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Informative priors can account for location uncertainty in stop-level analyses of the North American Breeding Bird Survey, allowing fine-scale ecological analyses

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ABSTRACT

Ecological inferences are often based on the locations at which species are present, but many species records have substantial uncertainty in spatial metadata, limiting their utility for fine-scale analyses. This is especially prevalent in historical records such as museum specimens, and in some citizen-science data. For example, the North American Breeding Bird Survey (BBS) has 55+ years of bird data from regular transects ("routes") across the continent but was not designed to capture the spatial component of point count events, limiting analyses of species-habitat relationships for which it would otherwise be well suited. We present a new methodology for quantifying location uncertainty in BBS records using digitized estimated stop locations, deriving the corresponding environmental covariate uncertainty distributions, and incorporating this information into hierarchical species distribution models using informative Bayesian priors. This approach allows for estimation of species–environment relationships in a way that fully accounts for underlying spatial uncertainty. We quantify stop-location uncertainty in BBS data across the central United States, model bird–land cover relationships in the upper Midwest, and validate our method by comparing posterior land cover estimates to known covariate values for a subset of Global Positioning System (GPS)-digitized stop locations. We provide code for implementing this method in R. Posterior land cover estimates (forest, grass/hay, and developed land cover), based on our informative priors, were highly correlated with known land cover values from GPS-digitized stop locations. Our approach thus makes it possible to responsibly leverage large historical and citizen-science databases, such as the BBS, for fine-scale ecological analyses.

Keywords: conservation planning, forest cover, grasslands, informative prior, location error, National Land Cover Database, North American Breeding Bird Survey, stop-level analyses

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LAY SUMMARY

- Ecologists can learn a lot about species by studying the precise locations in which they do (and do not) occur, but the location information associated with many species records is imprecise.
- This is true of the North American Breeding Bird Survey (BBS), in which volunteer observers have surveyed birds at points along consistent routes across the United States for over 55 years.
- As the BBS was designed for large-scale analyses, detailed location information for each bird count is not recorded.
- We estimate location uncertainty in point count locations for BBS data and present a modeling method that accounts for this uncertainty in a way that opens new possibilities for fine-scale uses of this extensive dataset, unlocking its potential to advance the study of the relationships between birds and their immediate habitat.

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Los valores informativos previos pueden tener en cuenta la incertidumbre de la ubicación en los análisis a nivel de parada del Censo de Aves Reproductoras de América del Norte, permitiendo análisis ecológicos a escala fina

RESUMEN

Las inferencias ecológicas a menudo se basan en las ubicaciones en las que están presentes las especies, pero muchos registros de especies tienen una incertidumbre sustancial en los metadatos espaciales, lo que limita su utilidad para análisis a escala fina. Esto es especialmente frecuente en registros históricos, como los especímenes de museos, y en algunos datos de ciencia ciudadana. Por ejemplo, el Censo de Aves Reproductoras de América del Norte (BBS por sus siglas en inglés) tiene más de 55 años de datos de aves de transectos regulares ("rutas") a lo largo del continente, pero no fue diseñado para capturar el componente espacial de los eventos de conteo puntual, lo que limita los análisis de las relaciones especie-hábitat para los cuales, de otro modo, sería adecuado. Presentamos una nueva metodología para cuantificar la incertidumbre de la ubicación en registros de BBS utilizando ubicaciones de paradas estimadas digitalizadas, derivando las correspondientes distribuciones de incertidumbre de covariables ambientales e incorporando esta información en modelos jerárquicos de distribución de especies utilizando valores bayesianos informativos previos. Este enfoque permite estimar las relaciones especie-ambiente de una manera que tiene en cuenta completamente la incertidumbre espacial subyacente. Cuantificamos la incertidumbre de las ubicaciones de parada en los datos de BBS en el centro de los Estados Unidos, modelamos las relaciones entre aves y cobertura del suelo en la parte superior del Medio Oeste, y validamos nuestro método comparando las estimaciones posteriores de la cobertura del suelo con valores conocidos de covariables para un subconjunto de ubicaciones de paradas digitalizadas con GPS. Proporcionamos el código para implementar este método en R. Las estimaciones posteriores de la cobertura del suelo (bosques, pastizales/hierba, y cobertura desarrollada), basadas en nuestros valores informativos previos, estuvieron altamente correlacionadas con los valores conocidos de cobertura del suelo de las ubicaciones de paradas digitalizadas con GPS. Nuestro enfoque, por lo tanto, hace posible aprovechar de manera responsable grandes bases de datos históricos y de ciencia ciudadana, como la BBS, para análisis ecológicos a escala fina.

Palabras clave: análisis a nivel de parada, Base de Datos Nacional de Cobertura del Suelo, Censo de Aves Reproductoras de América del Norte, cobertura forestal, error de ubicación, pastizales, planificación de la conservación, valores informativos previos

INTRODUCTION

Many ecological inferences rely on records of species abundance and occurrence, past and present (Elith et al. 2006, Guillera-Arroita 2017). This is especially true for macroecological questions covering broad geographic areas, for taxonomically rich study systems, and for inferences from the past where few other approaches are available (Wüest et al. 2020). Such species records can be overlaid with climate and habitat layers and linked via trait and phylogenetic information, producing valuable inferences (Xu et al. 2023). Nevertheless, species records present many analytical challenges, which differ according to their source (Farley et al. 2018).

One important challenge is variable precision and uncertainty in location metadata associated with species records (Braunisch and Suchant 2010, Bloom et al. 2018). Inferences based on species locations can be made only at and above the scale of precision in location metadata, limiting the utility of some large datasets for studies of species-habitat associations at the local scales that are often most relevant for many species and for land managers (Niemuth et al. 2017). Location information can be imprecise for many museum and herbaria specimens (Rowe 2005, Naimi et al. 2014, Ellwood et al. 2016), our primary source of information from the past and for many poorly known taxa.

Uncertainty or imprecision in locations associated with species records, however, does not imply a total lack of spatial information for those records. In some cases, a probability density function over space (Angermann et al. 2001) can be reasonably approximated, given the nature of the underlying sampling process. Spatial autocorrelation in habitat and climate, typical at many scales (Venter and Sydenham 2021), means that uncertainty in probability distributions of environmental covariates will often be lower than uncertainty in the location probability density functions (Zhang et al. 2018) from which they were derived (Naimi et al. 2014). Bayesian hierarchical models provide a method for incorporating this partial knowledge about a quantity (i.e., land cover), using informative priors in a way that is somewhat analogous to forms of Bayesian meta-analysis (Rhodes et al. 2016).

The North American Breeding Bird Survey (BBS) is recognized as a quantitative foundation for avian conservation and management in North America (Sauer et al. 2017, Rosenberg et al. 2019). The BBS methodology was designed to provide status, trends, and environmental associations of birds at regional and continental scales, but its results have also been successfully used to examine more localized effects of habitat heterogeneity (Farwell et al. 2020b), test for route-level habitat effects on temporal trends (Smith et al. 2024), and explore relationships between climate and bird diversity (Fogarty et al. 2020). The BBS operates more than 4,000 active roadside sample units throughout the continental United States and Canada, ~3,000 of which are surveyed annually. The sample units are called "routes" and are distributed along secondary and tertiary roadways using a random stratified design. Routes are sampled once per year, primarily in June. Each route is comprosed of a sequence of 50 roadside point counts ("stops") at intervals of roughly 0.8 km. The point counts are 3 min in duration and, during each, an assigned observer records all birds heard or seen within a 0.25-mile (0.4-km) radius. BBS count data had been collected and stored as aggregated 10-stop summaries up until 1997, and all subsequent data have been saved and released in unaggregated 50-stop format.

The national BBS office creates route paths, stores start location coordinates, and tasks the first observer on each route with creating the locations where the remaining 49 stops should occur. Survey instructions direct observers to use the same point count locations annually but give the flexibility to move point count locations as needed to accommodate safety and roadway issues (Hudson et al. 2017). At the discretion of the BBS national office, this can include the removal of five or fewer stops, which causes renumbering of existing stops and adding new replacements to the end. Differences in observer safety tolerances, or unclear or absent descriptions can lead to differences in annual point count locations between years and

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observers. The BBS design does not include the reporting of point count level spatial data, so there are no data describing where point count events occurred each year. However, the survey instructions ask observers to create and maintain personal stop descriptions for purposes of navigating to their same locations the following year. In coordination with the BBS office, some authors have compiled coordinate sets (hereafter "estimated stop locations") corresponding to observer stop descriptions for certain routes and years (Niemuth et al. 2017, Twedt 2020). For clarity, in this study, we refer to these digitized estimated locations as "estimated stop locations," whereas "annual point count locations" refer to the unknown and unrecorded true locations of stops (i.e., counts) in each year.

For the reasons described above, location uncertainty is associated with these stop locations and this has limited their utility for fine-scale ecological questions, such as habitat selection and use. The latest BBS Strategic Plan (U.S. Geological Survey and Canadian Wildlife Service 2020) and BBS Action Plan (U.S. Geological Survey et al. 2021) have identified the annual collection of spatial data from point count events as a priority, and although when implemented this will improve location precision going forward, analysis of past data will still require methods to account for uncertainty in locations (Sauer et al. 2017). Simplistic approaches (e.g., that assume consistent 800-m spacing between adjacent stops, or consistency in point count locations through time) are insufficient as they are likely to introduce errors. Hudson et al. (2017) highlight ways in which improved BBS stop-level analyses could enhance our understanding of bird–habitat relationships and the effects of land use change. Birds respond strongly to habitat effects at the scale of breeding home ranges (Holmes and Sherry 1988), for example, and for many bird species this corresponds roughly to the scale of individual BBS stops. This is also the scale of many management decisions and conservation actions (Niemuth et al. 2017).

The BBS offers advantages as a test case for modeling location uncertainty because, unlike, for example, museum records, BBS location uncertainty is largely one-dimensional (i.e., along a defined route path, although deviations and detours along these routes can occasionally occur). Additionally, compiled coordinate sets that correspond to observer stop descriptions are available from a small but representative subset of years and routes. These stop locations allow quantification of the variation (and thus uncertainty) in point count locations along BBS route paths. The resulting location uncertainty distributions can then be used to derive corresponding land cover uncertainty distributions, using land cover layers such as the National Land Cover Database (NLCD) (Dewitz 2021), which aligns temporally to the available stop-level BBS count data (1997–present) (Ziolkowski et al. 2022). These land cover uncertainty distributions can thus be included in Bayesian models via informative priors, resulting in estimates of bird–habitat relationships that fully account for annual point count location uncertainty.

In this study, we estimate location uncertainty for BBS stops and the corresponding uncertainty in land cover. We then develop a Bayesian hierarchical logistic regression model that incorporates land cover uncertainty information using informative priors to examine the effects of land cover covariates on bird occurrences across the upper Midwest in the United States. We use stop-level BBS data, generating land cover uncertainty distributions by pairing uncertainty in annual point count locations with NLCD data layers. Our objectives are thus to (1) quantify variation in BBS annual point count locations along routes; (2) quantify uncertainty in stop-level land cover covariates, given this underlying location uncertainty; (3) incorporate this land cover uncertainty into our stop-level analyses via informative Bayesian priors in hierarchical models; (4) estimate bird responses to small-scale (400-m radius) forest, grassland, and developed land cover while simultaneously estimating these land cover covariates from our informative priors; (5) evaluate the accuracy of our posterior land cover estimates; and (6) provide a framework for future nationwide stop-level BBS analyses.

We provide quantified estimates of annual point count location uncertainty for the central United States (Burner et al. 2024), as well as code (Burner 2024) for quantifying the corresponding land cover uncertainty and extracting BBS data for input into our modeling framework. We evaluate the effectiveness of our method by comparing posterior land cover estimates to known land cover values for Global Positioning System (GPS)-digitized stop locations. Additionally, we fit a second model in which we systematically modify informative land cover covariate priors to be misleading, relative to known land cover, for these stop locations. We also compare these posterior land cover estimates to their known values. Finally, we compare model fit and parameter estimate precision between our primary land cover uncertainty model and a third model that assumes consistent 800-m annual point count spacing and the resulting land cover values.

MATERIALS AND METHODS

Study Area

We selected a 17-state focal region in the central United States for which to compile BBS route and stop information (Figure 1) in order to quantify uncertainty in annual point count locations and land cover across this region. We then selected a subset of these states (Minnesota, Wisconsin, and Michigan; Figure 1A) for modeling. These focal states each contain BBS routes that vary in amount and configuration of forest, grassland, and developed land cover. GPS-digitized stop locations are available for many routes (one year each) in Wisconsin, and we use these to test our method. BBS routes in the modeled states fall into four Bird Conservation Regions (BCRs) (Sauer et al. 2003).

Selecting Bird Species

Our method is based on the premise that land cover influences bird assemblages (Melo et al. 2018, Farwell et al. 2020), and so we needed to include bird species that differ in their optimum land cover ranges and that occur regularly enough in suitable habitat to inform land cover covariate estimates. We also needed bird species that are readily detectable in point counts and that have small enough breeding territories to be regularly present for detection. To this end, we downloaded stop-level BBS data (Ziolkowski et al. 2022) using the *bbsAssistant* R package (Burnett et al. 2019) and selected passerines that occurred in ≥5% of point counts in our modeled dataset (described below). We excluded non-passerines because many are wide-ranging (e.g., Accipitriformes) or are poorly detected in point counts during much of the year (e.g.,

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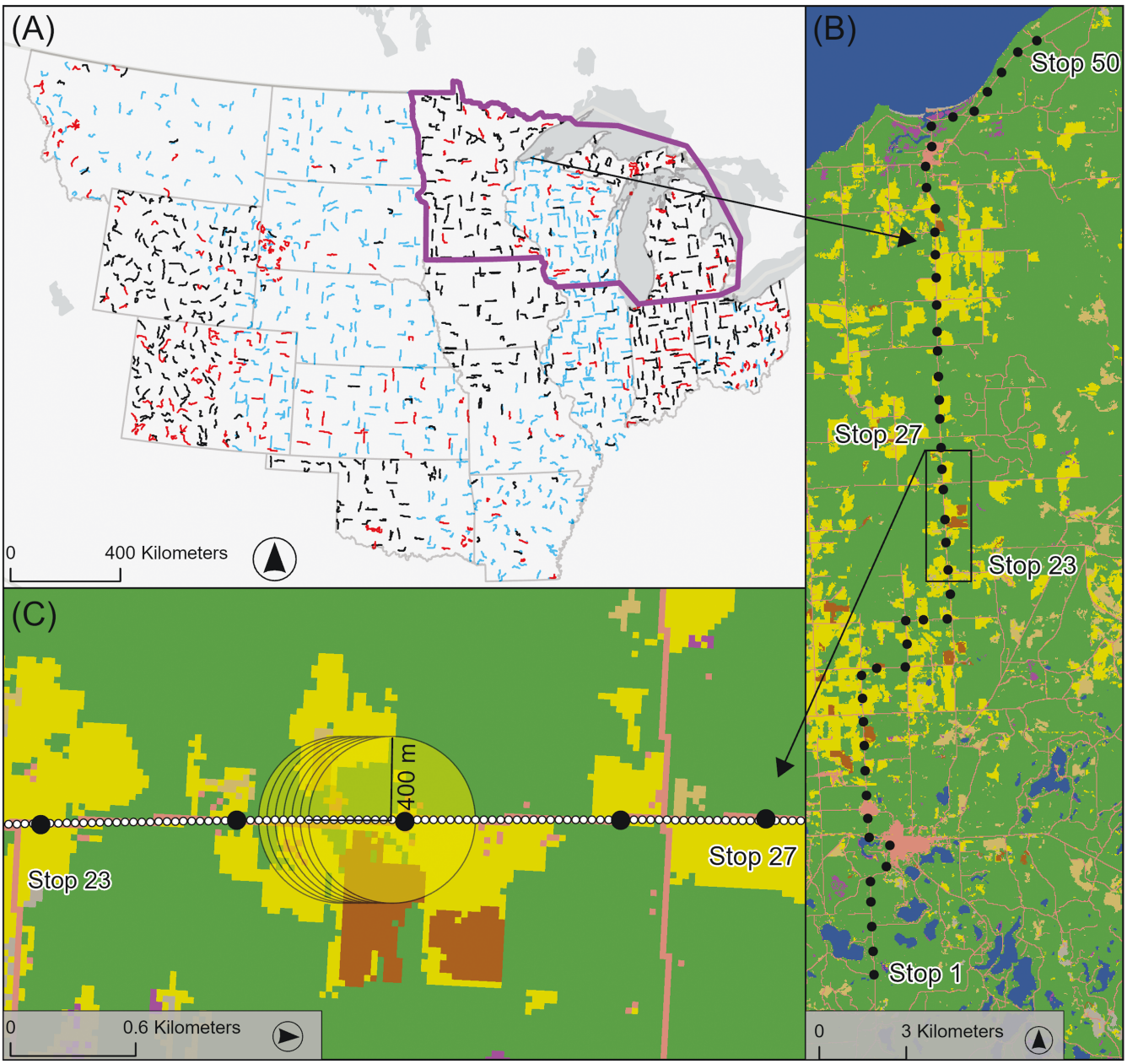


FIGURE 1. North American Breeding Bird Survey (BBS) route paths in the central United States. Includes all routes (**A**) that met inclusion criteria for the initial phase of our study (black and cyan) as well as those that were eliminated (red). Exclusion criteria are available in methods. Routes for which digitized estimated stop locations were available (each for a single year) are shown in cyan. These stop locations were used to quantify uncertainty in BBS annual point-count locations. For modeling, we chose those routes found in Minnesota, Wisconsin, and Michigan (purple border in panel **A**). Right panel (**B**) shows a single route, with 50 hypothetical point count locations for a given year. The BBS design does not include the reporting of point-count-level spatial data, so no data describe where point-count events had occurred in each year. Along each route, we generated evenly spaced points (C; white dots) every 40 m and extracted proportion of land cover within a 400-m radius for each of these autogenerated points (several example circles are illustrated). Land cover maps are based on the 2019 National Land Cover Database (NLCD) (Dewitz 2021) as detailed in Table 2. Forest is shown in green, grass/hay as mustard, development as peach, wetlands as purple, shrubs as light brown, and cultivated land as dark brown.

Galliformes), and we also excluded corvids (Corvidae) and swallows (Hirundinidae) for the same reasons. This resulted in selection of 37 species that varied in their core habitats and prevalences (Table 1).

Given the geographic breadth of our modeled states, ranges of some modeled species did not span the full region. We defined breeding ranges for each species and indicated species as NA (i.e., not applicable) rather than absent (or present) on BBS routes outside their breeding ranges. To quantify breeding ranges, we downloaded breeding range shapefiles from the *ebirdst* R package (Strimas-Mackey et al. 2022) and designated a BBS route as out of range for a species when the route start point did not fall within the breeding range. All analyses were conducted in R version 4.4.0 (R Core Team 2024).

Quantifying Location Uncertainty for BBS Stops

Our workflow for quantifying location and land cover uncertainty and incorporating these into BBS models consisted of 3 main steps: (1) estimate overall uncertainty in annual point

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TABLE 1. Bird species chosen for modeling of Breeding Bird Survey (BBS) data from the upper Midwest of the United States. All passerines detected during at least 5% of modeled BBS count events ("Counts detected (%)") were included. Model fit for each species was assessed using TjurR^2 (Tjur 2009). Species are ordered by forest association (positive to negative) estimated in our study. Taxonomy follows Chesser et al. (2023).

Scientific name	Common name	Counts detected (%)	TjurR^2	Forest optimum [a]	Grass/hay optimum[a,b]	Developed optimum[a,b]	Forest niche breadth [c]	Grass/hay niche breadth[b,c]	Developed niche breadth[b,c]
Catharus guttatus	Hermit Thrush	14.8%	0.262	25% to 100%	0% to 100%	0% to 24%	0.75	1	0.24
Contopus virens	Eastern Wood-Pewee	7.5%	0.156	19% to 100%	0% to 97%	0% to 67%	0.81	0.97	0.67
Vireo olivaceus	Red-eyed Vireo	31.6%	0.417	17% to 100%	0% to 100%	0% to 100%	0.83	1	1
Seiurus aurocapilla	Ovenbird	28.5%	0.488	15% to 100%	0% to 100%	0% to 53%	0.85	1	0.53
Poecile atricapillus	Black-capped Chickadee	12.3%	0.139	13% to 100%	0% to 81%	19% to 100%	0.87	0.81	0.81
Myiarchus crinitus	Great Crested Flycatcher	6.5%	0.092	13% to 100%	0% to 100%	0% to 33%	0.87	1	0.33
Pheucticus ludovicianus	Rose-breasted Grosbeak	10.2%	0.099	12% to 100%	0% to 85%	0% to 11%[d]	0.88	0.85	0.11[d]
Leiothlypis ruficapilla	Nashville Warbler	20.7%	0.296	13% to 100%	0% to 36%	0% to 7%	0.87	0.36	0.07
Catharus fuscescens	Veery	10.3%	0.217	10% to 100%	0% to 14%	0% to 5%[d]	0.90	0.14	0.05[d]
Setophaga pensylvanica	Chestnut-sided Warbler	14.7%	0.221	9% to 100%	0% to 36%	0% to 14%	0.91	0.36	0.14
Setophaga ruticilla	American Redstart	7.7%	0.198	9% to 100%	0% to 18%	0% to 86%	0.91	0.18	0.86
Passerina cyanea	Indigo Bunting	16.1%	0.203	11% to 100%	0% to 69%	0% to 34%	0.89	0.69	0.34
Zonotrichia albicollis	White-throated Sparrow	21.3%	0.314	9% to 100%	0% to 15%	0% to 5%[d]	0.91	0.15	0.05[d]
Cardinalis cardinalis	Northern Cardinal	20.7%	0.237	10% to 96%	0% to 87%	15% to 100%	0.86	0.87	0.85
Sayornis phoebe	Eastern Phoebe	5.6%	0.068	9% to 89%	0% to 69%	0% to 81%	0.80	0.69	0.81
Dumetella carolinensis	Gray Catbird	11.5%	0.173	9% to 86%	0% to 65%	0% to 17%[d]	0.77	0.65	0.17[d]
Molothrus ater	Brown-headed Cowbird	17.2%	0.128	1% to 88%	0% to 65%	0% to 100%	0.87	0.65	1
Bombycilla cedrorum	Cedar Waxwing	8.6%	0.106	5% to 81%	0% to 61%	0% to 100%	0.76	0.61	1
Spinus tristis	American Goldfinch	18.9%	0.124	5% to 80%	0% to 72%	0% to 100%	0.75	0.72	1
Geothlypis trichas	Common Yellowthroat	30.3%	0.223	7% to 77%	0% to 86%	0% to 5%	0.70	0.86	0.05
Troglodytes aedon	House Wren	18.4%	0.194	8% to 75%	0% to 71%	15% to 100%	0.67	0.71	0.85
Spizella passerina	Chipping Sparrow	28.2%	0.174	0% to 100%	0% to 65%	11% to 100%	1	0.65	0.89
Icterus galbula	Baltimore Oriole	7.3%	0.095	7% to 75%	0% to 60%	0% to 100%	0.68	0.6	1
Setophaga petechia	Yellow Warbler	11.2%	0.243	8% to 73%	0% to 57%	0% to 5%	0.65	0.57	0.05
Melospiza melodia	Song Sparrow	38.2%	0.232	3% to 63%	0% to 71%	0% to 13%	0.6	0.71	0.13
Vireo gilvus	Warbling Vireo	5.5%	0.122	5% to 55%	0% to 61%	0% to 23%	0.5	0.61	0.23
Spizella pallida	Clay-colored Sparrow	6.9%	0.223	3% to 57%	9% to 92%	0% to 9%	0.54	0.83	0.09

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Table 1. Continued.

Scientific name	Common name	Counts detected (%)	TjurR²	Forest optimum [a]	Grass/hay optimum[a,b]	Developed optimum[a,b]	Forest niche breadth [c]	Grass/hay niche breadth[b,c]	Developed niche breadth[b,c]
Turdus migratorius	American Robin	54.7%	0.176	0% to 67%	0% to 68%	11% to 100%	0.67	0.68	0.89
Pooecetes gramineus	Vesper Sparrow	9.9%	0.271	0% to 30%	0% to 9%[d]	0% to 24%	0.30	0.09[d]	0.24
Agelaius phoeniceus	Red-winged Blackbird	40.4%	0.390	0% to 27%	0% to 100%	0% to 9%	0.27	1	0.09
Quiscalus quiscula	Common Grackle	19.2%	0.283	0% to 17%	0% to 65%	10% to 100%	0.17	0.65	0.90
Sturnella magna	Eastern Meadowlark	7.6%	0.259	0% to 12%	16% to 100%	0% to 7%	0.12	0.84	0.07
Dolichonyx oryzivorus	Bobolink	8.9%	0.272	0% to 13%	28% to 100%	0% to 5%	0.13	0.72	0.05
Sturnus vulgaris	European Starling	19.2%	0.264	0% to 12%	0% to 82%	10% to 100%	0.12	0.82	0.90
Passerculus sandwichensis	Savannah Sparrow	16.8%	0.398	0% to 11%	41% to 100%	0% to 12%	0.11	0.59	0.12
Passer domesticus	House Sparrow	19.1%	0.251	0% to 9%	0% to 74%	10% to 100%	0.09	0.74	0.90
Eremophila alpestris	Horned Lark	13.2%	0.284	0% to 4%	0% to 5%[d]	0% to 12%	0.04	0.05[d]	0.12

[a]Optimum range is defined as the range of proportion land cover at which predicted occupancy is at least 75% as high as the maximum predicted occupancy.

[b]Developed and grass/hay optimum range and niche breadth values are calculated from model predictions across the full gradient of percent cover, but cover values above 60% are rare in the model training data and so predictions for this portion of the gradients are likely less reliable.

[c]Niche breadth values are defined as the difference between the maximum and minimum of the optimum range.

[d]These species had concave-up relationships with Grass/hay or Development, resulting in split optima (one near 0, one near 100) that are probably not biologically realistic and are likely caused by poor sampling above 60% on these gradients. The lower optimum range is presented here; refer to Figure 4 for detailed responses of each species.

count locations for each BBS stop number using digitized estimates of stop locations available from some BBS routes; (2) calculate land cover uncertainty for each BBS stop on each route in each year using the NLCD and our stop-location uncertainty distributions; and (3) specify these land cover uncertainty distributions as informative priors in a stop-level BBS model.

We obtained BBS route paths based on U.S. Geological Survey (2012) and start points from the BBS dataset (Ziolkowski et al. 2022). Beginning with all routes in our 17-state focal region (n = 1,361; Figure 1), we then removed routes that were not conducive to our method of quantifying location uncertainty. We excluded nonrandom (i.e., 900-series) routes (n= 72), nonlinear routes (with forks, 'T's, loops, or multiple GIS line segments; n = 42), route lines farther than 1,000 m from their designated start points (n = 26), and routes with abnormally long (>48 km; n = 79) or short (<37 km; n = 5) BBS route lines. Finally, we removed routes for which estimated stop locations indicated a direction of travel opposite that indicated by route start points (n = 18; 2.8% of all routes with digitized stop-location estimates). We thus retained 1,119 routes (82%). In preparation for quantifying the distributions of estimated stop locations along BBS routes and extracting corresponding land cover distributions, we first used ArcGIS Pro 3.1.2 (ESRI 2023) to generate sequentially numbered points every 40 m along each route. These points (hereafter "autogenerated points") were numbered (e.g., 1–1,000 for a 40-km route), starting at the end of the route nearest the start point. These autogenerated points therefore function as a measure of distance along a route line (hereafter "route distance"), such that, for example, autogenerated point 201 on any route is (201 – 1) × 40 m = 8,000 m from the starting end of the route line.

To quantify uncertainty in annual point count locations for each stop number (1 to 50) across BBS routes (Dobbyn and Couturier 1998), we assumed that digitized stop-location estimates were representative of the overall variation in annual point count locations along BBS routes in the region. We used digitized estimated locations, which were available from 13 of 17 states in our focal region in the central United States (Figure 1). This includes digitized stop-location estimates from Ohio (Burner 2024), Illinois (Thogmartin 2002), Wisconsin (Anich and Striegel 2019), parts of Missouri, Arkansas, and Oklahoma (Twedt 2020), and Kansas, Nebraska, South Dakota, North Dakota, and parts of Colorado, Wyoming, and Montana (Niemuth et al. 2017). In total, we used 25,078 stop locations across 568 routes. Refer to Supplementary Material Table 1 for digitized routes used by state, and for years and location estimation methods.

For each of these digitized stop-location estimates, we located the nearest autogenerated point on the appropriate route. We then extracted the distributions of autogenerated point numbers nearest each BBS stop number across the entire dataset of digitized stop estimates. This produced

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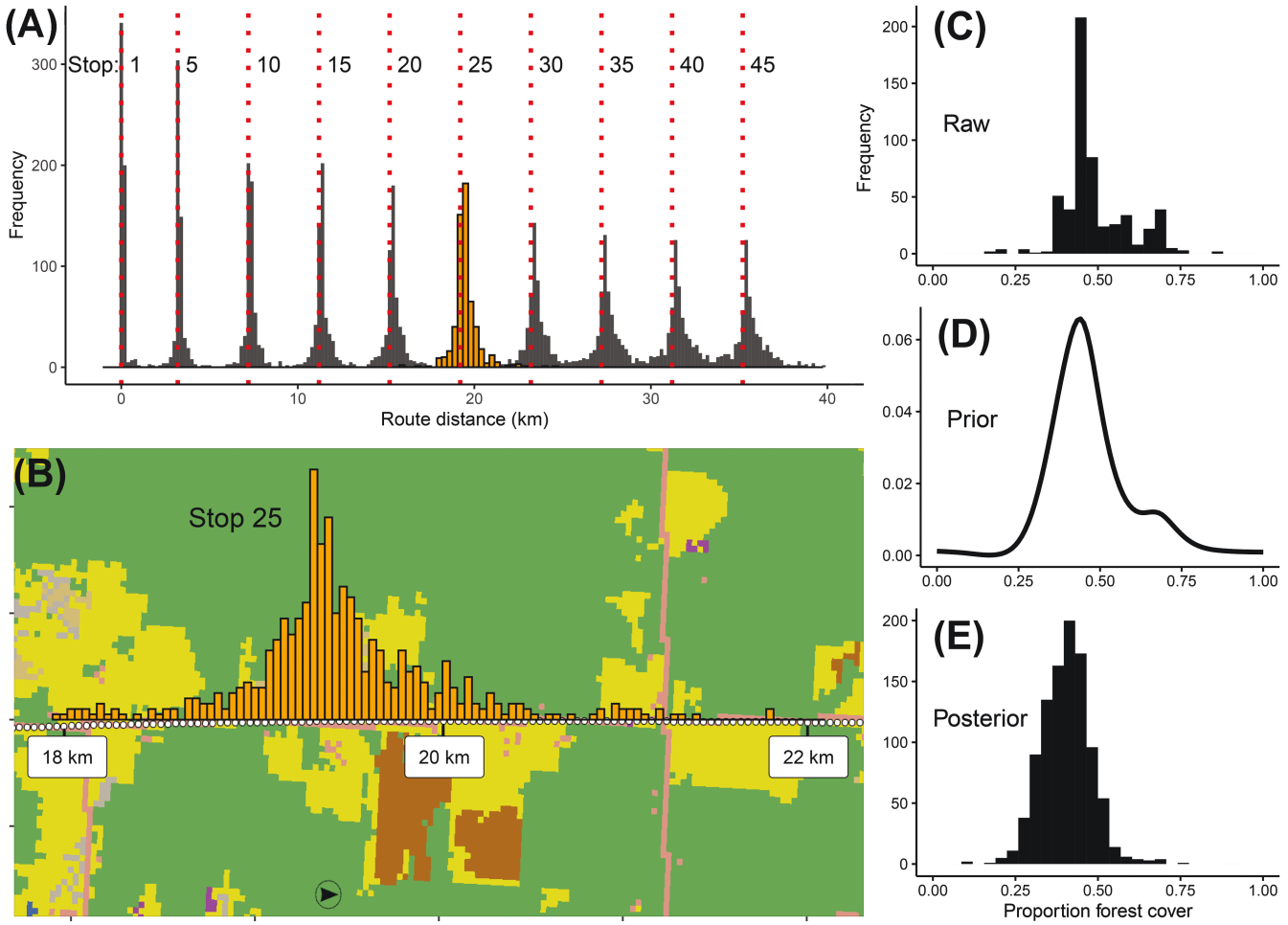


FIGURE 2. Quantification of stop-location uncertainty and resulting land cover uncertainty for North American Breeding Bird Survey (BBS) stops. Histograms (**A**) show variation in the locations of selected stops along BBS route lines, based on digitized stop location estimates from 13 states (Figure 1). As an example, histograms show just 10 of the 50 calculated stops (number labels), and red vertical dotted lines indicate the hypothetical location of each stop given even 800-m stop spacing along route lines. In practice, stop spacing varies among routes, years, and observers. We generated points every 40 m along each route line (**B**; white dots) and calculated proportion of each land cover (e.g., proportion forest cover) in a 400-m radius around each of these autogenerated points. For each stop number along each route, we then extracted land cover values from those autogenerated points in proportion to the height of the stop location probability histogram (**B**; in orange, showing stop 25 as an example). This produced unique raw land cover probability distributions (**C**) for each land cover covariate for each stop number in each route and year. To use these distributions as prior probability distributions in our Bayesian models, we then converted each to a smoothed custom distribution (**D**). These distributions were then used as informative priors to produce posterior land cover covariate estimates (**E**) for each stop in our model. Our land cover layers (**B**) are based on the National Land Cover Database (NLCD) (Dewitz 2021), merging NLCD land cover categories as detailed in Table 2. Forest is shown in green, grass/hay as mustard, development as peach, wetlands as purple, shrubs as light brown, and cultivated land as dark brown.

binned distributions (40-m bins, corresponding to spacing of autogenerated points) of distance along routes for each stop number (1 to 50) (Figure 2A). BBS stops beyond stop 45 were often beyond the end of 40-km route lines (e.g., on 28% of routes for stop 50), so we eliminated stops 46–50 from further analysis. We also excluded all stops for which the distance to the nearest autogenerated point was > 200 m ($n = 457$; 1.8% of all stops), which typically indicated a minor route deviation. A subset of digitized stop locations ($n = 837$) was collected using GPS units in a known year in Wisconsin, and these were used as a validation test of our method (described below).

Quantifying Habitat Uncertainty at BBS Stops

To quantify habitat uncertainty at each BBS stop using these stop-location uncertainty distributions (Figure 2A), we first defined our land cover covariates of interest. We used NLCD layers (Dewitz 2021) for the year closest to each BBS survey year and merged some NLCD categories to simplify cover classes for our analyses (Table 2). NLCD has been shown to be relatively accurate for these land cover classes (Wickham et al. 2021). For modeling, we chose to focus on 3 broad land cover categories—forest, grass/hay, and development—to assess their effects on bird occurrences. A fourth land cover of interest, crop lands, was correlated with the others and so was excluded. We defined our radius of interest as 400 m, which minimizes overlap between adjacent stops, corresponds to the BBS protocol maximum aural detection distance, and is consistent with other studies examining local-scale habitat effects on birds (Cunningham and Johnson 2019, De Souza Leite et al. 2022, Van Der Burg et al. 2023). We then calculated proportion cover (proportion of 30-m NLCD cells of that cover class) within a 400-m radius for each of our merged land cover classes. We did this for each autogenerated point

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(Figure 2B) on each route for each NLCD year (2001, 2004, 2006, 2008, 2011, 2013, 2016, 2019), using the focal statistics tool in ArcGIS Pro 3.1.2.

For the purposes of our analyses, all annual point count locations were assumed to be unknown as a test of our method and we thus withheld the known land cover information from GPS-digitized stops to use in the model validation stage. For each BBS stop and year in our model (described below), we then extracted land cover values from autogenerated points along the appropriate route (using the corresponding NLCD year) in proportion to the location probability distributions generated above (i.e., the probability that a given stop was located at each autogenerated point; Figure 2B). Extracting land cover from autogenerated points in proportion to the stop-location histograms thus resulted in a land cover probability distribution (Figure 2C) for each land cover covariate at each stop in each route in each year. We then calculated the standard deviation (SD) of each of these land cover distributions, and land cover values with very low SDs (≤ 0.02) were treated as fixed covariates in models. Those with higher SDs were treated as estimated parameters.

To estimate these land cover parameters in our Bayesian models (described below), we used these land cover probability distributions as custom informative prior distributions. To do this, we first binned each land cover uncertainty distribution into 101 bins from 0 to 1 and calculated the proportion of total values in each bin (i.e., the probability) (Figure 2D) for each stop on each route in each year. We then fit smooth curves using the *smooth.spline* (spar = 0.7) R function to the non-zero values in each of these distributions, flanked by small but non-zero values such that the resulting curve is always positive on the interval from 0 to 1. These curves were then used to create custom prior distributions in the *nimble* 1.2.0 R package (de Valpine et al. 2017, de Valpine et al. 2023). Model posterior land cover covariate estimates (Figure 2E) were based on these priors.

Statistical Modeling

We developed a Bayesian hierarchical logistic regression model in *nimble*. We used stop-level BBS data (Ziolkowski et al. 2022), retaining only those routes that we selected earlier for autogenerated points from a three-state region (n = 210; Figure 1). Land cover covariates with non-trivial uncertainty were treated as parameters to be estimated in the model, with informative priors specified that were generated as described above. We included the 37 species (Table 1) detected in ≥ 5% of modeled stop events and used presence/absence as our response. For computational efficiency, we selected 5 years (2004, 2008, 2011, 2013, 2016) that were NLCD years and that also covered GPS-digitized locations for Wisconsin routes (Supplementary Material Table 1) so that we could use these known locations to validate our method.

We defined our logistic regression model as follows:

$$\text{logit}\left(P_{\text{species,route,stop,year}}\right) = \alpha_{\text{species,BCR,route}} + \alpha 2_{\text{obs,species}} + \left(\beta_{\text{cov,species}} * X_{\text{cov,route,stop,year}}\right)$$

$$Y_{\text{species,route,stop\_year}} \sim \text{Bernoulli}\left(P_{\text{species,route,stop,year}}\right)$$

where P is probability of a species being present and detected, Y is whether a species was detected, α is the route-level intercept, $\alpha 2$ is the observer-level (obs) intercept, and each β is a slope coefficient for each covariate (cov) X. Intercepts (α) for each species on each route were drawn from model-estimated intercept priors for each species in each BCR, which in turn were drawn from overall priors for each bird species, drawn from a single global intercept hyperprior. This global hyperprior was given a broad prior as follows:

$$\mu \sim \text{TruncatedNormal}\left(0, \text{SD} = 10, -10, 10\right)$$

$$\mu_{\text{species}} \sim \text{Normal}\left(\mu, \sigma\right)$$

$$\mu_{\text{species,BCR}} \sim \text{Normal}\left(\mu_{\text{species}}, \sigma_{\text{species}}\right)$$

$$\alpha_{\text{species, BCR,route}} \sim \text{Normal}\left(\mu_{\text{species,BCR}}, \sigma_{\text{species,BCR}}\right)$$

The SD prior had a similar hierarchical structure, with a global hyperprior of $\sigma \sim$ Uniform (0, SD = 10). Our BCR intercept helps to account for many of the potentially influential covariates that vary at large geographic scales (i.e., climate, dominant forest type, and east–west or north–south gradients in species prevalence). Observer effects have also been shown to be important in BBS analyses (Sauer et al. 2017), and our observer (obs) intercept for each species ($\alpha 2$) was drawn from a prior mean effect for that observer across all species, drawn from an overall observer hyper-prior. This observer hyper-prior was given a broad prior as follows:

$$\mu 2 \sim \text{TruncatedNormal}\left(0, \text{SD} = 10, -10, 10\right)$$

$$\mu 2_{\text{obs}} \sim \text{Normal}\left(\mu 2, \sigma 2\right)$$

$$\alpha 2_{\text{obs,species}} \sim \text{Normal}\left(\mu 2_{\text{obs}}, \sigma 2_{\text{obs}}\right)$$

The standard deviation (SD) prior had a similar hierarchical structure, with a global hyperprior of $\sigma 2 \sim$ Uniform (0, SD = 10). Routes and stops not sampled in a given year were excluded from the model using route-specific indexing. Values marked NA in *nimble* are treated as missing and do not affect parameter estimates, so detection values for species on stops outside of their breeding range (described above) were marked NA. Beta slope coefficients for each species and covariate were also given broad priors as follows:

$$\beta_{\text{cov,species}} \sim \text{TruncatedNormal}\left(0, \text{SD} = 15, -25, \quad 25\right)$$

Our models included land cover covariates that reflected habitat at each stop, covariates for latitude and longitude (as proxies for environmental gradients across the region), and covariates meant to account for potential variation in detectability. Our land cover covariates included proportion cover of forest, grass/hay, and development (Table 2). These covariates ranged from 0 to 1 and were treated as estimated (rather than known) quantities in the model, except for those with very low uncertainty (described above). We also included a quadratic term for each, squared on the fly as each quantity was estimated during the model fitting process. We specified custom prior distributions for these land cover covariates, based on land cover probability distributions described above, as follows:

$$X_{\text{cov,route,stop,year}} \sim \text{customDistribution}_{\text{cov,route,stop,year}}$$

Our covariates meant to account for imperfect detection included stop number (a proxy for time of day because routes

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TABLE 2. National Land Cover Database (NLCD) cover classes merged to create our land cover covariates.

Covariate	NLCD land cover classes[a]
Forest	Deciduous forest; evergreen forest; mixed forest; woody wetlands
Grass/hay	Grassland/herbaceous; pasture/hay; sedge/herbaceous
Development	Developed, open space; developed, low intensity; developed, medium intensity; developed, high intensity
[Not included]	Open Water; Barren Land; Cultivated Crops; Shrub/Scrub; Emergent Herbaceous Wetlands

[a]From Dewitz (2021).

are run from stop 1 to 50), day of year (DOY; and DOY^2), and a binary covariate indicating if it was an observer's first year on the route. Each of the non-binary detection covariates was scaled to a SD of one and centered on zero prior to modeling. We examined the variance inflation factor (Naimi et al. 2014) of all covariates (using the modes of distribution priors for estimated land cover covariates) and all values were < 2.02.

Testing Model Performance

In addition to accounting for location uncertainty, we wanted to test whether our method resulted in posterior land cover estimates that are closer to true land cover than land cover priors. To test this, we first extracted the land cover covariate values for each GPS-digitized stop (if any; n = 837 stops in Wisconsin) for the year in which it was digitized. We then compared posterior land cover estimates to these known land cover values. Additionally, as a test of model performance for stops that occur far from their most likely locations, we fitted a second model in which we modified land cover priors for each of the known land cover stops to be intentionally misleading and compared posterior estimates to known values (details in Supplementary Material Figure 1). Finally, to compare the performance of our informative prior method to a naive assumption of fixed 800 m spacing between adjacent stops and consistent stop locations over years, we fit an additional model with fixed habitat covariates based on assumed 800-m spacing.

Fitting and Evaluating the Model

Our model was compiled to C++ for Markov chain Monte Carlo (MCMC) sampling in *nimble* (de Valpine et al. 2023). We sampled using three MCMC chains for 40,000 iterations each, with the first 6,000 discarded as burn-in. Remaining iterations were thinned by 68 to produce 500 samples per chain (1,500 samples in total). We checked potential scale reduction factors (psrf) and effective sample sizes using the *MCMCvis* 0.15.5 R package (Youngflesh 2018) to confirm model convergence. To evaluate model fit, we calculated TjurR^2 (Tjur 2009) for each bird species.

To quantify bird niches with respect to land cover covariates, we extracted mean β covariates and used these to predict each species' probability of being present and detected (p) across the range of each land cover covariate that were well represented in the training data (0 to 1.0 for forest, 0 to 0.6 for grass/hay and development). For each of these predictions, non-focal covariates (i.e., all the others) were held to their overall mean across the dataset. We then quantified optimum land cover covariate ranges for each species as the range of a covariate for which p was ≥ 75% of its maximum value.

To evaluate the effectiveness of our informative prior method in estimating land cover covariates, we compared posterior mean cover values to known values for each GPS-digitized stop location in the appropriate year (except in cases where the covariate values were fixed). We also tested whether these correlations differed based on stop's known land cover and based on the number of modeled species detected at each site. We assessed these relationships and correlations using linear models. We did the same for our additional model in which a subset of priors was modified to be intentionally misleading (Methods section in Supplementary Material).

To compare our informative prior model to our model assuming fixed 800-m spacing between adjacent stops we compared model fit between the 2 models (TjurR^2) for each bird species and compared the SDs of posterior distributions of beta coefficients indicating the effects of land cover on bird distributions.

RESULTS

Quantifying Location Uncertainty

We quantified location uncertainty in BBS stops using digitized estimates of stop locations from 568 routes in 13 states. The median distance along route lines for each stop number was consistent with standard 800-m stop spacing (Figure 2A), with median locations 0 and 280 m beyond predicted locations for stops 1 and 45, respectively. However, uncertainty increased considerably with stop number (and route distance), with the SD of distance along routes increasing from 190 (stop 1) to 1,040 m (stop 45) (Figure 3). Data underlying histograms in Figure 2A are included in the data release associated with this study (Burner et al. 2024).

Quantifying Habitat Uncertainty

Habitat uncertainty was quantified by extracting land cover values for each stop and year in proportion to the corresponding location probability distributions. Across a 17-state region in the central United States (Figure 1), the median SD of uncertainty distributions increased with stop number for more common land cover types (forest and grass/hay; Figure 3), but remained relatively low and constant for developed land, which is less common on BBS routes in the region. The proportion of BBS stops with very low land cover uncertainty (SD < 0.02) was highest for the rarest land cover (development) and decreased somewhat with stop number for all land covers (Figure 3). In our modeled three-state region, we treated land cover covariates as fixed (SD < 0.02) for forest at 16% of stop-year combinations, 31% for grass/hay, and 52% for developed land (refer to Supplementary Material Table 2 for region-wide values). For the remaining land cover covariates, we parameterized custom distributions (Figure 2D) to best fit the raw distributions (Figure 2C). Our posterior mean land cover estimates (Figure 2E),

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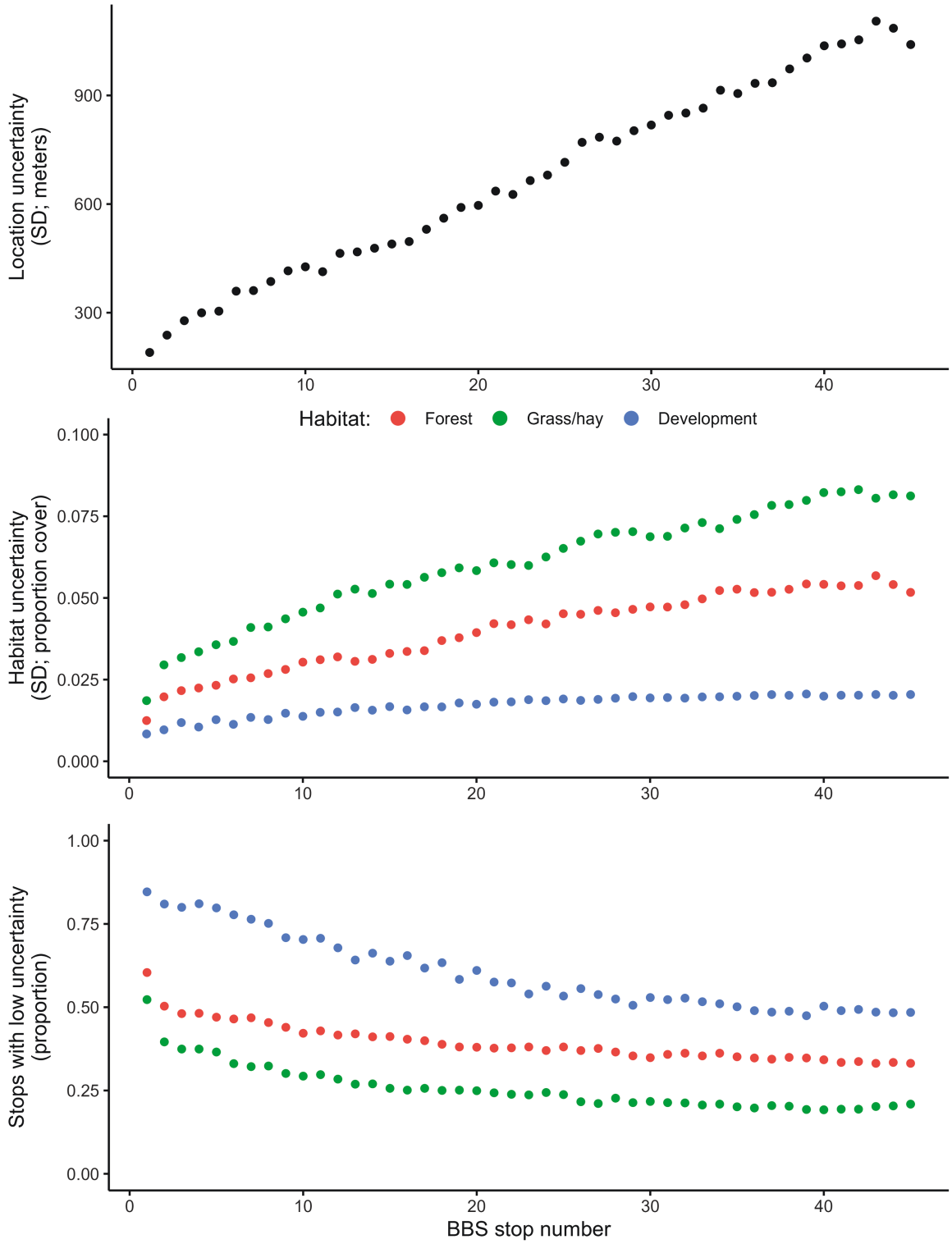


FIGURE 3. Stop location uncertainty and corresponding land cover uncertainty along Breeding Bird Survey (BBS) routes in the central United States. Sequential BBS stops occur at varying distances along route lines. Black points (top facet) show the standard deviation (SD) of stop locations in meters along BBS routes for each stop number (*x* axis). Land cover uncertainty results from this underlying location uncertainty. The center facet shows the median SD of proportion cover for each land cover (color) and stop number (*x* axis). The bottom facet shows the proportion of stops with very low uncertainty (SD < 0.02) for each land cover and stop number. Stop location uncertainty is based on digitized estimates of stop locations from 568 BBS routes the central United States. Land cover uncertainty is calculated by applying location uncertainty to 1,119 BBS routes using the 2019 National Land Cover Database (NLCD) (Dewitz 2021), with land cover classes merged as in Table 2. Location uncertainty and corresponding land cover uncertainty increase along the length of BBS routes, and more common land cover classes have more uncertainty.

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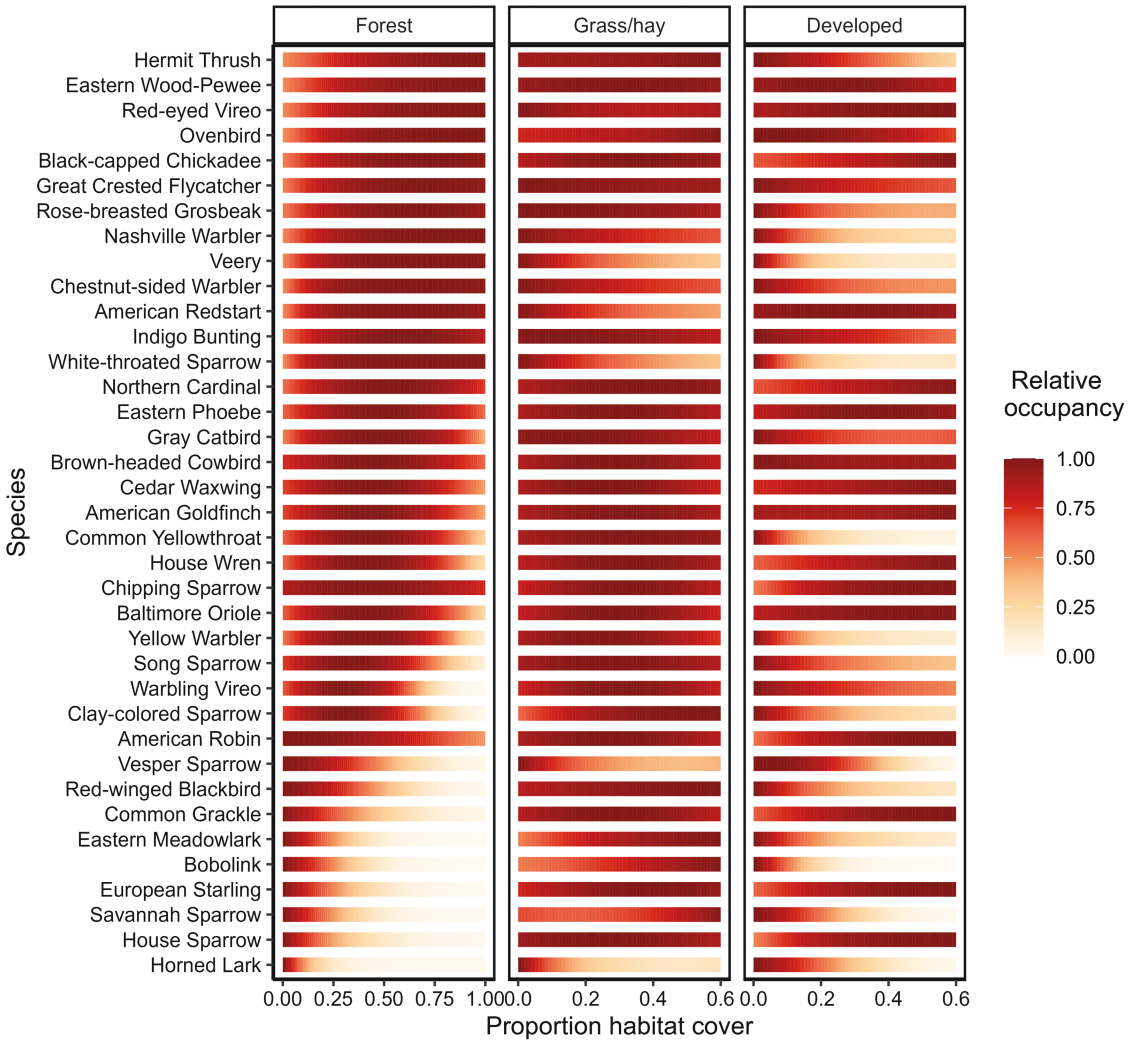


FIGURE 4. Mean predicted relative occupancy of bird species across gradients of land cover. Species differ in overall prevalence, so values for each species are scaled to the maximum occupancy for that species. Proportion land cover is based on proportion of grid cells dominated by each cover type within a 400-m radius of the sampling point, based on the National Land Cover Database (NLCD) (Dewitz 2021). Refer to Table 2 for land cover classes. Bird names follow Chesser et al. (2023); refer to Table 1 for species scientific names and Supplementary Material Figures 3 and 4 for covariate response coefficients.

combined with values from fixed land cover covariates, indicated that our modeled stops represent the full range of possible forest cover. However, almost all modeled stops have grass/hay cover below 50% and developed land cover below 25% (Supplementary Material Figure 2), meaning that higher values of these less common land cover types are rare in model training data.

Quantifying Bird Responses

Most bird species responded to forest, grass/hay, and developed land cover (i.e., had land cover effect coefficients with 95% credible intervals that did not overlap zero; Supplementary Material Figure 3). More species responded strongly and positively to forest cover than to grass/hay or development. Non-land cover covariates were also important for some species (Supplementary Material Figure 4). TjurR^2 values had a mean of 0.17 across all bird species (range: 0.07–0.49) (Table 1). For each land cover covariate, some species had wide optimum ranges along the gradient (range of values at which mean predicted occupancy was ≥ 75% of the maximum value) whereas others inhabited only a narrow part of the gradient (Figure 4 and Table 1).

Evaluating Habitat Covariate Estimates

For land cover covariates for which the true proportion cover was known from GPS-digitized stop locations for a given year, known forest covered varied evenly from 0 to almost 1 (Figure 5). Grass/hay and developed land cover were mostly below 0.2, with few stops above 0.5, which was representative of the patterns observed across the entire modeled region (Supplementary Material Figure S2). Mean posterior cover estimates were highly correlated to known proportion cover for forest (R^2 = 0.88), grass/hay (0.52), and development (0.61). Linear relationships indicate that estimated proportion cover was on average a bit lower than the known value (slope = 0.89, 0.64, and 0.78 for forest, grass/hay, and development, respectively; Figure 5). Accuracy of posterior land cover estimates was not correlated with number of modeled bird species detected at a stop (R^2 < 0.02).

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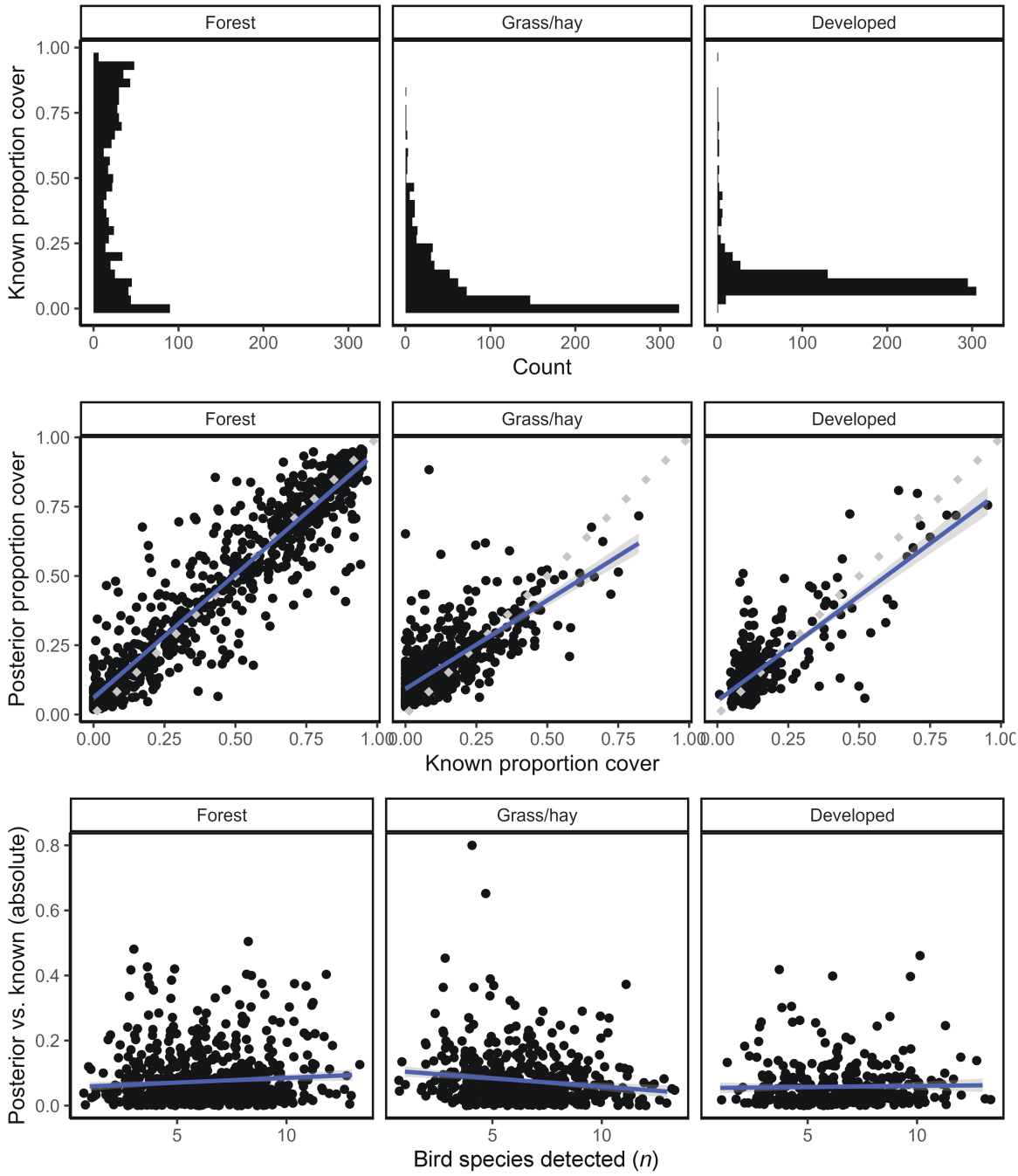


FIGURE 5. Comparison of posterior land cover estimates to known cover from GPS-digitized Breeding Bird Survey (BBS) stop locations in Wisconsin. Top panel shows histograms of known land cover distributions across all GPS-digitized stops. Middle panel shows mean posterior estimates (*y* axis) compared to known values (*x* axis). Dotted diagonal line shows 1:1 relationship. Bottom panel shows the absolute difference between mean posterior estimates and known values (*y* axis) as a function of number of modeled bird species detected at each stop (*x* axis; values jittered slightly). Each point represents one BBS stop (n = 788, 560, and 383, respectively). Solid lines in scatter plots show linear models with 95% confidence interval on the slope. Land cover covariates (facet columns; proportion cover in a 400 m radius) are based on the National Land Cover Database (NLCD) (Dewitz 2021) as described in Table 2. Posterior land cover estimates are similar to known land cover irrespective of the number of bird species detected during a count.

When we deliberately specified strongly misleading priors as a test of our method, posterior land cover estimates of forest cover were closer to known cover values compared to the priors (Supplementary Material Figure 5), with a mean score of 0.62 (where 0 is equal to the known value and 1 is equal to the prior mean). Corresponding values for grass/hay (1.06) and development (0.91) indicate that posterior estimates remained on average near the prior values for these land covers. More modeled bird species detected at a stop, however, did result in posterior estimates marginally closer to known cover values for each land cover (regression slopes negative with P-values < 0.001; Supplementary Material Figure 5).

When we compare our model with informative priors to a model that makes a naive assumption of consistent 800-m stop spacing, model explanatory power is higher for all species in the informative prior model (Figure 6). Posterior distributions

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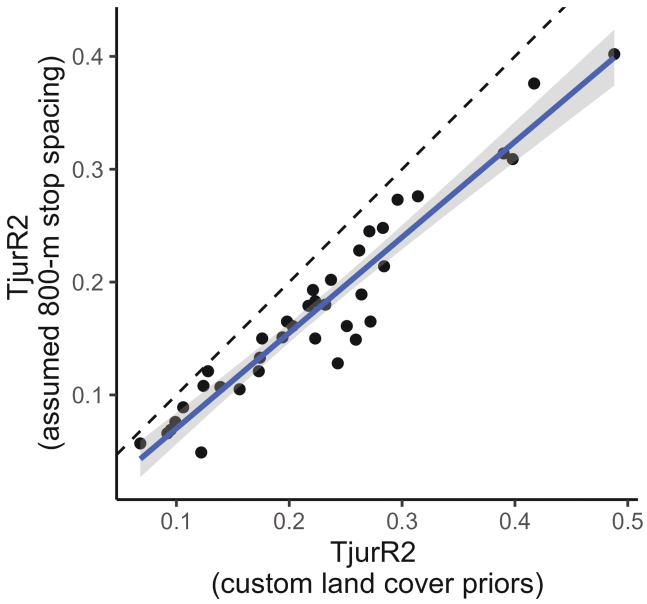


FIGURE 6. Comparison of model fit for bird species when using custom land cover priors versus a naive assumption of consistent 800 m stop spacing. TjurR^2 shows model explanatory power when location uncertainty is incorporated via informative priors representing the corresponding land cover uncertainty (*x* axis) and under assumed 800-m spacing (*y* axis). Each point represents one modeled bird species. Dotted line shows a 1:1 relationship between values, and the solid line shows a linear model with 95% confidence interval on the slope. Model explanatory power is higher for all species when land cover uncertainty is included.

of beta regression coefficients are narrower (i.e., have lower SD) under an assumed 800-m spacing model (Supplementary Material Figure 6), implying that this assumption introduces artificial precision in covariate estimates.

DISCUSSION

A lack of precise location information for annual point counts has often precluded use of the extensive BBS dataset for fine-scale studies of habitat associations. We estimated annual point count location uncertainty for BBS routes across the central United States and quantified the resultant land cover uncertainty (Figures 2 and 3). We then demonstrated the effectiveness of incorporating this land cover information into models using Bayesian priors. Our use of informative priors, rather than treating land cover covariates as fixed quantities, accounts for the uncertainty in annual point count locations and is thus a conceptual advance relative to simpler approaches that do not explicitly account for this uncertainty (Van Der Burg et al. 2023). Our method resulted in posterior land cover estimates that were close to known true land cover, allowing for estimation of species-habitat relationships in a way that explicitly incorporates habitat uncertainty. It also resulted in higher explanatory power for all species when compared to a model assuming consistent 800-m spacing between stops.

Spatial and Habitat Uncertainty Increases Along Routes

As expected, stop-location uncertainty increases along BBS routes and the mean expected location of subsequent stops shifts farther beyond the location that would be expected under uniform 800-m stop spacing (Figures 2 and 3). Our distributions of location uncertainty for each BBS stop number, available from Burner et al. (2024), could be used to extract habitat distributions for each stop using different habitat layers and spatial scales. BBS routes have been shown to represent the habitat in the larger landscape fairly well (Veech et al. 2017). We found that uncertainty in land cover (400-m radius) associated with each BBS stop increases in proportion to location uncertainty along BBS routes for common landcover types (forest and grasslands in the central United States; Figure 3) but is less variable along routes for development, which was less prevalent (Zhang et al. 2021). The proportion of stops where there is no meaningful uncertainty in one or more habitats, despite location uncertainty, is relatively high (26% to 60%, depending on habitat category; Figure 3 and Supplementary Material Table 2) across the central United States. Most of these habitat values with low uncertainty are very near zero or one, indicating that a substantial number of route segments are lacking in (or dominated by) certain habitat classes.

Posterior Habitat Estimates

For a subset of BBS stop events with GPS-digitized stop locations and thus with known land cover, our mean posterior habitat estimates were highly correlated with known cover values (Figure 5). Our known-habitat sites spanned a wide range of forest cover, the habitat for which performance was strongest. Stops with high proportion cover of grass/hay or development, although rare in our known-habitat dataset, also resulted in fairly accurate posterior estimates. Our results thus indicate that this informative prior method is effective for estimating land cover and bird–habitat relationships. The method is only as precise, however, as the responses of the bird species, and habitat estimates will thus be most accurate for habitats that are most important for the modeled species. Our 37 bird species had optimum habitat niches that spanned the full range of our habitat covariates (Figure 4), likely increasing the precision of estimates. When we experimentally modified priors for known-habitat stops to be intentionally misleading, our method nonetheless resulted in posterior habitat estimates that were much closer to known values for forest cover (Supplementary Material Figure 5), but not for grass/hay and development. This is likely due to the relatively limited range of these covariates across the modeled region (few stops with > 25% cover; Supplementary Material Figure 2), which limits the model's ability to correctly estimate the effects of high cover values on bird communities and hence to improve posterior estimates for low proportion cover stops that we gave misleadingly high prior distributions. Nonetheless, the strong performance in estimating forest cover despite strongly misleading priors indicates that, for cover types well represented in a region's BBS routes, land cover estimates are expected to be relatively accurate even in the case of stops that are placed far from their most likely locations, or in small patches of unique habitat. When compared to a model that assumed fixed 800 m spacing among stops, posterior regression coefficients for the effects of land cover covariates in our model had higher (and probably more realistic) uncertainty. Model explanatory power was higher for all species when land cover uncertainty was included (Figure 6).

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Use of Method for BBS Stop-Level Analyses

Our methods (and R code) provide a way to incorporate location uncertainty into stop-level BBS analyses, allowing future users to define and calculate their own habitat measures and extract habitat distributions for each stop and year. These habitat distributions could then be specified as prior distributions in models like the ones presented in this article. Depending on the project goals and the scale of the data being analyzed, future users could add model constraints (e.g., restricting the mean of all stops in a route to equal the route-level mean for a given habitat) that are simple to implement in *nimble* and may further increase accuracy but are computationally expensive. For large-scale (i.e., multi-year, continent-wide) studies, the computational intensity of our informative prior methods may be a challenge. In this case, users could perhaps first fit a series of regional models to get more precise habitat estimates for each stop and then use the means of those posterior habitat distributions as fixed habitat covariates in larger-scale models for computational efficiency. Future research could expand this method to the full extent of the BBS dataset and address questions on the effects of habitat loss and fragmentation at various scales to breeding birds (Trzcinski et al. 1999), and in particular the effects of gradients of agricultural intensity on breeding grassland birds (Filloy and Bellocq 2007).

BBS analyses with different response variables that currently aggregate bird observations to the route level could also benefit from switching to the stop level and accounting for stop-location uncertainty. Models that tie BBS relative abundance and change in relative abundance over time to habitat covariates are a prime example (Donovan and Flather 2002, Fearer et al. 2007, Betts et al. 2022). Because bird detection is fundamentally a stop-level process, moving from route-level to stop-level analyses may also allow analysts to account for detection probabilities and therefore estimate true abundance (Edwards et al. 2023).

Implications for the BBS Program

The BBS dataset is unparalleled globally in its spatial and temporal extent and structured nature and continues to fulfill its core purpose of providing estimates of population change for hundreds of bird species (Rosenberg et al. 2019), with important implications both for public awareness and for conservation and policy (Sauer et al. 2017). However, its lack of spatial coordinates for point counts in each sampling year limits its utility for many fine-scale ecological questions for which it could otherwise be well suited. The BBS program faces substantial challenges as it administers a program with many volunteer coordinators and observers and strives to maintain the methodological continuity necessary for long-term trend analyses. Nevertheless, contemporary research questions and methods require precise location metadata, as recognized in BBS strategic planning documents (U.S. Geological Survey and Canadian Wildlife Service 2020, U.S. Geological Survey et al. 2021). Route-level aggregations, although sufficient for trend analyses, are limited in their ability to reveal associations between birds and habitat at the scale of bird home ranges and human management actions (Ciuzio et al. 2013, Niemuth et al. 2017, Niemuth et al. 2021).

We quantified stop-location uncertainty, and the resulting habitat uncertainty, for BBS stops across the central United States and provided a methodology and code to do so for the full extent of the BBS. This fulfills an often-stated need from the BBS literature (Niemuth et al. 2017, Sauer et al. 2017, Clement et al. 2019). We demonstrated the effectiveness of accounting for this underlying uncertainty in Bayesian modeling using informative prior distributions, uncovering relationships between fine-scale habitat cover and bird distributions. We also demonstrated the utility of fully documented stop locations, even from a subset of routes and years, in quantifying uncertainty and informing stop-level BBS analyses. Our method, however, does not alleviate the need for collection of location metadata. Rather, our models could become even more powerful if paired with precise spatial information from future BBS data, which would provide more fixed habitat covariates to inform parameter estimates and likely increase precision of estimated habitat parameters. In this way, expansion of future BBS protocols to record precise location information annually (U.S. Geological Survey and Canadian Wildlife Service 2020, U.S. Geological Survey et al. 2021) could inform and benefit analyses of past, as well as future, BBS data.

Limitations

We quantified location uncertainty in BBS stops for the central United States as a whole, but location uncertainty likely differs across the continent. Uncertainty may be lower on routes with a regular gridded road system, lower human population density, and less topography (and the reverse). Researchers in other regions with access to digitized estimates of stop locations could quantify location uncertainty for alternate geographic areas. We treated all digitized stop-location estimates that were available as representing an unbiased snapshot of BBS annual point count locations through time, but instances of route modifications due to external factors such as road closures could be underrepresented, biasing uncertainty estimates downwards. We eliminated some routes that were not conducive to our study due to, for example, nonlinear route paths, which could increase the chances that observers would vary the order of route segments. These routes were geographically scattered and were not expected to introduce bias. The strong performance of our models even in cases of misleading habitat priors indicates that our method is robust to many of these challenges. Of course, location uncertainty is only one form of variation inherent in these analyses, albeit a major one. Land cover layers are necessarily coarse and can have their own errors and biases (Wickham et al. 2021), and birds recorded at a BBS stop can be anywhere within a 400 m radius and thus occupy quite different habitat patches.

Implications Beyond the BBS

Location uncertainty is a pervasive problem in species records, especially in the case of museum specimens and other historical records (Rowe 2005). This could also apply to eBird (Munson et al. 2010), the largest collection of bird occurrence records in the world, because historical eBird lists can span large areas that contains multiple habitats and were often snapped to hotspots that reduced location precision (Steen et al. 2023). Even when locations are precisely defined, some aspects of local conditions (e.g., elevation, habitat, water availability, microclimate, human disturbance) may have high uncertainty, such as when including parts of the world for which detailed habitat layers are not available. In all such cases, using informative

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priors allows researchers to incorporate the information that is available without implying unrealistic certainty by artificially fixing uncertain covariate values. We have shown that for large datasets, prior probability distributions for covariates (if relatively unbiased) can contribute substantial information. For each application, one could quantify uncertainty in the value(s) of interest (whether through some empirical method or by making informed assumptions) and, if possible, include some fixed covariate cases for which values are known to further inform model estimates.

Conclusions

Location uncertainty reduces the utility of extensive historical and contemporary species occurrence datasets for fine-scale ecological analyses. We present a method of accounting for this uncertainty, demonstrated in stop-level analyses of the BBS that could increase the breadth of research questions for which this dataset is suited. More broadly, our method of quantifying uncertainty and incorporating it via informative Bayesian priors could be applicable to other cases of uncertainty in location, habitat, and other covariate information prevalent in ecological data.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

This research followed the U.S. Geological Survey Fundamental Science Practices.

Conflict of interest

The authors have no conflict of interest to declare.

Author contributions

R.C.B., A.K., and N.N. conceived the ideas; R.C.B., A.K., D.T., and J.A.H designed the methodology; N.M.A. and E.D.S. digitized location information for Wisconsin BBS routes; A.K. extracted spatial data and created spatial figures; D.J.Z. guided interpretation of BBS data and location uncertainty; R.C.B. analyzed the data, visualized and validated the results, led the writing of the manuscript, and obtained the funding; All authors contributed critically to the drafts and gave final approval for publication.

Data availability

Analyses reported in this article can be reproduced using the data available from Burner et al. (2024) https://doi.org/10.5066/P1CLSQED and code available from Burner (2024) https://doi.org/10.5066/P1HY6LDF.

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