



# Predicting Species Distributions from Samples Collected along Roadsides

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**Abstract:** *Predictive models of species distributions are typically developed with data collected along roads. Roadside sampling may provide a biased (nonrandom) sample; however, it is currently unknown whether roadside sampling limits the accuracy of predictions generated by species distribution models. We tested whether roadside sampling affects the accuracy of predictions generated by species distribution models by using a prospective sampling strategy designed specifically to address this issue. We built models from roadside data and validated model predictions at paired locations on unpaved roads and 200 m away from roads (off road), spatially and temporally independent from the data used for model building. We predicted species distributions of 15 bird species on the basis of point-count data from a landbird monitoring program in Montana and Idaho (U.S.A.). We used hierarchical occupancy models to account for imperfect detection. We expected predictions of species distributions derived from roadside-sampling data would be less accurate when validated with data from off-road sampling than when it was validated with data from roadside sampling and that model accuracy would be differentially affected by whether species were generalists, associated with edges, or associated with interior forest. Model performance measures ( $\kappa$ , area under the curve of a receiver operating characteristic plot, and true skill statistic) did not differ between model predictions of roadside and off-road distributions of species. Furthermore, performance measures did not differ among edge, generalist, and interior species, despite a difference in vegetation structure along roadsides and off road and that 2 of the 15 species were more likely to occur along roadsides. If the range of environmental gradients is surveyed in roadside-sampling efforts, our results suggest that surveys along unpaved roads can be a valuable, unbiased source of information for species distribution models.*

**Keywords:** breeding birds, monitoring programs, niche models, occupancy models, road effects, sample bias, species distribution models

Predicción de la Distribución de Especies a Partir de Muestras Recolectadas a lo Largo de Carreteras

**Resumen:** *Los modelos predictivos de la distribución de especies típicamente son desarrollados con datos recolectados a lo largo de carreteras. El muestreo en carreteras puede producir una muestra sesgada (no aleatoria); sin embargo, actualmente se desconoce si los muestreos en carreteras limita la precisión de predicciones generadas por los modelos de distribución de especies. Probamos si los efectos del muestro en carreteras afecta la precisión de las predicciones generadas por modelos de distribución de especies mediante la utilización de una estrategia de muestreo prospectivo diseñado específicamente para abordar este tema. Construimos modelos a partir de datos recolectados en carreteras y validamos las predicciones de los modelos en localidades pareadas en caminos no pavimentados y a 200 m de carreteras (fuera de la carretera), espacial y temporalmente independientes de los datos utilizados para la construcción del modelo. Pronosticamos la distribución de 15 especies de aves con base en datos de conteos por puntos de un programa de monitoreo de*

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*aves terrestres en Montana e Idaho (E.U.A.). Utilizamos modelos jerárquicos de ocupación para considerar la detección imperfecta. Esperábamos que las predicciones de distribución de especies derivadas de los datos de muestreo en carreteras serían menos precisas cuando fueron validadas con datos de muestreo fuera de la carretera que cuando fueron validadas con datos de muestreo en carreteras y que la precisión del modelo sería afectada diferencialmente si las especies eran generalistas, asociadas con bordes o asociadas con el interior del bosque. Las medidas de rendimiento del modelo ( $\kappa$ , área bajo la curva de una parcela característica operada por receptor y estadística de habilidad real) no difirieron entre las predicciones de la distribución de especies en carreteras y fuera de carreteras. Más aun, las medidas de rendimiento no difirieron especies de borde, generalistas o de interior, no obstante diferencias en la estructura de la vegetación en carreteras y fuera de carreteras y que 2 de las 15 especies tuvieron una mayor probabilidad de ocurrencia a lo largo de carreteras. Si el rango de gradientes ambientales es muestreado en esfuerzos a lo largo de carreteras, nuestros resultados sugieren que los muestreos en caminos no pavimentados pueden una fuente valiosa, no sesgada, de información para modelos de distribución de especies.*

**Palabras Clave:** aves reproductoras, efectos de carreteras, modelos de distribución de especies, modelos de nicho, modelos de ocupación, programas de monitoreo, sesgo de muestreo

## Introduction

Understanding species distributions across space and time is essential to ecology, evolution, and conservation biology. Models of species distributions are often used in the examination of conservation issues, such as to evaluate potential management actions and interpret the effects of climate change, and are frequently used in spatial conservation planning (Loiselle et al. 2003; Penman et al. 2009; Lawler et al. 2010). However, their accuracy is limited by several factors (Guisan & Thuiller 2005), including the fact that data used in model building are often spatially biased.

Spatial bias in species distribution data arises for several reasons (Reddy & Davalos 2003; Phillips et al. 2009). Perhaps the most common reason is that sampling often occurs near roads for logistical purposes (Kadmon et al. 2004; Weir & Mossman 2005). Indeed, roadside sampling is often biased because roads occur nonrandomly across landscapes, such that land cover and vegetation near roads are not representative of the region of interest (Keller & Scallan 1999; Harris & Haskell 2007; Niemuth et al. 2007). Although there is increasing evidence that roads affect species distributions and community structure (Trombulak & Frissell 2000; Fahrig & Rytwinski 2009), it is currently unknown whether roadside sampling affects the predictive accuracy of species distribution models generated from such data. To date, only retrospective evaluations of existing data have occurred, either by adding road-related covariates to models (Griffith et al. 2010) or by contrasting the performance of models built at coarse resolutions from road-biased, presence-only data to those built from post hoc rectifications of data (Kadmon et al. 2004). Tests of whether species distribution models built from road-biased data can accurately predict occurrence at locations away from roads (hereafter off-road locations) are needed to deter-

mine whether inferences made on the basis of species distribution models are robust.

A further limitation to efforts that have assessed road effects and potential biases that arise from roadside sampling is that they have failed to account for imperfect detection (i.e., a species is present but not observed) (MacKenzie et al. 2006). Perfect detection is unlikely in natural systems and, because several factors can alter the detectability of species near roads, assuming equivalent accuracy in detection when conducting surveys along roads versus off road may be unwarranted (e.g., Hutto et al. 1995). For example, variation in traffic volume may influence detectability of species near roads (Griffith et al. 2010). Recently developed methods to account for imperfect detection in occupancy modeling address this potential shortfall by estimating both the probability of occurrence and the probability that a species is detected (MacKenzie et al. 2006). Such methods can improve the performance of species distribution models (Rota et al. 2011) and could reduce detection biases that may result from roadside sampling. However, to our knowledge, occupancy models have yet to be implemented to account for potential road-based sampling biases when developing species distribution models.

We assessed whether road-based sampling limits the accuracy of predictions of species distributions of breeding birds. We used hierarchical Bayesian occupancy modeling (Rota et al. 2011) to develop species distribution models from road-based sampling and contrasted predictive accuracy of these models with survey data that were strategically collected at paired roadside and off-road locations independent in time and space from the data used for model building. We expected that the potential bias in roadside sampling would result in models that predicted occurrence away from roads less accurately than they predicted occurrence along roadsides and that model performance would be affected by whether species were generalists, associated with edges (hereafter

edge species), or associated with interior forests (hereafter interior species). These ecological groupings are relevant to understanding limitations in predictions because they reflect variation in the likelihood that a species occurs near roads (Harris & Haskell 2007). For edge species, we expected detections at fewer off-road locations than predicted because roadside locations typically have a greater proportion of early-successional and other edge features than areas away from roads (Keller & Scallan 1999). For interior species, we expected detections at a higher number of off-road locations than predicted. For generalist species, we expected little difference in the number of sites with detections and in predicted levels of detection at off-road locations. We used data on breeding bird distributions across Montana and Idaho (U.S.A.) to test these expectations.

## Methods

### Breeding Bird Monitoring Program

We used data from the ongoing Northern Region Land-bird Monitoring Program (NRLMP), which has coordinated point-count surveys across western Montana and northern Idaho since 1994 (Hutto & Young 2002). The NRLMP data are collected at 482 permanently marked transects stratified across public and private lands (Hutto & Young 2002). Transects, each consisting of 10 permanently marked points spaced approximately 250 m apart, were located along roads or trails. At each point, 10-min, 100-m-radius point counts were conducted to estimate the occurrence of bird species in the area. Each point was surveyed once per breeding season, between late-May and mid-July (Hutto & Young 2002). Although a single count provides only a sample of the bird community and cannot be used to estimate within-season variation of bird occurrence, we used this protocol because it allowed us to have broader spatial coverage throughout the region than would be possible with repeated within-season counts (Hutto & Young 2002).

During each survey, all birds seen or heard were recorded by trained observers. In 1994, 1995, and 2004, 2007, and 2008 each 10-min survey was divided into 2 consecutive 5-min sampling intervals. In these surveys, observers recorded the interval of first detection for each observed species, which is effectively a "removal" sampling design (MacKenzie et al. 2006; Rota et al. 2009). This method allows one to estimate detection probability in occupancy modeling.

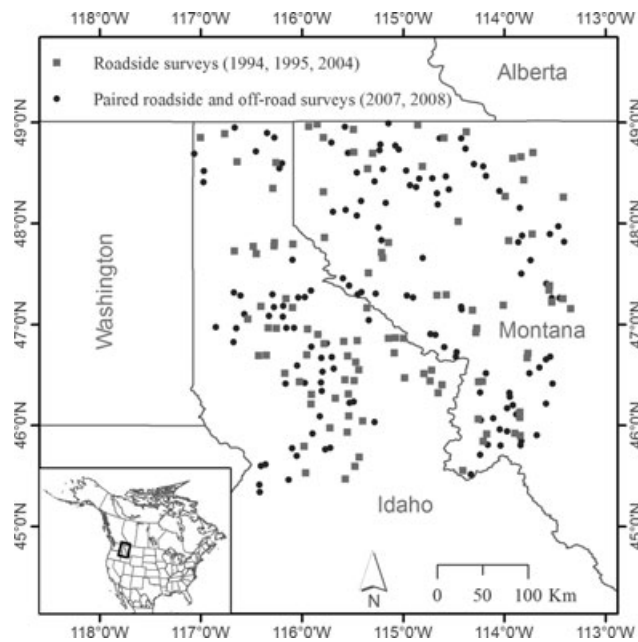
In 2007 and 2008, we designed a new sampling protocol to test the potential limitations of the road-biased NRLMP. Along 136 NRLMP transects (see Transect and Species Selection), we surveyed an additional 4 off-road points that we paired with NRLMP roadside points. We added these off-road points to determine whether mod-

els built from roadside data could be used to model distributions of species away from roads. We visited these paired points once during either 2007 or 2008. Because of the paired design, anomalous interannual variation in bird occurrence should not affect comparisons of roadside and off-road locations. Off-road points were approximately 200 m from and perpendicular to roads with paired roadside points (cf. Keller & Scallan 1999). Placing off-road points farther than 200 m from paired roadside points often resulted in the point being positioned within 200 m of another road, so we chose this distance as a reasonable and logistically feasible compromise. The roads used in the NRLMP are generally unpaved, U.S. Forest Service roads that produce less roadside effect than larger paved roads (Hutto et al. 1995), so our results may have limited application to networks of paved roads.

### Transect and Species Selection

We first filtered the NRLMP data to include only transects and points for which high resolution (30 × 30 m), spatially explicit land-cover data were available and had been incorporated into a geographic information system (GIS). We then filtered the data to include only transects that were along roads. For model building, we used only data from transects sampled in 1994, 1995, and 2004 that did not later have paired off-road points included. Consequently, our model-building data were temporally and spatially independent of the paired roadside-off-road surveys conducted in 2007–2008. This filtering resulted in 1908 individual point counts on 105 transects that spanned 3 different years (1994, 1995, and 2004) (Fig. 1). For model validation, we used data only from transects in 2007 and 2008 for which we had paired roadside-off-road surveys, which resulted in 1096 point counts along 136 transects (518 off road, 578 roadside).

We considered only those species detected on >5% of point-count locations. To classify each remaining species into edge, interior, and generalist categories, we consulted 4 experts familiar with the avian communities in this region. Each expert was sent a description of our 3 categories along with a list of potential species. We asked each expert to categorize individual species on the basis of their life-history traits and vegetation requirements. Reviewers were blind to the objective of this study. We defined the edge category as species with strong associations with early-mid seral forests, open forests, shrubby areas, recently logged areas, or edges. The interior category included species with strong associations with mature, old-growth, or late-seral forests and that may use interior or natural openings within contiguous forests. The generalist category included species that have no strong vegetation associations and can be found across most vegetation types. We further asked experts to assign strength to their selected classification. Strength ranged from low (i.e., species fits loosely in the chosen category)



**Figure 1.** Location of permanently marked Northern Region Landbird Monitoring Program transects used to estimate the distribution of forest birds in Idaho and Montana, 1994–2008.

to strong (i.e., species is well defined by this categorization, rarely being considered as associated with other vegetation types).

Within each category we sorted species by the percent agreement among experts and then by the average strength of that categorization. We selected the top species (highest level of agreement and highest average strength) from each category to include in our analyses: Olive-sided Flycatcher (*Contopus cooperi*), Dusky Flycatcher (*Empidonax oberholseri*), Chipping Sparrow (*Spizella passerina*), MacGillivray's Warbler (*Oporornis tolmiei*), and Townsend's Solitaire (*Myadestes townsendi*) for the edge category; Dark-eyed Junco (*Junco hyemalis*), American Robin (*Turdus migratorius*), Brown-headed Cowbird (*Molothrus ater*), and Pine Siskin (*Carduelis pinus*) for the generalist category; and Townsend's Warbler (*Dendroica townsendi*), Red-breasted Nuthatch (*Sitta canadensis*), Western Tanager (*Piranga ludoviciana*), Hammond's Flycatcher (*Empidonax hammondi*), Golden-crowned Kinglet (*Regulus satrapa*), and Varied Thrush (*Ixoreus naevius*) for the interior category.

### Environmental Covariates

We modeled occupancy as a function of several environmental covariates. We identified relevant covariates for each species from published accounts of habitat use (Supporting Information). For all species, we also modeled occupancy as a function of survey date. Sur-

vey date likely influences the probability of occurrence, especially early in the breeding season because species are arriving from wintering grounds and making territory decisions.

We used GIS-based vegetation measures to derive environmental covariates. Original GIS layers for diameter at breast height (dbh), canopy cover, and land-cover type were 15-m resolution digital land-cover maps developed by the U.S. Forest Service Northern Region Vegetation Mapping Program (USFS R1-VMP) with Landsat Thematic Mapper imagery and aerial photography (Brewer et al. 2004). We derived vegetation variables from 3 R1-VMP GIS layers: tree diameter, canopy cover, and life form. We used a principal components analysis (PCA) to reduce the number of dbh variables from 4 to 2 and the number of canopy cover variables from 3 to 2. In each case, one principal component reflected a linear gradient of canopy cover or dbh, whereas the other component reflected a nonlinear gradient (high factor loadings on intermediate) (Rota et al. 2011). The R1-VMP life-form layer includes the relative canopy cover of several vegetative communities for each cell. From this layer, we extracted variables describing the presence or absence of subalpine forest, mesic forest, and shrubby vegetation in the surrounding 100 m and the percentage of land cover in the surrounding 1 km that contained conifer forest. We used a 1-km extent because results of other investigations in this region showed strong correlations of avian distribution at this extent (e.g., Fletcher & Hutto 2008).

We determined road density by merging TIGER (Topologically Integrated Geographic Encoding and Referencing system) data for Idaho and Montana (Montana Department of Commerce 2002) with U.S. Forest Service Region 1 road data (USFS 2008) and calculating the total road length within a 1-km radius from each cell. We derived elevation from a 30-m resolution digital elevation model and stream distances from the U.S. Geological Survey National Hydrography Dataset (USGS 2009). We acquired mean annual precipitation data from the PRISM Climate Group at Oregon State University (2010). Prior to analysis we aggregated all GIS layers to a common 200-m resolution, which reflects the grain of our sampling unit (100-m radius point counts). In doing so, paired roadside and off-road counts were typically located in adjacent cells on our GIS layers.

Occupancy models allowed us to model detection probability as a function of covariates. For each species, we modeled detection probability as a function of canopy cover, dbh, date of survey, time of survey, wind speed, stream noise, cloud cover, and precipitation during surveys. We included linear and quadratic effects for date of survey and time of survey. We standardized all noncategorical vegetation and detectability covariates to have a mean of 0 and a variance of 1 in the model-building data and adjusted covariates in the validation data set on the



basis of these values to ensure predictions were scaled appropriately.

### Modeling Species Distributions

We used hierarchical occupancy modeling developed specifically for this monitoring program to predict bird distributions (Rota et al. 2011). To account for imperfect detection, we used a removal sampling protocol (Rota et al. 2009) in which a species was surveyed only until it was first detected. We assumed detection or nondetection of a species at point  $i$  along transect  $t$  in year  $r$  depended on the latent occupancy state,  $z_{irt}$  ( $z_{irt} = 1$  if a species is present and  $z_{irt} = 0$  if a species is absent). Our general process model was described by

$$z_{irt} \sim \text{Bernoulli}(\psi_{irt}). \quad (1)$$

We modeled  $\psi_{irt}$  as a function of both fixed and random effects:

$$\text{logit}(\psi_{irt}) = \beta_0 + \beta_{\text{cov}} \times \mathbf{x}_{ir} + \tau_t + \gamma_r, \quad (2)$$

where  $\beta_0$  is the intercept,  $\beta_{\text{cov}}$  is a vector of regression parameters associated with the covariates,  $\mathbf{x}_{ir}$  is a vector of explanatory covariates,  $\tau_t$  is a random effect of transect  $t$ , and  $\gamma_r$  is a random effect of year  $r$  (for more details, see Rota et al. 2011). To account for imperfect detection, our general observation model of detection or nondetection of a species was

$$y_{ir} \sim \text{Bernoulli}\{1 - [1 - (p_{ir} \times z_{ir})^J]\}, \quad (3)$$

where  $y_{ir}$  is a binary indicator of whether a species was detected at point  $i$  ( $y_i = 1$ ) or not detected ( $y_i = 0$ ) in year  $r$ ,  $p_{ir}$  is the probability of detecting a species at point  $i$  in year  $r$ , and  $J$  is the maximum number of sampling intervals, such that  $J = 2$  in our sampling protocol (Rota et al. 2011). We modeled  $p_{ir}$  as a function of covariates likely to influence detection probability as

$$\text{logit}(p_{ir}) = \alpha_0 + \alpha_{\text{cov}} \times \mathbf{v}_{ir} + \rho_o, \quad (4)$$

where  $\alpha_0$  is the intercept,  $\alpha_{\text{cov}}$  is a vector of regression parameters,  $\mathbf{v}_{ir}$  is a vector of detection covariates, and  $\rho_o$  is a random effect of observer  $o$  (Rota et al. 2011). We include the potential for observer effects because comparable data sets (e.g., the Breeding Bird Survey) have shown strong effects of observers (Sauer et al. 1994).

We specified vague, normal, prior distributions with mean zero and precision of 0.001 for all fixed effects (Royle & Dorazio 2008). For  $\alpha_0$  and  $\beta_0$ , we specified a noninformative uniform (0,1) prior distribution, transformed to the logit scale. We specified noninformative uniform (0,10) prior distributions for all standard deviation parameters of random effects (Gelman 2006).

We selected models by averaging coefficients on the basis of the posterior probability of all possible combinations of fixed effects (Kuo & Mallick 1998; Royle &

Dorazio 2008). To do so, we specified a latent indicator variable,  $w_\theta$ , for each fixed effect,  $\theta$ , with a vague prior of  $w_\theta \sim \text{Bernoulli}(0.5)$ . We then estimated the posterior probability of each model by calculating the proportion of times each combination of fixed effects appeared in the posterior distribution. We estimated the regression coefficient of each fixed effect by model averaging over all possible model combinations,  $R$ :

$$\hat{\theta} = \sum_{i=1}^R \delta_i \hat{\theta}_i, \quad (5)$$

where  $\delta_i$  is the posterior probability of model  $i$ , and  $\hat{\theta}_i$  is the mean of the posterior distribution of fixed effect  $\theta$  for model  $i$ . Because the posterior distributions of the inclusion parameters are sensitive to the choice of prior distributions for the fixed effects (Royle & Dorazio 2008: 111), we also ran models with more-informed priors for fixed effects (mean 0 and precision 0.1). Relative predictive performance along roadsides and off-road was similar to using less informed priors for all but one species, Olive-sided Flycatcher (Supporting Information), which suggests that our results are not sensitive to our choice of priors and model averaging.

We ran all models in WinBUGS (Lunn et al. 2000) version 1.4 via R version 2.10 (R Development Core Team 2009) in package R2WinBUGS (Sturtz et al. 2005). We estimated posterior distributions with 2 independent Markov chains, each with 150,000 iterations. We discarded the first 50,000 as burn-in and saved every fifth iteration thereafter as model output. We assessed convergence by comparing the posterior distributions from each independently run chain. See Rota et al. (2011) for an example of the WinBUGS code used for modeling.

### Contrasting Model Performance along Roads and Off Road

We used the fixed effects from the models to predict the probability of detecting individual species at validation points located along the roadside and off roads. The problem of imperfect detection was still present in the validation data, so we adjusted occupancy model predictions to account for imperfect detection and predict the probability of detecting a species rather than the probability of occupancy, following Rota et al. (2011). We used R version 2.10 with package PresenceAbsence (Freeman & Moisen 2008) to assess predictive performance of each species-specific model. We calculated the area under the curve (AUC) of a receiver operating characteristic (ROC) plot, the kappa statistic, and the true skill statistic (TSS) to assess overall predictive performance for both roadside and off-road validation data (Fielding & Bell 1997; Allouche et al. 2006). We further assessed false-positive and false-negative error rates in models to better interpret the sources of prediction error. All metrics considered except AUC are threshold-dependent measures; we

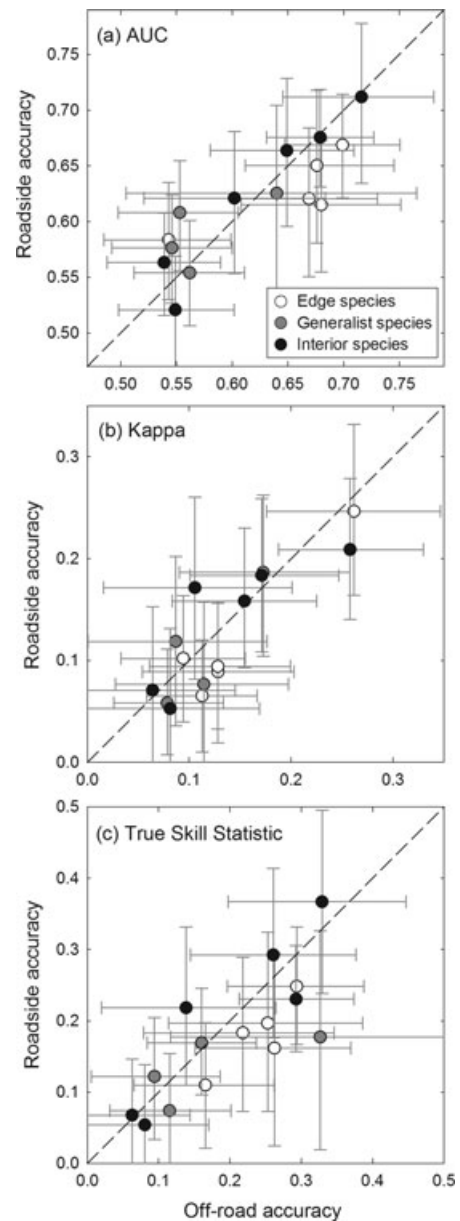
used the MaxSens+Spec criteria in PresenceAbsence to select thresholds for each model that maximized the sum of sensitivity and specificity (Freeman & Moisen 2008). We used nonparametric bootstrapping with 2000 replicates to generate 95% CI for each metric roadside and off roads.

## Results

Contrary to our expectations, model performance did not differ consistently when predicting species distributions at roadside versus off-road points on the basis of kappa, AUC, and the TSS (Fig. 2 & Supporting Information). Mean (SD) roadside performance measures (kappa = 0.13 [0.06]; AUC = 0.62 [0.05]; TSS = 0.18 [0.09]) and mean off-road performance measures (kappa = 0.13 [0.06]; AUC = 0.62 [0.06]; TSS = 0.20 [0.09]) were similar as were performance measures among species groups (Fig. 2). Error rates in predictions were variable for roadside (false positive = 0.38 [0.13]; false negative = 0.44 [0.12]) and off roads (false positive = 0.39 [0.14]; false negative = 0.40 [0.14]), depending on the species. One species, the Dark-eyed Junco, had greater false-positive error rates off roads and had greater false-negative error rates along roadsides. Nonetheless, there were no consistent differences in error rates among groups (Fig. 3).

Overall, these results on predictive performance were surprising, given that in our validation data paired roadside and off-road points also showed variation in the environmental covariates we used for modeling (discriminant analysis:  $F_{16,1079} = 5.44$ ,  $p < 0.001$ ; Fig. 4). On the basis of standardized loadings of the canonical variate that discriminated roadside and off-road points, off-road points tended to be at higher elevations, farther from streams, less frequently contained shrubs, and had greater canopy cover than roadside points (Fig. 4 & Supporting Information).

These results raised the question of whether our models achieved similar predictive performance roadside and off roads by accounting for habitat variability or because species occupancy did not vary between roadside and off-road validation points. Consequently, we ran a second series of hierarchical occupancy models with only the validation data to test for variation in species occupancy roadside and off roads, where we fit  $\psi_i$  as a function of a single, binary indicator variable regarding whether the point was roadside or off road. Although point estimates for the coefficients showed patterns across species groups that were relatively consistent with expectations, for all but 2 species (MacGillivray's Warbler and Chipping Sparrow) 95% CI around the coefficient overlapped zero (Fig. 5). In addition, average coefficients were generally small, with the resulting differences in the probabilities of occurrence roadside and off roads ranging from 0% to 9.7%.



*Figure 2. Three measures: (a) area under the curve (AUC) of a receiver operating characteristic plot, (b) kappa, and (c) true skill statistic (95% CI), of accuracy of predictions of roadside and off-road distributions of 15 breeding bird species made with hierarchical occupancy models built from independent roadside point counts from the Northern Region Landbird Monitoring Program in Montana and Idaho (dashed line, 1:1 ratio for roadside and off-road predictive accuracy, such that when CI overlap this line, there is no evidence of variation in predictive accuracy at roadside and off roads; CI above the dashed line, evidence of greater off-road predictive accuracy; CI below the dashed line, evidence of greater roadside predictive accuracy). Accuracy is differentiated by species type (edge, generalist, forest interior).*

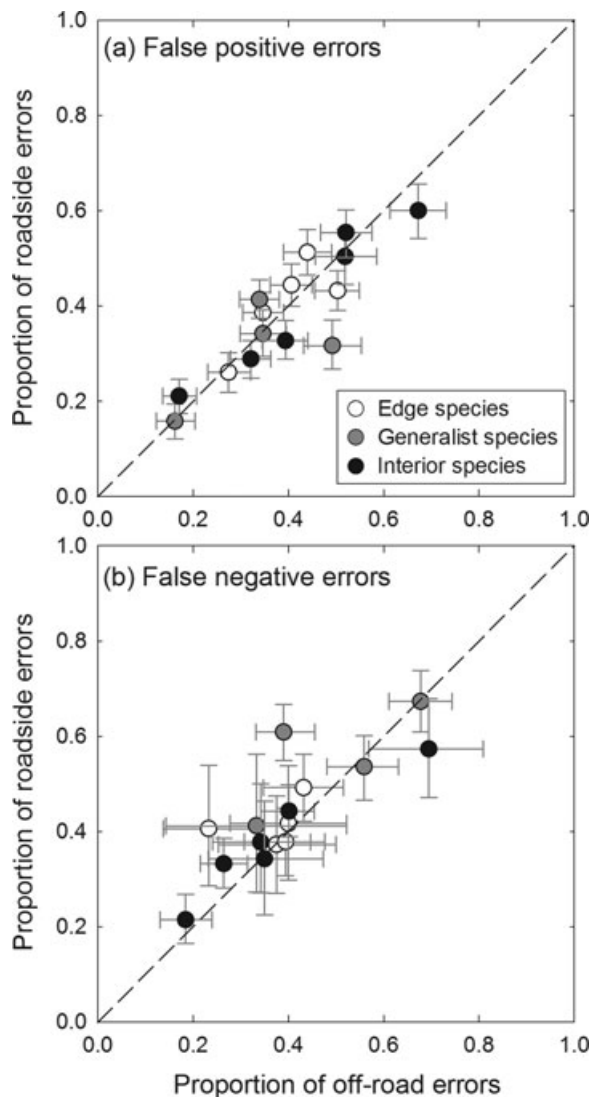


Figure 3. Proportion of (a) false-positive and (b) false-negative errors (95% CI) by type of species (edge, generalist, forest interior) in predictions of roadside and off-road distributions on the basis of hierarchical occupancy models built from independent (not used for model building) roadside point counts in the Northern Region Landbird Monitoring Program in Montana and Idaho (dashed line, 1:1 ratio for roadside and off-road error rates in predictions; when CI overlap the dashed line, there is no evidence of variation in error rates at roadsides and off roads).

## Discussion

Sample bias is common in monitoring programs (e.g., North American Breeding Bird Survey [BBS] and North American Amphibian Monitoring Program) (Bart et al. 1995; Weir & Mossman 2005), data from which are frequently used to predict species distributions for the purpose of conservation planning. For example, analyses of

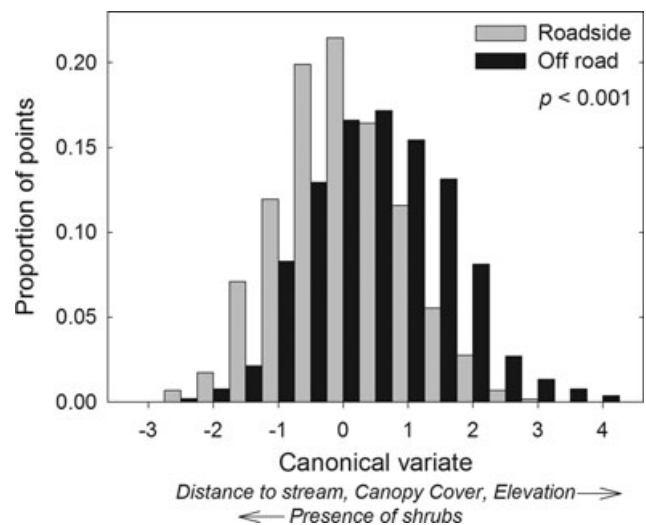
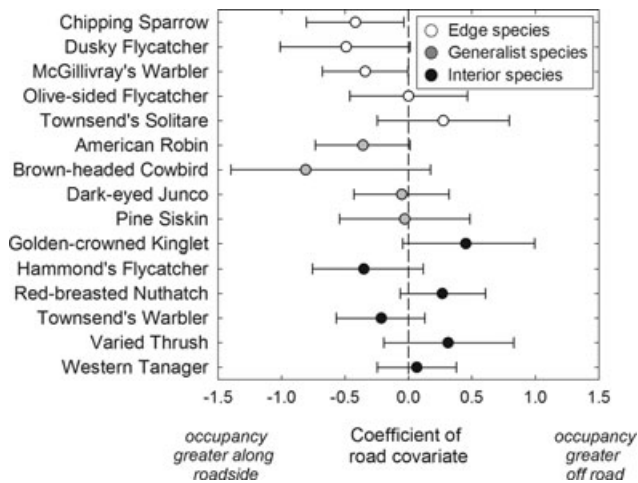


Figure 4. Results of discriminant analysis of environmental covariates at paired roadside and off-road transects surveyed in 2007–2008 as part of the Northern Region Landbird Monitoring Program in Montana and Idaho (x-axis, first canonical variate with the strongest factor loadings [distance to stream, canopy cover, elevation, and presence of shrubs]; y-axis, proportion of both roadside and off-road points associated with different levels of the canonical variate).

BBS data have informed conservation priorities for several groups of birds and have increased knowledge of several conservation issues, including effects of exurbanization and climate change (Thogmartin et al. 2004; Pidgeon et al. 2007; Albright et al. 2010). Road bias is also prevalent in museum data, which are used to build presence-only models (Reddy & Davalos 2003; Kadmon et al. 2004). Despite the ubiquity of this sample bias, ours is the first example, to our knowledge, of a test that is based on a prospective sampling strategy designed to measure the performance of road-based species distribution models when extrapolated to locations away from roads (off-road locations).

Our models of species distributions of breeding birds were moderately accurate compared with some other assessments of species distribution models (e.g., Elith et al. 2006), which was likely due, in part, to the fact that our models were validated with data that were truly independent in space and time from the data used for model building. Despite observed variation in environmental covariates and the occupancy of some species near roads, we found neither evidence of reduced accuracy of models built with roadside data when predicting distributions off roads nor evidence of consistent variation across species groups. For example, we expected false-positive error rates would be consistently greater for off-road edge species than other species because models



**Figure 5.** Coefficients (95% credible intervals) (logit scale) of a binary road covariate used to test for variation in roadside versus off-road bird occupancy at paired roadside and off-road transects surveyed in 2007–2008 and used for model validation. Positive values suggest a greater probability of species occurrence at off-road than roadside locations.

built from roadside data for edge species may overpredict occurrence of these species off roads. However, 2 key properties of occupancy models and 2 aspects of our data set help explain our results and provide context for when road-based sampling may be adequate to develop reliable models.

First, occupancy models and other modeling approaches that use presence-absence data (or more frequently detection-nondetection data) can account for the effect of vegetation on species site occupancy. If variation in environmental covariates sampled on roads captures variation in the environment throughout the system, then observed species-environment relations can be uncovered (assuming no interactions of habitat use and roads occur). In our study region, a random sample of point locations showed that land cover varies as a function of distance from roads (Wilk's  $\Lambda = 0.886$ ,  $p < 0.001$ ) (Supporting Information). However, overall variation in land cover was captured at distances  $< 200$  m from a road (Supporting Information). Given adequate variation in surveyed land cover, occupancy models may be able to reliably identify species-environment relations that can be used to predict species distributions.

Second, our species distribution models accounted for variation in detectability. Such accounting could keep the effects of detectability along roadsides from limiting the predictive performance of a model for off-road areas. Nonetheless, we also considered logistic regression models that did not correct for detectability to determine whether such models reduced performance by removing the observation component of our hierarchical model

(K.M., unpublished). The predictions of these models at roadside and off-road locations had similar accuracy, such that variation in detectability appears not to be driving the similarity in model accuracy.

In addition to the above properties of occupancy models, 2 aspects of the monitoring data can further explain similar predictive performance of roadside and off-road species distribution models. First, most of the roads along which sampling was conducted were U.S. Forest Service roads, which are relatively narrow, unpaved (primarily dirt or gravel), and have less vehicle traffic compared with some other types of roads. These roads likely have smaller effects on vegetation and species occupancy than other types of roads that cause greater changes in vegetation and noise (Hutto et al. 1995; Griffith et al. 2010). Indeed, while vegetation sometimes differed between our paired roadside and off-road points, only 2 of the species we considered were consistently more likely to occur close to roads (MacGillivray's Warbler and Chipping Sparrow), and none of the species were more likely to occur away from roads (Fig. 5). Second, off-road validation locations were also only 200 m from roads, such that predictions farther from roads might be less accurate than those we made. However, most investigations of the effects of roads on bird distributions show that strong effects tend to occur  $< 200$  m from roads (Benitez-Lopez et al. 2010). In addition, 39% of area in this region was  $< 200$  m from roads (Supporting Information). The lack of differences in model predictions was not likely due to a lack of power, given that our validation data set for roadside and off-road locations was relatively large ( $n = 578, 518$ , respectively).

Species distribution models are often built with presence-only data, and sample bias in such models is more problematic than for models built with presence-absence data, in part because sample bias influences presence points but not pseudo absences frequently used for making comparisons (Phillips et al. 2009). Results of the few systematic evaluations of potential sample bias in such investigations suggest that sample bias may reduce the predictive performance of these models (Kadmon et al. 2004; Phillips et al. 2009). The only example to our knowledge of tests whether road-based sampling bias influenced the accuracy of species distribution models is that of Kadmon et al. (2004). In their study, bioclimatic models had slightly reduced performance when built from data collected near roads ( $< 432$  m), on the basis of models for 129 species that were assessed with validation data taken from  $5 \times 5$  km grain cells across their study region. Their assessment suggests potential roadside biases in presence-only data can be reduced by using a subset of road-biased data to achieve a distribution of distances to roads that is similar to the distribution throughout the region; see also Supporting Information. We think future efforts to predict distributions with presence-only data should attempt to



address this potential bias, either through the use of subsets of data that reflect the distribution of road distances in the region or alternatively through the use of pseudo absences included to capture similar biases in spatial distribution (Kadmon et al. 2004; Phillips et al. 2009).

Our results suggest that in circumstances in which roads are typically dirt or gravel and sampling covers wide environmental gradients, roadside sampling should not be problematic for building species distribution models. Consequently, some current monitoring programs and species-diversity databases may be adequate for the development and application of distribution maps. We recommend that monitoring programs address roadside bias in a series of steps. First, estimate the extent to which roadside samples reflect environmental variation across the region of interest (e.g., Supporting Information). Second, conduct additional sampling away from roads to test whether model results can be extrapolated to off-road locations or use a subset of existing data to reduce road bias (Kadmon et al. 2004), particularly if roadside samples do not cover the range of environmental variation. Third, limit other sources of potential bias that may arise from sampling along roadsides, such as variation in detectability of species near roads. Often many of these biases can be accounted for with only minor changes to sampling protocols (Griffith et al. 2010; Kéry et al. 2010). Finally, if models built with data collected along roads cannot adequately predict species distributions away from roads, monitoring programs will need to carefully weigh the trade-offs between sample coverage (e.g., Bart et al. 2004) and reliable predictions of species distributions relative to other goals of the monitoring programs.

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## Supporting Information

Environmental covariates used to model species distributions (Appendix S1), accuracy assessment with more informed priors (Appendix S2), model coefficients for occurrence and detectability for each species (Appendix S3), and analysis of environmental variation as a function of distance from roads throughout the study

region (Appendix S4) are available online. Queries (other than absence of the material) should be directed to the corresponding author.

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