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Point count offsets for estimating population sizes of north American landbirds

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Bird monitoring in North America over several decades has generated many open databases, housing millions of structured and semi-structured bird observations. These provide the opportunity to estimate bird densities and population sizes, once variation in factors such as underlying field methods, timing, land cover, proximity to roads, and uneven spatial coverage are accounted for. To facilitate integration across databases, we introduce NA-POPS: Point Count Offsets for Population Sizes of North American Landbirds. NA-POPS is a large-scale, multi-agency project providing an open-source database of detectability functions for all North American landbirds. These detectability functions allow the integration of data from across disparate survey methods using the QPAD approach, which considers the probability of detection (q) and availability (p) of birds in relation to area (a) and density (d). To date, NA-POPS has compiled over 7.1 million data points spanning 292 projects from across North America, and produced detectability functions for 338 landbird species. Here, we describe the methods used to curate these data and generate these detectability functions, as well as the open-access nature of the resulting database.

Keywords: availability, data integration, detectability, distance sampling, perceptibility, QPAD, removal sampling, roadside effects, sound attenuation.

The broad-scale monitoring of birds in North America over the past several decades has resulted in the availability of millions of bird observations in open databases that span most of the continent. Individual programmes such as the North American Breeding Bird Survey (BBS; Hudson *et al*. 2017, Sauer *et al*. 2017), the Integrated Monitoring in Bird Conservation Regions (IMBCR; Pavlacky *et al*. 2017), the Boreal Avian Modelling Project (BAM; Cumming *et al*. 2010) and eBird (Sullivan *et al*. 2014) provide a great deal of information on relative abundance over time and space. Partners in Flight (PIF) has previously estimated population sizes of landbirds using BBS data and a series of sophisticated expert-informed equations

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to extrapolate survey-level counts to total abundance within defined geographical regions (Rosenberg & Blancher 2005, Will *et al.* 2020). These population sizes have been used to inform reports such as the 2019 State of Canada's Birds report (North American Bird Conservation Initiative Canada 2019) and to show the loss of nearly 3 billion North American birds since the 1970s (Rosenberg *et al.* 2019).

An estimate of detectability is needed to translate survey-level counts into estimates of total abundance (Rosenberg & Blancher 2005, Stanton *et al.* 2019). For a bird, the overall probability of detection (i.e. its detectability) can be broken down into two independent probabilities: availability and perceptibility (Marsh & Sinclair 1989, Johnson 2008). Availability is defined as the probability of a bird giving a cue (auditory or visual) during a survey. This probability is a function of a bird's cue rate, defined as the expected number of cues per unit time, and can be calculated using surveys that employ removal sampling (Barker & Sauer 1995, Farnsworth *et al.* 2002, Alldredge *et al.* 2007). Perceptibility is defined as the probability of an observer detecting a cue from a bird, provided the bird is actually giving a cue. This probability is a function of the bird's effective detection radius (EDR), defined as the distance at which the same number of birds go detected and undetected, and can be calculated using data from surveys that employ distance sampling (Buckland 2001, Buckland *et al.* 2015).

Detectability in landbirds is generally nonconstant. Factors such as time of day, time of year, habitat type and presence of roads have been shown to affect both the availability and the perceptibility of birds (Wilson & Bart 1985, Sólymos *et al.* 2013, Johnston *et al.* 2014, Cooke *et al.* 2020). Additionally, the length of time an observer surveys for a bird, and the maximum survey distance the observer is surveying, can account for some variation in how many birds are detected and recorded for any given survey (Alldredge *et al.* 2007, Sólymos *et al.* 2013, Buckland *et al.* 2015).

The QPAD method developed by BAM is a flexible approach to accounting for heterogeneity in survey conditions and survey methodology (Sólymos *et al.* 2013). It can calculate availability and perceptibility independently, while allowing for multiple surveying methods to be accounted for at once. In other words, any dataset that employs a removal sampling approach with two or more time bins can be jointly used to calculate availability, and any dataset that employs a distance sampling approach with two or more distance bins can be jointly used to calculate perceptibility (Sólymos *et al.* 2013). Additionally, by recognizing that availability is a function of cue rate, and that perceptibility is a function of EDR, the QPAD method allows for variation in cue rate and EDR as a function of covariates that affect detectability (time of day, time of year, habitat type, roadsides, etc.), and for estimates of perceptibility as a function of survey radius or other covariates (Sólymos *et al.* 2013). Finally, the QPAD method allows for estimates of true density to be derived from any survey, by allowing the detectability function to act as a statistical offset to account for differences among survey types. An offset term is used in linear models to adjust the expected value with a known quantity. In our case the detectability function quantity is not known but is estimated through QPAD. However, as a result, the offsets allow all survey-observed counts to be translated into an estimate of true density. A more in-depth review of how each component of QPAD is derived can be found in Supporting Information Text S1, or in the Appendix of the original manuscript describing the method (Sólymos *et al.* 2013).

The current PIF population size estimates use coarse binned estimates of detection distance for each landbird, and calculate uncertainty around the detection distance using a uniform distribution (Stanton *et al.* 2019). However, the methods by which these binned estimates are determined are not consistent across species, and often rely only on expert opinion. There is therefore a need for a systematic approach to estimating these detection distances for all landbirds, while accounting for variation in environmental conditions and survey types (Stanton *et al.* 2019). BAM has already made huge strides in accomplishing this, by first generating estimates of cue rate and EDR for 75 North American boreal birds (Sólymos *et al.* 2013), and then further extending that to cue rates of 151 boreal birds (Sólymos *et al.* 2018a), each time using data harmonization techniques (Barker *et al.* 2015) and the QPAD methodology (Sólymos *et al.* 2013) to allow multiple survey types and survey conditions to be accounted for. Additionally, QPAD offsets produced by BAM have been used extensively to adjust survey point count data to account for detectability (Hobson & Kardynal 2019, Zlonis *et al.* 2019, Knaggs *et al.* 2020, Leston *et al.* 2020) and to estimate population sizes and distribution of boreal birds (Crosby *et al.* 2019, Sólymos *et al.* 2020b). Thus, the next frontier is to extend these methods developed by BAM and use the millions of rigorously collected bird observations and covariates (i.e. landcover and road networks) that are now available on a continental scale to derive detectability estimates for as many North American landbirds as possible.

We have therefore created the collaborative project NA-POPS: Point Count Offsets for Population Sizes of North American Landbirds, to apply the QPAD approach developed by BAM to a compilation of point counts across North America. Our overarching goal is to generate an open-source database of detectability functions, thus creating a systematic and standardized approach to generating detectability estimates across North American landbird species. NA-POPS includes a GitHub organization (Blischak *et al.* 2016, Crystal-Ornelas *et al.* 2022) to store the databases securely, a series of fitted models to estimate cue rates and EDRs in common observation conditions, and an R-package for users to access the estimates. Here, we detail the methods surrounding the following key components of achieving this large-scale project: (1) data acquisition and standardization, (2) derivation of covariates and modelling of cue rate and EDR, and (3) the software infrastructure used to curate the data, generate model runs and host results. We summarize the results of the data collection and modelling efforts, and highlight the species-specific results of American Robin *Turdus migratorius*, a suitable species for a case study as it is a wide-ranging North American landbird well covered in the NA-POPS database. Finally, we discuss some applications for these detectability offsets, and invite further data contributions to enable additional refinement of the offsets produced by NA-POPS.

METHODS

Data acquisition and standardization

We solicited point count datasets from across Canada and the USA that used removal sampling or distance sampling, or both. Each dataset was subject to data cleaning and standardization before being added to the NA-POPS database, following techniques initially developed for North America's boreal region by BAM (Cumming *et al.* 2010, Barker *et al.* 2015). For the purposes of this analysis, we considered one 'sampling event' to be a single visit to a specific location to conduct a point count survey. Some surveys were designed to include a transect or grid of point counts; in these cases, each of those point counts were considered unique sampling events. Details of this standardization process can be found in Supporting Information Text S2.

Modelling and covariates

Removal models

We fitted nine removal models per species (Farnsworth *et al.* 2002, Alldredge *et al.* 2007) using the 'detect' R package (Sólymos *et al.* 2020a) and different combinations of time-since-sunrise (TSSR), Ordinal day (OD) and their quadratic terms to account for possible unimodal relationships (Supporting Information Text S3). The null model (i.e. intercept only) was a part of these candidate models. For all models, we analysed only the subset of data that contained two or more subintervals of time, and for species for which we had $\geq$ 75 sampling events that contained at least one detection (Matsuoka *et al.* 2012, Sólymos *et al.* 2018a). We ranked candidate models using Akaike's information criterion (AIC) to select the best supported model (i.e. lowest AIC score) for each species.

Time-since-sunrise was calculated in R using the 'maptools' package, which has functionality to calculate the sunrise time for a location given a date (Bivand & Lewin-Koh 2020). Only data that included locational information (latitude and longitude), start time and date were able to have TSSR calculated, otherwise the data had to be filtered out. For each species, we centred each TSSR value prior to modelling by the species-specific median TSSR, and divided all values by their maximum possible value of 24.

Ordinal day was calculated by converting the standardized coordinated universal time (UTC) into the day of the year. For each species, we centred each OD value prior to modelling by the species-specific median OD, and divided all OD values by 365.

Distance models

We fitted five distance models per species using different combinations of roadside status and forest coverage, to account for differences in sound attenuation and visibility in these different environments (Yip *et al.* 2017; Supporting Information Text S4). The null model (i.e. intercept only) was a part of these candidate models. We analysed only the subset of data that contained two or more subintervals of distance, and for species for which we had ≥ 75 sampling events that contained at least one detection (Matsuoka *et al.* 2012, Buckland *et al.* 2015). For each point count location in the database, two spatial covariates were calculated: (1) the distance to the nearest road and (2) land cover type. Only data that included locational information (latitude and longitude) were able to have these covariates calculated, otherwise the data had to be filtered out. As we did for removal models, the best supported model for each species was evaluated using AIC.

Road data from Statistics Canada (Statistics Canada 2019), the United States Census Bureau (U.S. Geological Survey, National Geospatial Technical Operations Center 2020) and the Mexican National Institute of Statistics, Geography and Informatics (National Institute of Statistics, Geography and Informatics, Red Nacional de Caminos 2019) were assembled, reprojected and clipped to retain only data within 10 km of each point count location. For each point count location, the distance to the nearest road was calculated using the 'Near' tool in ArcGIS 10.7 (Environmental Systems Research Institute 2011).

The 2015 North American Land Change Monitoring System (NALCMS) provided a standardized and seamless landcover dataset for the entire study area (Natural Resources Canada, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Comisión Nacional Forestal, Instituto Nacional de Estadística y Geografía, U.S Geological Survey, 2020). The classification includes 19 landcover classes defined using the Level II Land Cover Classification System (LCCS) standard developed by the Food and Agriculture Organization (FAO) of the United Nations. The 19 cover classes were collapsed into two classes: forested and non-forested. We then calculated the proportion of forested area (hereinafter, forest coverage) surrounding each point count location at a 150-m resolution (5 × 5 pixel analysis).

NA-POPS infrastructure

We used GitHub Organizations (https://docs.github.com/en/organizations) to organize both raw data from individual projects, and for scripts related to combining these data and generating the detectability functions. This allowed open access to the results in a central repository, and all original data from data providers to be private. Details on the organization of scripts and data in GitHub Organizations can be found in Supporting Information Text S5 and Figure S1.

RESULTS

The full suite of results is visualized on the NA-POPS dashboard at https://na-pops.org/. Additionally, researchers can begin to explore and apply these offsets by using the R package 'napops' (Edwards & Smith 2022). This R package includes a README file that demonstrates how to use access estimates of cue rate and EDR through the package, as well as estimating probability of availability and probability of perceptibility. All post-hoc analyses, including generation of figures and tables, were performed with this R package.

For the sake of reproducibility, and to archive a snapshot of the results at the time of this paper, we have supplied a .zip file containing all generated covariates, analysis scripts (without raw data due to data shareholder agreements) and raw results, as well as a local copy of the NA-POPS dashboard (see Supporting Information).

Data collection

The NA-POPS Github organization can be found at https://github.com/na-pops. At the time of this paper, the NA-POPS database contains data from 292 individual projects (listed in Supporting Information Table S3). These projects contributed a total of 7 144 709 landbird observations across 712 138 sampling events, 422 514 of which had sufficient ancillary data for removal modelling and 522 820 of which had sufficient ancillary data for distance modelling. These sampling events contributed enough data to derive estimates of cue rate or effective detection radius for 338 species of North American landbirds, 319 of which had sufficient data for both (Supporting Information Table S4). The sampling events represent a wide geographical range across Canada and the United States, including data from all but two (BCR 20: Edwards Plateau, and BCR 36: Tamaulipan Brushlands) of the 37 Bird Conservation Regions (BCRs) in Canada and the USA (Fig. 1a). In general, areas with greater numbers of

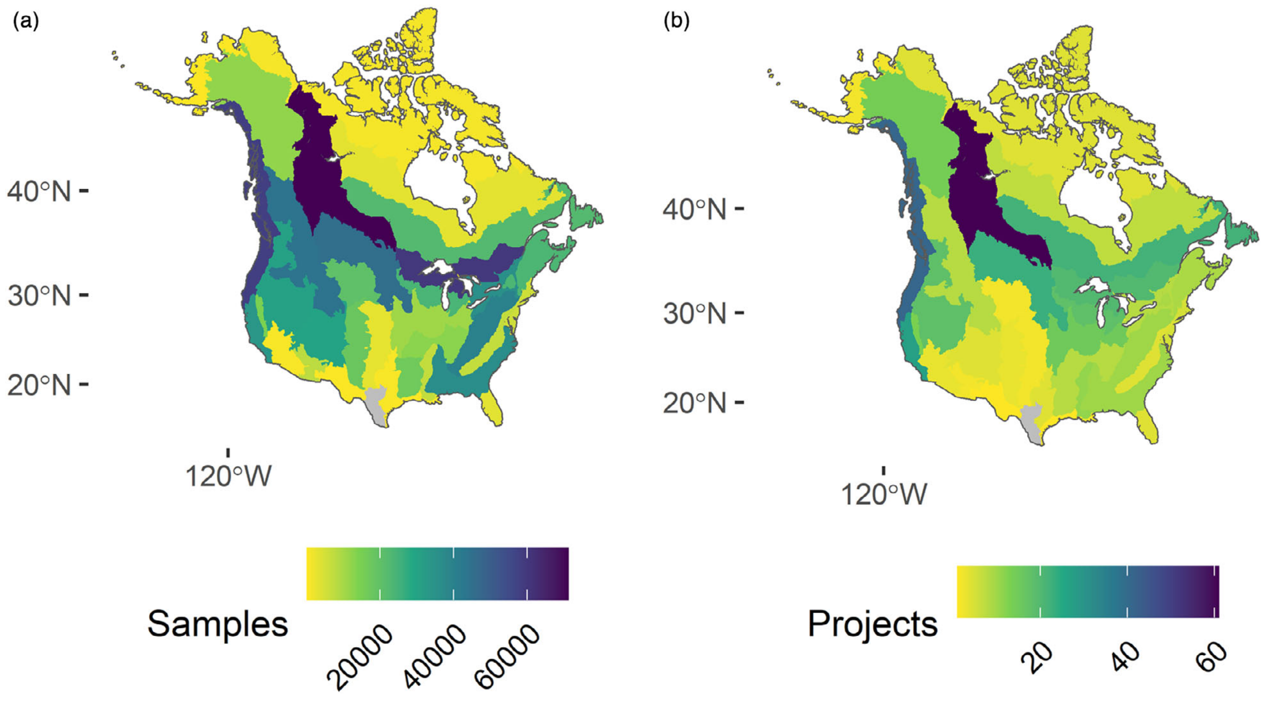

Figure 1. Spatial coverage map of all sampling events considered in the analysis of this paper (a), and number of individual projects that contributed data to each stratum (b), stratified by Bird Conservation Region (BCR). Grey regions indicate no data (BCR 20: Edwards Plateau, and BCR 36: Tamaulipan Brushlands).

sampling events corresponded to areas where there were a greater number of projects contributing data. Some exceptions to this were the montane regions of the USA, and the Great Lakes region, where a small number of projects contributed the majority of the data (Fig. 1b).

We were able to compile observations that span a wide range of sampling covariates (Fig. 2). For removal modelling, OD covariates ranged from 61 to 244, with a median of 160; TSSR covariates ranged from −3.00 to 14.4, with a median of 1.64 (Fig. 2a). Of those samples used for removal modelling, 43.6% had a maximum survey duration of 10 min and 34.1% a maximum survey duration of 6 min. The remaining 22.3% of removal samples consisted of maximum survey durations of 3, 5 or 8 min (Fig. 2b). For distance modelling, forest coverage covariates ranged from 0 to 1, with most sampling events having a value of either 0 (i.e. open canopy) or 1 (i.e. closed canopy); there was a bias toward off-road surveys (n = 414 555) compared with on-road surveys (n = 108 265, Fig. 2c). Of those samples used for distance modelling, 88.1% used infinite radius point counts and 11.2% a maximum radius of 400 m. The remaining 0.70% of the distance samples had a maximum survey radius of 30, 75, 100 or 150 m (Fig. 2d).

Model selection

For the 319 species that had sufficient data for both removal modelling and distance modelling, the best model included at least one of the removal or distance covariates for all but seven species (Fig. 3). In all, 280 species (87.8%) had a removal model selected that included at least one covariate; of these, 237 species included an OD term, 147 of which included the quadratic OD term; and 215 included a TSSR term, 108 of which included the quadratic TSSR term. Of the 319 species, 51 had the full model (Model 9) selected. A total of 296 species (92.8%) had a distance model selected that included at least one covariate; of these, 261 species included a roadside status term and 269 included a forest coverage term. The full model (Model 5) was selected in 171 species.

Species with more sampling events tended to have more complex models chosen (Fig. 4). For removal modelling, the mean sample size of species with null models selected was 1650, with a

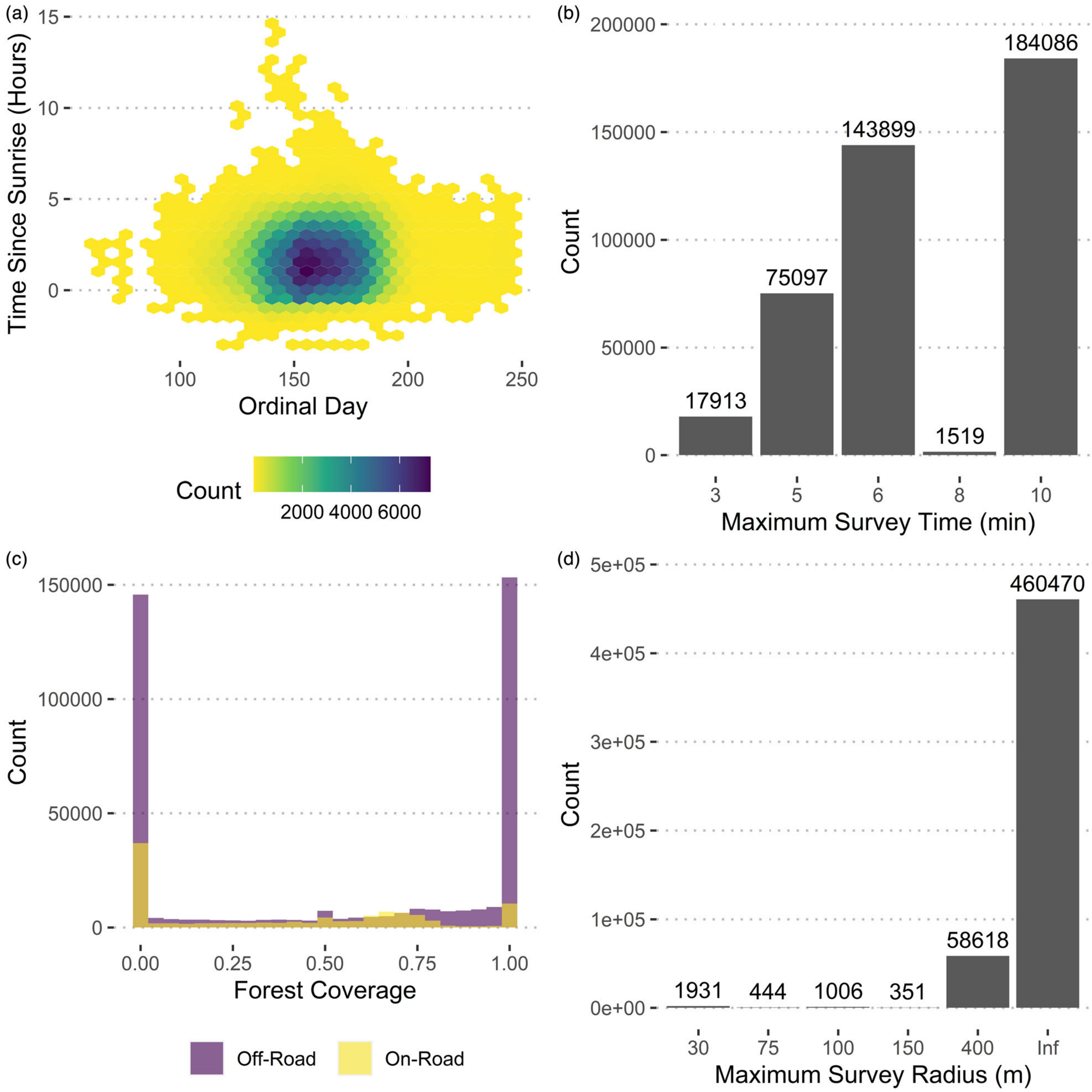

Figure 2. Covariate space for all covariates considered for both removal modelling and distance modelling. (a) 2D density plot for all values of ordinal day (OD) and time since sunrise (TSSR) collected by NA-POPS. (b) Bar chart for the number of surveys containing each maximum survey time. (c) Histogram for forest coverage values colour-coded by roadside status. (d) Bar chart for the number of surveys containing each maximum survey radius.

range between 87 (Florida Scrub-Jay *Aphelocoma coerulescens*) and 10 120 (MacGillivray's Warbler *Geothlypis tolmiei*). For distance modelling, the mean sample size of species with null models selected was 1612, with a range between 121 (Ferruginous Hawk *Buteo regalis*) and 19 760 (Vesper Sparrow *Pooecetes gramineus*).

The effects of ordinal day and time since sunrise on availability

We had sufficient data to analyse 332 species of landbirds across 46 families using removal models that contained OD, TSSR and/or their quadratic terms as covariates (Supporting Information

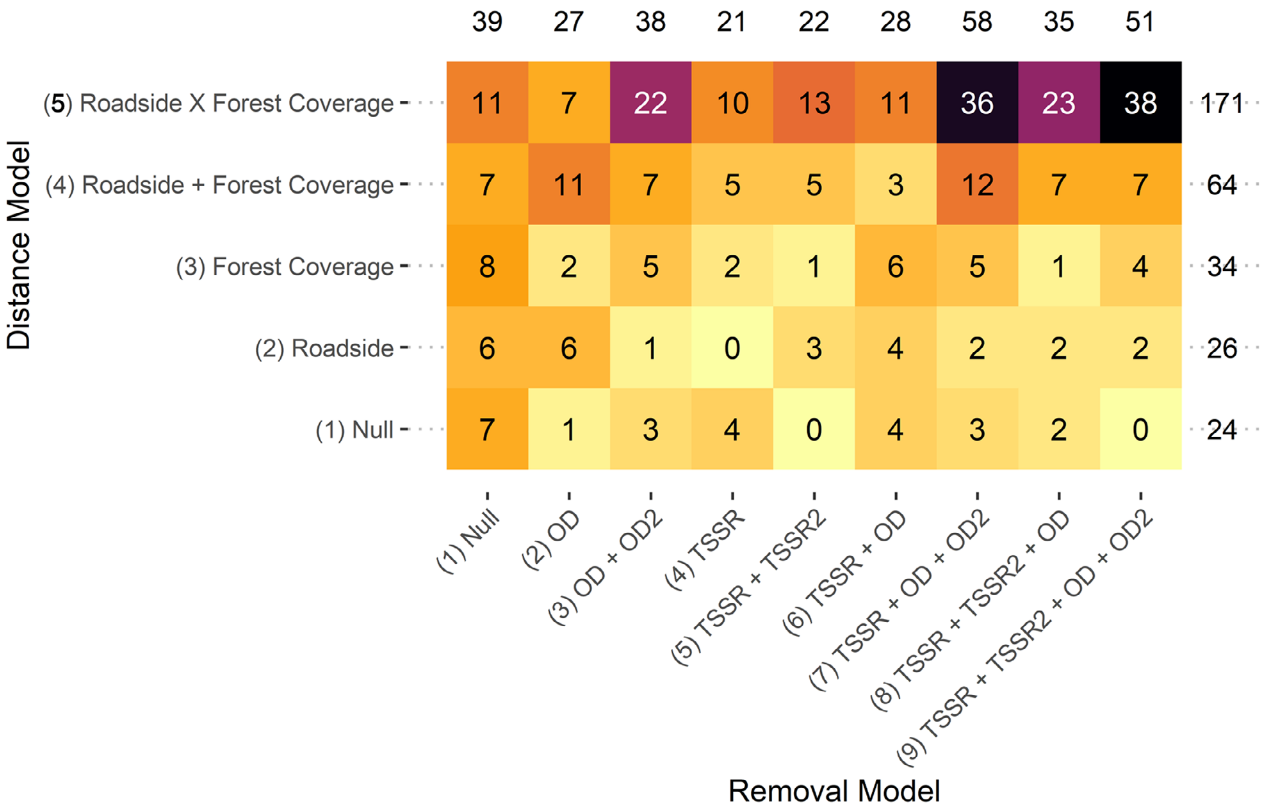

Figure 3. Heatmap of model selection (chosen by AIC) for species that had sufficient data for both removal and distance modelling. Numbers inside squares indicate the number of species that had that particular removal model/distance model combination selected. Numbers in the margin are total number of species for that particular removal model or distance model.

Table S5). Note that this total includes species that may not have had sufficient sample size for distance modelling. Figure 5 shows predicted availability curves for species in the top four families by sample size modelled by NA-POPS, plotted against varying values of OD and TSSR, for surveys of 5 min in duration. For most of these species, availability peaked around the 160th–180th ordinal day (9–29 June in a non-leap year) when keeping TSSR constant at its median of 1.6, and tended to decrease as time since sunrise increased, with some species showing some slight peaks between 0 and 2 h after sunrise.

The effects of roadside status and forest coverage on perceptibility

We had sufficient data to analyse 325 species of landbirds across 45 families using distance models that contained roadside status, forest coverage and their interaction as covariates (Supporting Information Table S6). Note that this total includes species that may not have had sufficient sample size for removal modelling. Figure 6 shows predicted effective detection radii for species in the top four families by sample size modelled by NA-POPS, plotted against varying values of forest coverage, for roadside and off-road surveys. In both roadside and off-road surveys, the effective detection radius, on average, decreased as forest coverage increased, with variability in the magnitude of decrease among species within each family.

For most species, roadside EDRs are greater than off-road EDRs (i.e. detectability is greater on roadsides than off-road) when forest coverage is high and the opposite is true (detectability is greater off-road than on roadsides) when forest coverage is low (Fig. 7). The effects of roadside vs. off-road surveys and their interaction with forest coverage can be seen in Figure 7, where the change in EDR going from a roadside survey to an off-road survey (i.e. $\Delta EDR = EDR_{Roadside} - EDR_{Offside}$) is plotted against increasing forest coverage; that is, positive values of ΔEDR mean that the roadside EDR is

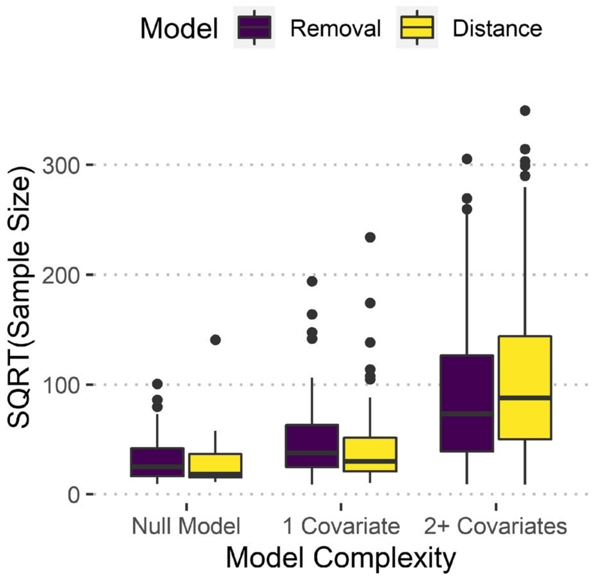

Figure 4. Species sample size (i.e. square root of the number of sampling events) grouped by complexity of the best model (based on number of covariates) as determined by AIC, for both removal (purple) and distance (yellow) modelling. See Supporting Information Material for the list of models.

greater than the off-road EDR, and negative values of ΔEDR mean that the roadside EDR is less than the off-road EDR. For the four families considered here, there is a small increase in EDR moving from roadside to off-road surveys when forest coverage is lower (< 0.50), and then a slight decrease in EDR moving from roadside to off-road surveys when forest coverage is higher (> 0.50). The exception appears to be the family Picidae, where the change in EDR is negative throughout the values of forest coverage, indicating that EDR increases from roadside to off-road surveys regardless of the forest coverage.

Case study: American Robin *Turdus migratorius*

For removal modelling, the most parsimonious model for American Robin (n_{removal} = 72 620) was Model 9, which contained linear and quadratic terms for TSSR and OD (Table 1). In the current version of the NA-POPS database, there are at least some removal data from much of this species' range, but also a strong spatial bias where most data are from the west and relatively few data cover the core of the species' range in the east (Fig. 8). The removal data for American Robin were much more balanced across the relevant parameter space, covering the standard seasons and times of day for point counts. The species' relative availability is at a peak in late June (approximately OD 180) and 0.5 h before sunrise, and its absolute availability is very high (almost 1.0) within a 10-min point count conducted at the peak time of day and season.

For distance modelling, American Robin (n_{distance} = 98 775) had the full model of roadside effect, forest coverage effect and an interaction term (Model 5) selected as most parsimonious by AIC (Table 2). There are some distance data for this species across the southern and eastern portion of the species' range, and also a strong western bias similar to the removal data (Fig. 9). The current version of the NA-POPS database includes distance data for on- and off-road, and in both forested and non-forested landscapes, but there is also some bias in the parameter space, with more data from forested landscapes and from off-road survey sites. Perceptibility of American Robin is generally greater in non-forested sites than in forested sites, and greater off-road than on-road.

DISCUSSION

NA-POPS: Point Count Offsets for Population Sizes of North American Landbirds is a collaborative project that has generated empirical estimates of detectability in a range of common observation conditions for 338 species of landbirds in North America. This accounts for 75.4% of the 448 species of landbirds considered in Partners in Flight's 2016 Landbird Conservation Plan (Rosenberg *et al.* 2016). This monumental effort fills a well-known gap in the literature, in that we have previously lacked a systematic way to generate detection estimates across species (Stanton *et al.* 2019). Past efforts by BAM (Matsuoka *et al.* 2012, Sólymos *et al.* 2013, 2018a) have started to target this, and NA-POPS serves as an extension of their work. The NA-POPS estimates of detectability can be used to integrate observations among diverse survey protocols (variations in duration and distance) and under varying survey conditions (forest cover, roadside vs. off-road, time of day, etc.), including BBS counts, eBird stationary counts and IMBCR point counts. They can also be used to inform detectability corrections in individual studies, as offsets or informative priors for detectability estimation. Most directly, these offsets provide an

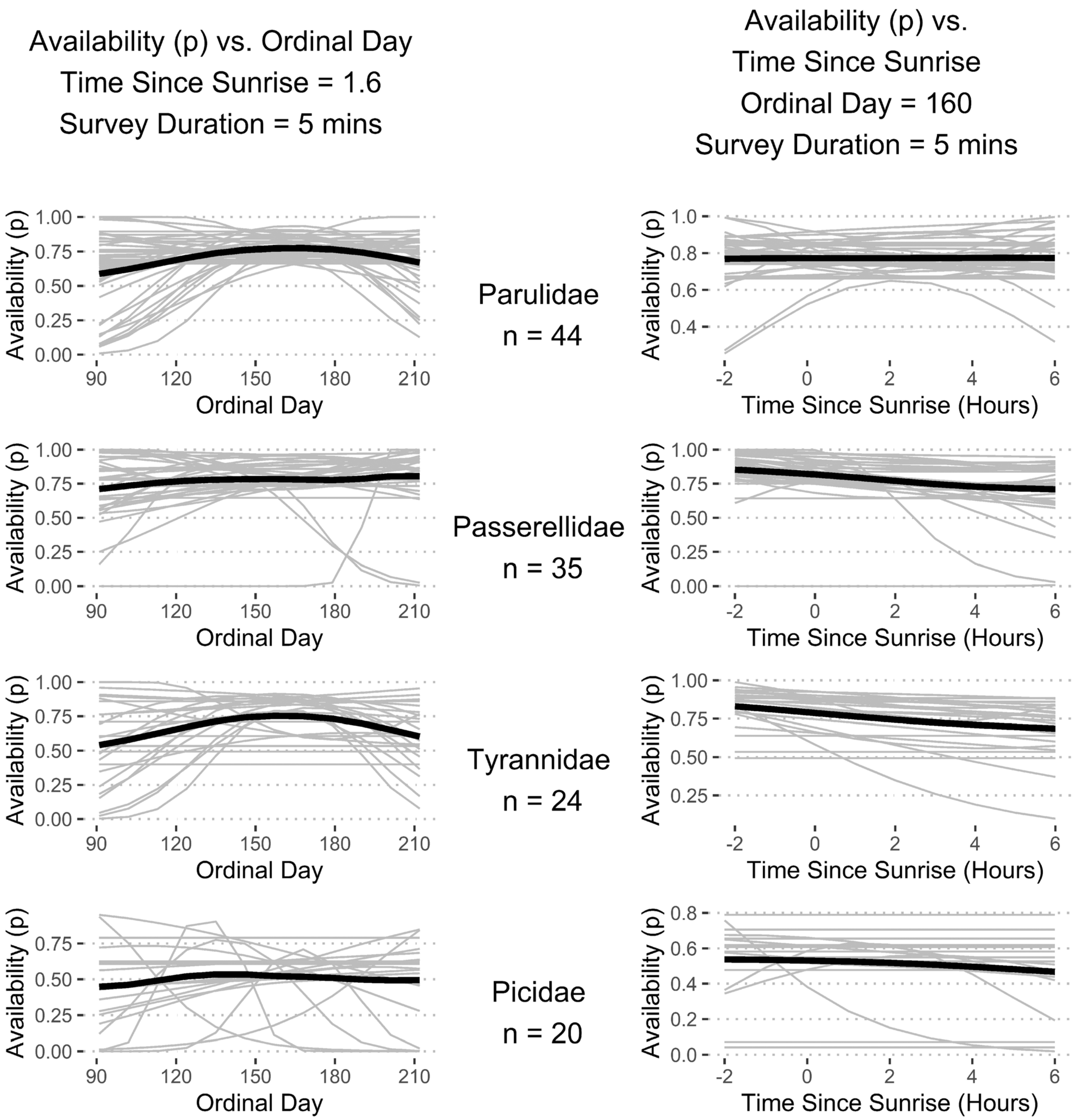

Figure 5. Plots of availability vs. ordinal day (left) and time since sunrise (right) for the four top families (by sample size) modelled in NA-POPS. Grey lines are species-specific availability curves within a family, and black lines are family-specific mean availability curves.

analytically coherent and empirical approach to improving estimates of population sizes of North American landbirds.

NA-POPS has relatively good overall coverage in the west due to data contributed from the Avian Knowledge Network, and the boreal region with data contributed from the Boreal Avian Modelling project. By contrast, there are gaps in the NA-POPS coverage in the south-central and south-eastern portions of the continent. This could be supplemented with state/province-specific Breeding Bird Atlas point counts, which are key

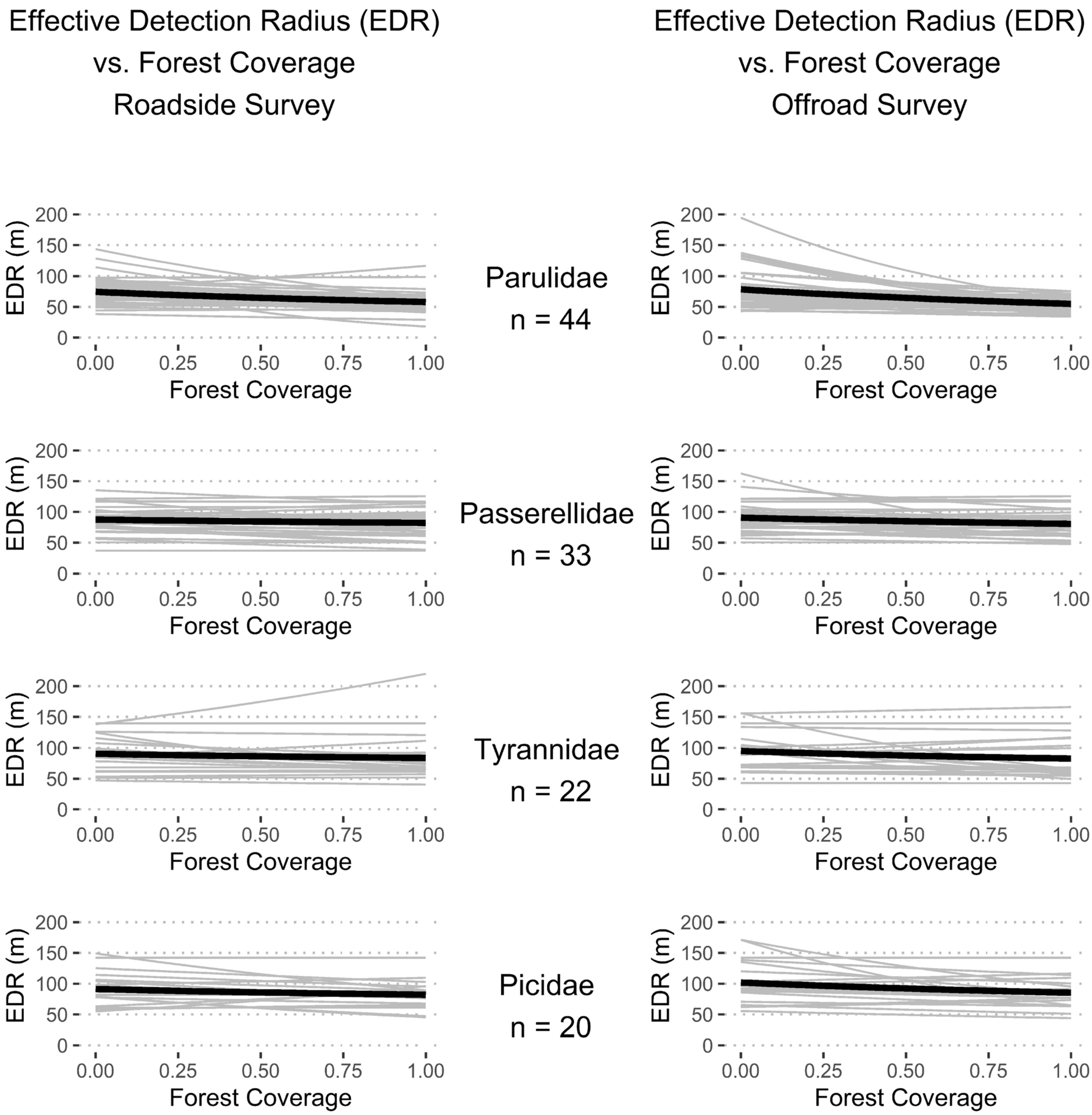

Figure 6. Plot of effective detection radius vs. forest coverage for roadside and off-road surveys for the four top families (by sample size) modelled in NA-POPS. Grey lines are species-specific effective detection radii within a family, and black lines are family-specific mean effective detection radius curves.

targets for future data to be added to NA-POPS. Additionally, NA-POPS requires better coverage of the large number of species that occur in Mexico and the south-western USA (Ruiz Gutiérrez *et al.* 2020). Finally, with the increase in creation and use of bioacoustic data from tools such as autonomous recording units (ARUs), localization techniques (Hedley *et al.* 2017) and sound pressure level curves (Yip *et al.* 2020) could be used to estimate distances to singing birds from sound recordings, which could allow for a plethora of additional data to be added in to the NA-POPS database to inform detectability estimates. The gaps mentioned here mean that the species

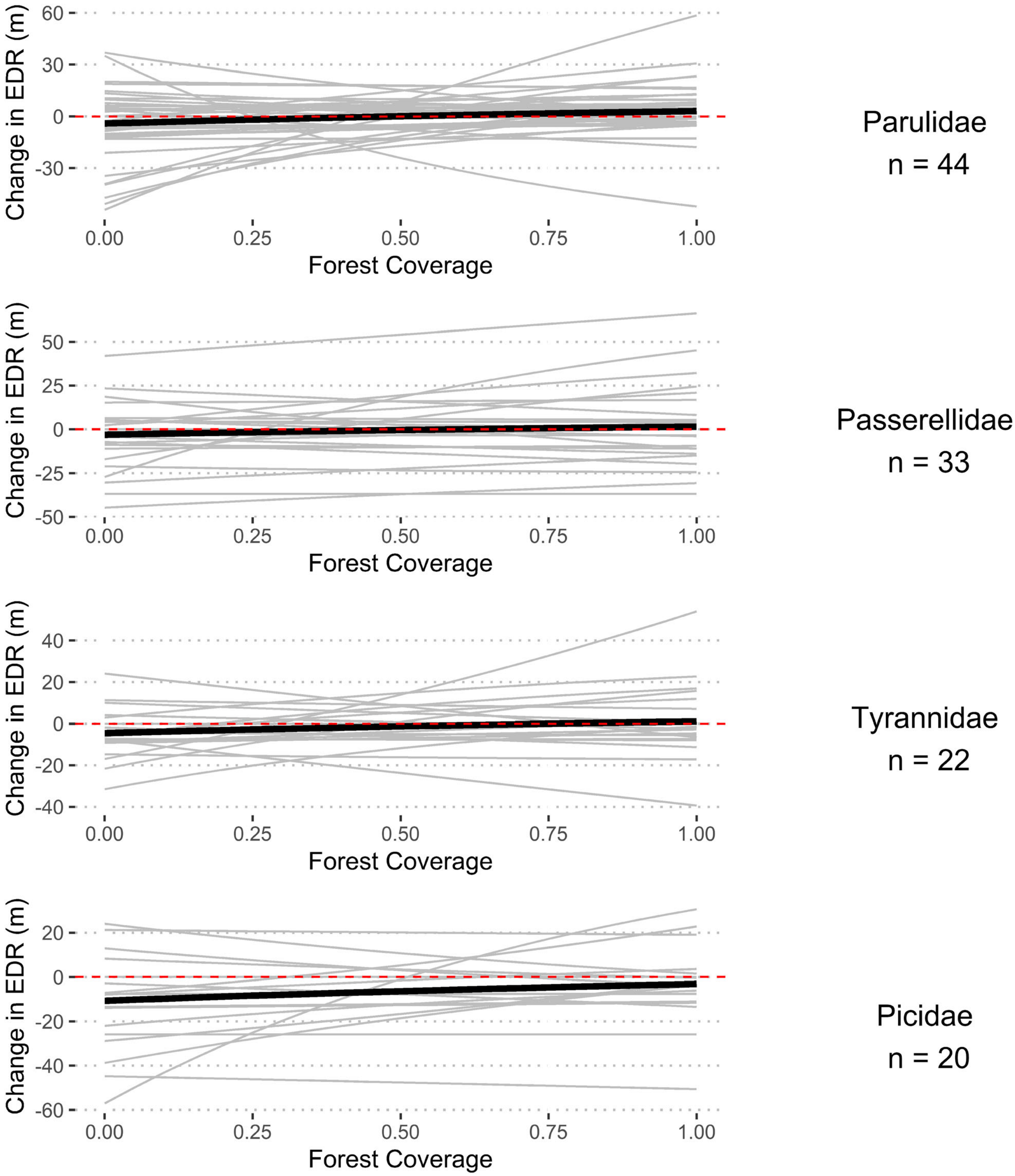

Figure 7. Change in effective detection radius when moving from a roadside survey to an off-road survey (i.e. $\Delta EDR = EDR_{Roadside} - EDR_{Off-road}$) against varying values of forest coverage, for the four top families (by sample size) modelled in NA-POPS. Red dashed line indicates a change in EDR of 0. Grey lines are species-specific changes in EDRs within each family, and black lines are mean family changes in EDR. Lines below the red dashed line indicate that the EDR for roadside surveys is less than the EDR for an off-road survey for that species, and lines above the red dashed line indicate that the EDR for roadside surveys is greater than the EDR for an off-road survey for that species.

Table 1. Coefficients for all nine removal models for American Robin *Turdus migratorius* (n = 72 620), ranked by difference in AIC from the top model.

Model	Delta AIC	Intercept	TSSR	TSSR2	OD	OD2
9	0	−1.36	−1.42	11.68	1.49	−8.36
8	29.76	−1.38	−1.47	12.24	1.47	
7	52.13	−1.32	−1.15		1.48	−8.71
6	86.3	−1.34	−1.18		1.47	
3	141.08	−1.32			1.53	−9.25
5	148.85	−1.38	−1.53	12.31		
2	181.03	−1.34			1.51	
4	205.64	−1.34	−1.24			
1	309.47	−1.35				

See Table S5 for removal coefficients for all species modelled in NA-POPS.

modelled in NA-POPS probably have some taxonomic bias toward it, in that species that occur in the south-western USA (e.g. desert specialists, species whose range occurs more in Mexico than the USA) or species that have low population sizes to begin with (e.g. Kirtland's Warbler *Setophaga kirtlandii*, Bicknell's Thrush *Catharus bicknelli*) will be systematically underrepresented. By making use of targeted data mentioned here, we can attempt to correct these taxonomic biases.

The infrastructure of NA-POPS on the GitHub Organization has been set up for quick and simple continual integration of datasets, whether they are brand new to the analyses or updates of previous datasets. For any incoming dataset, a new repository is created, and all steps in the Methods section of this paper are followed to standardize these data, add them to the dataset to be modelled, and create a new set of covariates for each species given these new data. Updates to previous datasets can be done using the same approach, except that a new project repository does not have to be created. This ease of incorporating new data means that the geographical, temporal and species coverage of NA-POPS can continue to improve, allowing for estimates of coefficients to be refined as new data are integrated.

Removal modelling and estimation of cue rate

In many cases, the NA-POPS results of model selection among removal models and cue rate estimation align with previous studies using comparable methods (Sólymos *et al.* 2013, 2018a). For the removal models, we used TSSR, OD and their quadratic terms as covariates, because it is well known that bird availability is affected by both of these variables (Wilson & Bart 1985). As expected, most species (88%) had at least one of these covariates in their AIC-selected best model, and the best model for approximately half of species included at least one quadratic term.

We found that 50.2% of species included non-linear effects of TSSR on availability in their best model, somewhat fewer than the 70% reported by Sólymos *et al.* (2018a). This could be due to NA-POPS modelling more species and therefore picking up more species that had only linear responses to TSSR. It could also be due to the range of the covariates of TSSR, in that many point count surveys tend to begin just before, or even at, the peak of dawn chorus, and so in species where most data are from the peak of dawn chorus or later, there may be insufficient data to support a curved relationship.

We found much greater support for non-linear effects of OD on availability than did Sólymos *et al.* (2018b), which may be partly due to variation in the included species and also a result of an improved estimation approach. Whereas Sólymos *et al.* (2018a) found that only 29% of modelled species had non-linear responses to OD, this was the case for 62% of species modelled by NA-POPS. Although this could also be due to modelling more species, it is probably because we standardized our OD variables slightly differently than in previous studies, in that we both scaled and centred our OD variables (where previous studies only scaled them). This additional centring of the variables ensured that models with an OD and OD^2 term do not suffer from collinearity of the two variables because squaring strictly positive terms will result in terms that are also strictly positive and therefore will be highly correlated. Thus, our models that included an OD and OD^2 term probably performed better than previous analyses that did not centre the variables (Sólymos *et al.* 2013, 2018a).

Distance modelling and estimation of effective detection radius

For the distance models, we used forest coverage and roadside status as covariates. The effect of forest coverage was expected to account for the attenuation of sound and light through forested vs.

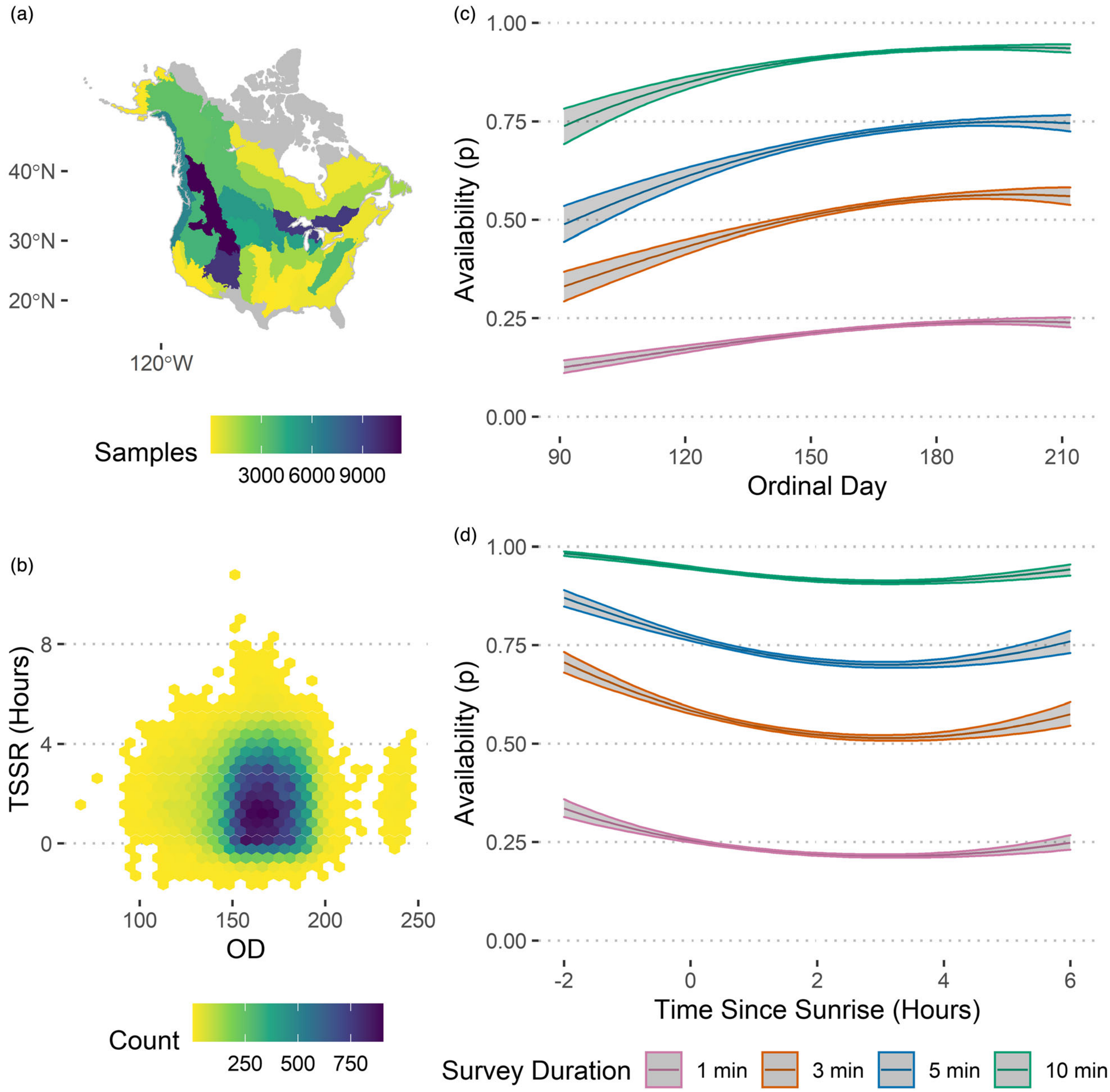

Figure 8. Summary of removal modelling for American Robin *Turdus migratorius* (n = 72 620), including (a) spatial coverage of removal sampling, (b) covariate space for ordinal day and time since sunrise, (c) predicted probability of availability against ordinal day for surveys of 1, 3, 5 and 10 min in duration, and (d) predicted probability of availability against time since sunrise for surveys of 1, 3, 5 and 10 min in duration.

non-forested environments; that is, we would expect to be able to hear and/or see the same species at a further distance in a non-forested environment than in a forested environment (Yip *et al.* 2017). The effect of roadside status was expected to account for lesser sound attenuation on a road than on an off-road environment (Yip *et al.* 2017), but to also potentially account for the ability of an observer to perceive bird sounds when near a potentially loud road, compared with an off-road environment (Pacifici *et al.* 2008, Cooke *et al.* 2020). The roadside status of a survey could also influence the ability of an observer visually to detect birds, with potentially higher detectability

Table 2. Coefficients for all five distance models for American Robin *Turdus migratorius* (n = 98 775), ranked by difference in AIC from the top model.

Model	Delta_AIC	Intercept	Road	Forest	RoadForest
5	0	4.63	−0.04	−0.19	−0.02
4	2.13	4.63	−0.05	−0.19	
3	191.55	4.61		−0.18	
2	2066.81	4.56	−0.01		
1	2072.63	4.55			

See Table S6 for distance coefficients for all species modelled in NA-POPS.

during roadside surveys where views are less obstructed compared with intact habitats. We also examined the effect of the interaction between these two variables. Given these previous studies of the effects of open/closed environments and roads on sound attenuation, and the results of Sólymos *et al.* (2013) when considering tree cover, we also expected that most species modelled in NA-POPS would have at least one of these covariates in their selected best model as chosen by AIC. Indeed, this was the case, as only 7.5% of species had the null model chosen.

When considering forest coverage as a covariate, our results were similar to those found in previous studies (Sólymos *et al.* 2013, Yip *et al.* 2017) in that there was a small but non-zero effect of forest coverage on effective detection radius. That is, as forest coverage increases, the effective detection radius of a bird tends to decrease. This aligns with previous studies that have found that sound tends to attenuate more quickly in forested than non-forested environments (Yip *et al.* 2017).

Interestingly, the effective detection radius was greater in off-road surveys than roadside surveys for many species, contrary to earlier studies that have shown greater detectability on roadsides (Yip *et al.* 2017). This was true for the American Robin example (Fig. 9): for both forested and non-forested environments, the perceptibility of American Robin was greater in off-road surveys than in roadside surveys. However, this pattern varied greatly by species, and appeared to interact with forest coverage (Fig. 7). Although Yip *et al.* (2017) showed that effective detection radius (and therefore perceptibility) is increased with roadside surveys due to decreased sound attenuation from the road surface, Cooke *et al.* (2020) showed that bird detectability with a selection of European birds was negatively associated with roadside surveys, particularly roadsides with heavier traffic. With this in mind, effects of roadside surveys compared with off-road surveys may be more difficult to pick up without accounting for traffic, and future versions of NA-POPS should consider differences in road types (e.g. major arterial road vs. minor road), or an estimate of traffic.

Selection of null removal or distance models

Models that include covariates were favoured over the null models for most species (Fig. 4). However, even for some of the species where the null model was best, the covariate models are probably still useful. For example, the null removal model was selected for MacGillivray's Warbler and the null distance model was selected for Vesper Sparrow, despite the fact that both species had a large number of detections (10 120 and 19 760, respectively). In both cases, the differences in AIC between the top selected null model and the more complex models were very close: for MacGillivray's Warbler, the four next best models were models 4, 2, 6 and 5 with ΔAICs of 1.01, 1.33, 2.33 and 2.96, respectively; for Vesper Sparrow, the four next best models (i.e. the remaining distance models) were models 3, 2, 4 and 5 with ΔAICs of 1.59, 2.00, 3.58 and 5.45, respectively. Essentially, the models could be considered 'tied'. This pattern holds for several species with null models selected as their best model, but with large sample sizes.

While it is certainly possible that these species' detectabilities are not in fact affected by the covariates used for these models, researchers wanting to apply these detectability offsets to their own point count datasets could consider using the more complex models of detectability if they have the ancillary data in their own point counts. In the 'napops' R package, although we have an explicit 'best model' argument for all the species when choosing covariates, we also allow for other covariates to be chosen if the researcher feels those covariates are relevant. For example, a practitioner wishing to generate densities for a species where the 'null' model is chosen as the best model for explaining EDR could still consider using the 'road' model of EDR if they have the roadside status of each survey available to them; the BBS data would always be a roadside status survey, so the researcher could simply opt to use the roadside

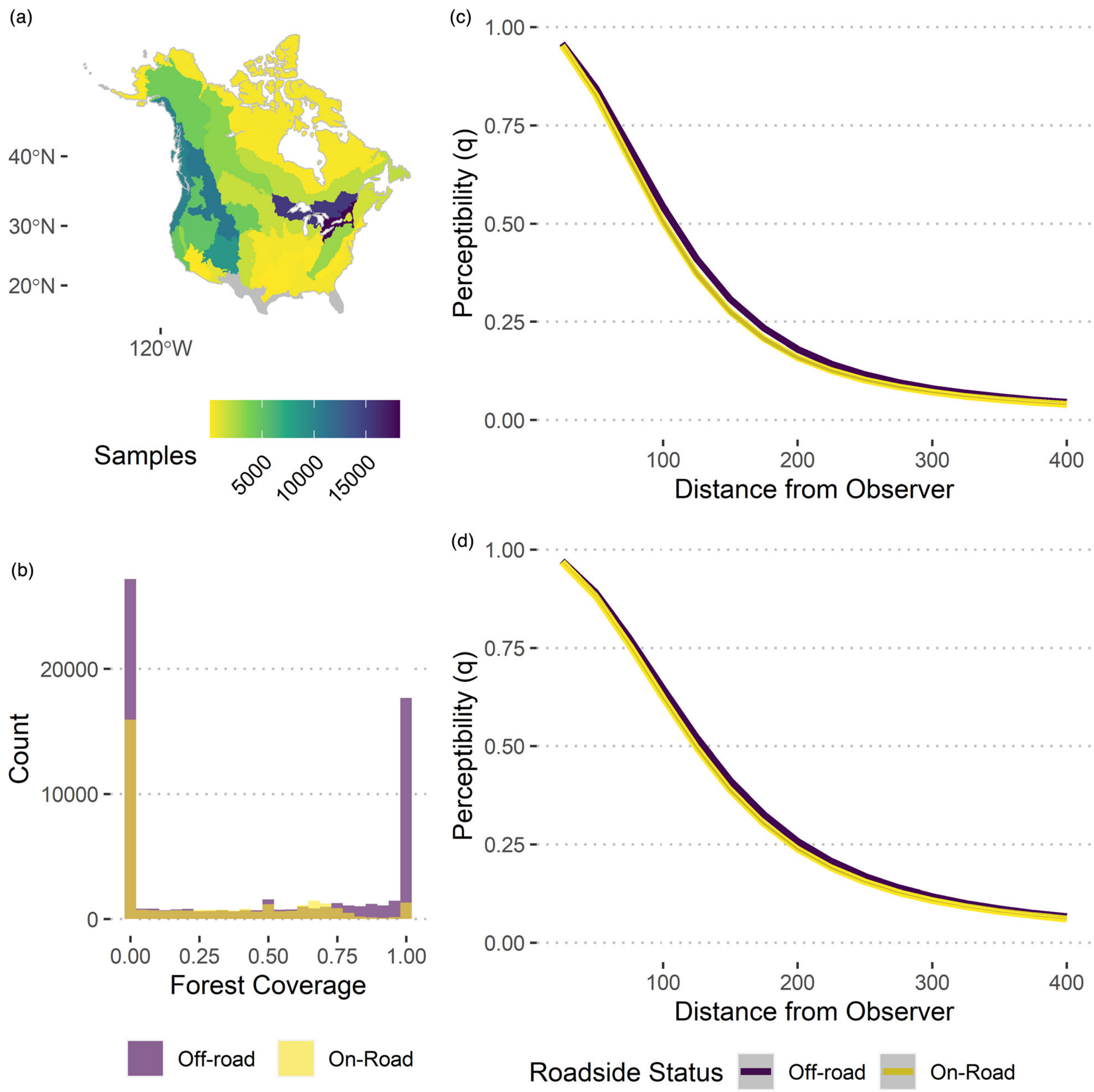

Figure 9. Summary of distance modelling for American Robin *Turdus migratorius* (n = 98 775), including (a) spatial coverage of distance sampling, (b) covariate space for forest coverage and roadside status, and predicted perceptibility against distance from observer for off-road and on-road surveys in (c) forested environments and (d) non-forested environments.

EDR for that roadside survey. On the other hand, if a practitioner feels that a model with forest coverage as a variable or time since sunrise as a variable is more useful, then they will have access to those models and should use those models. Finally, if the practitioner has none of these ancillary data for a given survey, they could still simply use the null model for a species, even if a full model was chosen. We note that generally the 'best' model is a compromise given the data, which is why the 'best' model could change when we have more data. Focused research (i.e. more data collected) allows for these shifts and, in the meantime, one can pick a different model if its biological mechanism is favoured.

Model improvements

Given the large number of observations compiled by NA-POPS to date, and the potential for many more datasets to be added, the NA-POPS project is in an excellent position to use more sophisticated modelling techniques that take full advantage of all the data we have. For example, we could consider more specific covariates to be used in both the removal and the distance modelling aspects. For removal modelling, we could consider adding an effect that accounts for differences in timing of breeding and territorial defence across the continent. For example, in a widespread species such as American Robin, local spring times in the western part of the continent mean that peak singing day could be significantly earlier in those areas than in eastern North America, where local spring happens much later. One further suggestion would be to use a landcover variable that captures local plant emergence times, similar to the 'Local Spring' variable used in Sólymos *et al.* (2018a). Alternatively, a more complex version would be to include latitude and longitude spline functions in a generalized additive model (GAM), which could facilitate the sharing of information across BCRs (Crainiceanu *et al.* 2005, Wood 2017, Pedersen *et al.* 2019). For distance modelling, a random observer effect could be incorporated into the model to account for differences in observer abilities. This could be particularly important if different projects train observers to detect birds differently (e.g. exact distances with rangefinders vs. estimating binned distances), but could also be important to account for potential differences in hearing ability for particularly high-pitched birds such as Blackpoll Warblers *Setophaga striata*. We note that although there is a plethora of additional variables we could consider, one of the main goals of NA-POPS is to make these estimates available and usable to the end-user, and so we must balance modelling with potentially relevant variables and modelling with variables that the end user will be able to access for their point count data.

We can also consider ways to share information across multiple species. For example, we could share information phylogenetically by taking advantage of patterns of detectability within families (e.g. Figs. 5–7) or by sharing information among species based on traits that are known to account for some differences in detectability (Johnston *et al.* 2014, Sólymos *et al.* 2018b). This could be done by developing a multi-species modelling framework that allows the sharing of information between similar species. That is, data-deficient species could borrow information from data-rich species that share similar phylogeny/traits.

A flexible way to share information between units is through the use of hierarchical Bayesian modelling. These models have the additional benefit of allowing informative priors when we have existing information for a particular species (e.g. singing rate or effective detection radius). Bayesian models with informative priors would allow us to incorporate expert opinion into the analysis, such as the 'Detection distance adjustment' used in the Partners in Flight Population Estimation Database, which are similar to our empirically derived EDRs (Rosenberg *et al.* 2016, Will *et al.* 2020). Additionally, in developing a hierarchical Bayesian framework, data-poor BCRs or data-poor species could have a well-chosen, informative prior to fall back on to improve estimates. Previous studies have had success with using hierarchical Bayesian modelling for estimating detectability (Amundson *et al.* 2014, Sollmann *et al.* 2016) and so a Bayesian implementation of the QPAD methodology could serve as a useful addition to these previous successes by taking advantage of the ability of QPAD to analyse heterogeneous data.

Applications and implications for conservation practitioners

Improving population size estimates

Detectability offsets derived from NA-POPS can be used to improve population estimates of landbirds in North America. Because they include separate estimates for on- vs. off-road surveys, the NA-POPS offsets would represent an improvement over the current PIF population estimates, which assume that the roadside BBS is representative of the entire landscape (Rosenberg *et al.* 2016, Stanton *et al.* 2019), even though it is well known that detectability of birds changes with on- vs. off-road surveys (Sauer *et al.* 2017, Yip *et al.* 2017, Cooke *et al.* 2020), and estimates of bird populations have been shown to improve when accounting for roadside bias (Sólymos *et al.* 2020b).

Generating population sizes using EDRs that account for roadside status and forest coverage may improve the accuracy of continental estimates of population for many landbird species. Additionally, integrating more refined information on density would have the simultaneous benefits of accounting for potential variations in detectability, reducing biases within and among monitoring programmes and generating useful information on local population sizes of birds that could inform conservation prioritizations (Veloz *et al.* 2015).

Correcting for detectability in long-term studies

The NA-POPS detectability offsets can be used to correct for changes in the landscape for long-term programmes such as the BBS. It is well known that landscapes for any given route within the BBS will have probably changed over the potentially 50+ years that the route has been run (Sauer *et al.* 2017); for example, increased agricultural and housing needs in some areas have come at the expense of forest cover, and some of the roads used by the BBS have become larger and busier. NA-POPS, in combination with time-series of long-term habitat changes at BBS point locations, could be used to generate detectability offsets to adjust for landscape alterations over time.

Data integration

Any single programme has gaps in coverage that may bias the estimates. For example, the BBS data have provided the basis for estimates of trends in relative abundance for North American landbirds, but there are known biases in the sampling framework that cannot be filled using the BBS field methods (Thogmartin 2010, Sólymos *et al.* 2020b, U.S. Geological Survey, Canadian Wildlife Service 2020). As a roadside survey, the BBS has excellent coverage in areas where there are roads, such as the eastern USA, and poor coverage where there are few roads, such as the north (boreal and arctic regions of Canada and Alaska), Mexico and alpine regions. Possibilities exist to fill these gaps by taking advantage of data available through other existing monitoring programmes. For example, the IMBCR programme collects data from montane and grassland regions in western and central USA (Pavlacky *et al.* 2017), and the Avian Knowledge Network (Iliff *et al.* 2009) and eBird data (Sullivan *et al.* 2014) can be used to fill in gaps throughout the continent. Additionally, the PROALAS programme has good coverage in Mexico (Ruiz Gutiérrez *et al.* 2020), which could allow for better estimates of southern North American birds. Integrating these data into a single modelling framework could fill spatial gaps, address limitations, and complement BBS data and analyses (Miller *et al.* 2019, Isaac *et al.* 2020).

NA-POPS estimates can be used for data integration across variations in survey duration and timing during the day and season, as well as observation conditions such as forest coverage and roadside status. Integrating information across disparate field programmes and sampling protocols remains a key challenge to analysing compilations of heterogeneous survey data because the observed counts of birds during any particular survey do not provide comparable estimates of the true density of birds. For example, the BBS conducts 3-min, 400-m, roadside point count surveys, whereas the IMBCR programme conducts mostly off-road, 6-min, unlimited-distance point count surveys and records detection distances. However, using the QPAD offsets produced by NA-POPS, we can transform raw, survey-level counts into estimates of true density and account for differences among survey method and conditions (Stralberg *et al.* 2015, Sólymos *et al.* 2020b). For example, BBS counts for a given species can be adjusted using QPAD offsets from NA-POPS for a 3-min, 400-m-radius count on a roadside, so that the BBS counts can be integrated with 6-min, unlimited-distance off-road counts from IMBCR. This can allow us to include disparate datasets in the same model, so we no longer have to make broad-scale inferences from a single survey (such as status and trends of North American birds derived solely from the BBS). Instead, we can begin deriving broad-scale inferences with broad-scale information via multiple surveys.

Additionally, these QPAD offsets can then also be applied to semi-structured citizen science data that come from eBird (Sullivan *et al.* 2014), if we are able to filter and derive checklists that meet a stationary count protocol for a reasonably short period of time. Several promising studies have demonstrated the utility of community science programmes such as eBird in filling spatial gaps in abundance and species distribution models (Pacifici *et al.* 2017, Robinson *et al.* 2020, Joseph *et al.* 2021). With data from eBird being available for researchers to download, future studies could consider generating roadside status and forest coverage variables for stationary protocol checklists which are reasonably short in length (e.g. < 10 min). Using GIS software, roadside status and forest coverage variables could be derived and, along with the temporal information from the checklist, can be used as input for the detectability functions to produce the estimate of density for that checklist.

Facilitating open science and future detectability research

NA-POPS is an open-access database, with several avenues available for researchers to explore and access these results. The unprocessed results can simply be downloaded from the GitHub Organization (https://github.com/na-pops/results), the summarized results and predictions can be visualized using the NA-POPS dashboard (found at https://na-pops.org), and the processed results can be accessed using the R package *napops* (Edwards & Smith 2022). Ease of use of these detectability functions will allow researchers from across North America to use these estimates where they see fit, scrutinize these estimates where there is disagreement, and explore deeper into species-specific estimates that are surprising or counterintuitive.

We also hope that this broad-scale synthesis of detectability estimates will inspire future work in landbird detectability across North America, as well as on a global scale. We have mentioned here several surprising findings, including some unexpected results concerning off-road vs. on-road surveys. Additionally, we have highlighted several future avenues for more specific detectability research, including investigating spatial effects on cue rate and/or EDR, investigating potential observer effects on EDR, and the need for additional data from several geographical regions of North America. Because detectability is an important consideration in several modelling exercises and carries several conservation implications with it, we recommend that researchers wanting to run bird surveys strategically design their surveys such that the survey protocols allow for detectability estimates to be derived (i.e. Matsuoka *et al.* 2014).

CONCLUSION

NA-POPS is the first open-access database of detectability functions for over 300 species of North American landbirds. Our goal is to continue to grow the database to include more species and broaden the spatial coverage, and to refine the models further. The detectability functions generated from NA-POPS can be used to translate bird abundance into estimates of true density, and can play a crucial role in integrating disparate data sources into an integrated modelling framework. Additionally, systematic estimates of effective detection radius produced by the distance modelling component of NA-POPS, using covariates of roadside status and forest coverage, can be used to improve population estimates of North American landbirds, by accounting for detection biases in roadside surveys such as the BBS. NA-POPS is already a collaborative project, involving several agencies from across North America, but more partners are required to address spatial gaps and facilitate improved modelling. We invite researchers with bird point count data that use a removal or distance sampling approach to contribute to the further growth of the NA-POPS database.

We thank the hundreds of skilled observers across North America who have collected point count data for the projects used here. NA-POPS curated data from several projects across North America, and we have listed and acknowledged the data owners at https://na-pops.org. We thank the members of the Partners in Flight Population Estimates working group and the Boreal Avian Modelling project for their crucial feedback throughout this study. We thank all constructive reviewers for their extremely valuable feedback to improve the manuscript. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

AUTHOR CONTRIBUTIONS

Brandon P. M. Edwards: Conceptualization; data curation; formal analysis; investigation; methodology; software; visualization; writing – original draft; writing – review and editing. **Adam Smith:** Conceptualization; data curation; formal analysis; investigation; methodology; supervision; writing – original draft; writing – review and editing. **Teegan D. S. Docherty:** Data curation; methodology; writing – original draft; writing – review and editing. **Marcel A. Gahbauer:** Writing – original draft; writing – review and editing. **Caitlyn R. Gillespie:** Data curation; writing – original draft; writing – review and editing. **Alexis R. Grinde:** Data curation; writing – original draft; writing – review and editing. **Taylor Harmer:** Methodology; writing – original draft; writing – review and editing. **David T. Iles:** Writing – original draft; writing – review and editing. **Steven Matsuoka:** Writing – original draft; writing – review and editing. **Nicole L. Michel:** Writing – original draft; writing – review and editing. **Andrew Murray:** Methodology; writing – original draft; writing – review and editing. **G. J. Niemi:** Data curation; writing – original draft; writing – review and editing. **Jon Pasher:** Methodology; writing – original draft; writing – review and editing. **David C. Pavlacky Jr:** Writing – original draft; writing – review and editing. **Barry G. Robinson:** Data curation; methodology; writing – original draft; writing – review and editing. **Brandt Ryder:** Writing – original draft; writing – review and editing. **Péter Sólymos:** Data curation; formal analysis; methodology; software; writing – original draft; writing – review and editing. **Diana Stralberg:** Data curation; formal analysis; writing – original draft; writing – review and editing. **Edmund Zlonis:** Writing – original draft; writing – review and editing.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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ETHICAL NOTE

None.

Data Availability Statement

All source code for detectability derivations, post-hoc analyses, as well as results and covariates used are available at the NA-POPS GitHub Organization: https://github.com/na-pops.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. General structure of the NA-POPS Github Organization. Raw data (a) in the form of metaprojects (black boxes) or individual projects (blue boxes) are made into their own GitHub (b) project repository (red boxes), where the raw data are run through a script to standardize the data into a common format. These standardized data sets, along with the landcover and temporal covariates, are combined in the 'analysis' repository where the data are modelled using the removal and distance sampling models. The coefficients from these are calculated and output into a public 'results' repository.

Table S1. Design matrix for removal modelling. Method represents the specific method used to split the overall time into subintervals, and Level represents the individual subintervals per method. The numbers corresponding to each Method–Level combination are the max cut-off time for that subinterval.

Table S2. Design matrix for distance sampling modelling. Method represents the specific method used to split the overall radius into subintervals, and Level represents the individual subintervals per method. The numbers corresponding to each Method–Level combination are the maximum cut-off distance for that subinterval.

Table S3. List of all projects that were used in NA-POPS analysis. Metaprojects denote an organization or network that is the 'parent project' for several smaller monitoring projects.

Table S4. List of all species that had sufficient data for removal modelling, distance modelling or both. Species that had sufficient data for only one method of modelling are noted in the Notes column.

Table S5. Removal coefficients for all species in NA-POPS, for the best model chosen by AIC.

Table S6. Distance coefficients for all species in NA-POPS, for the best model determined by AIC.

Supplemental Text S1. Background on QPAD methodology.

Supplemental Text S2. Data standardization details.

Supplemental Text S3. Removal models.

Supplemental Text S4. Distance models.

Supplemental Text S5. NA-POPS GitHub Organization.