two species because they are found in different densities in residential areas. Because of the large standard error of the regression coefficients in the simulation (Table 7), these differences were statistically significant for Eastern Towhee in narrow buffers, but not for other buffer sizes or for any buffers sizes for Prairie Warbler.

We draw two main conclusions from the simulated estimates of population size and population trends. First, the roadside biases that we report (Tables 4 and 5) have the potential to produce substantial distortions in estimates of both population sizes (Table 6) and population trends (Table 7). Population sizes were particularly poorly estimated by roadside surveys in the cases of European Starling, Prairie Warbler, and Eastern Towhee. These species live in land cover categories that are either undersampled (early-successional forests) or oversampled (residential areas) by roadside surveys, causing a large difference between population size estimates based on roadside surveys and population size estimates based on the whole landscape. Population trends were likewise poorly estimated by roadside surveys for species that live in early-successional forests and residential areas. These trend estimates were affected by both the yearly magnitude of land cover bias and the extent to which this bias changed from year to year. The size of the roadside bias in these estimates of population trends was large enough in some cases to potentially produce serious distortions in trend estimates. For example, for both Prairie Warbler and European Starling, the annual trend estimate (i.e., percent population change per year) was > 2% per year smaller in roadside surveys than for the whole landscape (Table 7). Given that for actual BBS data the mean annual population trend of declining species in the BBS is –1.09% (± 0.12 SE, range: –4.9 to –0.1%) and of increasing species is 2.16% (± 0.28 SE, range: 0.1–12.4%), the biases that we found in our simulations are well within the range that could change the conclusions of analyses of BBS data. It is important to note that these BBS means were obtained from the survey-wide 1966–2005 trends published on the BBS website using only those species with the highest reliability index, i.e., species with at least 14 samples over the long term, with moderate precision, and with moderate abundance on routes (Sauer et al. 2005*a*). We provide this information as a context for our results only and not as a quantitative analysis of actual BBS trends. Because temporal data on roadside bias were only available for a subregion of the Cumberland Plateau, and not the whole of Tennessee, our simulation focused on this subregion. Only part of one BBS route passes through this subregion; therefore, we cannot compare our simulated trends to trends reported by the BBS. Such comparisons will be possible when more detailed data on changing land cover at a large scale become available.

Our second main conclusion from the simulation is that our data suggest that the effect of roadside land cover sampling bias differs markedly among species. Each of the five species that we analyzed had its own set of distortions of population sizes or population trends. This heterogeneity results from the different land cover preferences of the species in question. Thus, although Wood Thrush and Kentucky Warbler both nest primarily in mature forest, their differing preferences for pine plantations and residential areas (Table 3) caused our simulations of their populations to respond quite differently to roadside bias. Similarly, although Eastern Towhee inhabits early-successional habitat and some residential areas, the roadside bias that we quantified in the simulation differed between Eastern Towhee and Prairie Warbler (which is rarely found in residential areas) and European Starling, which is only found in residential areas. Thus, correcting for roadside bias in BBS surveys will require data on the abundance of each species in each land cover type.

Our simulation assumed a linear relationship between land cover area and bird population size. In reality, bird populations often show nonlinear responses to changes in land cover (e.g., Meents et al. 1983). These nonlinear responses will affect roadside bias in complex ways, depending on the exact nature of the nonlinearity and the extent of habitat fragmentation. For example, if bird populations become disproportionately low in small habitat fragments compared to large fragments, then the extent of the roadside bias will depend on whether roads give a representative sample of habitat fragment sizes on the landscape. This question is beyond the scope of our study, but previous work suggests that roads may not provide random samples of fragment sizes, partly because roads are themselves causes of fragmentation (Heilman et al. 2002).

General implications

Our quantification of bias has two main implications for conservation biologists and land managers. First, our study, along with that of Betts et al. (2007), suggests that roadside surveys give biased samples of the landscape in some regions of North America. In contrast, Bart et al. (1995) and Keller and Scallan (1999) tentatively concluded that roadside survey land cover sampling bias is relatively minor. We recommend that future studies further quantify these biases in other regions and evaluate ways of correcting biases in existing survey data. The correction of this bias is conceptually straightforward: species abundance in each year can be weighed by the extent to which each species' preferred land cover types are sampled by roads. However, the empirical data that are required to make these corrections are not yet available: temporal and spatial variation in the extent of roadside bias has not been quantified for most regions and data on bird abundance across land cover types are scattered throughout the literature or are unavailable. Nevertheless, these biases must be removed if the scientific community is to move toward statistically rigorous methods of interpreting BBS data.

Second, the biases that we quantified in the study area suggest that conservation recommendations based on uncorrected roadside survey data may need reinterpretation. For example, early-successional bird species have been the focus of a number of studies that recommend increasing rates of forest disturbance to create habitat for these species (Brawn et al. 2001, Hunter et al. 2001, DeGraaf and Yamasaki 2003, Dettmers 2003, Litvaitis 2003, Oehler 2003). However, we found that in the study area, industrial forestry activities that created large areas of early-successional habitat were poorly sampled by roads, suggesting that populations of species that inhabit these areas are faring much better than roadside surveys suggest. Unquantified reports of similar biases in other regions (Hagan et al. 1997) indicate that the problem of undersampling early-successional habitat on industrial timberland may be widespread within the BBS database. Betts et al. (2007) also emphasize that industrial timberlands tend to be located away from roads. However, biases may be weaker in areas that have little industrial forestry (Bart et al. 1995, Keller and Scallan 1999). If these results are confirmed elsewhere, the high priority currently assigned to early-successional bird species may need to be reassessed.

Our analysis focused on the effects of roadside bias on surveys of breeding birds. However, because roads provide a convenient means of access to many habitats, roadside surveys have been used to sample taxa other than birds. For example, the spread of invasive dogwood anthracnose in the southern Appalachians has been monitored through the use of roadside surveys (Sherald et al. 1996). Roadside surveys have also been used to quantify populations of amphibians (Royle and Link 2005) and mammals (Drake et al. 2005). The biases that we report here suggest that the results of these roadside surveys should be interpreted in light of the nonrandom distribution of roads on the landscape.

Responses to this article can be read online at:
http://www.ace-eco.org/vol2/iss2/art12/responses/

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