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Using Human Footprint Models and Land-Cover Variability to Predict Ecological Processes

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ABSTRACT

Transformation of landscapes for human use underlies most conservation problems. Biologists are increasingly using human footprint models with massive global and national spatial datasets to gauge the effects of humans on ecosystems. These models use spatial data to estimate the influence of human activities on natural landscapes. We examined 3 models to determine how accurately human footprint models predict effects of land use on ecological processes. Models were evaluated using bird data and anuran data from the eastern United States, as well as Breeding Bird Survey data and invasive cheatgrass data from the western United States. Bird and anuran species were organized into guilds and the incident rate for each guild was related to the human footprint intensity. We mapped occurrence of invasive species to compare to human footprint intensity. We predicted that when human footprint intensity was low incident rates of bird and anuran species that are sensitive to human activities should be highest and there should be fewer occurrences of invasive species. We found that Leu et al.'s (2008) model was the best at predicting all synanthropic species, while Theobald et al.'s (2012) model was the most accurate at predicting invasive species and avian species that are sensitive to humans. None of these models were accurate at predicting anuran guild abundance. The results of this study can inform future land-use decisions with potential to influence the spread of invasive species or the occurrence of species that are sensitive to anthropogenic land use, spread of invasive species, and future land use decisions.

Human-land modification is widespread and occurs throughout every land-cover type in the United States. How a species might respond to human land modification varies; human-dependent species thrive in anthropogenic land-cover, while species that are sensitive to human-dominated landscapes tend to avoid certain aspects of land use. Which particular features of human dominated land-cover are avoided across species (e.g. agriculture, highways, urban areas, etc.). We compared how different anthropogenic features predicted where certain species occurred. We extracted land-cover data from USGS Landfire (2013) datasets and compared them to data collected from the Breeding Bird Survey (BBS) for the entire conterminous United States. We compared natural and anthropogenic land-cover types to species occurrence of a human dependent species, the European starling (*Sturnus vulgaris*), and a sample of thought to be associated with unaltered habitats: bushtit (*Psaltriparus minimus*), marsh wren (*Cistothorus palustris*), swainson's thrush (*Catharus ustulatus*), hermit thrush (*Catharus guttatus*), northern parula (*Parula americana*), ovenbird (*Seiurus aurocapillus*), and grasshopper sparrow (*Ammodramus savannarum*). The species were chosen because they are thought to be sensitive to anthropogenic disturbance where their preferred breeding land-cover type was available and avoided high levels of human development. These results will enable land managers to improve current human footprint models and create habitat suitability models for species in relation to human landscapes.

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This M.S. degree is dedicated to my parents, family, and friends who have
helped me countless times along the way

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Chapter 1: Introduction

One of the first publications depicting how humans change landscapes and the subsequent effects on ecological processes was *Man and Nature* (Marsh 1864). In that early publication, Marsh (1864) described the extent of human impacts on the environment and the need to understand the complex interactions between man and the environment (Turner et al. 1990). Recent studies have proposed that by 2100, land-cover change will be the largest stressor for terrestrial ecosystems (Sala et al 2000), altering ecosystems and reducing biodiversity throughout the world (Vitousek et al. 1997). In their landmark study, Wilcove et al. (1998) state that the most common cause of faunal extinction is loss of land-cover, followed by over exploitation, the introduction of invasive species, pollution, and disease; all directly or indirectly influenced by the creation of human-dominated landscapes.

Human population growth has been extensive from 1950 to 2000 (Brown et al 2005). The human population has surpassed seven billion people in 2013 and is projected to reach eleven billion by 2100 (U.S. Census 2010). The need to provide food, fiber, water, and shelter to the increasing human population drives the conversion of "natural" landscapes (i.e. intact landscapes where dispersal is not impeded) to anthropogenic landscapes (Foley et al. 2005). Croplands, pastures, plantations, and urban areas have expanded in recent decades, accompanied by large increases in energy, water, and fertilizer consumption resulting in considerable losses of biodiversity (Foley et al. 2005).

The most common land use conversions in the United States are urban development (Brown et al. 2005), agriculture (Foley et al. 2005) and most recently, energy production (Krijgsveld et al. 2009). Although urban areas likely have the largest effect on wildlife, areas of rural development incur reduced species survival and reproduction near homes. Native species richness (i.e. total number of species in an area) generally drops with increased rural development (Hansen et al. 2005; Merenlender et al. 2009). Areas of human housing also increase the number of synanthropic species (i.e., species that are commonly associated with humans [Johnston et al. 2001]), which have negative effects on population growth and survival of the native fauna that are sensitive to anthropogenic features. American crows (*Corvus brachyrhynchos*), raccoons (*Procyon lotor*), rats *(Rattus sp.*), and many others are all commonly associated with human dominated land cover.

Roads and traffic directly affect animal populations through decreasing natural land cover amount and quality, increasing mortality due to collisions with vehicles, and preventing access to resources. Roads also indirectly affect populations by subdividing them into smaller and more vulnerable subpopulations (Jaeger et al. 2004). Roads also have an effect zone, which is an area over which significant ecological effects extend outward. Larger, busier roads will have a greater effect zone than smaller local roads (Forman and Alexander 1998).

Areas of heavy agriculture can be as detrimental to a species as an urban landscape. Agriculture intensification has led to declines in biological diversity among several taxa (Benton et al. 2003). For example, an area dominated by natural land cover can turn into a land cover dominated by invasive alien plants if existing grasslands are converted into an agricultural field for corn. These land-cover types can subsequently become an ecological sink for wildlife. Donal et al. (2001) found that population declines in species and range contractions were significantly greater in areas of intensive agriculture.

Several modeling approaches have been developed to measure and weigh the effects of land use on ecological processes. These models can be used to provide valuable information for land use, transportation, conservation, and urban planning efforts (Girvetz et al. 2000). Sanderson et al. (2002) assigned impact values to each human feature based on landscape modifications, whereas Leu et al. (2008) created models to evaluate the effects of anthropogenic habitat features on anthropogenic predators and habitats. Lastly, Theobald (2012) evaluated the ability of species to move through different land-cover types to model human land use effects spatially.

While human footprint models have the potential to be important planning tools to land managers and biologists, they all have assumptions, which in turn are based on expert opinion or studies conducted outside of the inference space of a human footprint model (Theobald 2010). The first objective of our study is to compare different human footprint models' abilities to predict effects of human stressors on ecological processes. Specifically, we will compare human footprint model intensity to avian guild presence using point counts, the Breeding Bird Survey (BBS), anuran survey data, and occurrence of an invasive species. This method of validating footprint intensity based on different anthropogenic components to actual ecological processes has not been done across multiple taxa before.

Anthropogenic activity varies across ecosystem types and the response of the species within that ecosystem varies based in part on their tolerance toward humans (Vitousek 2006). By looking at the functional response of species to human-dominated land-cover types, we can create a model of the biological response of each species to anthropogenic features. If we can potentially make parallels between certain types of species concerning what predicts their occurrence, we can parameterize human footprint models based on empirical data.

As the human population continues to increase, species that avoid human dominated land-cover will likely experience a reduction in populations (Wilcove et al. 1997). Zuidema et al. (1996) found that proximity to urban centers affects many aspects of the ecosystem including water supply, wildlife, habitat availability, and overall habitat quality. However, human impact on natural land-cover types can be minimized if the species requirements are known (Matlack 1993). It is therefore important to know minimum land -cover requirements and determents for sensitive species and whether there are any parallels in those requirements among species that are sensitive to anthropogenic land-cover. The second objective of this study was to evaluate if there are underlying minimum requirements that predict the occurrence of sensitive species.

We created models based on land-cover classification for seven species that avoid anthropogenic land-cover and one species that predominately exists in anthropogenic land-cover. The species we analyzed include the bushtit (*Psaltriparus minimus*), marsh wren (*Cistothorus palustris*), Swainson's thrush (*Catharus ustulatus*), hermit thrush (*Catharus guttatus*), northern parula (*Parula americana*), ovenbird (*Seiurus* *aurocapillus*), and grasshopper sparrow (*Ammodramus savannarum).* We compared these species to the European starling (*Sturnus vulgaris*), which is common throughout land-cover heavily dominated by anthropogenic features.

Modeling European starling occurrence served to compare how land-cover preferences and avoidances between the different species compare in model weight. From this comparison, we can determine if anthropogenic land-cover types are ranked highly and negatively in species that are sensitive to human dominated land-cover types and positively for species that thrive in anthropogenic land cover.

In addition, by finding parallels between sensitive species and land-cover types, a more species specific and biologically accurate human footprint model can be created. Land managers and city planners can also potentially incorporate more natural and biologically diverse habitats into urban and suburban designs. Even small changes in the spatial patterning of resources can produce dramatic ecological responses, like an increase in biodiversity (Turner and Gardner 1991).

Proper planning by land managers and regional planners can also reduce the inclusion and subsequent spread of invasive species into urban and suburban areas (Kowarik 2008). Previous research has suggested that the inclusion of diverse plant communities in anthropogenic land-cover increased wildlife species diversity (Vale and Vale 1976). With the information obtained from this study, the amount, type, and quality of land-cover required for sensitive species occurrence can be determined and evaluated for future regional planning.

In addition, by looking into how effective human footprint models are at predicting ecological processes and whether there are particular land-cover elements that influence the occurrence of species that are sensitive to humans, land managers can improve habitats for species that are declining as a result of anthropogenic activities. As the human population continues to increase and more land cover becomes influenced by land use, it will be ever more important to protect land-cover important for species that avoid human dominated land-cover types (Robinson et al. 2005).

Chapter 2: Can Human Footprint Models Accurately Predict Human Impact on Ecological Processes?

Introduction

The three most well documented global changes from humans are: alterations of biogeochemistry of the global Nitrogen cycle, increasing Carbon concentrations in the atmosphere, and the process of land-cover and land use change (Vitousek 1994). Humans have altered the Nitrogen cycle through fertilizer production and agriculture practices and increased Carbon concentrations primarily through combustion of fossil fuel. Humans have converted "natural" land-cover (i.e. intact landscapes where floral and faunal dispersal is not impeded) to croplands, pastures, plantations, and urban areas, accompanied by an increase in demands for energy, water, and fertilizer (Foley et al. 2005). Global increase in land-cover change and increased consumption of limited resources result in biodiversity loss and reduction in ecosystem health (Vitousek 1994; Wilcove et al. 1998).

Effects of humans on ecological processes are delineated in human footprint models (Sanderson et al. 2002). Spatially explicit models that delineate and predict land-cover change were first created by theoretical ecologists to document species presence and movement (Kareiva and Wennergren 1995). Recent advances in satellite imagery classification and availability of spatial data sets delineating land use and anthropogenic features, such as roads and power lines, resulted in an explosion of human footprint models. Human footprint models have been created, for example, at a global extent for terrestrial (Sanderson et al. 2002) and marine environments (Halpern et al. 2008), at national extents, such as for the conterminous United States (Theobald 2010; Theobald et al. 2012), at the sub-national extent (Leu et al. 2008; Nuñez et al 2012), and at the ecosystem level (Davis and Hansen 2011; Wade et al. 2011; Portman et al. 2012; Walston et al. 2012). Human footprint models have also been developed to predict the impacts of specific human land use practices, including, construction activities in wetlands (Fuertes 2013) and the impact of industrial processes on the local environment (Li and Hui 2001). In conjunction with increasing availability of human footprint models, land managers and environmental planners are using them increasingly to predict species presence, habitat availability, and the cost of humans to the functioning of environmental services (Bicknell et al. 1998; Moran et al. 2008).

While human footprint models have the potential to be important planning tools to land managers and biologists, they are based on expert opinion or on studies conducted outside of the inference space of a human footprint model (Theobald 2010). If these models do not accurately predict human impacts on ecological processes, their use could result in ineffective land use planning or management of species of concern (van Kooten and Bulte 2000; Fiala 2008). It is therefore important to test whether these models accurately predict effects of human land use on ecological processes.

In this paper, we evaluate the predictive abilities of three human footprint models, by Sanderson et al. (2002), Leu et al. (2008), and Theobald et al. (2012). These models have been used by land managers and environmental planners to develop remediation plans, define suitable habitat for endangered species, predict the spread of invasive species, and create corridors for species movement. Published studies based on Sanderson et al.'s (2002) model include modeling the potential spread of invasive species (Bean et al. 2012), mapping of the human influence on mountain ecosystems (Rodríguez-Rodríguez et al. 2012), and linking fragmented landscapes (Alagador 2012). Leu et al.'s (2008) model has been specifically used to model persistence of greater sage-grouse leks (*Centrocercus urophasianus*) (Knick et al. 2013) and factors influencing the distribution of chytrid fungus (*Batrachochytrium dendrobatidis*) presence, associated with declines in Pacific-Northwest frog populations (Adams et al. 2011). Theobald et al.'s (2012) paper was a recent publication and has not yet directly been used by other authors, but methods similar to Theobald et al. (2012) have been used to estimate land-cover permeability (Nuñez et al 2012; Galic et al 2013).

The objectives of this study were to compare predicted human footprint intensity of three models (Sanderson et al. 2002; Leu et al 2008; Theobald et al. 2012) to four avian guild incident rates, two anuran guild incident rates, and the occurrence of an invasive plant, cheatgrass (*Bromus tectorum*). We evaluated these models at the extent of the conterminous United States, and two of the three models (Sanderson et al. 2002, Theobald et al. 2012) were also tested at the regional extent, in the state of Virginia, and the eastern United States.

We compared human footprint intensity predicted by the three models to species guild responses. For birds, we assigned species to four different guilds, depending on how species utilize human land use (Johnston et al. 2001). For anurans we assigned species to conservation status based on classifications by Nature Serve (2013) and

International Union of Conservation (IUCN 2013), and for the invasive cheatgrass we used occurrence data used from satellite imagery for the western United States (GAP Analysis Program, 2004).

We used Johnston et al.'s (2001) avian synanthrope classification to classify bird species into four guilds: "full synanthrope", species that depend on anthropogenic features throughout their entire annual cycle; "casual synanthrope" species that exploit anthropogenic features; "tangential synanthrope", species that occasionally exploit anthropogenic features; and "non-synanthrope" (anthrophobic), species that avoid anthropogenic features. As human footprint intensity increases, we predict an increase in incident rate for synanthropic species and a decrease for anthrophobic species. For full synanthropes, we predict that incident rate relates positively and linearly to human footprint intensity. For casual synanthropes we predict a logarithmic function between incident rate and human footprint intensity. As human footprint intensity increases, there will be an initial increase in incident rate but the incident rate will remain constant at higher human footprint intensity. For tangential synanthropic species we predict a quadratic function between incident rate and human footprint intensity because these species do not use areas where human footprint intensity is low or high. For anthrophobic species we predict that as the human footprint value increases, there will be a decrease in incident rate.

We classified anuran species into two guilds, common and sensitive (includes locally declining, threatened, near threatened, and imperiled species). Several studies have found that the presence of suitable land cover plays the most important role in anuran species presence (Cushman 2006; Birx-Raybuck et al. 2009; Adams 2011; Mushet et al. 2012). We predicted that as the human footprint intensity increases, richness of species that are sensitive to land use or are habitat specialists will decrease. We predicted for anuran species that are more common and are habitat generalists, including some anthropogenic land-cover types, such as storm water retention ponds, should increase as human footprint intensity increases.

Cheatgrass was identified as present or absent at each survey location (GAP Analysis Program 2004). The presence of cheatgrass has been called one of the most dramatic land-cover changes observed in western landscapes (Billings 1994; Alldredge et al. 2007; Hanser et al. 2011). Nielsen-Pincus et al. (2010) found that this change in land-cover to cheatgrass dominance has been primarily caused by land-cover disturbance and degradation through intensive livestock grazing and heavy off-road vehicle use.

Methods

Human footprint models

We analyzed how three different human footprint models from Sanderson et al. (2002), Leu et al. (2008), and Theobald et al. (2012) performed when evaluated against synanthropic avian guilds, amphibian conservation guilds, and occurrence of cheatgrass. Each model was built using different methods, land-cover classification, resolution, anthropogenic features, and human impact calculations (Table 1).

Sanderson et al. (2002) created a human impact model built on human land-cover modification. The authors summed anthropogenic features based on four types of human influence on the environment: population density, land transformation, accessibility, and electrical power infrastructure. The scores for each variable were summed across the model, resulting in a model that ranged from 1 to 1000 in human impact.

Leu et al. (2008) created seven models, based on anthropogenic features, anthropogenic predators, and habitat. The seven models included three top-down predator models (domestic dogs, domestic cats, and corvids) and four bottom-up models (exotic plant invasion, human-caused fires, wildland fragmentation, and energy extraction). The authors then standardized all models and binned them into 10 classes, creating a model that ranged from 1 to 10 in human impact.

Theobald et al. (2012) created a human impact model that included anthropogenic features that affect wildlife movement, creating a landscape connectivity map. The authors modeled least-cost calculations based on the ability of an animal to move through different land-cover types. The final model ranged in values from 1 to 1000.

Datasets Used in Model Validation

We validated human footprint models using point counts, North American Breeding Bird Survey (BBS) data, North American Amphibian Monitoring Program (NAAMP) data, and invasive cheatgrass occurrence (GAP Analysis Program 2004). For the avian validation, we derived guild incident rates from BBS data and guild abundance using point count surveys. Guilds were assigned from Johnston et al.'s (2001) avian guild classification (Appendix 1). Anuran validation was based on calling indexes for each guild (Nelson and Graves 2004, NAAMP). Guilds were assigned from the Nature Serve (2013) and International Union of Conservation (IUCN 2013) (Appendix 2). Cheatgrass validation was classified as presence/absence based on vegetation surveys used to classify satellite imagery (GAP Analysis Program 2004).

Point count data were collected over a 3 year period, 2 years of point counts (2012-2013) were collected from the Virginia Peninsula and 2 years (2011 and 2012) from the Shenandoah Valley (Figure 1). Locations of point counts were stratified randomly across deciduous, coniferous and riparian forest land cover. Each point was visited once (between the end of May to June) in the Shenandoah Valley and four times during the season (between the end of May to July) in the Virginia Peninsula. Point counts were conducted over 8 min, during which all birds seen or heard were recorded (Ralph et al. 1995). Observers estimated the distance to each object using a laser range finder (800 LH, Opti-Logic). All point counts were conducted during the morning hours of peak bird activity (15 min after sunrise to 10:00 A.M.) (Robbins 1981).

Breeding bird survey routes were obtained from the USGS (ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles/). The model developed by Leu et al. (2008) covers the entire western United States, for this reason, the routes used in this analysis are located in the western United States (Figure 2). BBS routes were visited once a year, either by the same or a different observer each year. Each survey route was 39.4-km long with stops at 800 m intervals. At each stop, a 3 min point count was conducted where all birds seen and heard within a 400 m buffer were recorded (BBS 2013).

We validated models using anuran survey datasets that were provided by NAAMP. Survey routes used in this analysis were located within the eastern United States (Figure 3). Each route consists of 10 stops and is surveyed based on land-cover present. In wetland land cover, surveys stops are spaced at least 0.80-km apart. Survey routes not located in wetland land cover are stratified by bodies of water including, ponds, vernal pools, road side ditches, etc. (NAAMP).

Invasive plant species comparison datasets were obtained from vegetation surveys that were used to inform satellite land-cover classification (GAP Analysis Program 2004). Survey points were located throughout the western United States (Figure 4). On each survey point, percent cheatgrass cover was estimated. Samples were then verified independently using satellite imagery.

Response Metrics

To compare the human impact intensity to the avian point count datasets, we first eliminated the possibility of spatial auto-correlation at the resolution of Sanderson et al.'s (2002) model. We placed a 1-km grid on the point count locations within Sanderson et al.'s (2002) map and randomly selected one point count from those included within each 1-km^2 area. The total number of point count locations used in the analysis were 87 for the Virginia Peninsula and 466 for the Shenandoah Valley.

For the point count avian analysis, we used program Distance (2009) to calculate the effective detection radius, or the distance in which an object is as likely to be missed as it is detected beyond the distance, for each species (Appendix 3). All observations that were outside a species' effective detection radius were not included in analyses. We then calculated the total abundance of individuals for each guild at each point count location to estimate the representation of each guild type at each point count location. Full synanthrope species were not observed enough times across all years to be included as a response metric, as result, we omitted the full synanthrope guild from our analysis.

For the BBS avian analysis, all three human footprint models were validated using BBS data from 2009 to 2012. The most recent model, Theobald et al.'s (2012) oldest dataset is from 2006. To incorporate lag effects (Perkins 2012; Manning et al. 2013), we added an additional 3 years and included the most recent BBS data available. A total of 949 BBS routes were used for analysis. We included the area of each buffer as a covariate, as the different shapes of the routes could affect the size of the buffer.

We included only BBS routes that were surveyed more than 70% of the total survey years. We found that the numbers of route visits closer to cities were not more likely visited than routes located in rural areas. We used an Incident Rate (IR) to eliminate the possibility of observer bias in sampling, where the IR for each guild is the proportion of times the guild was observed along the route compared to all other guilds observed at that route. For example, if the anthrophobic guild was observed 2 times and the casual synanthrope was observed 1 time over all survey years, the IR of the anthrophobic guild would be 0.5 and the casual synanthrope would be 0.25.

We reduced the original amphibian broad-resolution datasets to eliminate the potential for spatial auto-correlation in GIS (Esri 2013) by removing any routes that had overlapping buffers. This resulted in a total of 888 survey routes for the analysis. In the anuran analysis we again included the area of each buffer. We used the calling index to estimate the abundance of each guild at each survey route. The calling index ranked the calling intensity of each frog species on a scale of 1-3. A score of "1" indicated that individuals can be counted and there was space between calls, "2" calls of individuals can be distinguished but there was some overlapping of calls, and "3" represented a full chorus, calls were constant, continuous and overlapping (NAAMP, http://www.pwrc.usgs.gov/naamp). IR was estimated by summing the calling index scores for each guild at each route and then dividing by the total calling index for both guilds on each route. For example, if the sensitive species guild had 3 instances of a level 2 calling index that would total to 6. If the common species guild had 4 instances of level 3 calling index, that would total to 12. The incident rate of the sensitive species guild at that particular route would be 6 divided by the total of 18, or 0.33.

Cheatgrass survey points were reduced from the original 79483 points surveyed to 1985 survey points to eliminate the potential for spatial auto-correlation. We selected survey points to maintain the same proportion of points as the original sampling extent. Cheatgrass data collection was calculated in percent cover. We changed all percent cover classifications to cheatgrass occurrence at each location. If cheatgrass was observed at a survey point, it was counted as an occurrence

Statistical Analysis

We buffered survey routes and points by 200 m, 1 km, 2 km, and 3 km, but limited the buffer to 200 m for the point-count analysis in ArcGIS 10.1 (ESRI, 2013). We chose buffers sizes to incorporate the variation in dispersal distances (Katherina and Peter 2001; Berven and Grudzien 1990; Funk et al. 2005), territory, and home range sizes for avian species (Anich et al. 2009), and dispersion distances for cheatgrass (Feis 2013). All species, even those with limited mobility that function at relatively small spatial extents will have life histories that require examination across multiple scales (Funk et al. 2002). Human footprint intensity was averaged for each buffer using zonal statistics in ArcGIS 10.1 (ESRI 2013) and Geospatial Modelling Environment (Beyer 2012).

All statistical analyses and modeling were conducted using the R statistical language v. 2.13.2 (R Development Core Team 2011). We examined the variation in guild IR and abundance indices for avian point counts, BBS routes, and anuran survey routes in relation to human footprint intensity values using a general linear model. We used logistic regression to analyze the presence/absence of the cheatgrass within each survey point. Tests for normality indicated that datasets were not normally distributed. We transformed the data using log-transformation or square-root transformation to meet assumptions of normality. We compared model fit using Akaike's Information Criterion (AIC; Akaike 1974, Lebreton et al. 1992; Burnham and Anderson 2002). We chose the model with the lowest AIC value as the most parsimonious model with the best fit to the data.

Results

Avian Validation Results

For the point count analysis, Theobald et al.'s (2012) model outperformed Sanderson et al.'s (2002) and the null model for all guilds (ΔAIC>54 for casual synanthropes; ΔAIC>9 for tangential synanthropes; ΔAIC>77 for anthrophobic) (Appendix 2). Sanderson et al.'s (2002) model performed worse than the null model for the causal and anthrophobic guild (Appendix 2). Model performance did not differ between our predicted linear relationships, a logarithmic shape for casual synanthropes, and a quadratic shape for tangential synanthropes (Table 2; Appendix 2).

For the BBS analyses, Leu et al.'s (2008) model outperformed Sanderson et al.'s (2002), Theobald's et al.'s (2012) and the null model for every guild except the anthrophobic guild (ΔAIC>37 for full synanthropes; ΔAIC>29 for casual synanthropes; ΔAIC>25 for tangential synanthropes; Table 3 and Appendix 3), in which Theobald et al.'s (2012) model was the best predictor (ΔAIC>13). Results differed slightly across resolutions for all guilds (Appendix 3). For the full synanthrope guild, Leu et al.'s model performed best at the 1-km neighborhood, outperforming other models on every neighborhood when corrected for area of BBS route. Sanderson et al.'s (2002) model also greatly outperformed the null model at all resolutions for full synanthropes (ΔAIC>50), while Theobald et al.'s (2012) model did not outperform the null model at any neighborhood size (null ΔAIC>996). For the casual synanthropes, Leu et al.'s (2008) model performed best at the 200-m neighborhood with our predicted threshold relationship between human footprint intensity and species observations. Leu et al.'s (2008) model outperformed other models at all neighborhood with the exception of the 3-km neighborhood, where Sanderson et al.'s (2002) model outperformed the other models. All models outperformed the null model at every neighborhood (ΔAIC>7). Leu et al.'s (2008) model also performed best at the 200-m neighborhood for the tangential synanthropes, again matching our prediction of a quadratic relationship between human footprint intensity and species present. Leu et al.'s (2008) outperformed all models for all neighborhood sizes, with the exception of the 3-km neighborhood, where Theobald et al.'s (2012) model performed the best. All models outperformed the null model except for Sanderson et al.'s (2002) model when the area variable was included for both the linear and quadratic predicted relationships. Theobald et al.'s (2012) model outperformed every model at every neighborhood size for the anthrophobic guild (ΔAIC>13), whereas Leu et al.'s (2008) and Sanderson et al.'s (2002) model performed worse than the null model at any neighborhood size (Appendix 3).

Anuran validation results

Neither Theobald et al.'s (2012) model nor Sanderson et al.'s (2002) model performed better than the null model for either guild at any neighborhood (ΔAIC<2; Table 4).

Invasive species validation results

Theobald et al.'s (2012) model outperformed all models at every neighborhood for predicting the occurrence of cheatgrass (ΔAIC>13). Neither Leu et al.'s (2008) model nor Sanderson et al.'s (2002) model outperformed the null model at any neighborhood (ΔAIC<2; Table 5).

Discussion

Our validation and comparison of different human impact models to ecological processes is the first such systematic comparison in the literature. Although Leu et al. (2008) tested model predictions for different inputs (i.e., synanthropic predator model and exotic invasion model), and human footprint model, evaluation of predictions were limited to birds and exotic plants.

We evaluated human footprint intensity predictions across three taxa. In our analysis, we found that human footprint models can be used to predict certain ecological processes. Leu et al.'s (2008) model was a superior predictor for all avian species that use anthropogenic land-cover types whereas Theobald et al.'s (2012) model was best at predicting anthrophobic species, fine-resolution point count avian guilds, and invasive species occurrence. However, none of the models functioned as a completely predictive model.

In the point count analyses, Theobald et al.'s (2012) model outperformed Sanderson et al.'s (2002) model and the null model for all guilds. This could be due to differences in model resolution, Theobald et al. (2012) model input data were at a resolution of 30 m and 120 m, while Sanderson et al. (2002) model input data was at a 1-km resolution. The maximum distance for a species' effective area surveyed was 159.33 m for the American crow (*Corvus brachyrhynchos*). This is much smaller than the resolution of Sanderson et al.'s (2002) model. The difference in resolution and species detection could have resulted in the incorrect predictions from their model. Cooper and Belmaker (2010) argued that differences in forest habitat use could not be detected unless habitat types are more finely classified. The Sanderson et al. (2002) model was created at not only a larger resolution, but he also had a narrower classification of land-cover types. Land cover was classified into 5 types, "built-up", "agriculture", "mixed-use", and a few natural types. The "built-up" areas, which represented the largest cities as polygons in the National Imagery and Mapping Agency (NIMA) database, were assigned a score of 10. Scores 6-8 were assigned to different types of agricultural land, depending on level of input. Lower scores of 4 were assigned to mixed-use cover, and a value of 0 was given to other land-cover types, such as forests, grasslands, and Mediterranean ecosystems. Sanderson et al. (2002) also stated that given their method of land-cover classification, the land-cover types with a value of 0 were also subjected to various kinds of land uses. Given that some land-cover types classified as natural likely had some degree of anthropogenic disturbance, these classifications may have been too narrow to accurately predict where certain guilds would occur. Theobald et al.'s (2012) finer-scale resolution and more detailed land-cover classification likely made it a superior model at predicting avian species guilds at a fine-scale resolution.

In the BBS analyses, Leu et al.'s (2008) model outperformed Sanderson et al.'s (2002), Theobald's et al.'s (2012) and the null model for every guild except the anthrophobic guild, in which Theobald et al.'s (2012) model was the best predictor. The better fit for the other guilds could be due to the submodels incorporated into Leu et al.'s (2008) analysis. In their analysis, Leu et al. (2008) focused on the presence of synanthropic species, as well as land-cover change from humans including presence of invasive plant species and habitat fragmentation. Both of these habitats are likely to hold edge and generalist species (Klaus et al. 2004; Lampila et al 2005) which fall into the synanthropic, casual, and tangential synanthrope guilds. However, Leu et al.'s (2008) model was not the best predictor for casual synanthropes or tangential synanthropes at the 3-km neighborhood. Sanderson et al.'s (2002) model performed the best at the 3-km resolution and predicted a positive linear relationship for casual synanthropes. This model was based on comparatively larger resolution and more generalized land-cover types, which may increase predicative capabilities of this model for casual synanthropes. In addition, Theobald et al.'s (2012) model outperformed all other models at the 3-km neighborhood for the tangential synanthropes, predicting a negative linear relationship. Averaging the human footprint intensity to the larger neighborhoods may have resulted in Theobald et al.'s (2012) model predicting that tangential synanthrope species would have a similar relationship to human footprint intensity as anthrophobic species.

Leu et al.'s (2008) model emphasized land-cover types that were dominated by anthropogenic features and risks from anthropogenic predators, fires, and invasive species. The authors did not incorporate models that emphasized habitat suitable for anthrophobic species. Theobald et al.'s (2012) model, in contrast, incorporated land-cover features that were not dominated by anthropogenic land-cover features, including canopy cover, which has been suggested to serve as an accurate predictors for bird biodiversity (Radford et al 2005; Philpott and Bichler 2012). Sanderson et al.'s (2002) model may not predict well due to generalized land cover classifications. Although Sanderson et al.'s (2002) model performed better than the null model at predicting synanthrope and casual synanthrope species, the generalized land-cover classifications likely made their model a poor predictor in comparison to Leu et al.'s (2008) and Theobald et al.'s (2012) models.

In the anuran validation, neither Theobald et al.'s (2012) model nor Sanderson et al.'s (2002) model performed better than the null model for either guild at any resolution. This could be a result of models not including variables important to capture variation in amphibian movement across the landscape (Eigenbrod 2008). Neither model included agricultural ditches as potential habitat; ditches often serves as amphibian habitat for multiple species (Bonin et al. 1997; Ouellet et al. 1997). In addition, the time frame in which the data were collected (2000-2010) included three droughts in 2001, 2007, and 2008 (Cook et al. 2009). This may have affected amphibian distributions, which could have contributed to population decreases of the species in the survey areas at different times (Adams et al. 2011).

Theobald et al.'s (2012) model was the only model that validated well with the presence of invasive cheatgrass, despite Leu et al.'s (2008) model incorporating exotic plant invasion in a submodel. The differences in model prediction could be that the survey sites for cheatgrass were located in low human impact areas of Theobald et al.'s (2012) model. Rivera et al. (2011) found that the main predictors of cheatgrass spread and invasion did not include just land use, but also temperature, humidity, precipitation, and elevation. The combination of including topography, multiple agriculture land-cover types, sparse grassland, disturbed lands, and roads Theobald et al.'s (2012) model may have improved validation.

Overall, the models performed better than the null model in most validations. Sanderson et al.'s (2002) model had a better fit than the null model for the full and casual avian synanthropes, but did not validate with other taxa. This is particularly worrisome given that this model was cited the most for use in studies involving conservation of sensitive species (Alagador 2012; Bean et al. 2012; Rodríguez-Rodríguez et al. 2012) Leu et al.'s (2008) model performed the best for synanthrope, casual, and tangential synanthrope avian species, but was not accurate in predicting anthrophobic species or cheatgrass presence. Theobald et al.'s (2012) model proved to be the best model in the point count analysis at predicting all avian guilds (full synanthropes were not included), anthrophobic avian species in the BBS analysis, and presence of cheatgrass. The differences in model fit could be due to the input variables or the scales at which they were evaluated (Table 1). There was disagreement in spatial datasets included in three models, and we did not break down each model to compare input variables. Further analysis on what factors are more likely to contribute to species distribution is recommended. Although we did not compare individual model inputs, variables that likely increased the model accuracy included finer resolution; Leu et al. (2008) and Theobald et al. (2012) both used finer resolution (180m and 30m/120 resolution, respectively) than Sanderson et al.'s (2002) 1-km resolution. Detailed land-cover classification, including variation in types of agriculture also appeared to be important variables in a model's predictive capabilities. This level of detail used by Leu et al. (2008) was important for predicting all avian guilds that used anthropogenic habitat.

Each model incorporates critical information of the human footprint on the landscape and has the potential to cast preliminary forecasts of the effects of land use change on the environment (Theobald 2010). As the human population continues to increase and land-cover change expands, it is becoming even more important to set aside important landscapes and refuges for species that are sensitive to human sprawl (Robinson et al. 2005). Human footprint models provide a spatial representation of land uses, allowing land managers and environmental planners to develop priorities at the local and potentially regional scales (Leu et al. 2008). These models have proven to be an important tool in predicting where certain species are likely to occur. However, with the degree of variability in landscapes and climate, the use of these models as predictors must be applied cautiously (Kareiva and Wennergen 1995) as we found that not all models are created equal; model inputs and seasonal variability greatly affect how well each model performs. Species' occurrence can be affected by more than just proximity to urban areas. Distances to road, suburban land-cover, elevation, intensity of agricultural, amongst other variables all have profound effects on ecological processes (Citation). The resolution of each study area is also an important factor to include in any use of these models for management purposes.

As humans continue to overuse finite resources, the importance of understanding how specific species respond to human dominated landscapes will become essential in maintaining ecosystem health (Foley 2005). Human footprint models have the potential to be used to link fragmented landscapes (Alagador 2012), create species suitability models (Nuñez et al 2012; Galic et al 2013; Knick et al. 2013), observe the spread of disease in anuran populations (Adams et al. 2011), and predict the spread of contamination (Li and Hui 2001; Fuertes 2013), among many other uses. With the right input variables, these models have the potential for habitat design and great predictive capabilities, provided that land-cover detail and species specific responses are included.

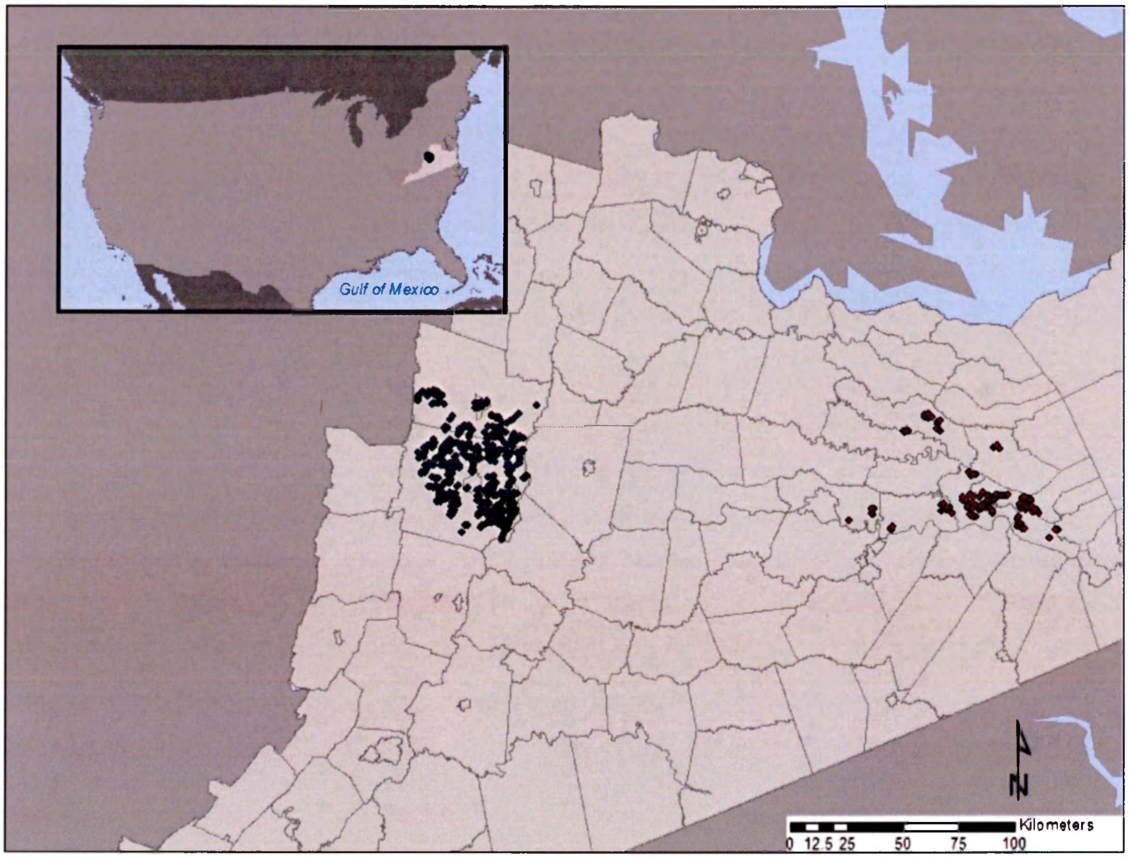

Figure 1. Location of avian point count survey data. Blue dots represent surveys conducted in the Shenandoah Valley (n=466), red dots represent surveys conducted in the Virginia Peninsula (n=67).

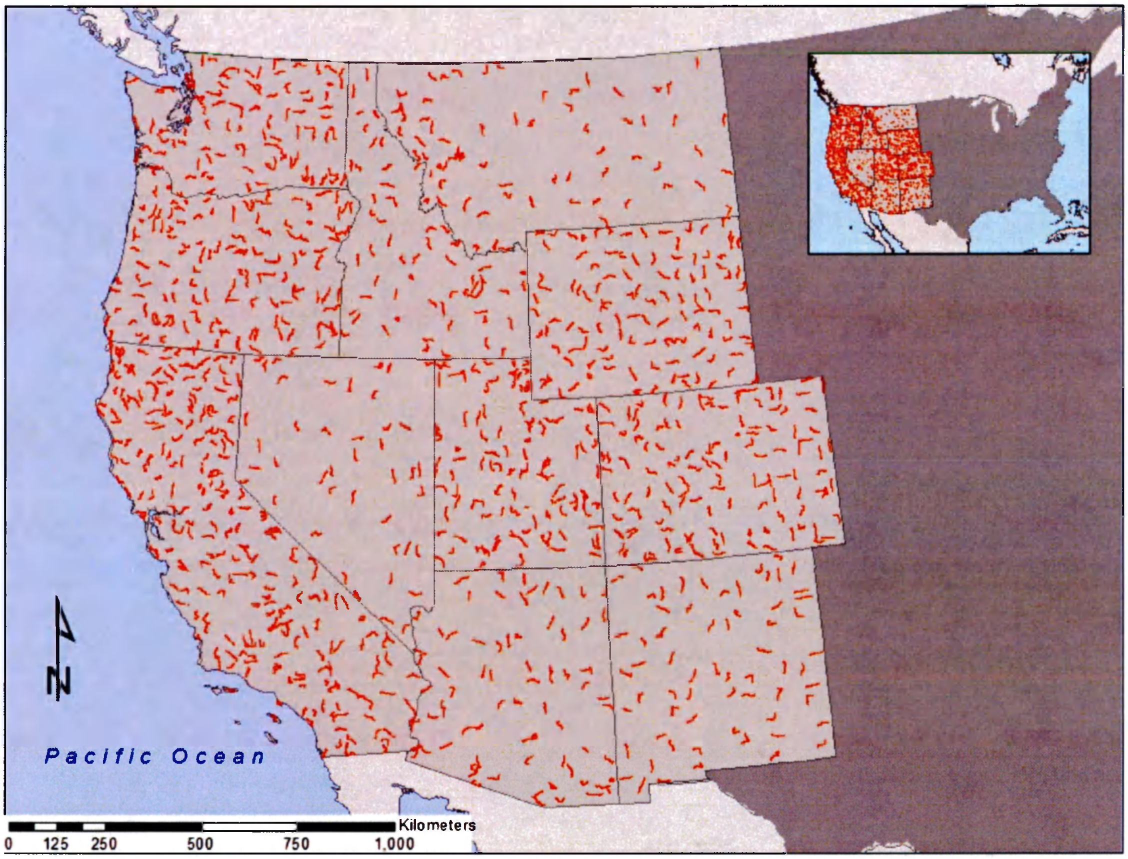

Figure 2. Breeding bird survey (BBS) route locations. Each line denotes a single BBS route (n=949).

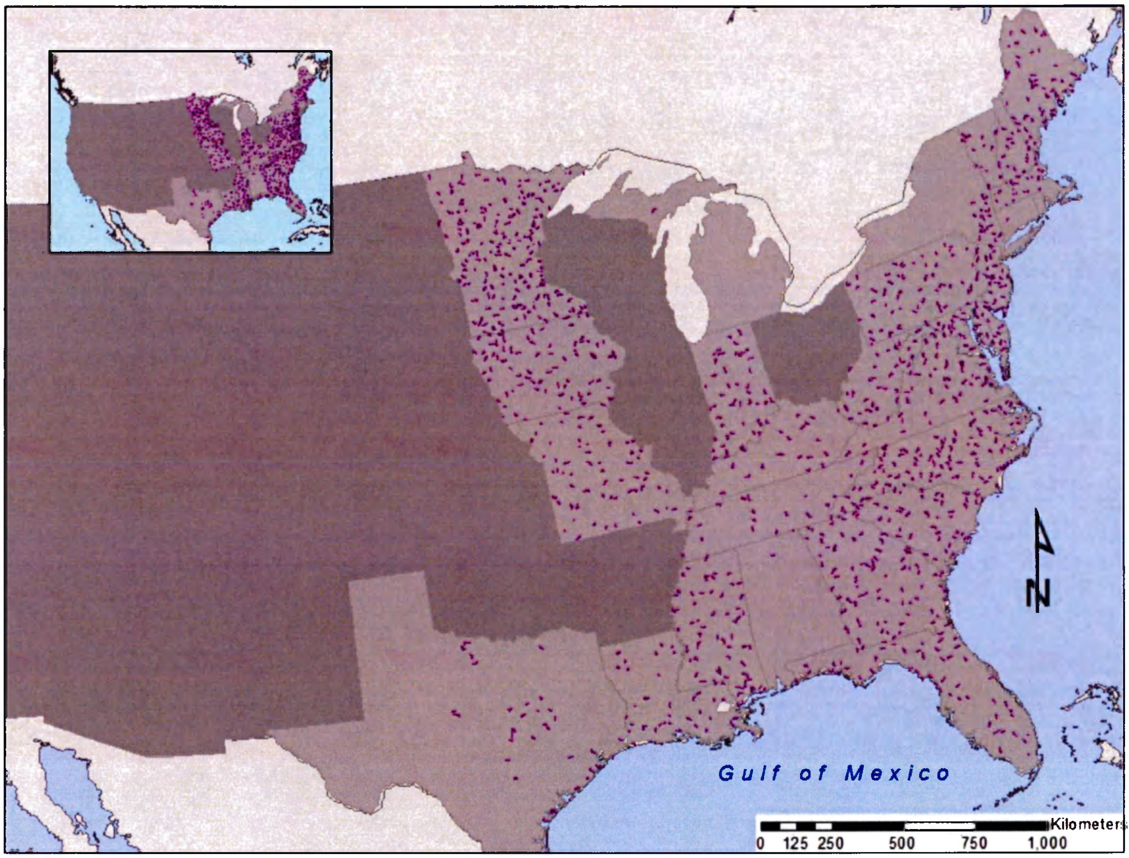

Figure 3. Location of NAAMP survey routes. Each line denotes a single route (n=888).

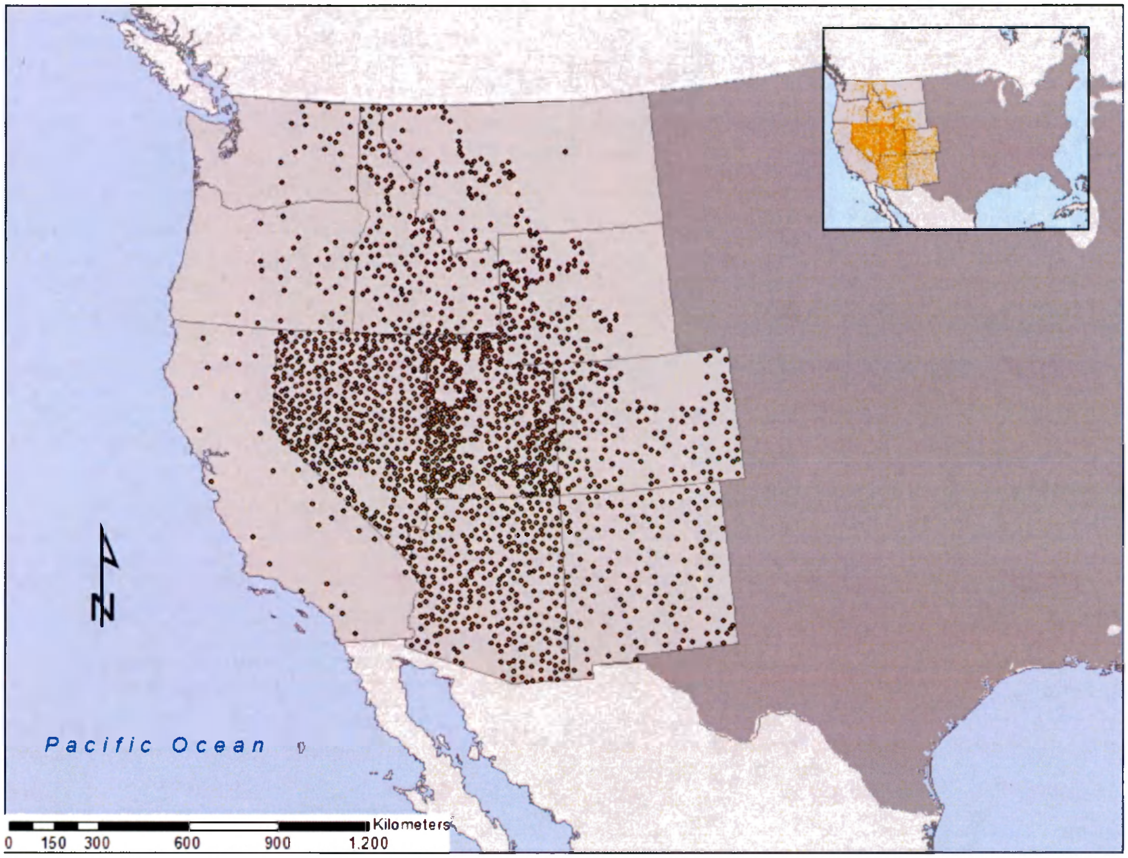

Figure 4. Location of the cheatgrass survey points. Each point denotes a single survey location (n=1984).

Table 1. Comparison of time frame of input variables, input variables, input variable resolution used in the development of Sanderson et al (2002), Leu et al. (2008) and Theobald et al. (2012) human footprint models.

	Sanderson, et al.	Leu, et al.	Theobald, et al.
Time frame of input variables (Publishing date)	1993-2001	1998-2006	2006-2011
Housing			X
Interstate highways	X	X	X
State highways	X	X	X
Secondary roads	X	X	X
Traffic volume			X
Walking distance	X		
Power lines	X	X	X
Agriculture	X	X	X
Oil and gas		X	X
Topography and Canopy Cover			X
Populated areas	X	X	X
Light pollution	X		
Human induced fires		X	
Global Biodiversity model (Globio)	X	X	
Resolution	1km	180m	120m (built on 30m model)
Model verified with	Point Counts, BBS, Amphibian, Cheatgrass	BBS, Cheatgrass	Point Counts, BBS, Amphibian, Cheatgrass

Table 2. Comparison of human footprint model performance based on regressing incident rate of three synanthropic avian guilds against human footprint intensity. Shown are all models within 2 Δ AIC values (for complete set of models see Appendix 2). For each models log likelihood (LL), slope (Beta), standard error for slope, AIC, and AIC weight (Wi) are shown.

Guild	Model	Scale	LL	AIC	delta AIC	Wi
Casual-Linear	Theobald	200m	101.55	-197.6	0.0	1
Casual-Threshold	Theobald	200m	101.00	-196.0	1.6	0.4503
Casual	Null	-		-143.3	54.3	2E-12
Casual-Linear	Sanderson	200m	-74.28	-142.6	55.0	1E-12
Casual-Threshold	Sanderson	200m	-73.95	-141.9	55.7	8E-13
Tangential-X	Theobald	200m	-20.65	49.3	0.0	1
Tangential-X^2	Theobald	200m	-	-	-	-
Tangential-Linear	Theobald	200m	-22.13	50.3	1.0	0.6145
Tangential-X	Sanderson	200m	-25.54	59.1	9.8	0.0075
Tangential-X^2	Sanderson	200m	-	-	-	-
Tangential	Null	-	-	61.0	11.7	0.0029
Tangential-Linear	Sanderson	200m	-28.23	62.5	13.2	0.0014
Anthrophobic	Theobald	200m	7.62	9.2	0.0	1
Anthrophobic	Null	-	-	86.8	77.6	1E-17
Anthrophobic	Sanderson	200m	88.81	88.8	79.6	5E-18

Table 3. Comparison of human footprint model performance based on regressing incident rate of four synanthropic avian guilds against human footprint intensity. Shown are all models within 2 Δ AIC values (for complete set of models see Appendix 2). For each models log likelihood (LL), slope (Beta), standard error for slope, and AIC weight (W_i) are shown.

Guild	Model	LL	Scale	Beta	Standard Error	AIC	delta AIC	W_i
Full	Leu	2777.90	Area+1km	-	-	5577.2	0.0	5.3E-01
Full	Null		-	-	-	4980.5	596.7	1.4E-130
Casual-Threshold	Leu	-547.95	200m	2.815	0.168	1101.9	0.0	7.1E-01
Casual-linear	Leu	-553.02	200m	0.231	0.014	1112.0	10.1	4.6E-03
Casual	Null		-	-	-	1346.2	244.3	6.4E-54
Tangential-X	Leu	1110.37	200m	0.076	0.021	2212.7	0.0	3.8E-01
Tangential-X^2	Leu	1110.37	200m	0.005	0.002	-	-	-
Tangential-Linear	Leu	1107.01	200m	0.021	0.002	2208.0	4.7	3.7E-02
Tangential	Null		-	-	-	2141.7	71.0	1.5E-16
Anthrophobic	Theobald	-563.38	Area+3km	-	-	1135.5	-0.5	6.8E-01
Anthrophobic	Null	-	-	-	-	1151.4	15.4	2.4E-04

Table 4. Comparison of human footprint model performance based on regressing incident rate of two anuran guilds against human footprint intensity derived from NAAMP data. Shown are all models. For each models log likelihood (LL), slope (Beta), standard error for slope, AIC, and AIC weight (W_i) are shown.

Guild	Model	Scale	LL	Beta	Standard Error	AIC	Delta AIC	W_i
Sensitive	Null	-	-	-	-	-1850.4	0	0.19
Sensitive	Sanderson	200m	927.481	-0.001877	0.022563	-1849	1.4	0.09
Sensitive	Sanderson	1km	927.387	-0.001519	0.00258	-1849	1.4	0.09
Sensitive	Sanderson	2km	927.397	-0.001566	0.002582	-1848.8	1.6	0.08
Sensitive	Sanderson	3km	927.352	-0.001361	0.002582	-1848.7	1.7	0.080
Sensitive	Theobald	200m	927.736	0.002962	0.002558	-1849.8	0.6	0.14
Sensitive	Theobald	1km	927.667	0.002437	0.002558	-1849.3	1.1	0.11
Sensitive	Theobald	2km	927.669	0.00244	0.002558	-1849.3	1.1	0.11
Sensitive	Theobald	3km	927.685	0.002485	0.002558	-1849.4	1	0.11
Common	Null	-	-	-	-	-2049.7	0	0.20
Common	Sanderson	200m	1027.100	0.001617	0.002243	-2048.2	1.5	0.09
Common	Sanderson	1km	1027.002	0.001287	0.002258	-2048	1.7	0.09
Common	Sanderson	2km	1027.014	0.00138	0.00226	-2048	1.7	0.09
Common	Sanderson	3km	1026.966	0.001138	0.00226	-2047.9	1.8	0.08
Common	Theobald	200m	1027.451	-0.002474	-0.002239	-2048.9	0.8	0.13
Common	Theobald	1km	1027.265	-0.002064	0.002239	-2048.5	1.2	0.11
Common	Theobald	2km	1027.266	-0.002068	0.002239	-2048.5	1.2	0.11
Common	Theobald	3km	1027.282	-0.002106	0.002239	2048.28	1.4	0.01

Table 5. Comparison of human footprint model performance based on occurrence of cheatgrass (*Bromus tectorum*) against human footprint intensity derived from Gap Analysis data. Shown are all models. For each models log likelihood (LL), slope (Beta), standard error for slope, AIC, and AIC weight (W_i) are shown.

Model	Scale	LL	Beta	Standard Error	AIC	delta AIC	W_i
Theobald	2km	724.783	0.200	0.07739	1453.6	0	0.434163
Theobald	1km	724.852	0.196	0.07581	1453.7	0.1	0.412989
Theobald	3km	725.903	0.165	0.07655	1455.8	2.2	0.14452
Leu	1km	730.427	0.118	0.06697	1464.9	11.3	0.001527
Leu	3km	730.629	0.103	0.06698	1465.3	11.7	0.00125
Leu	2km	730.130	0.122	0.06621	1464.3	10.7	0.002061
Null	-	-	-	-	1465.6	12	0.001076
Sanderson	3km	731.221	0.068	0.07371	1466.4	12.8	0.000721
Sanderson	2km	731.346	0.057	0.07294	1466.7	13.1	0.000621
Sanderson	1km	731.484	0.043	0.07185	1467.0	13.4	0.000534

Appendix 1. Johnston et al. (2001) Classification for species observed on BBS routes.

Common Name	Scientific Name	Classification
Montezuma Quail	*Cyrtonyx montezumae*	Non-Synanthrope
Northern Bobwhite	*Colinus virginianus*	Casual synanthrope
California Quail	*Callipepla californica*	Casual synanthrope
Gambel's Quail	*Callipepla gambelii*	Non-Synanthrope
Scaled Quail	*Callipepla squamata*	Non-Synanthrope
Mountain Quail	*Oreortyx pictus*	Non-Synanthrope
Chukar	*Alectoris chukar*	Non-Synanthrope
Gray Partridge	*Perdix perdix*	Non-Synanthrope
Ring-necked Pheasant	*Phasianus colchicus*	Non-Synanthrope
Spruce Grouse	*Falcipennis canadensis*	Non-Synanthrope
White-tailed Ptarmigan	*Lagopus leucura*	Non-Synanthrope
Ruffed Grouse	*Bonasa umbellus*	Non-Synanthrope
Sharp-tailed Grouse	*Tympanuchus phasianellus*	Non-Synanthrope
Lesser Prairie-Chicken	*Tympanuchus pallidicinctus*	Non-Synanthrope
Greater Prairie-Chicken	*Tympanuchus cupido*	Non-Synanthrope
Gunnison Sage-Grouse	*Centrocercus minimus*	Non-Synanthrope
Greater Sage-Grouse	*Centrocercus urophasianus*	Non-Synanthrope
Wild Turkey	*Sphyrapicus thyroideus*	Tangential synanthrope
Mourning Dove	*Zenaida macroura*	Tangential synanthrope
White-winged Dove	*Meleagris gallopavo*	Casual synanthrope
Eurasian Collared-Dove	*Streptopelia decaocto*	Casual synanthrope
Spotted Dove	*Spilopelia chinensis*	Non-Synanthrope
Inca Dove	*Scardafella inca*	Non-Synanthrope
Ruddy Ground-Dove	*Columbina talpacoti*	Non-Synanthrope
Common Ground-Dove	*Columbina passerina*	Non-Synanthrope
Rock Pigeon	*Columba livia*	full synanthrope
Band-tailed Pigeon	*Patagioenas fasciata*	Casual synanthrope
Yellow-billed Cuckoo	*Coccyzus americanus*	Tangential synanthrope
Black-billed Cuckoo	*Coccyzus erythropthalmus*	Non-Synanthrope
Greater Roadrunner	*Geococcyx californianus*	Non-Synanthrope
Common Poorwill	*Phalaenoptilus nuttallii*	Tangential synanthrope
Mexican Whip-poor-will	*Caprimulgus arizonae*	Non-Synanthrope
Common Nighthawk	*Chordeiles minor*	Tangential synanthrope
Lesser Nighthawk	*Chordeiles acutipennis*	Non-Synanthrope
Vaux's Swift	*Chaetura vauxi*	Non-Synanthrope
Chimney Swift	*Chaetura pelagica*	full synanthrope
Black Swift	*Cypseloides niger*	Non-Synanthrope
White-throated Swift	*Aeronautes saxatalis*	Non-Synanthrope

Violet-crowned Hummingbird	*Amazilia violiceps*	Non-Synanthrope
Broad-billed Hummingbird	*Cynanthus latirostris*	Non-Synanthrope
Blue-throated Hummingbird	*Lampornis clemenciae*	Non-Synanthrope
Magnificent Hummingbird	*Eugenes fulgens*	Non-Synanthrope
Anna's Hummingbird	*Calypte anna*	Tangential synanthrope
Costa's Hummingbird	*Calypte costae*	Non-Synanthrope
Black-chinned Hummingbird	*Archilochus alexandri*	Non-Synanthrope
Calliope Hummingbird	*Stellula calliope*	Tangential synanthrope
Broad-tailed Hummingbird	*Selasphorus platycercus*	Tangential synanthrope
Allen's Hummingbird	*Selasphorus sasin*	Non-Synanthrope
Rufous Hummingbird	*Selasphorus rufus*	Tangential synanthrope
Elegant Trogon	*Trogon elegans*	Non-Synanthrope
Belted Kingfisher	*Megaceryle alcyon*	Non-Synanthrope
Acorn Woodpecker	*Melanerpes formicivorus*	Non-Synanthrope
Red-headed Woodpecker	*Melanerpes erythrocephalus*	Non-Synanthrope
Lewis's Woodpecker	*Melanerpes lewis*	Tangential synanthrope
Gila Woodpecker	*Melanerpes uropygialis*	Non-Synanthrope
Williamson's Sapsucker	*Sphyrapicus thyroideus*	Tangential synanthrope
Red-breasted Sapsucker	*Sphyrapicus ruber*	Tangential synanthrope
Red-naped Sapsucker	*Sphyrapicus nuchalis*	Tangential synanthrope
Downy Woodpecker	*Picoides pubescens*	Tangential synanthrope
Hairy Woodpecker	*Picoides villosus*	Tangential synanthrope
American Three-toed Woodpecker	*Picoides dorsalis*	Non-Synanthrope
Black-backed Woodpecker	*Picoides arcticus*	Non-Synanthrope
Nuttall's Woodpecker	*Picoides nuttallii*	Tangential synanthrope
Ladder-backed Woodpecker	*Picoides scalaris*	Non-Synanthrope
Arizona Woodpecker	*Picoides arizonae*	Non-Synanthrope
White-headed Woodpecker	*Picoides albolarvatus*	Non-Synanthrope
Gilded Flicker	*Colaptes chrysoides*	Non-Synanthrope
(Red-shafted Flicker) Northern Flicker	*Colaptes auratus*	Tangential synanthrope
Pileated Woodpecker	*Dryocopus pileatus*	Non-Synanthrope
Northern Beardless-Tyrannulet	*Camptostoma imberbe*	Non-Synanthrope
Greater Pewee	*Contopus pertinax*	Non-Synanthrope
Olive-sided Flycatcher	*Contopus cooperi*	Tangential synanthrope
Western Wood-Pewee	*Contopus sordidulus*	Tangential synanthrope
Eastern Wood-Pewee	*Contopus virens*	Non-Synanthrope
Pacific-slope Flycatcher	*Empidonax difficilis*	Tangential synanthrope
Cordilleran Flycatcher	*Empidonax occidentalis*	Tangential synanthrope
Willow Flycatcher	*Empidonax traillii*	Tangential synanthrope

Alder Flycatcher	*Empidonax alnorum*	Non-Synanthrope
Least Flycatcher	*Empidonax minimus*	Tangential synanthrope
Hammond's Flycatcher	*Empidonax hammondii*	Tangential synanthrope
Dusky Flycatcher	*Empidonax oberholseri*	Tangential synanthrope
Gray Flycatcher	*Empidonax wrightii*	Tangential synanthrope
Buff-breasted Flycatcher	*Empidonax fulvifrons*	Non-Synanthrope
Black Phoebe	*Sayornis nigricans*	Tangential synanthrope
Eastern Phoebe	*Sayornis phoebe*	Tangential synanthrope
Say's Phoebe	*Sayornis saya*	Tangential synanthrope
Vermilion Flycatcher	*Pyrocephalus rubinus*	Non-Synanthrope
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	Non-Synanthrope
Ash-throated Flycatcher	*Myiarchus cinerascens*	Tangential synanthrope
Brown-crested Flycatcher	*Myiarchus tyrannulus*	Non-Synanthrope
Thick-billed Kingbird	*Tyrannus crassirostris*	Non-Synanthrope
Eastern Kingbird	*Tyrannus tyrannus*	Non-Synanthrope
Tropical Kingbird	*Tyrannus melancholicus*	Non-Synanthrope
Cassin's Kingbird	*Tyrannus vociferans*	Non-Synanthrope
Western Kingbird	*Tyrannus verticalis*	Non-Synanthrope
Scissor-tailed Flycatcher	*Tyrannus forficatus*	Non-Synanthrope
Sulphur-bellied Flycatcher	*Myiodynastes luteiventris*	Non-Synanthrope
Loggerhead Shrike	*Lanius ludovicianus*	Tangential synanthrope
Gray Vireo	*Vireo vicinior*	Non-Synanthrope
Red-eyed Vireo	*Vireo olivaceus*	Tangential synanthrope
Warbling Vireo	*Vireo gilvus*	Tangential synanthrope
Bell's Vireo	*Vireo bellii*	Tangential synanthrope
Hutton's Vireo	*Vireo huttoni*	Tangential synanthrope
Plumbeous Vireo	*Vireo plumbeus*	Non-Synanthrope
Cassin's Vireo	*Vireo cassinii*	Non-Synanthrope
Blue-headed Vireo	*Vireo solitarius*	Non-Synanthrope
Steller's Jay	*Cyanocitta stelleri*	Tangential synanthrope
Blue Jay	*Cyanocitta cristata*	Tangential synanthrope
Western Scrub-Jay	*Aphelocoma californica*	Tangential synanthrope
Mexican Jay	*Aphelocoma wollweberi*	Non-Synanthrope
Gray Jay	*Perisoreus canadensis*	Tangential synanthrope
Pinyon Jay	*Gymnorhinus cyanocephalus*	Non-Synanthrope
Clark's Nutcracker	*Nucifraga columbiana*	Tangential synanthrope
Black-billed Magpie	*Pica hudsonia*	Tangential synanthrope
Yellow-billed Magpie	*Pica nuttalli*	Non-Synanthrope
Common Raven	*Corvus corax*	Tangential synanthrope
Chihuahuan Raven	*Corvus cryptoleucus*	Non-Synanthrope
American Crow	*Corvus brachyrhynchos*	Tangential synanthrope

Northwestern Crow	*Corvus caurinus*	Non-Synanthrope
Horned Lark	*Eremophila alpestris*	Casual synanthrope
Purple Martin	*Progne subis*	full synanthrope
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	Tangential synanthrope
Bank Swallow	*Riparia riparia*	Tangential synanthrope
Violet-green Swallow	*Tachycineta thalassina*	Non-Synanthrope
Tree Swallow	*Tachycineta bicolor*	Tangential synanthrope
Cliff Swallow	*Petrochelidon pyrrhonota*	Tangential synanthrope
Cave Swallow	*Petrochelidon fulva*	Tangential synanthrope
Barn Swallow	*Hirundo rustica*	Tangential synanthrope
Bridled Titmouse	*Baeolophus wollweberi*	Non-Synanthrope
Oak Titmouse	*Baeolophus inornatus*	Non-Synanthrope
Juniper Titmouse	*Baeolophus ridgwayi*	Non-Synanthrope
Black-capped Chickadee	*Poecile atricapillus*	Tangential synanthrope
Mountain Chickadee	*Poecile gambeli*	Non-Synanthrope
Boreal Chickadee	*Poecile hudsonicus*	Tangential synanthrope
Mexican Chickadee	*Poecile sclateri*	Non-Synanthrope
Chestnut-backed Chickadee	*Poecile rufescens*	Non-Synanthrope
Verdin	*Auriparus flaviceps*	Non-Synanthrope
Bushtit	*Psaltriparus minimus*	Non-Synanthrope
Red-breasted Nuthatch	*Sitta canadensis*	Tangential synanthrope
White-breasted Nuthatch	*Sitta carolinensis*	Tangential synanthrope
Pygmy Nuthatch	*Sitta pygmaea*	Non-Synanthrope
Brown Creeper	*Certhia americana*	Tangential synanthrope
Bewick's Wren	*Thryomanes bewickii*	Non-Synanthrope
House Wren	*Troglodytes aedon*	Tangential synanthrope
Sedge Wren	*Cistothorus platensis*	Non-Synanthrope
Marsh Wren	*Cistothorus palustris*	Non-Synanthrope
Cactus Wren	*Campylorhynchus brunneicapillus*	Non-Synanthrope
Rock Wren	*Salpinctes obsoletus*	Non-Synanthrope
Canyon Wren	*Catherpes mexicanus*	Non-Synanthrope
American Dipper	*Cinclus mexicanus*	Tangential synanthrope
Wrentit	*Chamaea fasciata*	Non-Synanthrope
Golden-crowned Kinglet	*Regulus satrapa*	Tangential synanthrope
Ruby-crowned Kinglet	*Regulus calendula*	Tangential synanthrope
California Gnatcatcher	*Polioptila californica*	Non-Synanthrope
Black-tailed Gnatcatcher	*Polioptila melanura*	Non-Synanthrope
Blue-gray Gnatcatcher	*Polioptila caerulea*	Non-Synanthrope
Townsend's Solitaire	*Myadestes townsendi*	Tangential synanthrope

Mountain Bluebird	*Sialia currucoides*	Tangential synanthrope
Western Bluebird	*Sialia mexicana*	Tangential synanthrope
Eastern Bluebird	*Sialia sialis*	Non-Synanthrope
Varied Thrush	*Ixoreus naevius*	Tangential synanthrope
American Robin	*Turdus migratorius*	Casual synanthrope
Veery	*Catharus fuscescens*	Non-Synanthrope
Swainson's Thrush	*Catharus ustulatus*	Non-Synanthrope

Appendix 2. Nature Serve (2014) and IUCN (2014) Classification for species observed on NAAMP routes.

Common Name	Scientific Name	Classification
American Bullfrog	*Lithobates catesbeianus*	common
American toad	*Anaxyrus americanus*	common
Barking tree frog	*Hyla gratiosa*	Sensitive
Barking Treefrog	*Hyla gratiosa*	Sensitive
Boreal Chorus Frog	*Pseudacris maculata*	Sensitive
Brimley's Chorus Frog	*Pseudacris brimleyi*	common
Cajun Chorus Frog	*Pseudacris fouquettei*	common
Canadian toad	*Anaxyrus hemiophrys*	Sensitive
Carolina Gopher Frog	*Lithobates capito*	Sensitive
Carpenter Frog	*Lithobates virgatipes*	Sensitive
Cliff Chirping Frog	*Eleutherodactylus marnockii*	common
Coastal Plain Toad	*Incilius nebulifer*	common
Cope's gray tree frog	*Hyla chrysoscelis*	common
Couch's Spadefoot	*Scaphiopus couchii*	common
Crawfish Frog	*Lithobates areolatus*	Sensitive
Cuban Treefrog	*Osteopilus septentrionalis*	common
Eastern Narrow-mouthed Toad	*Gastrophryne carolinensis*	common
Eastern Spadefoot	*Scaphiopus holbrookii*	common
Florida Bog Frog	*Lithobates okaloosae*	Sensitive
Fowler's toad	*Anaxyrus fowleri*	Sensitive
Giant Toad	*Rhinella marina*	common
Gray Treefrog	*Hyla versicolor*	common
Great Plains Narrow-mouthed Toad	*Gastrophryne olivacea*	common
Great Plains toad	*Anaxyrus cognatus*	common
Green Frog	*Lithobates clamitans*	Sensitive
Green Treefrog	*Hyla cinerea*	common
Greenhouse Frog	*Eleutherodactylus planirostris*	common
Hurter's Spadefoot	*Scaphiopus hurterii*	common
Hyla avivoca	*Hyla avivoca*	common
Illinois Chorus Frog	*Pseudacris illinoensis*	Sensitive
Little Grass Frog	*Pseudacris ocularis*	common
Mink Frog	*Lithobates septentrionalis*	common
Mountain Chorus Frog	*Pseudacris brachyphona*	common
New Jersey chrous frog	*Pseudacris kalmi*	Sensitive
Northern cricket frog	*Acris crepitans*	common
Northern Leopard Frog	*Lithobates pipiens*	common

Oak toad	*Anaxyrus quercicus*	common
Ornate Chorus Frog	*Pseudacris ornata*	common
Pickerel Frog	*Lithobates palustris*	common
Pig Frog	*Lithobates grylio*	common
Pine Barrens Treefrog	*Hyla andersonii*	Sensitive
Pine Woods Treefrog	*Hyla femoralis*	common
Plains Leopard Frog	*Lithobates blairi*	Sensitive
Plains Spadefoot	*Spea bombifrons*	common
Rio Grande Chirping Frog	*Eleutherodactylus cystignathoides*	common
Rio Grande Leopard Frog	*Lithobates berlandieri*	common
River Frog	*Lithobates heckscheri*	common
Southern Chorus Frog	*Pseudacris nigrita*	common
Southern cricket frog	*Acris gryllus*	common
Southern Leopard Frog	*Lithobates sphenocephalus*	common
southern toad	*Anaxyrus terrestris*	common
Spotted Chorus Frog	*Pseudacris clarkii*	Sensitive
spring peeper	*Pseudacris crucifer*	common
Squirrel Treefrog	*Hyla squirella*	common
Strecker's Chorus Frog	*Pseudacris streckeri*	common
Upland Chorus Frog	*Pseudacris feriarum*	common
Western Chorus Frog	*Pseudacris triseriata*	Sensitive
Wood frog	*Lithobates sylvaticus*	Sensitive

Appendix 3. Comparison of human footprint model performance based on regressing incident rate of four synanthropic avian guilds against human footprint intensity derived Theobald et al. (2012) model. Shown are all models. For each models log likelihood (LL), AIC, and AIC weight (W_i) are shown.

Guild	Model	LL	Scale	AIC	deltaAIC	W_i
Full	Leu	2777.90	Area+1km	-5577.2	0.0	5.3E-01
Full	Leu	2790.66	1km	-5575.3	1.9	2.0E-01
Full	Leu	2790.46	200m	-5574.9	2.3	1.7E-01
Full	Leu	2777.90	Area+200m	-5573.9	3.3	1.0E-01
Full	Leu	2777.90	Area+2km	-5562.8	14.4	3.9E-04
Full	Leu	2781.46	2km	-5556.9	20.3	2.1E-05
Full	Leu	2777.90	Area+3km	-5547.8	29.4	2.2E-07
Full	Leu	2772.86	3km	-5539.7	37.5	3.8E-09
Full	Sanderson	2535.80	Area+3km	-5063.6	513.6	1.6E-112
Full	Sanderson	2534.83	Area+2km	-5061.7	515.5	6.1E-113
Full	Sanderson	2532.71	200m	-5059.4	517.8	1.9E-113
Full	Sanderson	2533.71	Area+1km	-5059.4	517.8	1.9E-113
Full	Sanderson	2532.23	3km	-5058.5	518.7	1.2E-113
Full	Sanderson	2532.18	1km	-5058.4	518.8	1.2E-113
Full	Sanderson	2531.97	2km	-5057.9	519.3	9.1E-114
Full	Sanderson	2532.75	Area+200m	-5057.5	519.7	7.4E-114
Full	Null		-	-4980.5	596.7	1.4E-130
Full	Theobald	2009.85	Area+2km	-4014.2	1563.0	0.0
Full	Theobald	2008.05	Area+3km	-4010.6	1566.6	0.0
Full	Theobald	2005.69	Area+1km	-4006.1	1571.1	0.0
Full	Theobald	2004.03	2km	-4005.5	1571.7	0.0
Full	Theobald	2002.16	1km	-4001.6	1575.6	0.0
Full	Theobald	2000.83	3km	-3999.2	1578.0	0.0
Full	Theobald	1989.64	200m	-3976.3	1600.9	0.0
Full	Theobald	1990.08	Area+200m	-3975.0	1602.2	0.0
Casual-Threshold	Leu	-547.95	200m	1101.9	0.0	7.1E-01
Casual-Threshold	Leu	-547.94	Area+200m	1103.9	2.0	2.6E-01
Casual-linear	Leu	-553.02	200m	1112.0	10.1	4.6E-03
Casual-linear	Leu	-553.02	Area+200m	1114.0	12.1	1.7E-03
Casual-Threshold	Leu	-558.00	1km	1122.0	20.1	3.1E-05
Casual-Threshold	Leu	-557.87	Area+1km	1123.7	21.8	1.3E-05
Casual-linear	Leu	-560.90	1km	1127.8	25.9	1.7E-06
Casual-linear	Leu	-569.53	Area+1km	1129.4	27.5	7.6E-07
Casual-linear	Sanderson	-663.46	3km	1131.8	29.9	2.3E-07
Casual-linear	Sanderson	-665.26	Area+1km	1138.5	36.6	8.1E-09

Casual-Threshold	Sanderson	-664.06	Area+1km	1138.5	36.6	8.1E-09
Casual-Threshold	Leu	-566.85	Area+2km	1141.7	39.8	1.6E-09
Casual-Threshold	Leu	-568.02	2km	1142.0	40.1	1.4E-09
Casual-linear	Leu	-560.71	Area+2km	1142.2	40.3	1.3E-09
Casual-linear	Leu	-568.48	2km	1143.0	41.1	8.5E-10
Casual-linear	Leu	-569.53	Area+3km	1147.1	45.2	1.1E-10
Casual-Threshold	Leu	-570.24	Area+3km	1148.5	46.6	5.4E-11
Casual-linear	Leu	-571.82	3km	1149.6	47.7	3.1E-11
Casual-Threshold	Leu	-571.82	3km	1150.5	48.6	2.0E-11
Casual-linear	Theobald	-652.70	Area+3km	1301.7	199.8	2.9E-44
Casual-linear	Theobald	-648.70	Area+2km	1302.8	200.9	1.7E-44
Casual-linear	Theobald	-648.33	2km	1303.3	201.4	1.3E-44
Casual-linear	Theobald	-648.58	3km	1303.8	201.9	1.0E-44
Casual-linear	Theobald	-648.93	1km	1304.5	202.6	7.2E-45
Casual-linear	Theobald	-646.99	Area+1km	1306.1	204.2	3.3E-45
Casual-linear	Theobald	-652.85	200m	1312.3	210.4	1.5E-46
Casual-linear	Theobald	-646.42	Area+200m	1314.0	212.1	6.3E-47
Casual-Threshold	Theobald	-653.71	Area+3km	1316.2	214.3	2.1E-47
Casual-Threshold	Theobald	-655.36	2km	1317.3	215.4	1.2E-47
Casual-Threshold	Theobald	-654.31	Area+2km	1317.4	215.5	1.1E-47
Casual-Threshold	Theobald	-655.49	3km	1317.6	215.7	1.0E-47
Casual-Threshold	Theobald	-655.90	1km	1318.4	216.5	6.9E-48
Casual-Threshold	Theobald	-655.76	Area+1km	1320.2	218.3	2.8E-48
Casual-Threshold	Theobald	-659.50	200m	1325.6	223.7	1.9E-49
Casual-Threshold	Theobald	-659.24	Area+200m	1327.1	225.2	9.0E-50
Casual-linear	Sanderson	-663.90	2km	1333.9	232.0	3.0E-51
Casual-linear	Sanderson	-663.22	Area+3km	1334.4	232.5	2.3E-51
Casual-Threshold	Sanderson	-665.38	Area+3km	1334.4	232.5	2.3E-51
Casual-Threshold	Sanderson	-664.64	3km	1335.3	233.4	1.5E-51
Casual-linear	Sanderson	-664.24	200m	1335.9	234.0	1.1E-51
Casual-linear	Sanderson	-664.15	1km	1336.1	234.2	1.0E-51
Casual-Threshold	Sanderson	-665.08	2km	1336.1	234.2	1.0E-51
Casual-linear	Sanderson	-664.22	Area+2km	1336.5	234.6	8.1E-52
Casual-Threshold	Sanderson	-661.88	Area+2km	1336.5	234.6	8.1E-52
Casual-Threshold	Sanderson	-665.33	1km	1336.7	234.8	7.4E-52
Casual-Threshold	Sanderson	-665.38	200m	1336.8	234.9	7.0E-52
Casual-linear	Sanderson	-665.06	Area+200m	1338.1	236.2	3.7E-52
Casual-Threshold	Sanderson	-663.96	Area+200m	1338.1	236.2	3.7E-52
Casual-linear	Null	-	-	1346.2	244.3	6.4E-54
Casual-Threshold	Null	-	-	1346.2	244.3	6.4E-54
Tangential-X	Leu	1110.37	200m	-2212.7	0.0	3.8E-01

Tangential-X^2	Leu	1110.37	200m	-	-	-
Tangential-$X+X^2$	Leu	1110.51	Area+200m	-2211.0	1.7	1.6E-01
Tangential-Linear	Leu	1107.01	200m	-2208.0	4.7	3.7E-02
Tangential-Linear	Leu	1107.09	Area+200m	-2206.2	6.5	1.5E-02
Tangential-X	Leu	1102.68	1km	-2197.4	15.3	1.8E-04
Tangential-X^2	Leu	1102.68	1km	-	-	-
Tangential-Linear	Leu	1101.03	1km	-2196.1	16.6	9.6E-05
Tangential-$X+X^2$	Leu	1102.68	Area+1km	-2195.4	17.3	6.7E-05
Tangential-Linear	Leu	1101.04	Area+1km	-2194.1	18.6	3.5E-05
Tangential-Linear	Leu	1097.37	2km	-2188.7	24.0	2.4E-06
Tangential-Linear	Leu	1096.02	Area+2km	-2187.4	25.3	1.2E-06
Tangential-Linear	Theobald	1096.62	1km	-2187.2	25.5	1.1E-06
Tangential-Linear	Theobald	1096.46	2km	-2186.9	25.8	9.6E-07
Tangential-Linear	Theobald	1094.75	3km	-2186.6	26.1	8.3E-07
Tangential-Linear	Theobald	1096.83	Area+2km	-2186.6	26.1	8.3E-07
Tangential-Linear	Theobald	1093.73	Area+3km	-2186.6	26.1	8.3E-07
Tangential-$X+X^2$	Leu	1096.14	Area+2km	-2186.2	26.5	6.8E-07
Tangential-X	Theobald	1097.04	1km	-2186.1	26.6	6.4E-07
Tangential-X^2	Theobald	1097.04	1km	-	-	-
Tangential-Linear	Theobald	1097.29	Area+1km	-2185.7	27.0	5.3E-07
Tangential-X	Theobald	1096.72	2km	-2185.4	27.3	4.5E-07
Tangential-X^2	Theobald	1096.72	2km	-2185.4	27.3	4.5E-07
Tangential-Linear	Leu	1095.61	3km	-2185.2	27.5	4.1E-07
Tangential-$X+X^2$	Theobald	1075.78	Area+2km	-2185.2	27.5	4.1E-07
Tangential-$X+X^2$	Theobald	1075.80	Area+3km	-2185.1	27.6	3.9E-07
Tangential-X	Theobald	1096.49	3km	-2185.0	27.7	3.7E-07
Tangential-X^2	Theobald	1096.49	3km	-	-	-
Tangential-$X+X^2$	Theobald	1075.67	Area+1km	-2184.5	28.2	2.9E-07
Tangential-Linear	Theobald	1093.69	200m	-2184.4	28.3	2.8E-07
Tangential-Linear	Leu	1096.02	Area+3km	-2184.0	28.7	2.3E-07
Tangential-X	Leu	1097.81	2km	-2183.5	29.2	1.8E-07

Tangential-X^2	Leu	1097.81	2km	-	-	-
Tangential-X	Leu	1095.76	3km	-2183.5	29.2	1.8E-07
Tangential-X^2	Leu	1095.76	3km	-	29.2	1.8E-07
Tangential-$X+X^2$	Leu	1096.14	Area+3km	-2182.3	-	-
Tangential-X	Theobald	1094.75	200m	-2181.5	31.2	6.5E-08
Tangential-X^2	Theobald	1094.75	200m	-2181.5	31.2	6.5E-08
Tangential-$X+X^2$	Theobald	1075.94	Area+200m	-2179.6	33.1	2.5E-08
Tangential-Linear	Theobald	1097.32	Area+200m	-2179.5	33.2	2.4E-08
Tangential-X	Sanderson	1075.67	1km	-2143.3	69.4	3.3E-16
Tangential-X^2	Sanderson	1075.67	1km	-	-	-
Tangential-X	Sanderson	1075.61	200m	-2143.2	69.5	3.1E-16
Tangential-X^2	Sanderson	1075.61	200m	-	-	-
Tangential-Linear	Sanderson	1074.57	3km	-2143.1	69.6	3.0E-16
Tangential-X	Sanderson	1075.50	2km	-2143.0	69.7	2.8E-16
Tangential-X^2	Sanderson	1075.50	2km	-	-	-
Tangential-X	Sanderson	1075.43	3km	-2142.9	69.8	2.7E-16
Tangential-X^2	Sanderson	1075.43	3km	-	-	-
Tangential-Linear	Sanderson	1074.11	2km	-2142.2	70.5	1.9E-16
Tangential-$X+X^2$	Sanderson	1075.80	Area+200m	-2141.9	70.8	1.6E-16
Tangential-Linear	Sanderson	1073.88	1km	-2141.8	70.9	1.5E-16
Tangential-Linear	Sanderson	1074.88	Area+3km	-2141.8	70.9	1.5E-16
Tangential-Linear	Null	-	-	-2141.7	71.0	1.5E-16
Tangential-X	Null	-	-	-2141.7	71.0	1.5E-16
Tangential-X^2	Null	-	-	-	-	-
Tangential-$X+X^2$	Sanderson	1075.78	Area+2km	-2141.6	71.1	1.4E-16
Tangential-$X+X^2$	Sanderson	1075.94	Area+3km	-2141.6	71.1	1.4E-16
Tangential-$X+X^2$	Sanderson	1075.67	Area+1km	-2141.3	71.4	1.2E-16
Tangential-Linear	Sanderson	1073.56	200m	-2141.1	71.6	1.1E-16
Tangential-Linear	Sanderson	1074.33	Area+2km	-2140.7	72.0	8.9E-17
Tangential-Linear	Sanderson	1073.94	Area+200m	-2139.9	72.8	6.0E-17
Tangential-Linear	Sanderson	1073.89	Area+1km	-2139.8	72.9	5.7E-17
Anthrophobic	Theobald	-563.38	Area+3km	1135.5	-0.5	6.8E-01
Anthrophobic	Theobald	-564.53	3km	1136.0	0.0	5.3E-01
Anthrophobic	Theobald	-564.20	Area+1km	1136.0	0.0	5.3E-01

Anthrophobic	Theobald	-564.62	1km	1136.2	0.2	4.8E-01
Anthrophobic	Theobald	-563.78	Area+2km	1136.3	0.3	4.5E-01
Anthrophobic	Theobald	-563.60	Area+200m	1136.4	0.4	4.3E-01
Anthrophobic	Theobald	-564.78	2km	1136.6	0.6	3.9E-01
Anthrophobic	Theobald	-565.18	200m	1137.4	1.4	2.6E-01
Anthrophobic	Leu	-570.72	Area+3km	1149.4	13.4	6.5E-04
Anthrophobic	Leu	-571.17	Area+2km	1150.3	14.3	4.1E-04
Anthrophobic	Sanderson	-571.52	Area+3km	1151.0	15.0	2.9E-04
Anthrophobic	Leu	-570.72	Area+1km	1151.0	15.0	2.9E-04
Anthrophobic	Null	-	-	1151.4	15.4	2.4E-04
Anthrophobic	Sanderson	-571.77	Area+200m	1151.5	15.5	2.3E-04
Anthrophobic	Sanderson	-571.84	Area+2km	1151.7	15.7	2.1E-04
Anthrophobic	Leu	-570.72	Area+200m	1151.7	15.7	2.1E-04
Anthrophobic	Sanderson	-571.89	Area+1km	1151.8	15.8	2.0E-04
Anthrophobic	Leu	-573.02	3km	1152.0	16.0	1.8E-04
Anthrophobic	Leu	-573.36	1km	1152.2	16.2	1.6E-04
Anthrophobic	Leu	-573.12	2km	1152.2	16.2	1.6E-04
Anthrophobic	Sanderson	-573.53	3km	1153.1	17.1	1.0E-04
Anthrophobic	Sanderson	-573.63	200m	1153.3	17.3	9.2E-05
Anthrophobic	Sanderson	-573.65	2km	1153.3	17.3	9.2E-05
Anthrophobic	Leu	-573.66	200m	1153.3	17.3	9.2E-05
Anthrophobic	Sanderson	-573.68	1km	1153.4	17.4	8.8E-05

Chapter 3: Linking Sensitive Species Occurrence to Land Cover Types

Introduction

Nearly half of the world's population lives in urban areas (Watson 1993). The proportion of the population living in cities has grown from 29% in 1950 to 50% in 2010 (UN 2011). By 2050, 69% or 6.3 billion people are projected to be living in urban areas and nearly as many humans will occupy cities as inhabit the earth today (Brown et al. 1995; UN 2011). Near the end of the last century, human settlements covered 1-6% of the earth's surface; agriculture covered another 12% (Meyer and Turner 1992). This conversion of land cover from natural to urban has been documented to produce some of the greatest local extinctions of native species (Marzluff 2001; McKinney 2002). The conversion of land cover to urbanization is often more lasting than other types of habitat loss (McKinney 2002). The infrastructure involved in creating skyscrapers, houses, power lines, and roads have permanent and lasting effects on ecosystem functioning (Hooke and Martín-Duque 2012).

As human populations continue to increase, there will be subsequent increases in urban areas, suburban areas, roads, and agriculture. Global croplands, pastures, plantations, and urban areas have expanded in recent decades, accompanied by large increases in energy, water, and fertilizer consumption compounded with considerable losses of biodiversity (Foley et al. 2005). The need to provide food, fiber, water, and shelter to the increasing human population drives the conversion of "natural" landscapes (i.e. intact landscapes where dispersal is not impeded) to anthropogenic landscapes (Foley et al. 2005).

The loss of habitat to urbanization has pronounced effects on native fauna. Large areas of land cover are first converted, creating degraded fragments and land cover dominated by exotic invasive plants. Over time, fragments continue to decrease in size and the spread of invasive species further degrades the landscape (Marzluff 2001).

It is the responses of individual organisms to a change in land cover that can disrupt ecosystem function, which can further compound the effects of the initial land cover change (Hansen et al. 2001). Species abundance and distribution are influenced by land use and land-cover quality (Pulliam 1988). Land-cover change also fragments habitats, which further increases the distances among habitat patches, and limits the ability of species to move across the landscape (Primack and Miao 1992; Andrén 1992; Hansen et al. 2001). Anthropogenic changes in land cover have direct effects on the species living within that area. Therefore, it is important for land managers to be able to predict which species will likely occur in a landscape (Lichstein 2002). While there are several studies that have addressed the need for understanding species response to land cover availability, additional studies are needed to further evaluate habitat use regarding amount and size of preferred land cover (Hansen and Urban 1992; Andrén 1992).

Habitat use depends on the area and type of land cover (Forman et al. 1976; Galli et al. 1976). Forman et al. (1976) found that the number of forest songbirds increased with increasing forest patch size and Mazerolle and Villard (1999) found that landscape characteristics were significant predictors of species presence. Identifying minimum land cover composition and configuration requirements for species that respond similarly to anthropogenic land cover can provide important information on species' population viability. Wood et al. (in press) found that there was an increase in synanthropic species associated with suburban developments but an overall decrease in species richness, even when those suburban developments were within protected reserves. Miller et al. (2003) found that bird species diversity decreased from rural to urban riparian areas. Identifying common habitat requirements among species improves management for species of concern, species richness, and diversity.

It is well established that some species are more sensitive to human-dominated landscapes than others. Johnston et al. (2001) classified avian species depending on their use of human-dominated land cover: "full synanthrope", species that depend on anthropogenic features throughout entire annual cycle; "casual synanthrope" species that exploit anthropogenic features; "tangential synanthrope", species that occasionally exploit anthropogenic features; and "non-synanthrope" (anthrophobic), species that avoid anthropogenic features.

As the human population continues to increase, species that avoid human-dominated land cover, anthrophobic species, may decline. It is therefore important to know minimum land cover requirements for sensitive species and whether there are parallels in land cover requirements among sensitive species. The objectives of this study were to evaluate 1) if there are underlying minimum land cover requirements for sensitive species and 2) the degree to which anthropogenic features and human land use influence the distribution of these species.

We created models based on land cover classification for seven anthrophobic species and one synanthropic species, for comparison. The anthrophobic species we selected included the bushtit (*Psaltriparus minimus*), marsh wren (*Cistothorus palustris*), Swainson's thrush (*Catharus ustulatus*), hermit thrush (*Catharus guttatus*), northern parula (*Parula americana*), ovenbird (*Seiurus aurocapillus*), grasshopper sparrow (*Ammodramus savannarum*). We compared these species to a full synanthropic species, one that is commonly found in areas dominated by anthropogenic land features, the European starling (*Sturnus vulgaris*). This species served as a control to evaluate signal strength of habitat-species interactions based on coarse-scale bird survey data and satellite imagery derived land-cover classifications. Moreover, we included the European starling to evaluate whether human land-cover types have similar weight in species occurrence models. From this comparison, we can determine if anthropogenic land-cover types are ranked highly for both anthrophobic species avoidance and on full synanthrope occurrence.

The results of this study will provide land managers and regional planners information on how natural and biologically diverse land cover can be integrated into urban and suburban designs. Even small changes in the spatial patterning of land cover can produce dramatic ecological responses (Turner and Gardner 1991). The information obtained from this study on the amount, and type of land cover required by sensitive species can be implemented for regional planning.

Methods

Study Area

Our study area included the conterminous United States (Figure 5). The cumulative species ranges included in our analysis spanned the conterminous United States and all major land cover types.

Avian Data

We used Breeding Bird Survey (BBS) data from 2005-2012 to estimate species occurrence. We used eight years of BBS data to derive robust species occurrence estimates. BBS routes were obtained from the USGS (ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles/) for the conterminous United States (Figure 5). BBS routes were visited once a year, either by the same or a different observer. Each survey route was 39.4 kilometers long with stops at 800-m intervals. At each stop, a 3 min point count was conducted in June where all birds seen and heard within a 400 m buffer were recorded (BBS, 2013).

The American bushtit is a year-round resident in the western United States ranging from coastal Washington to Utah, to western Texas (Figure 6). It breeds in deciduous woodland, coniferous forests, oak woodland, chaparral, scrub, and residential neighborhoods, often near streams (Alderfer 2006; Audubon 2014). The marsh wren is a resident along the coasts of the United States and breeds throughout the northern part of the conterminous United States (Figure 7). It prefers emergent vegetation for nesting habitat and inhabits freshwater and saltwater marshes, roadside ditches, and small agricultural runoff sites (Audubon 2014). The Swainson's thrush breeds throughout the Pacific Northwest and the Atlantic Northeast (Figure 8). Its breeding habitat includes coniferous woodlands with dense undergrowth and deciduous wooded areas in the Pacific Northwest and mixed forests in the Atlantic Northeast (Clements 2001; Audubon 2014). The hermit thrush breeds throughout the northern conterminous United States, along the West Coast and mountain regions in the Northwest (Figure 9). The hermit thrush breeds typically in conifer-dominated forests and deciduous forests, usually in areas with little undergrowth (Alderfer 2006). The northern parula breeds throughout the eastern United States from Maine to eastern Texas (Figure 10). This species is primarily a forest-dwelling species that breeds in habitat consisting of high tree diversity, variable canopy height, coniferous forests, and swamps (Ehrlich et al. 1988). The ovenbird breeds throughout the Northeast and northern plains, from Maine to Arkansas, to Montana (Figure 11). It breeds in mature deciduous and mixed forests, especially in areas with little undergrowth (Sibley 2000). The grasshopper sparrow breeds throughout most the conterminous United States, excluding the Southwest and parts of the Northwest (Figure 12). Preferred habitats include upland meadows, pastures, hayfields, and croplands (Arbib 1988; Vickery 1996; Smith 2008). The European starling breeds in human dominated habitats throughout the conterminous United States (Figure 13). This species is common in agriculture, suburban, and urban areas (Sibley 2000).

Land cover dataset

We obtained 706 land-cover types from the Landfire (USGS 2013) data set and reclassified some land-cover types in GIS (ESRI 2013) into natural and anthropogenic land cover that may be used by species included in the analysis. In this study, anthropogenic land cover is defined as any land cover that was classified as "developed", while natural land cover included all other types. We reclassified the land cover types into forest, grassland, shrubland, riparian, wetland, high development, medium development, low development, open development, developed grassland, developed forest, and agriculture. We also included extent of highways and secondary roads throughout each species' breeding range (TIGER 2000).

Statistical Analysis

We reduced the analyses extent to states where the species is known to breed (Sibley 2013; Figures 5-13). We also included the latitude demarking the center of each BBS route habitat use could change along latitudinal gradients.

We included only the BBS routes that were surveyed more than 70% of the total survey years from 2005-2012. We chose an 8-year interval to remove the possibility of observer bias in occurrence estimates. If a species was observed at least 70% of the time, that route was given a "1"and a "0" if a specie was observed less that 70% of the time. For example, if a bushtit was observed on a particular route 6 out of 8 years, a 75% occurrence, we code that route as "1". We chose the threshold of 70% because it eliminates observer bias and is most indicative that a species is present in this location.

We buffered BBS routes by 200 m, 1 km, 2 km, and 3 km to analyze proportion of land cover types. Buffers reflect within season movement for studied species. Wiens and Rotenberry (1987), Wittenberger (1991), and Pearson (1993) found that birds respond to their environment at multiple spatial scales, ranging from local scales to regional scales. Donovan et al. (1997) also found that it is important to look at multiple scales because the relative importance of different scales varies depending on land cover suitability. To calculate the proportion of land cover within each scales we used focal statistics in ArcGIS (ESRI 2013). We addressed the possibility of spatial autocorrelation by removing any route where 3-km buffers overlapped.

For each species we first ran a Spearman Rank correlation to check for multicolinearity among land cover types or buffers. We scaled all variables to allow comparison of parameter estimates. We then ran univariate general linear models to identify best scale for each land cover type and human disturbance. We included all variables that had a lower AIC value than the null model and did not correlate in the final models. If variables correlated, we chose the variable with the lowest AIC value for the analysis. All statistical analyses and modeling were conducted using the R statistical language v. 2.13.2 (R Development Core Team 2011).

We used the dredge function (MuMni package) to obtain the weight for each variable. To derive the final model for each species, we model averaged parameter estimates across all models whose combined AIC weights totaled 0.95(Burnham and Anderson 2004). To evaluate final model predictive capability, we calculated the area under the curve (AUC; pROC package). Calculating the AUC is a way to test the accuracy of the model; the scale of the AUC ranges from 0 to 1, where a value of 1 signifies a perfect model (Darlington 1990). For models with an AUC greater than 0.7 (Darlington 1990), we compared directionality and magnitude of parameter estimates to determine if there were any parallels in land cover type and scale.

Results

Developed Medium land cover was highly correlated to Developed High among all models. Developed Open land cover was highly correlated to Developed Low for all species but not the European starling. In addition, we removed Developed Open land cover from all models as it overlapped with less than 10% of BBS routes.

Bushtit

Correlations existed between Shrubland_{2km} and Shrubland_{3km} with Grassland_{2km} and Grassland_{3km}. The 95% candidate variable set included $\text{Agriculture}_{200m}$, Agriculture_{1km}, Development Medium_{1km}, Forest_{2km}, Secondary Roads_{200m}, Grassland_{3km},

Riparian_{3km}, Latitude, and Shrubland_{200m}, and Shrubland_{3km}. Variables with the highest AIC weights included Agriculture_{1km}, Development Medium_{2km}, and Shrubland_{200m} (Figure 14). A total of 4 models were used for the final model (Appendix 3):

Bushtit occurrence (SE) = -4.93 (0.21) -1.69 (0.05) Agriculture_{1km} -0.63 (0.03) Developed Medium_{2km} -1.05 (0.03) Forest_{2km} + 0.17 (0.10) Secondary Roads_{200m} + 0.72 (0.03) Shrubland_{200m}

The Bushtit model predicted well with an AUC value of 0.84. This model accurately predicts the species' occurrence.

Marsh wren

The 95% candidate variable set included Shrubland_{3km}, Wetland_{200m}, Highway_{3km}, Development High_{3km}, Riparian_{200m}, Riparian_{3km}, Secondary Roads_{1km}, $\text{Agriculture}_{200m}$, Agriculture_{1km}, Grassland_{3km}, and latitude. Variables with the highest AIC weights included Shrubland_{3km} and Latitude (Figure 15). A total of 12 models were used for the final model (Appendix 4):

Marsh wren occurrence (SE) = -6.98 (0.11) -1.67 (0.03) Shrubland_{3km} -1.67 (0.03) Latitude + 0.33 (0.01) Wetland_{200m} -0.90 (0.02) Development High_{3km} - 0.56 (0.02) Riparian_{200m} -1.11 (0.03) Secondary Roads_{1km}

The marsh wren model predicted well with an AUC value of 0.87. This model accurately predicts the species' occurrence.

Swainson's thrush

Variables included in the 95% candidate variable set were Ruparian_{200m}, Riparian_{2km}, Riparian_{3km}, Forest_{3km}, Shrubland_{200m}, Wetland_{200m}, Developed Grassland_{3km}, Agriculture_{3km}, Secondary Roads_{200m}, Highways_{1km}, Developed Forest_{2km}, Grassland_{200m},

Grassland_{3km}, and Development High_{1km}. Variables with the highest weights included Shrubland_{200m}, Riparian_{200m}, and Latitude (Figure 16). A total of 12 models were used for the final model (Appendix 5).

Swainson's thrush occurrence (SE) = -4.32 (0.07) - 0.63 (0.05) Shrubland_{200m} + 0.98 (0.07) Riparian_{200m} -1.43 (0.10) Latitude -1.44 (0.10) Wetland_{200m} + 0.09 (0.01) Forest_{2km} -0.11 (0.01) Developed Grassland_{3km} -0.11 (0.01) Highway_{1km}

The Swainson's thrush model had an AUC value of 0.39. This model does not accurately predict the species' occurrence.

Hermit thrush

Variables included in the 95% candidate model were Latitude, $\text{Agriculture}_{200m}$, Developed Medium_{3km}, Wetland_{1km}, Grassland_{200m}, Secondary Roads_{3km}, Shrubland_{200m}, Highway_{3km}, Riparian_{1km}, Developed Grassland_{200m}, Developed Forest_{200m}, and Forest_{200m}. Variables with the highest weight included; Riparian_{1km}, $\text{Agriculture}_{200m}$, Wetland_{1km} (Figure 17). A total of 8 models were used for the final model (Appendix 6):

Hermit thrush occurrence (SE) = -3.91 (0.40) + 1.17 (0.11) Riparian_{1km} -1.82 (0.08) $\text{Agriculture}_{200m}$ -2.66 (0.12) Wetland_{1km} + 0.32 (0.02) Shrubland_{200m} -1.07 (0.06) Development High_{3km} -0.32 (0.02) Secondary road_{3km} -0.21 (0.01) Highways_{3km}

The hermit thrush model had an AUC value of 0.29. This model does not accurately predict the species' occurrence.

Northern Parula

Correlations existed between all buffers for Agriculture and Riparian, with the exception of the 200 m buffer. Variables included in the 95% candidate variable set were Forest_{200m}, $\text{Agriculture}_{200m}$, Development High_{3km}, Riparian_{200m}, Highway_{3km},

$\text{Wetland}_{200\text{m}}$, Developed Forest_{200}, $\text{Riparian}_{3\text{km}}$, Secondary $\text{Roads}_{3\text{km}}$, $\text{Shrubland}_{1\text{km}}$, and Developed $\text{Grassland}_{2\text{km}}$. Variables in the final averaged model had equal weights, with the exception of $\text{Wetland}_{1\text{km}}$ and $\text{Highways}_{3\text{km}}$ (Figure 18). A total of 3 models were used for the final model (Appendix 7):

Northern parula occurrence (SE) = -4.52 (0.63) + 0.75 (0.09) Development $\text{High}_{3\text{km}}$ + 0.75 (0.09) Developed $\text{Forest}_{2\text{km}}$ - 0.89 (0.12)$\text{Shrubland}_{200\text{m}}$ + 0.85 (0.12) $\text{Riparian}_{200\text{m}}$ + 0.78 (0.11) Latitude - 0.50 (0.09) $\text{Wetland}_{1\text{km}}$ - 0.30 (0.09) $\text{Highways}_{3\text{km}}$

The northern parula model predicted well with an AUC value of 0.91. This model accurately predicts the species' occurrence.

Ovenbird

Correlations existed between $\text{Agriculture}_{1\text{km}}$, $\text{Agriculture}_{2\text{km}}$, and $\text{Agriculture}_{3\text{km}}$ with $\text{Riparian}_{2\text{km}}$, and $\text{Riparian}_{3\text{km}}$. Variables included in the model analysis were $\text{Grassland}_{200\text{m}}$, Forest_{200}, $\text{Forest}_{1\text{km}}$, $\text{Forest}_{2\text{km}}$, $\text{Forest}_{3\text{km}}$, $\text{Agriculture}_{200\text{m}}$, Developed $\text{High}_{1\text{km}}$, Secondary $\text{Roads}_{1\text{km}}$, Developed $\text{Grassland}_{2\text{km}}$, $\text{Riparian}_{200\text{m}}$, $\text{Riparian}_{3\text{km}}$, Highways3km, Developed Forest1km, $\text{Shrubland}_{3\text{km}}$, and $\text{Wetland}_{3\text{km}}$. Variables had equal weight in the model, with the exception of $\text{Agriculture}_{200\text{m}}$, which had a slightly less weight (Figure 19). A total of 2 models were used for the final averaged model (Appendix 8):

Ovenbird occurrence (SE) = -3.78 (0.23) - 1.67 (0.27) $\text{Grassland}_{200\text{m}}$ + 0.28 (0.09) $\text{Forest}_{200\text{m}}$ - 1.43 (0.10) Latitude - 1.44 (0.10) $\text{Wetland}_{200\text{m}}$ + 0.09 (0.01) $\text{Forest}_{2\text{km}}$ -0.11 (0.01) Developed $\text{Grassland}_{3\text{km}}$ - 0.11 (0.01) $\text{Highways}_{1\text{km}}$

The ovenbird model predicted well with an AUC value of 0.85. This model accurately predicts the species' occurrence.

Grasshopper Sparrow

Correlations existed between Agriculture$_{3km}$ and Riparian$_{3km}$. The candidate variable set included Developed Medium$_{2km}$, Riparian$_{200m}$, Developed Forest$_{1km}$, Secondary Roads$_{3km}$, Highways$_{3km}$, Shrubland$_{3km}$, Agriculture$_{3km}$, and Developed Grassland$_{200m}$. Variables with the highest AIC weights were Agriculture$_{3km}$, Wetland$_{3km}$, Riparian$_{200m}$, and Latitude (Figure 20). A total of 4 models were used for the final model (Appendix 9).

Grasshopper sparrow occurrence (SE) = -3.91 (0.40) + 1.17 (0.17) Agriculture$_{3km}$ - 1.71 (0.17) + Developed Medium$_{2km}$ 0.43 (0.05) Wetland$_{3km}$ - 0.96 (0.10) Riparian$_{200m}$ - 0.37 (0.04) Latitude - 0.26 (0.04) Highways$_{3km}$ + 0.01 (0.003) Developed Grassland$_{200m}$

The grasshopper sparrow model predicted well with an AUC value of 0.87. This model accurately predicts the species' occurrence.

European Starling

The candidate variable set included in the model average were Forest$_{200m}$, Agriculture$_{200m}$, development_High$_{3km}$, Grassland$_{200m}$, Riparian$_{200m}$, Highway$_{3km}$, Wetland$_{200m}$, Developed Forest$_{200m}$, Shrubland$_{2km}$, and Development Low$_{1km}$. All variables had equal AIC weights, with the exception of Development Low$_{1km}$, which had a slightly smaller weight (Figure 21). A total of 2 models were used for the final model (Appendix 10).

European Starling occurrence (SE) = 0.14 (0.05) + 0.48 (0.07) Agriculture$_{200}$ -0.36 (0.08) Developed Forest$_{200m}$ + 0.54 (0.07) Developed High$_{3km}$ + 0.24 (0.08)

Developed Low_{1km} - 0.66 (0.09) Riparian_{200m} + 0.37 (0.06) Shrubland_{2km} - 0.51 (0.07) Wetland_{200m}

The European starling model predicted well with an AUC value of 0.81. This model accurately predicts the species' occurrence.

Discussion

There were a few patterns and parallels between the species we modeled. Natural land cover types that each species was known to breed in generally had high AIC weights. Anthropogenic covariates commonly included in models were either Development High or Development Medium. Our analyses are consistent with previous research that suggests anthrophobic birds avoid highly developed areas (Galli et al. 1976; Beck and George 2000; Proppe et al. 2013). Highways and secondary roads were included in the models for grasshopper sparrow, marsh wren, and northern parula. These results are similar to previous research that suggests most species do not occur along roads and highways (Baumgartner 1934; Kuitunen 1998).

Natural land cover covariates with high weights occurred at the smaller buffer sizes of 200 m and 1km. In contrast, Development High and Medium covariates occurred at large buffer size classes of 1 km and 3 km. Road covariates also occurred at larger scales, ranging from 1 km to 3 km. These results suggest that breeding habitat use for species analyzed in this study occurs at smaller scales but that these species respond to development and roads at larger scales.

Human development covariates also had high model weight with the European starling; this suggests that human development is one of the biggest drivers for species' occurrence in all of the species we modeled. In addition, every type of natural land cover in the European starling model related negatively to occurrence.

Our models performed very well (AUC >0.8), with the exception of the hermit thrush (AUC = 0.29) and the Swainson's thrush (AUC = 0.39). Previous research has shown that habitat suitability models often do not perform well when tested on thrushes. Rittenhouse et al. (2010) found that habitat suitability indexes based on land cover requirements were inaccurate at predicting where wood thrush (*Hylocichla mustelina*) would occur. Thrushes could be keying in on more fine-scaled habitat features such as leaf litter (Laughlin et al. 2013), stem density (Chisholm and Leonarda 2008), or microhabitat foliage (Beck and George 2000).

The grasshopper sparrow occurrence model was also an outlier (Figure 20). Presence of agriculture and wetlands had the highest model weight. Developed grasslands, to a lesser extent, were also an indicator of species occurrence. Johnston et al. (2001) may have incorrectly identified the grasshopper sparrow as an anthrophobic species; several studies show that this species can successfully breed in pasture and hay field land cover (Wiens 1973; Benoît et al. 2008; Benoît et al. 2010; Irvin 2013). A further breakdown of the agriculture land cover types might add more insight into which types of agriculture this species uses during the breeding season.

Our results suggest that anthrophobic species avoid areas of high human development. These results are consistent with previous literature on rare and sensitive species occurrence (With and Crist 1995; McKinney 2000; Marzluff et al. 2001). This is problematic because urban areas are increasing in size. Since the 1950s, humans have been increasingly moving back to urban areas (UN 2011). This trend of more populated urban areas is occurring all over the world. Africa, for example, has the fastest rate of urbanization in the world (UN 2011). As cities continue to grow at a rapid rate, and merging together, it is becoming very important for regional planners to include habitat for local native species (Marzluff et al. 2001).

Several studies evaluated how to best manage urban land cover to promote native species. Beck and George (2000) found that the varied thrush (*Ixoreus naevius*) was more likely to occur near human settlements if the forest did not have an abrupt edge. Also, Zurita and Bellocq (2012) found that including variable tree height and tree densities in parks increases bird diversity. Smooth transitions from natural land cover to human settlement as well as diversity in land cover may have the potential to increase native species and biodiversity in land cover with anthropogenic influence. If regional planners and land managers make an effort to manage green spaces and rural lots for native species, there is potential for greater native bird diversity in anthropogenic land cover. Miller et al. (2003) studied riparian woodlands that were located within and outside human settlements. They found that as development increased, riparian woodlands had less native trees and shrubs, less ground cover and shrub cover, and lower bird species richness. This indicates a potential for better management of green spaces in areas of human development. Improved management practices can increase biodiversity, reduce the spread of invasive species, and increase the overall health of that ecosystem as well as surrounding ecosystems (McKinney 2002).

The results of this study can also be used to parameterize human footprint models that incorporate the biological response of species to anthropogenic land cover and land managers can incorporate these requirements into landscape management. Creating human footprint models that are based on biological response will be an important planning tool to gauge the effects of anthropogenic land cover types on anthrophobic species and ecological processes.

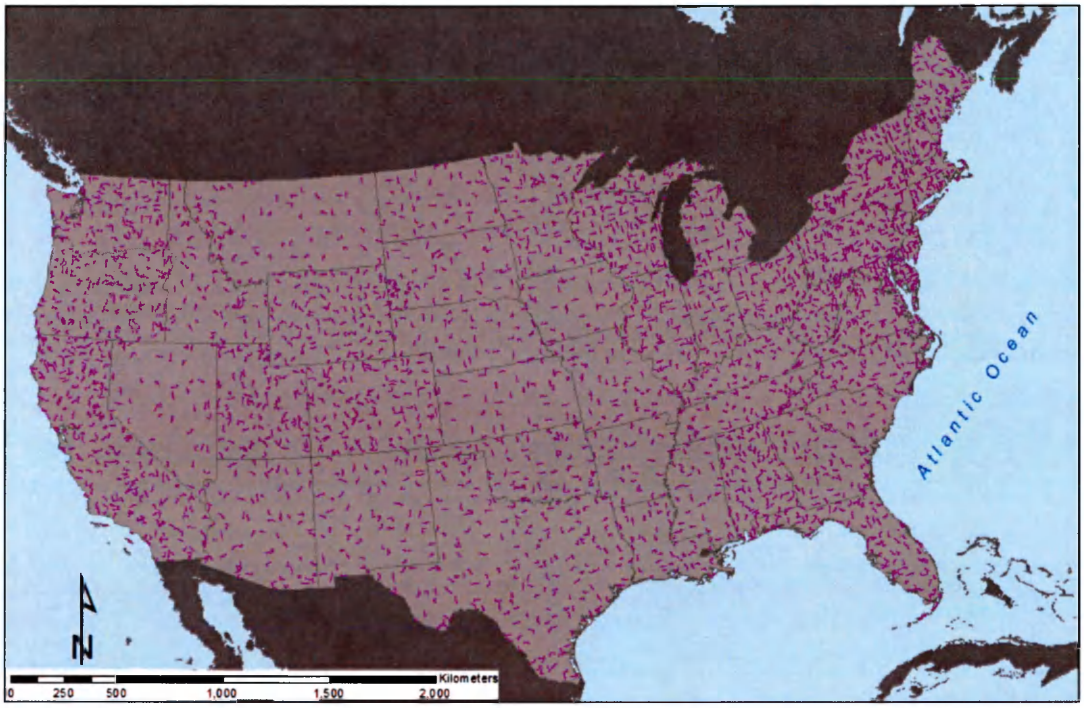

Figure 5. Breeding bird survey (BBBS) route locations. Each line denotes a single BBS route (n=3229).

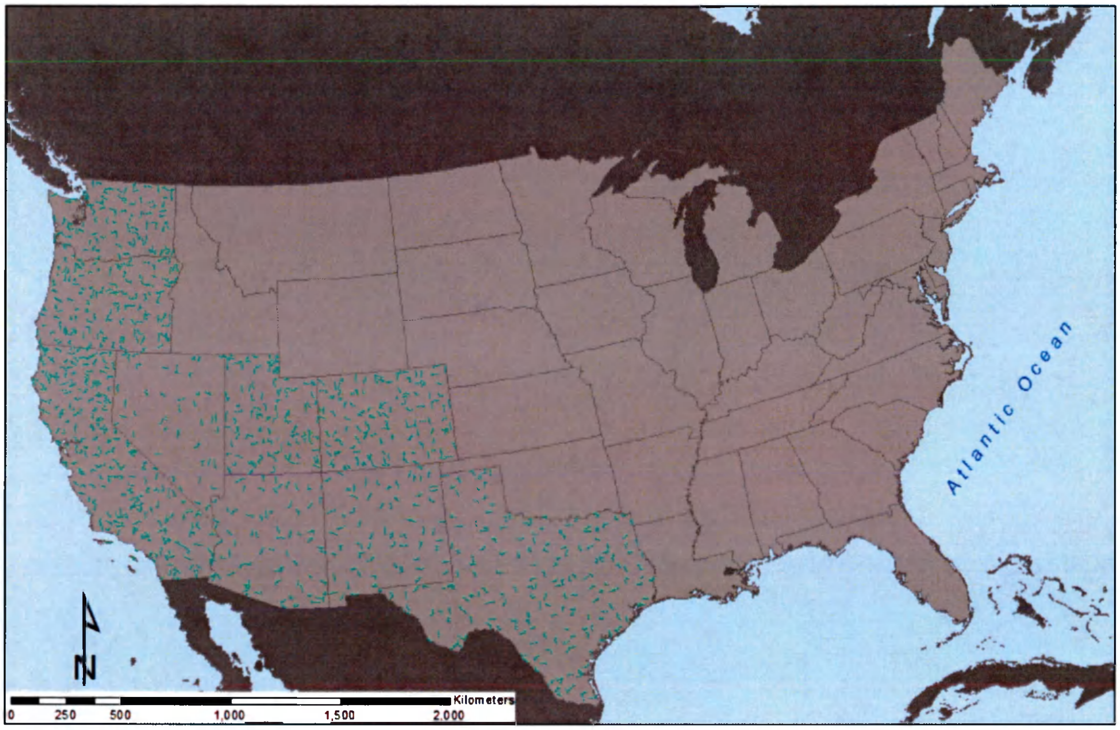

Figure 6. Breeding bird survey routes included in within the home range of the bushtit (*Psaltriparus minimus*) (n=1046).

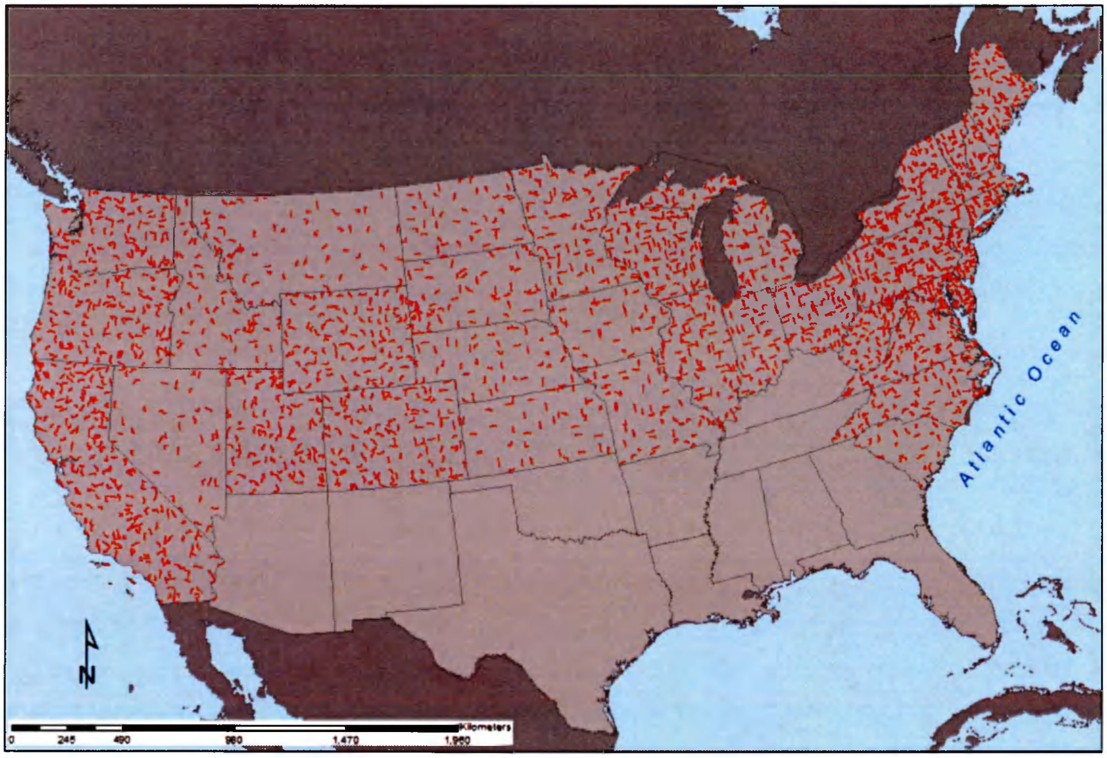

Figure 7. Breeding bird survey routes included in within the home range of the marsh wren (*Cistothorus palustris*) (n=2398).

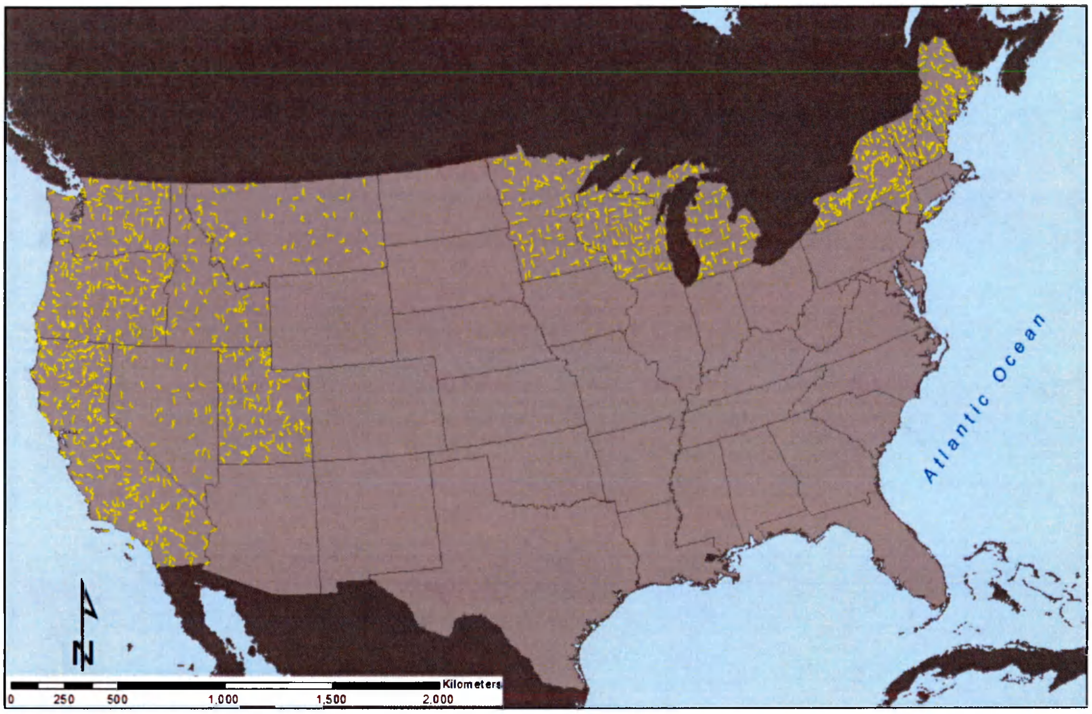

Figure 8. Breeding bird survey routes included in within the home range of the Swainson's thrush (*Catharus ustulatus*) (n=1209).

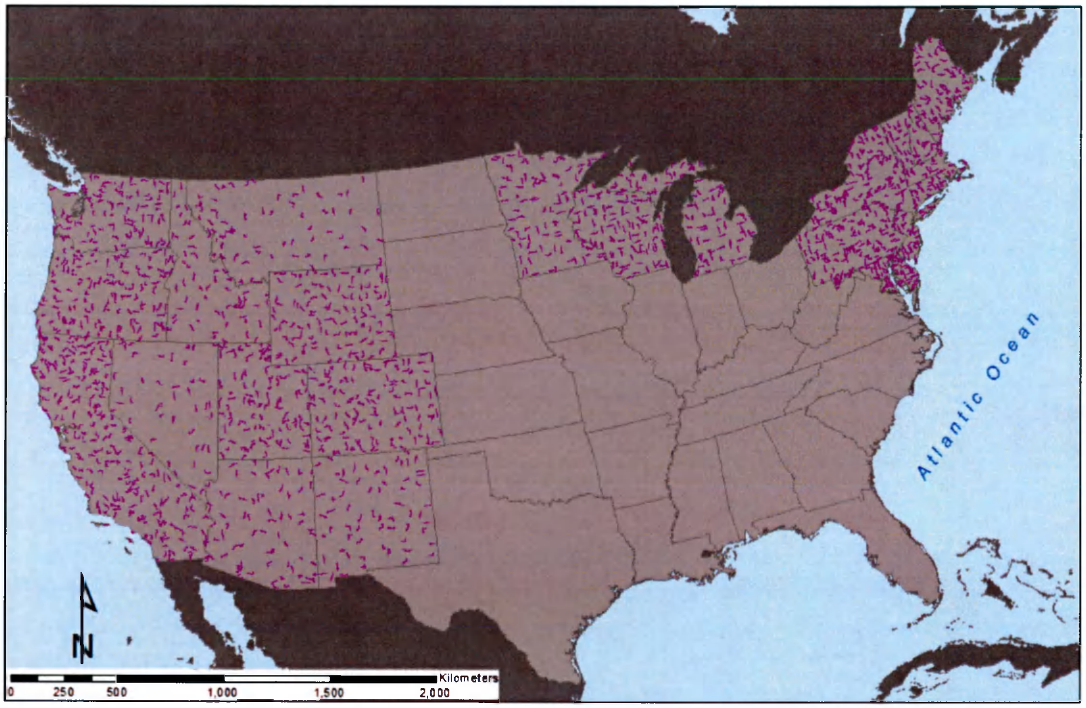

Figure 9. Breeding bird survey routes included in within the home range of the hermit thrush (*Catharus guttatus*) (n=1813).

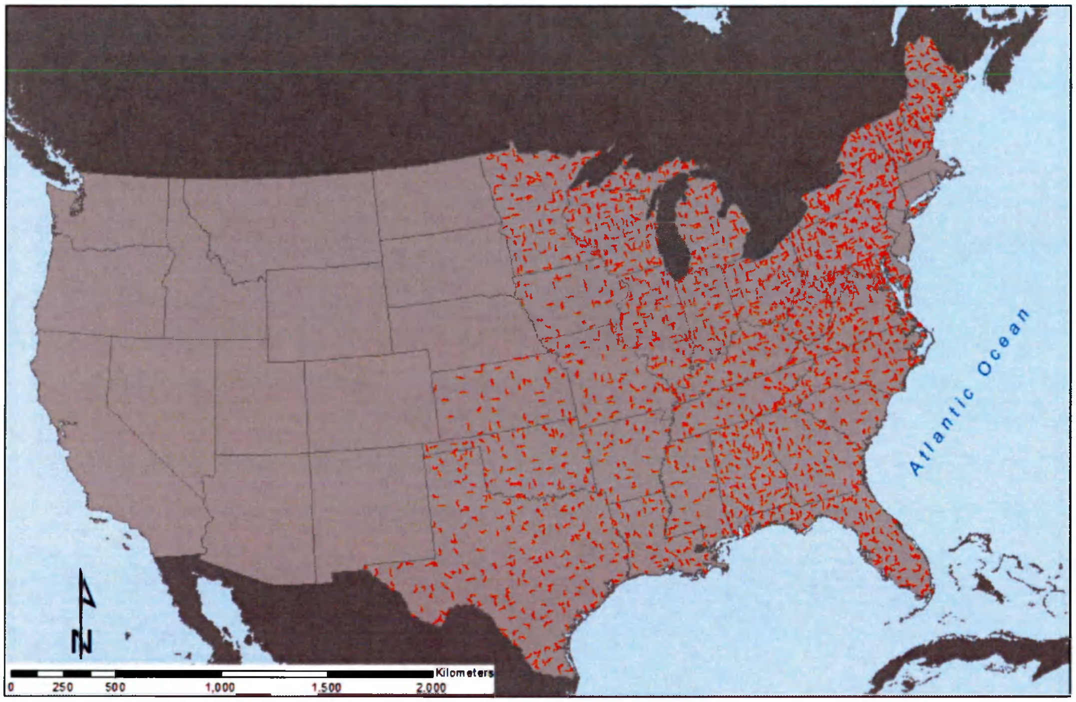

Figure 10. Breeding bird survey routes included in within the home range of the northern parula (*Parula americana*) (n=1913).

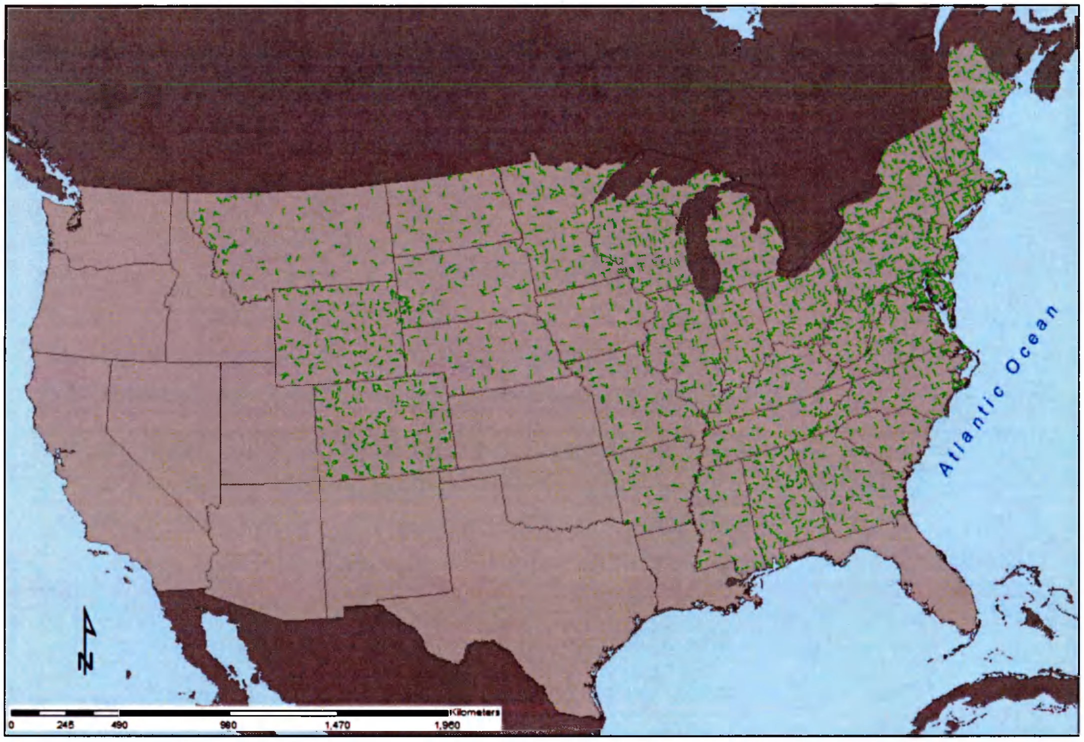

Figure 11. Breeding bird survey routes included in within the home range of the ovenbird (*Seiurus aurocapillus*) (n=1778).

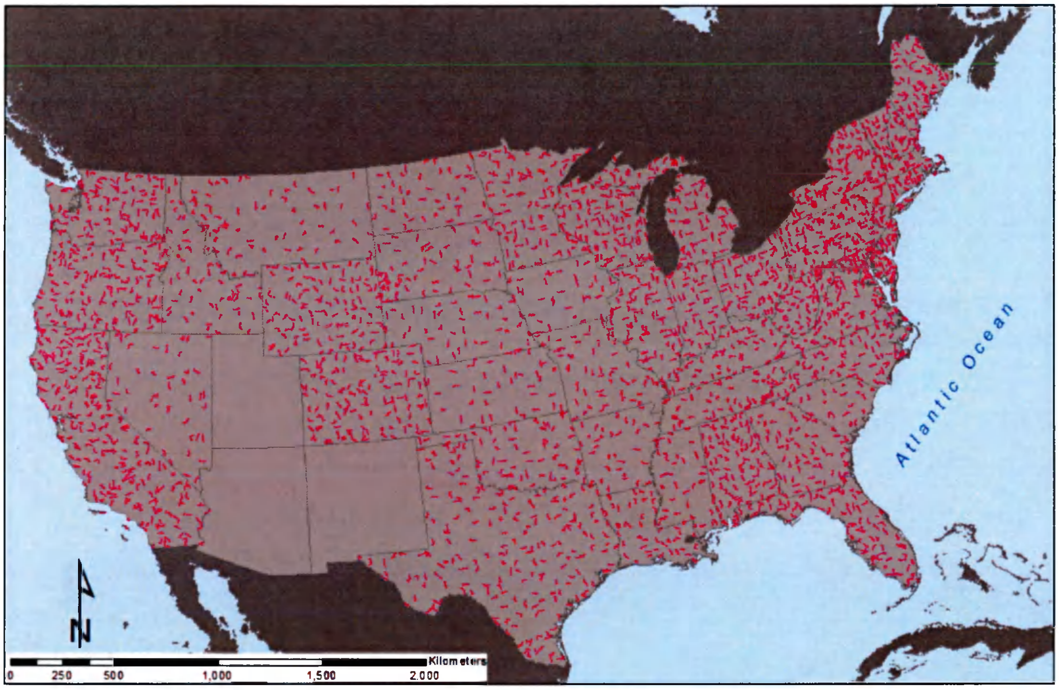

Figure 12. Breeding bird survey routes included in within the home range of the grasshopper sparrow (*Ammodramus savannarum*) (n=2988).

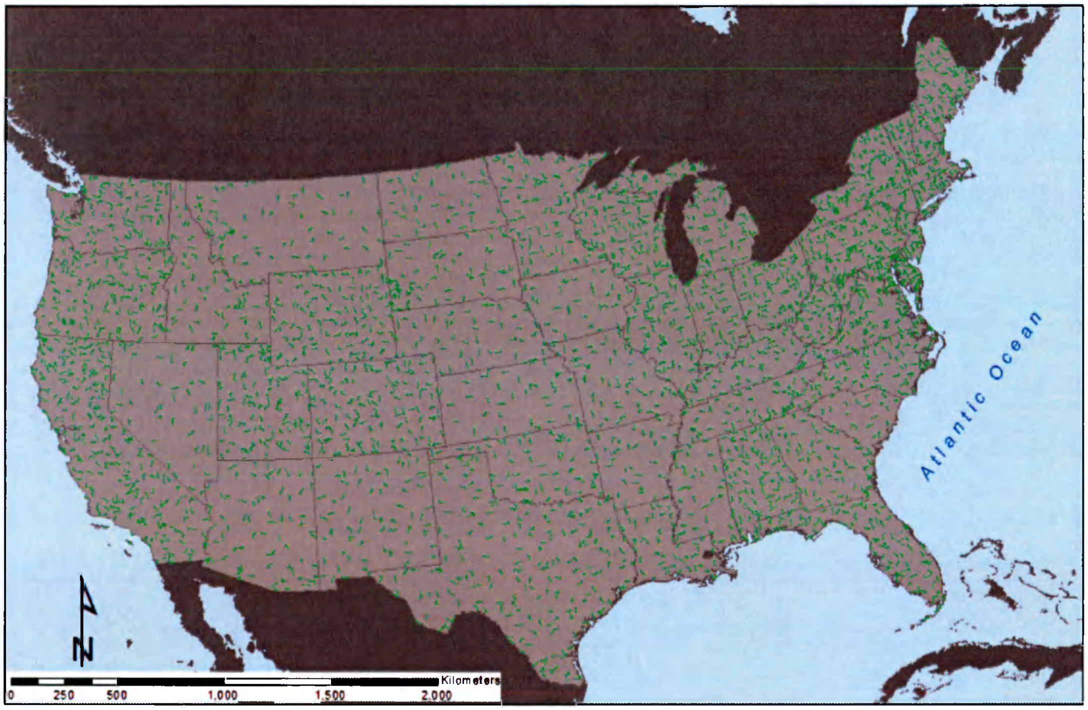

Figure 13. Breeding bird survey routes included in within the home range of the European starling (*Sturnus vulgaris*) (n=3229).

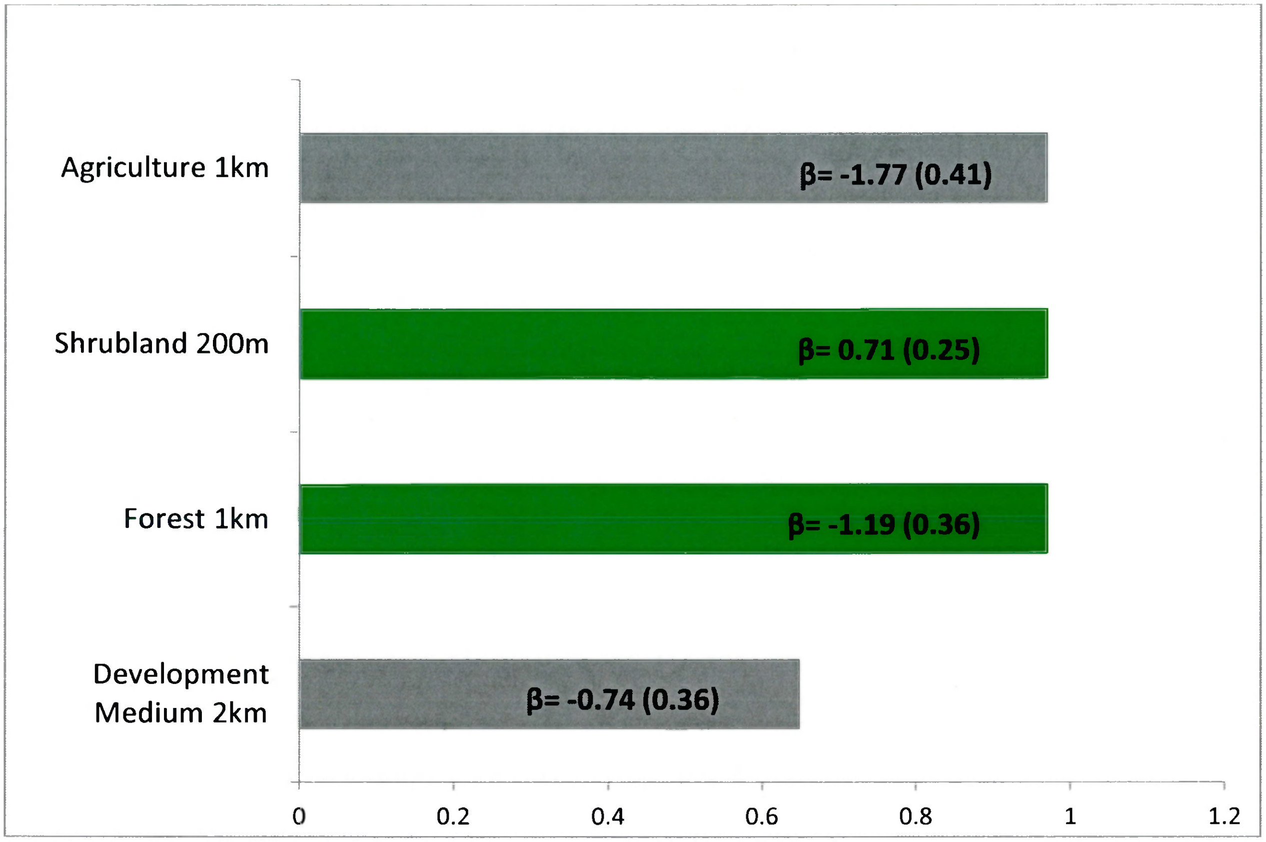

Figure 14. The relative effects of covariate on occupancy at the breeding life-history scale for the bushtit (*Psaltriparus minimus*); displayed as the cumulative AIC weights of the covariates falling within the confidence set, 95% of the highest Akaike weight, with the corresponding model averaged coefficients and standard errors (AICc 150.97; AUC = 0.85).

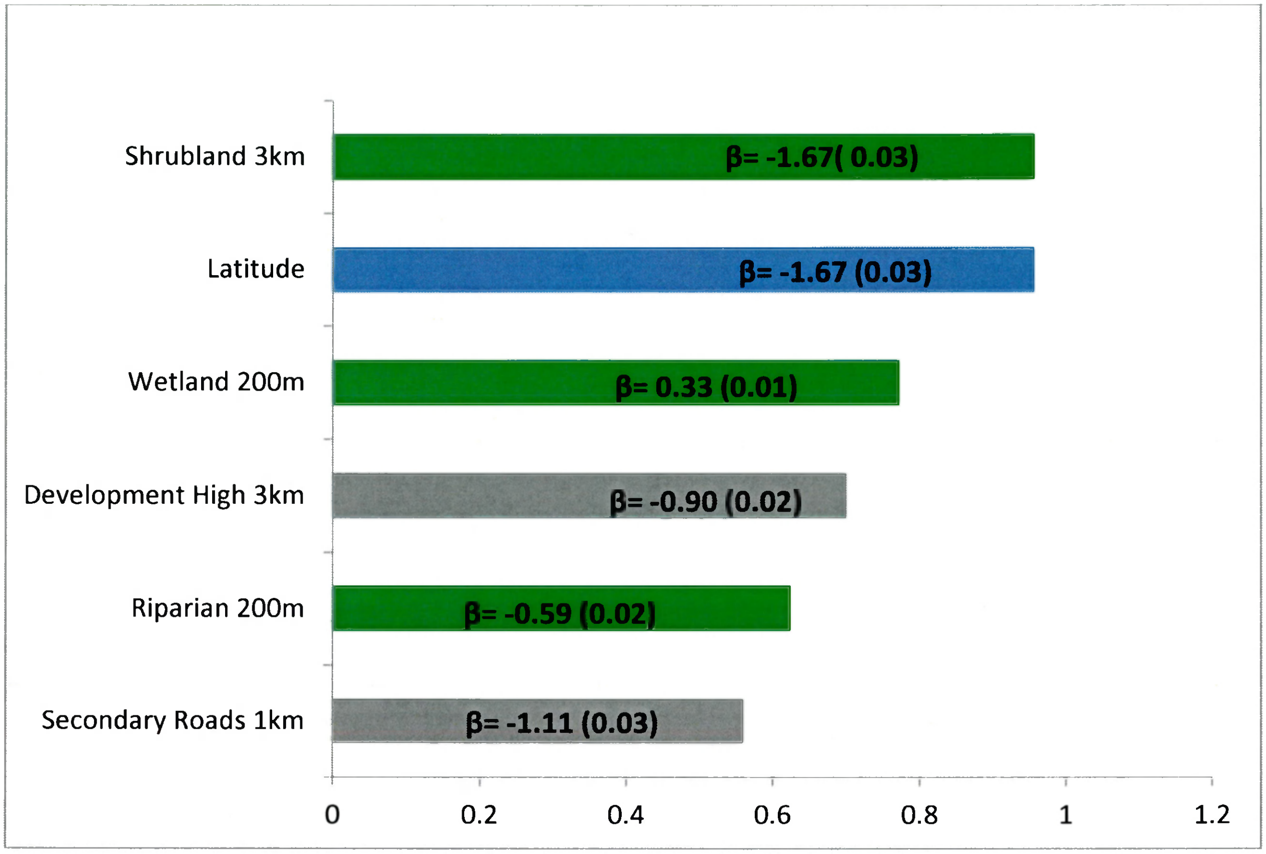

Figure 15. The relative effects of covariate on occupancy at the breeding life-history scale for the marsh wren (*Cistothorus palustris*); displayed as the cumulative AIC weights of the covariates falling within the confidence set, 95% of the highest Akaike weight, with the corresponding model averaged coefficients and standard errors (AICc = 138.80; AUC = 0.90).

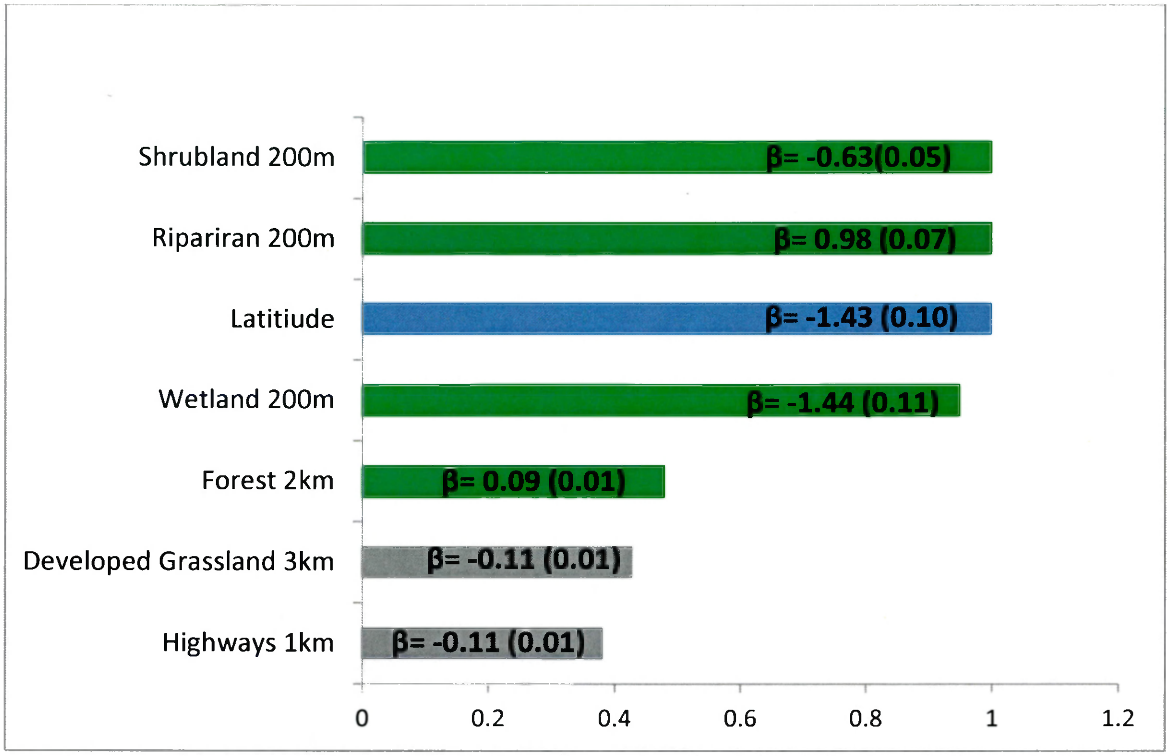

Figure 16. The relative effects of covariate on occupancy at the breeding life-history scale for the Swainson's thrush (*Catharus ustulatus*); displayed as the cumulative AIC weights of the covariates falling within the confidence set, 95% of the highest Akaike weight, with the corresponding model averaged coefficients and standard errors (AICc = 277.82; AUC = 0.39).

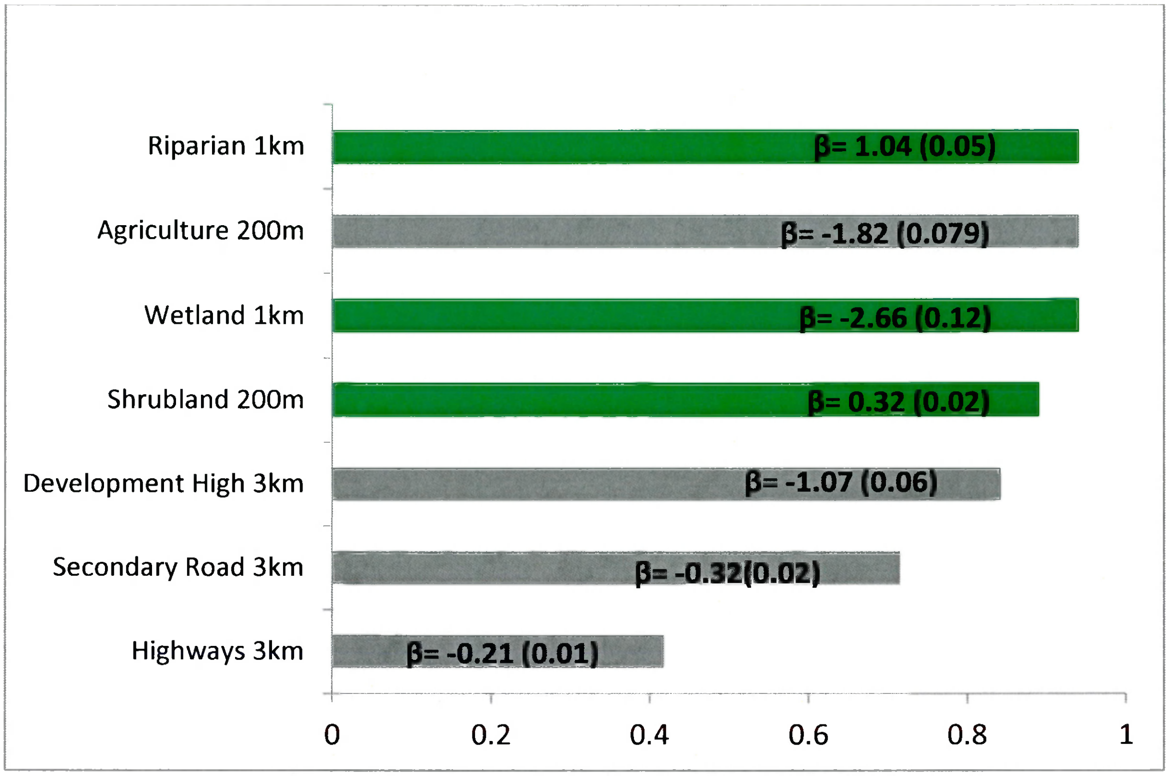

Figure 17. The relative effects of covariate on occupancy at the breeding life-history scale for the hermit thrush (*Catharus guttatus*); displayed as the cumulative AIC weights of the covariates falling within the confidence set, 95% of the highest Akaike weight, with the corresponding model averaged coefficients and standard errors (AICc = 437.31, AUC = 0.29).

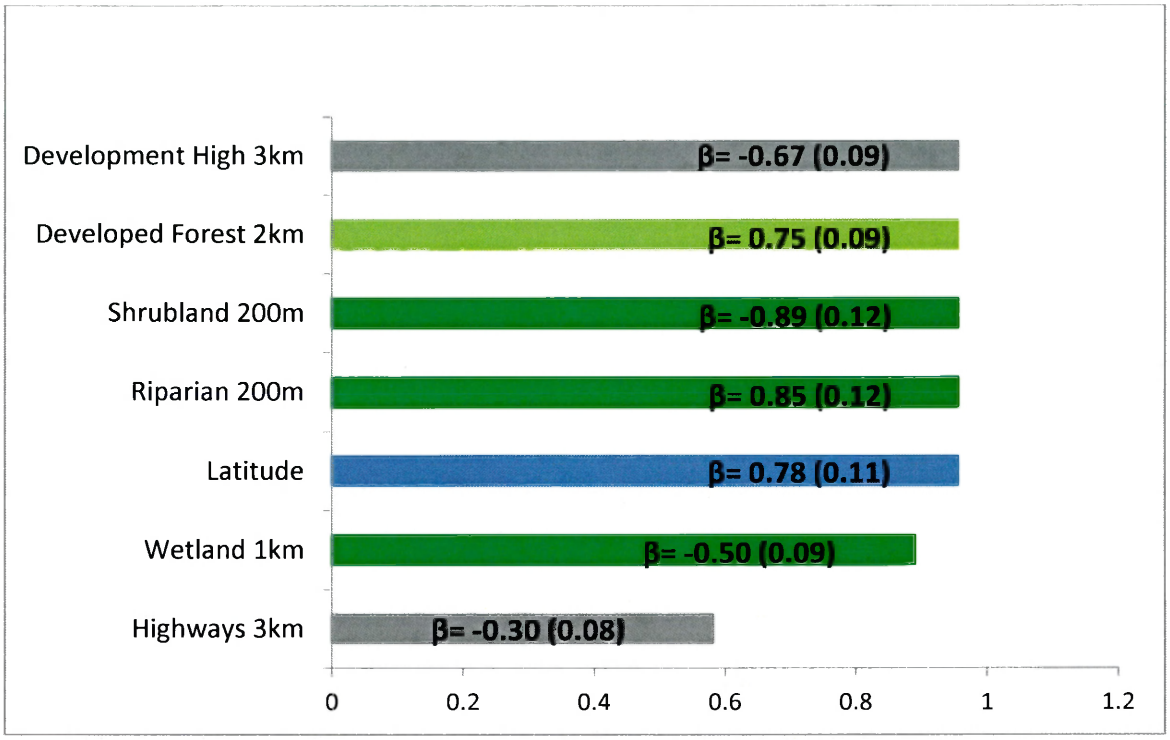

Figure 18. The relative effects of covariate on occupancy at the breeding life-history scale for the northern parula (*Parula americana*); displayed as the cumulative AIC weights of the covariates falling within the confidence set, 95% of the highest Akaike weight, with the corresponding model averaged coefficients and standard errors (AICc = 405.10; AUC = 0.91).

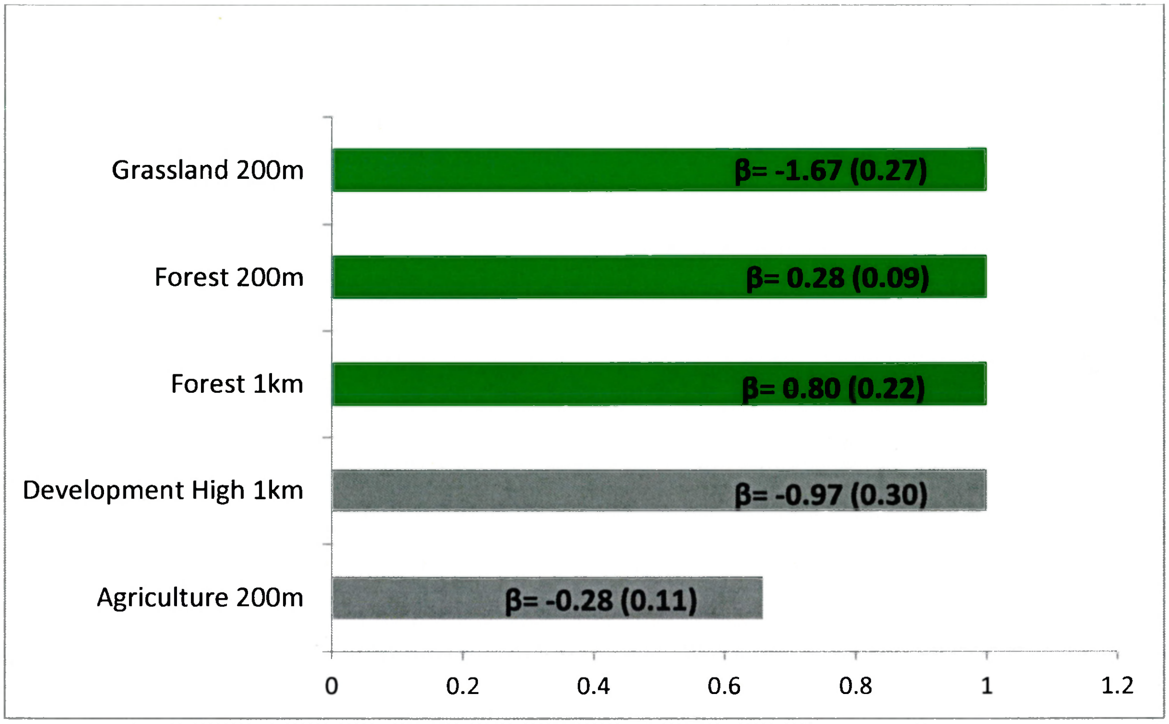

Figure 19. The relative effects of covariate on occupancy at the breeding life-history scale for the ovenbird (*Seiurus aurocapillus*); displayed as the cumulative AIC weights of the covariates falling within the confidence set, 95% of the highest Akaike weight, with the corresponding model averaged coefficients and standard errors (AICc = 604.48; AUC = 0.85).

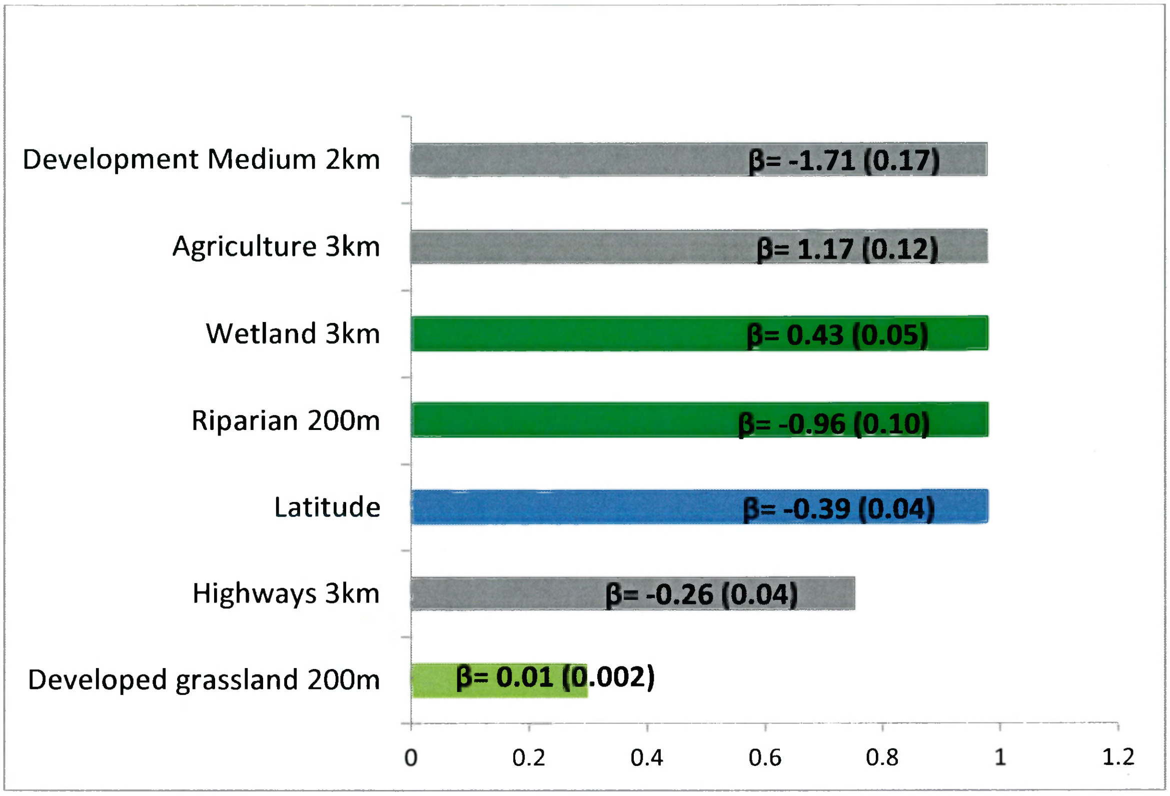

Figure 20. The relative effects of covariate on occupancy at the breeding life-history scale for grasshopper sparrow (*Ammodramus savannarum*); displayed as the cumulative AIC weights of the covariates falling within the confidence set, 95% of the highest Akaike weight, with the corresponding model averaged coefficients and standard errors (AICc = 405.10; AUC = 0.91).

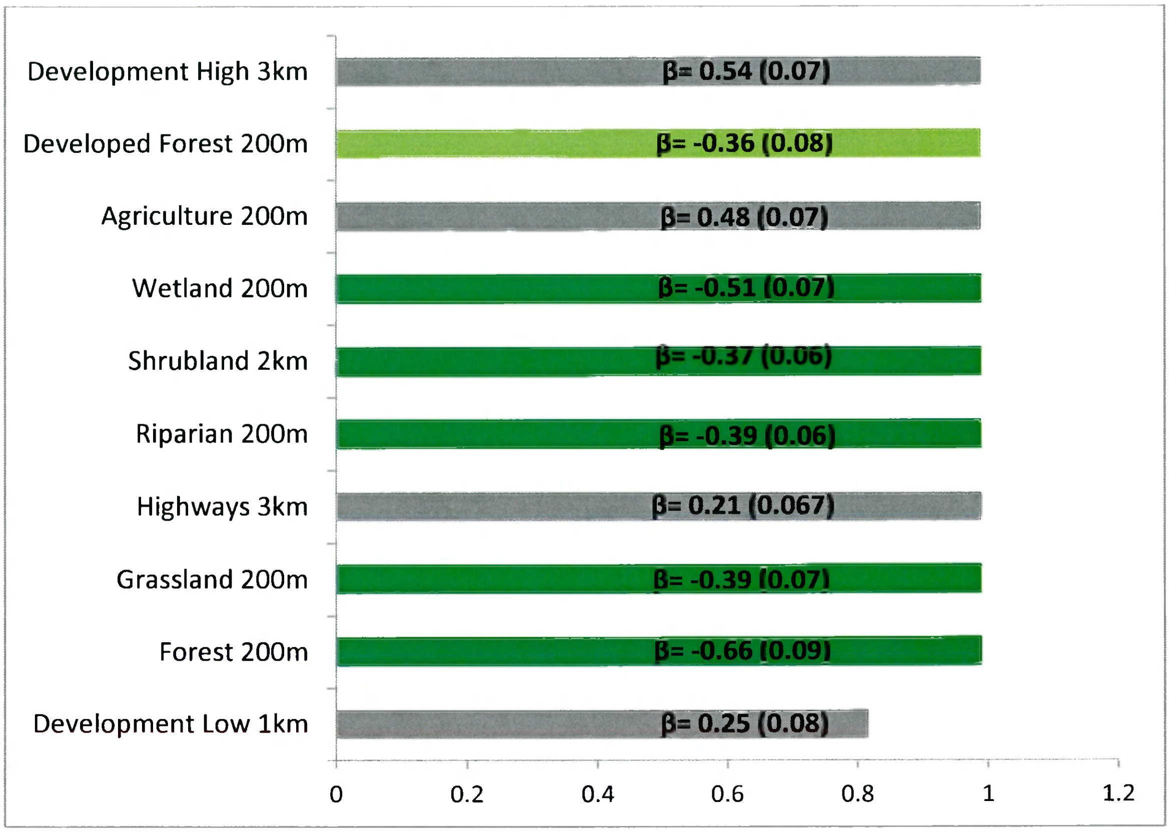

Figure 21. The relative effects of covariate on occupancy at the breeding life-history scale for European starling (*Sturnus vulgaris*); displayed as the cumulative AIC weights of the covariates falling within the confidence set, 95% of the highest Akaike weight, with the corresponding model averaged coefficients and standard errors (AICc = 2535.86, AUC = 0.81).

Appendix 4. Bushtit (*Psaltriparus minimus*) AIC model selection results for the analysis of occupancy. All candidate models within confidence set, 95% of the highest Akaike weight, are displayed, as well as the null model without covariates. For each models the number of parameters (K), log likelihood (LL), AIC_c, deltaAIC, and AIC weight (W_i) are shown.

Model	K	LL	AICc	ΔAIC	W_i
$Agriculture_{1km}$, $Development\ Medium_{2km}$, $Forest_{1km}$, $Shrubland_{200m}$	5	-70.69	151.48	0.00	0.65
$Agriculture_{1km}$, $Forest_{1km}$, $Shrubland_{200m}$	4	-72.41	152.89	1.40	0.32
Null	1	-110.84	223.69	72.21	1.36E-16

Appendix 5. Marsh wren (*Cistothorus palustris*) AIC model selection results for the analysis of occupancy. All candidate models within confidence set, 95% of the highest Akaike weight, are displayed, as well as the null model without covariates. For each models the number of parameters (K), log likelihood (LL), AIC, deltaAIC, and AIC weight (W_i) are shown.

Model	K	LL	AICc	ΔAIC	W_i
Development $High_{3km}$, Latitude, $Riparian_{200m}$, $Shrubland_{3km}$, $Wetland_{200m}$	6	-62.37	136.78	0.00	0.18
Development $High_{3km}$, Latitude, $Riparian_{200m}$, Secondary $Roads_{1km}$, $Shrubland_{3km}$, $Wetland_{200m}$	7	-61.47	137.00	0.22	0.16
Latitude, $Riparian_{200m}$, Secondary $Roads_{1km}$, $Shrubland_{3km}$, $Wetland_{200m}$	6	-62.70	137.45	0.67	0.13
Development $High_{3km}$, Latitude, Secondary $Roads_{1km}$, $Shrubland_{3km}$, $Wetland_{200m}$	6	-62.92	137.88	1.11	0.10
Development $High_{3km}$, Latitude, $Shrubland_{3km}$, Wetland200m	5	-63.93	137.90	1.12	0.10
Latitude, Secondary $Roads_{1km}$, $Shrubland_{3km}$, $Wetland_{200m}$	5	-64.33	138.70	1.92	0.07
Development $High_{3km}$, Latitude, $Riparian_{200m}$, $Shrubland_{3km}$, $Wetland_{200m}$	5	-64.62	139.27	2.49	0.05
Development $High_{3km}$, Latitude, $Riparian_{200m}$, Secondary $Roads_{1km}$, $Shrubland_{3km}$	6	-63.66	139.37	2.59	0.05
Latitude, $Riparian_{200m}$, Secondary $Roads_{1km}$, $Shrubland_{3km}$, $Wetland_{200m}$	5	-64.93	139.88	3.11	0.04
Development $High_{3km}$, Latitude, Secondary $Roads_{1km}$, $Shrubland_{3km}$	5	-65.07	140.17	3.39	0.03
Development $High_{3km}$, Latitude, $Shrubland_{3km}$	4	-66.20	140.42	3.64	0.03
Latitude, $Riparian_{200m}$, Secondary $Roads_{1km}$, $Shrubland_{3km}$	5	-65.38	140.80	4.02	0.02
Null	1	-82.40	166.81	30.03	5.34E-08

Appendix 6. Swainson's thrush (*Catharus ustulatus*) AIC model selection results for the analysis of occupancy. All candidate models within confidence set, 95% of the highest Akaike weight, are displayed, as well as the null model without covariates. For each models the number of parameters (K), log likelihood (LL), AIC$_c$, deltaAIC, and AIC weight (W$_i$) are shown.

Model	K	LL	AICc	ΔAIC	W$_i$
Forest$_{2km}$, Latitude, Riparian$_{200m}$, Shrubland$_{200m}$, Wetland$_{200m}$	6	-131.76	275.61	0	0.16
Latitude, Riparian$_{200m}$, Shrubland$_{200m}$, Wetland$_{200m}$	5	132.78	275.66	0.05	0.15
Developed Grassland$_{2km}$, Latitude, Riparian$_{200m}$, Shrubland$_{200m}$, Wetland$_{200m}$	6	-131.94	275.97	0.36	0.13
Developed Grassland$_{2km}$, Forest$_{2km}$, Latitude, Riparian$_{200m}$, Shrubland$_{200m}$, Wetland$_{200m}$	7	-131.00	276.13	0.52	0.12
Highways$_{1km}$, Latitude, Riparian$_{200m}$, Shrubland$_{200m}$, Wetland$_{200m}$	6	-132.20	276.49	0.88	0.10
Developed Grassland$_{2km}$, Highways$_{1km}$, Latitude, Riparian$_{200m}$, Shrubland$_{200m}$, Wetland$_{200m}$	7	-131.32	276.77	1.16	0.09
Forest$_{2km}$, Highways$_{1km}$, Latitude, Riparian$_{200m}$, Shrubland$_{200m}$, Wetland$_{200m}$	7	-131.34	276.81	1.20	0.09
Developed Grassland$_{2km}$, Forest$_{2km}$, Highways$_{1km}$, Latitude, Riparian$_{200m}$, Shrubland$_{200m}$, Wetland$_{200m}$	8	-130.57	277.30	1.69	0.07
Forest$_{2km}$, Latitude, Riparian$_{200m}$, Shrubland$_{200m}$	5	-135.11	280.29	4.68	0.02
Latitude, Riparian$_{200m}$, Shrubland$_{200m}$	4	-136.35	280.75	5.14	0.01
Highways$_{1km}$, Latitude, Riparian$_{200m}$, Shrubland$_{200m}$	5	-135.45	280.97	5.37	0.01
Forest$_{2km}$, Highways$_{1km}$, Latitude, Riparian$_{200m}$, Shrubland$_{200m}$	6	-134.49	281.07	5.46	0.01
Null	1	-172.43	346.89	71.26	5.26E-12

Appendix 7. Hermit thrush (*Catharus guttatus*) AIC model selection results for the analysis of occupancy. All candidate models within confidence set, 95% of the highest Akaike weight, are displayed, as well as the null model without covariates. For each models the number of parameters (K), log likelihood (LL), AIC_c, deltaAIC, and AIC weight (W_i) are shown.

Model	K	LL	AICc	ΔAIC	W_i
$Agriculture_{200m}$, Development $High_{3km}$, $Riparian_{1km}$, Secondary $Road_{3km}$, $Shrubland_{200m}$, $Wetland_{1km}$	7	-210.08	434.25	0.00	0.36
$Agriculture_{200m}$, Development $High_{3km}$, $Highway_{3km}$, $Riparian_{1km}$, Secondary $Road_{3km}$, $Shrubland_{200m}$, $Wetland_{1km}$	8	-209.50	435.11	0.86	0.23
$Agriculture_{200m}$, Development $High_{3km}$, $Highway_{3km}$, Riparian1km, $Shrubland_{200m}$, Wetland1km	7	-211.21	436.50	2.25	0.12
$Agriculture_{200m}$, Development $High_{3km}$, $Riparian_{1km}$, $Shrubland_{200m}$, $Wetland_{1km}$	6	-212.48	437.02	2.76	0.09
$Agriculture_{200m}$,$Highway_{3km}$, $Riparian_{1km}$, Secondary $Road_{3km}$, $Shrubland_{200m}$, $Wetland_{1km}$	7	-212.05	438.18	3.93	0.05
$Agriculture_{200m}$, $Riparian_{1km}$, Secondary $Road_{3km}$, $Shrubland_{200m}$, $Wetland_{1km}$	6	-213.09	438.24	3.98	0.05
$Agriculture_{200m}$, Development $High_{3km}$, $Riparian_{1km}$, Secondary $Road_{3km}$, $Wetland_{1km}$	6	-213.59	439.25	5.00	0.03
$Agriculture_{200m}$, Development $High_{3km}$, $Highway_{3km}$, $Riparian_{1km}$, Secondary $Road_{3km}$	6	-213.93	439.92	5.67	0.02
Null	1	-323.17	648.34	175.74	2.14E-39

Appendix 8. Northern parula (*Parula americana*) AIC model selection results for the analysis of occupancy. All candidate models within confidence set, 95% of the highest Akaike weight, are displayed, as well as the null model without covariates. For each models the number of parameters (K), log likelihood (LL), AIC_c, deltaAIC, and AIC weight (W_i) are shown.

Model	K	LL	AICc	ΔAIC	W_i
Developed Forest2km, Development High3km, Highways3km, Latitude, Riparian200m, Shrubland200m, Wetland1km	8	-193.71	403.51	0.00	0.52
Developed Forest2km, Development High3km, Latitude, Riparian200m, Shrubland200m, Wetland1km	7	-195.04	404.16	0.64	0.37
Developed Forest2km, Development High3km, Highways3km, Latitude, Riparian200m, Shrubland200m	7	-196.78	407.63	4.11	0.07
Null	1	-300.59	603.19	199.67	2.27E-44

Appendix 9. Ovenbird (*Seiurus aurocapillus*) AIC model selection results for the analysis of occupancy. All candidate models within confidence set, 95% of the highest Akaike weight, are displayed, as well as the null model without covariates. For each models the number of parameters (K), log likelihood (LL), AIC_c , deltaAIC, and AIC weight (W_i) are shown.

Model	K	LL	AICc	ΔAIC	W_i
$Agriculture_{200m}$, Development $High_{1km}$, $Forest_{1km}$, $Forest_{200m}$, $Grassland_{200m}$	6	-295.89	603.83	0	0.64
Development $High_{1km}$, $Forest_{1km}$, $Forest_{200m}$, $Grassland_{200m}$	5	-297.55	605.14	1.31	0.33
Null	1	-425.44	852.88	249.06	5.31E-55

Appendix 10. Grasshopper sparrow (*Ammodramus savannarum*) AIC model selection results for the analysis of occupancy. All candidate models within confidence set, 95% of the highest Akaike weight, are displayed, as well as the null model without covariates. For each models the number of parameters (K), log likelihood (LL), AIC_c, deltaAIC, and AIC weight (W_i) are shown.

Model	K	LL	AICc	deltaΔ	W_i
$Agriculture_{3km}$, Developed $Medium_{2km}$, $Highway_{3km}$, Latitude, $Riparian_{200m}$, $Wetland_{3km}$	7	-387.27	788.60	0.00	0.52
$Agriculture_{3km}$, Developed $Grassland_{200m}$, Developed $Medium_{2km}$, $Highway_{3km}$, Latitude, $Riparian_{200m}$, $Wetland_{3km}$	8	-387.10	790.26	1.66	0.23
$Agriculture_{3km}$, Developed $Medium_{2km}$, Latitude, $Riparian_{200m}$, $Wetland_{3km}$	6	-389.49	791.02	2.42	0.16
$Agriculture_{3km}$, Developed $Grassland_{200m}$, Developed $Medium_{2km}$, Latitude, $Riparian_{200m}$, $Wetland_{3km}$	7	-389.28	792.61	4.01	0.07
Null	1	-508.47	1018.95	230.35	5.01E-51

Appendix 11. European starling (*Sturnus vulgaris*) AIC model selection results for the analysis of occupancy. All candidate models within confidence set, 95% of the highest Akaike weight, are displayed, as well as the null model without covariates. For each models the number of parameters (K), log likelihood (LL), AIC_c , deltaAIC, and AIC weight (W_i) are shown.

Model	K	LL	AICc	deltaΔ	W_i
$Agriculture_{200m}$, Developed $Forest_{200m}$, Development $High_{3km}$, Development Low_{1km}, $Forest_{200m}$, $Grassland_{200m}$, $Highways_{3km}$, $Riparian_{200m}$, $Shrubland_{2km}$, $Wetland_{200m}$	11	-1256.10	2534.31	0.00	0.82
$Agriculture_{200m}$, Developed $Forest_{200m}$, Development $High_{3km}$, $Forest_{200m}$, $Grassland_{200m}$, $Highways_{3km}$, $Riparian_{200m}$, $Shrubland_{2km}$, $Wetland_{200m}$	10	-1258.66	2537.41	3.09	0.17
Null	1	-1668.01	3338.02	803.70	2.45E-175

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