Changes in bird distributions in Illinois, USA, over the 20th century were driven by use of alternative rather than primary habitats

Authors: Ward, Michael P., Stodola, Kirk W., Walk, Jeffery W., Benson, Thomas J., Deppe, Jill L., et al.

Source: The Condor, 120(3) : 622-631

Published By: American Ornithological Society

URL: https://doi.org/10.1650/CONDOR-17-153.1

THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 120, 2018, pp. 622–631
DOI: 10.1650/CONDOR-17-153.1

RESEARCH ARTICLE

Changes in bird distributions in Illinois, USA, over the 20th century were driven by use of alternative rather than primary habitats

Michael P. Ward,[1,2]* Kirk W. Stodola,[1,2] Jeffery W. Walk,[3] Thomas J. Benson,[2] Jill L. Deppe,[4] and Jeffrey D. Brawn[1]

[1] Department of Natural Resources and Environmental Sciences, University of Illinois, Urbana-Champaign, Urbana, Illinois, USA
[2] Illinois Natural History Survey, Prairie Research Institute, University of Illinois, Urbana-Champaign, Champaign, Illinois, USA
[3] The Nature Conservancy, Peoria, Illinois, USA
[4] Department of Biological Sciences, Eastern Illinois University, Charleston, Illinois, USA
* Corresponding author: mpward@illinois.edu

Submitted August 15, 2017; Accepted May 11, 2018; Published July 25, 2018

ABSTRACT

Most species are distributed such that their density and occupancy is greatest in one habitat, although they are found in other habitats. For example, a species with a high affinity for forests (its primary habitat) may also use urban areas and shrublands (its alternative habitat), although occupancy of these habitats would be lower. While habitat loss is the main conservation threat for most species, less is known about how changes in primary and alternative habitats impact populations. We used a systematic bird survey of the state of Illinois that spanned the past century to investigate how use of specific habitats was related to population changes. Specifically, we used a hierarchical Bayesian model to investigate the relationship between changes in statewide occupancy (probability a species would occur in a study site) and use of specific habitats (probability a species would be in a specific habitat within our study sites) for 66 species sampled in 1906–1909 and 2006–2008. Changes in the use of alternative habitats, and not primary habitats, was related to overall changes in statewide occupancy. Many species that increased over the past century did so by increasing their use of urban areas, while declining species declined the most in agricultural and grassland areas. Although primary habitats form the core of a species' distribution, alternative habitats may provide opportunities for a species to expand its distribution; conversely, declining species may abandon alternative habitats and contract into primary habitats. Consequently, alternative habitats may play an important role in the future of many species. Understanding this role could be crucial for successful conservation.

Keywords: habitat loss, long-term population trends, novel habitats, urban habitats

Los cambios en las distribuciones de aves en Illinois, EEUU a lo largo del siglo 20 fueron impulsados por el uso de hábitats alternativos en lugar de hábitats primarios

RESUMEN

La mayoría de las especies están distribuidas de tal modo que sus densidades y ocupaciones son mayores en un hábitat, aunque se las encuentra en otros hábitats. Por ejemplo, una especie con alta afinidad por los bosques (su hábitat primario) también puede usar áreas urbanas y arbustales (su hábitat alternativo), aunque la ocupación de estos hábitats fuera menor. Aunque la pérdida de hábitat es la principal amenaza de conservación para la mayoría de las especies, se sabe menos sobre cómo los cambios en hábitats primarios y alternativos impactan a las poblaciones. Usamos un censo sistemático de aves del estado de Illinois que abarcó el siglo pasado para investigar cómo el uso de hábitats específicos se relacionó con los cambios poblacionales. Específicamente, usamos un modelo bayesiano jerárquico para investigar la relación entre cambios de ocupación a escala de estado (probabilidad de que una especie estuviera presente en un sitio de estudio) y uso de hábitats específicos (probabilidad de que una especie estuviera en un hábitat específico adentro de nuestros sitios de estudio) para 66 especies muestreadas en 1906-1909 y 2006-2008. Los cambios en el uso de hábitats alternativos, y no hábitats primarios, se relacionaron con los cambios globales en la ocupación a escala de estado. Muchas especies que aumentaron a lo largo del siglo pasado lo hicieron aumentando su uso de áreas urbanas, mientras que las especies que disminuyeron lo hicieron en gran medida en áreas agrícolas y pastizales. Aunque los hábitats primarios forman el núcleo de la distribución de una especie, los hábitats alternativos podrían brindar oportunidades a una especie de expandir su distribución; contrariamente, las especies que disminuyeron podrían abandonar los hábitats alternativos y contraerse a los hábitats primarios. Consecuentemente, los hábitats alternativos pueden jugar un rol importante en el futuro de muchas especies. Entender este rol podría ser crucial para una conservación exitosa.

Palabras clave: hábitats nuevos, hábitats urbanos, pérdida de hábitat, tendencias poblacionales de largo plazo

INTRODUCTION

Humans have caused unprecedented environmental change through impacts on climate (Parmesan and Yohe 2003, Root et al. 2003), establishment and spread of invasive species (Vitousek et al. 1996, Blackburn et al. 2004), and, most importantly, changes in land cover and land use (Jetz et al. 2007). Over the last century, natural areas have been reduced considerably, urban and suburban areas have greatly expanded (Brown et al. 2005, Foley et al. 2005), and agricultural practices have shifted away from small fields with varied grain crops toward intensive row-crop agriculture (Walk et al. 2010). Consequently, land cover and land use change is often cited as the major driver of species population trends, and there are numerous examples of species declining as a result of habitat loss (Fahrig 2003).

Rarely are all areas with suitable habitat fully occupied by a given species (Gaston 2009). Most species are distributed such that their density and occupancy is greatest in one habitat (primary habitat) with other habitats used to a lesser extent (alternative habitats). The availability of a species' primary habitat may be the major driver of population change, but species use of alternative habitats may also influence long-term population persistence. As novel habitats are created in the landscape, certain species may utilize these as alternative habitats. Therefore, the fate of a species is not necessarily determined solely by changes to its primary habitat, but may also be influenced by its ability to use alternative and potentially novel habitats (Stralberg et al. 2009). For instance, a species can potentially increase in abundance or distribution irrespective of changes in its primary habitat if it increases its use of alternative habitats.

Understanding the influence of habitat use on population change requires information on populations across multiple habitats and over long periods of time. The state of Illinois had one of the earliest systematic bird surveys in North America, beginning >100 yr ago, with surveys across the entire state. The location and time span of these surveys provide a unique opportunity to investigate how changes in agricultural practices and urbanization impact bird populations. In the early to mid-20th century, agriculture in Illinois transitioned from small diverse farms powered by manual labor and draft animals to large farms reliant on mechanical equipment to produce corn and soybean monocultures. The state has also nearly tripled in population from 4.8 million in 1900 to 12.6 million residents today, with a corresponding increase in urban areas (Walk et al. 2010). These large changes in agriculture and development create novel habitats that birds may use as alternative habitat, providing a backdrop for understanding changes in bird populations.

We took advantage of one of the earliest systematic bird surveys in North America to understand how breeding bird populations changed across the 20th century in Illinois (>500 km north–south). We used land cover–specific bird data collected during 2 time periods (1906–1909 and 2006–2008) to estimate occupancy of a transect and use of specific habitats within that transect for 66 species. We evaluated long-term changes in population for each species and examined how these changes are manifested across various habitats. The specific objectives of this study were to (1) investigate how use of primary and alternative habitat influenced changes in species occupancy across the 20th century, and (2) examine which land cover types appeared to be most important for driving changes in species occupancy. These results allow us to anticipate how bird populations may continue to change in the 21st century in Illinois and throughout the developing world.

METHODS

100-year Bird Survey

Birds were surveyed along transects from 1906 to 1909 and again from 2006 to 2008. Each survey took place between mid-May and early-July (i.e. when most birds breed in Illinois). Transects traversed various land cover types, including grassland, forest, agriculture, urban, and other habitats (e.g., marsh/wetland and shrublands). Forbes (1907) gives this brief summary of the methods used to count birds: "Two acute and thoroughly reliable ornithological observers…were sent into the field under instructions to traverse the state in various directions, traveling always in straight lines and always thirty yards apart, and noting and recording the species, numbers, and exact situation of all birds flushed by them on a strip fifty yards in width, including also those crossing this strip within one hundred yards to their front." We repeated these exact methods in 2006 to 2008, with 2 observers moving at the same speed, 27 m apart, recording only birds visually observed within a width of 46 m and within 91 m in front of the observers. Observers recorded the time associated with the start of each transect, each time they crossed from one habitat type into a different habitat type, and the habitat type associated with bird observations. In the 1900s observers recorded their paces in each habitat type whereas we used GPS in the 2000s. Surveyors in both the 1900s and 2000s sampled habitat types in approximately the same proportion as their availability on the landscape. To acquire a robust sample size for occupancy modeling, we combined cover types into grassland, forest, agriculture, urban, and other habitats (Table 1). Grasslands included areas classified as idle grass, grazed pastures, hay fields, and linear grass areas. Forests included both upland and floodplain forests, savannas, and coniferous forest. Agriculture was primarily corn and soybeans, but also included wheat, oats, and fruits or vegetables. Urban consisted of low- and high-density urban areas, and urban open space

TABLE 1. Species-specific habitat affinities based on literature and 1900s surveys, along with absolute change in overall occupancy between the 1900s and 2000s surveys.

Species (taxonomic order)	Agriculture	Urban	Forest	Grassland	Shrubland / Wetland	Change in occupancy
Northern Bobwhite (*Colinus virginianus*)	medium	low	medium	high	high	−0.3061
Mourning Dove (*Zenaida macroura*)	high	medium	medium	high	high	0.0031
Yellow-billed Cuckoo (*Coccyzus americanus*)	low	low	high	low	high	−0.1989
Chimney Swift (*Chaetura pelagica*)	medium	high	high	medium	medium	0.3443
Ruby-throated Hummingbird (*Archilochus colubris*)	low	low	high	low	medium	0.3442
Killdeer (*Charadrius vociferus*)	high	medium	low	medium	high	0.1715
Upland Sandpiper (*Bartramia longicauda*)	high	low	low	high	low	−0.5105
Red-tailed Hawk (*Buteo jamaicensis*)	medium	low	medium	high	medium	0.2631
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	medium	medium	high	medium	medium	−0.2643
Red-bellied Woodpecker (*Melanerpes carolinus*)	low	low	high	low	high	0.2454
Downy Woodpecker (*Picoides pubescens*)	low	medium	high	low	high	0.1274
Hairy Woodpecker (*Picoides villosus*)	low	low	high	low	medium	0.2747
Northern Flicker (*Colaptes auratus*)	medium	high	high	medium	high	−0.0943
Eastern Wood-Pewee (*Contopus virens*)	low	low	high	low	low	0.325
Acadian Flycatcher (*Empidonax virescens*)	low	low	high	low	low	−0.0257
Eastern Phoebe (*Sayornis phoebe*)	medium	high	medium	low	medium	0.2906
Great Crested Flycatcher (*Myiarchus crinitus*)	low	low	high	low	low	−0.0831
Eastern Kingbird (*Tyrannus tyrannus*)	medium	medium	medium	high	high	−0.1322
Loggerhead Shrike (*Lanius ludovicianus*)	medium	low	low	high	high	−0.297
White-eyed Vireo (*Vireo griseus*)	low	low	low	low	high	0.0947
Red-eyed Vireo (*Vireo olivaceus*)	low	low	high	low	low	−0.0268
Blue Jay (*Cyanocitta cristata*)	low	medium	high	low	low	−0.0934
American Crow (*Corvus brachyrhychos*)	high	medium	high	high	high	−0.1965
Horned Lark (*Eremophila alpestris*)	high	low	low	medium	low	0.0808
Purple Martin (*Progne subis*)	medium	high	medium	medium	medium	−0.1672
Tree Swallow (*Tachycineta bicolor*)	medium	medium	medium	high	high	0.2992
N. Rough-winged Swallow (*Stelgidopteryx serripennis*)	medium	low	low	medium	medium	0.5309
Barn Swallow (*Hirundo rustica*)	high	high	high	high	high	0.503
Carolina Chickadee (*Poecile carolinensis*)	low	low	high	low	low	0.2462
Black-capped Chickadee (*Poecile atricapillus*)	low	low	high	low	low	0.3568
Tufted Titmouse (*Baeolophus bicolor*)	low	low	high	low	low	0.0985
White-breasted Nuthatch (*Sitta carolinensis*)	low	low	high	low	low	0.4633
House Wren (*Troglodytes aedon*)	low	high	high	low	medium	0.4696
Carolina Wren (*Thryothorus ludovicianus*)	low	low	high	low	low	0.0865
Blue-gray Gnatcatcher (*Polioptila caerulea*)	low	low	high	low	low	0.6162
Eastern Bluebird (*Sialia sialis*)	high	medium	medium	high	high	0.0114
Wood Thrush (*Hylocichla mustelina*)	low	low	high	low	low	0.033
American Robin (*Turdus migratorius*)	high	high	high	high	high	0.0599
Gray Catbird (*Dumetella carolinensis*)	low	medium	high	medium	high	0.1325
Brown Thrasher (*Toxostoma rufum*)	low	low	low	medium	high	−0.2262
Northern Mockingbird (*Mimus polyglottos*)	low	high	low	low	medium	−0.2461
Cedar Waxwing (*Bombycilla cedrorum*)	low	medium	high	medium	medium	0.4548
American Goldfinch (*Spinus tristis*)	high	high	high	high	high	0.1796
Eastern Towhee (*Pipilo erythrophthalmus*)	low	low	high	low	high	−0.1844
Chipping Sparrow (*Spizella passerina*)	medium	medium	medium	high	high	0.317
Field Sparrow (*Spizella pusilla*)	medium	low	low	high	high	−0.0386
Vesper Sparrow (*Pooecetes gramineus*)	high	low	low	high	low	0.1989
Lark Sparrow (*Chondestes grammacus*)	medium	low	low	high	medium	−0.2742
Savannah Sparrow (*Passerculus sandwichensis*)	low	low	low	high	medium	0.1224
Grasshopper Sparrow (*Ammodramus savannarum*)	medium	low	low	high	low	−0.2014
Song Sparrow (*Melospiza melodia*)	medium	medium	medium	high	high	0.1582
Yellow-breasted Chat (*Icteria virens*)	low	low	low	low	high	−0.0292
Bobolink (*Dolichonyx oryzivorus*)	low	low	low	high	low	0.2263
Eastern Meadowlark (*Sturnella magna*)	high	low	low	high	medium	−0.0494
Orchard Oriole (*Icterus spurius*)	low	low	high	medium	high	−0.1387
Baltimore Oriole (*Icterus galbula*)	low	medium	high	medium	high	−0.0568
Red-winged Blackbird (*Agelaius phoeniceus*)	high	low	low	high	high	0.0637
Brown-headed Cowbird (*Molothrus ater*)	high	low	medium	high	high	0.1439

TABLE 1. Continued.

Species (taxonomic order)	Agriculture	Urban	Forest	Grassland	Shrubland / Wetland	Change in occupancy
Common Grackle (*Quiscalus quiscula*)	high	high	medium	high	high	0.0695
Kentucky Warbler (*Geothlypis formosa*)	low	low	high	low	low	0.3772
Common Yellowthroat (*Geothlypis trichas*)	low	low	medium	high	high	−0.0181
Yellow Warbler (*Setophaga petechia*)	low	high	high	high	high	0.3144
Summer Tanager (*Piranga rubra*)	low	low	high	low	high	0.2149
Northern Cardinal (*Cardinalis cardinalis*)	low	medium	high	low	high	0.1192
Indigo Bunting (*Passerina cyanea*)	low	low	high	low	medium	0.1369
Dickcissel (*Spiza americana*)	medium	low	low	high	medium	−0.0755

(i.e. parks). The other category was primarily wetlands and shrublands, but also included some barren land.

During the breeding seasons from 1906 to 1909, 59 transects were surveyed with an average length of 8,671 m. Transects were ~42% in agriculture (compared to 52% of the Illinois landscape in agriculture at that time), 0.4% in urban habitats (1% of the landscape), 3% in forest (11% of the landscape), 52% in grassland (32% of the landscape), and 3% in shrublands and wetlands (4% of the landscape). Land cover estimates for the early 1900s came from interpolating across multiple sources; more information about derivation of these estimates can be found in Walk et al. (2010).

The logistics (mainly landowner permission) of conducting surveys has changed dramatically over the past century, resulting in shorter transects in the 2000s than in the 1900s. During the breeding seasons from 2006 to 2008, we surveyed 76 transects averaging 3,674 m in length. We had information on the approximate location of the 1900s transects (e.g., started 1.5 miles south of a given town), therefore we surveyed in the same general area as the 1900s transects to maintain the same geographic extent. We also attempted to sample habitats in proportion to their availability, but advances in crop-breeding technology have resulted in corn being >2 m high in early June, leading to difficulty visually detecting birds in cornfields (our methods only used visual detections); consequently, we surveyed less agriculture in the 2000s, even though it remained the most commonly surveyed habitat type. In the 2000s, transects were 29% in agriculture (compared to 64% of the Illinois landscape in agriculture), 20% in urban areas (8% of the landscape), 18% in forest (15% of the landscape), 23% in grasslands (11% of the landscape), and 10% in shrubland/wetlands (2% of the landscape). Given that transects were essentially random samples of Illinois landscapes, and observers recorded each time they crossed into a different cover type, transects generally were composed of multiple segments of each habitat type. For example, a transect may have included 3 grassland fields, 4 distinct forest patches, and 2 agricultural fields. This repeat sampling of habitat segments within a transect formed the basis for our multi-scale occupancy approach.

Multi-scale Occupancy Modeling

We used a multi-scale occupancy modeling approach (Mordecai et al. 2011) to investigate the probability a transect was occupied (ψ) and, if occupied, the probability a specific habitat within that transect was used (θ_h with h representing the 5 habitats). Similar to Mordecai et al. (2011), a species occupies a site according to a Bernoulli trial with the parameter ψ. The species uses a particular habitat within that transect according to another Bernoulli trial with the parameter θ_h, that is conditional on the respective site occupancy state (ψ). The observation portion of the model is another Bernoulli trial that is conditional on the state of the use of a specific habitat (θ_h), which is determined through the detection and non-detection encounter array unique to each habitat type within each transect. Therefore, if a species uses a particular habitat within an occupied transect, then the species is detected in that habitat according to a Bernoulli trial with the parameter *P*.

We used a spatial rather than temporal approach for fitting models (MacKenzie et al. 2006) since surveys were not repeated within years. While this approach may lead to a slight positive bias in occupancy estimates (Kendall and White 2009), we were primarily interested in comparisons among time periods and use of specific habitats rather than absolute estimates of occupancy. Transects often had habitat segments of varying length, which could also influence detection probability and estimation precision. Although we had information on the length of individual segments from the 2000s, the data for length was not available from the 1900s. Therefore, we randomly combined individual segments to create up to 5 replicates for each land cover type, artificially creating replicate units that were more comparable in size. Consequently, we created a detection history for each transect that consisted of 5 distinct habitat types (i.e. agriculture, urban, forest, grassland, other) and up to 5 subsamples from each habitat, thereby creating a 3-dimensional array of 1s and 0s representing detections or non-detections for a species along each transect–habitat–subsample combination. We excluded introduced species from analyses, because all of the species exhibited extremely rapid increase in abundance and distribution across multiple habitats (e.g., European Starling [*Sturnus vulgaris*], House Finch [*Haemorhous mexicanus*]). We also excluded species with naïve (uncorrected for detection) occupancy estimates of <5% or with <10 detections in their primary habitat across all 3 time periods; this resulted in a total of 66 species for which we could estimate habitat-specific occupancy (Table 1). To determine overall change in occupancy for a given species, we subtracted occupancy in 2000s from occupancy in 1900s.

Habitat Affinity

We determined habitat affinity (high, medium, low) of each species in the 1900s survey using historical literature (Ridgway 1889, Howell 1911, Musselman 1921, Ford et al. 1934) as well as data from the 1900s surveys (Table 1). For nearly all species, the historical literature would indicate habitat(s) in which the species was commonly found or where abundance was the greatest (high), where they were uncommon or occasionally found (medium), or where they did not occur (low). If historical information was not available, we used the 1900s data to determine habitat affinity. Specifically, habitat affinity was considered high in habitats where >50% of the detections occurred, medium in 5–49%, and low in <5%. For the vast majority of species, the historical literature and 1900s data were consistent in our categorization of habitat affinities; in the few instances where there was a discrepancy (always between medium or low affinity), we classified that habitat as medium affinity. Thirty-one species exhibited a high affinity for only 1 habitat, 23 species exhibited a high affinity for 2 habitats, 5 species exhibited a high affinity for 3 habitats, 3 species exhibited a high affinity for 4 habitats, 3 species exhibited a high affinity for all 5 habitats, and for 1 species we were unable to assign high affinity to any habitat. Primary habitat for each species was considered all habitat(s) of high affinity, while alternative habitat was all habitat of medium and low affinity (Table 1).

Statistical Analyses

We estimated occupancy using a hierarchical Bayesian multi-scale occupancy approach (Mordecai et al. 2011). For each species, we fit a model where overall occupancy (ψ) and use of specific habitats (θ_h) was estimated during each time period on the logit scale. Detection (probability of detecting an individual if it was present, P) was estimated as a function of time period, habitat cover type, total area of habitat type surveyed, and time of transect initiation on the logit scale. Unfortunately, we did not have information on the length of specific habitat segments within transects from the 1900s and were therefore unable to use a covariate for segment-specific area sampled. We used relatively vague priors for overall occupancy (ψ) and all detection (P) covariates (normal distribution, mean = 0, precision = 0.5). However, when estimating use of specific habitats (θ_h) we included prior information into the habitat-specific covariates. Incorporating prior information allowed us to account for the biologically reasonable assumption that most species do not use all habitats equally. Specifically, we believed the probability of using high-affinity habitats would be greater than medium-affinity habitats, which would be greater than low-affinity habitats. Consequently, the prior distributions for high-affinity habitat covariates were normally distributed with a mean of 2 with a precision of 0.5, medium-affinity habitat covariates were normally distributed with a mean of 0 with a precision of 0.5, and low-affinity habitat covariates were normally distributed with a mean of –2 with a precision of 0.5 (see Appendix Figure 3). Models were fit using OpenBUGS software (Lunn et al. 2009). We ran 3 chains of at least 10,000 iterations with a 5,000 iteration burn-in period, keeping 1 out of 10 iterations. We evaluated model convergence using the Gelman–Rubin statistic for each species model (Gelman et al. 2003). We ran additional iterations (10,000 at a time) until the Gelman–Rubin statistic was below 1.1. Consequently, for each species, inferences were made via ≥15,000 iterations.

We investigated whether changes in overall occupancy were more strongly associated with changes in the use of primary (high-affinity) or alternative (medium- and low-affinity) habitats by calculating the Pearson's correlation coefficient for overall change in occupancy versus average change in habitat use. Average change in primary (or alternative) habitat use was calculated as the difference between time periods in the probability a habitat was used (given a transect was occupied) for all habitats considered primary (or alternative) habitat. This analysis used 62 species with defined primary and alternative habitats (excluding American Goldfinch [scientific names in Table 1], American Robin, Barn Swallow, which had high affinity for all habitats, and Northern Rough-winged Swallow, which did not have any habitats of high affinity). Finally, we used ANOVAs to investigate changes (difference among time periods in the probability a specific habitat was used given a transect was occupied) in the use of specific land cover types for species that increased and for species that decreased over the 100-yr time frame. Specifically, we compared changes in the use of the 5 habitats (i.e. land cover types) for species that we estimated increased and species that we estimated decreased in overall occupancy.

RESULTS

We estimated that 26 of the 66 species we analyzed decreased in overall occupancy between the 1900 and 2000 surveys, while 40 species increased. Loggerhead Shrike, Upland Sandpiper, and Northern Bobwhite declined the most over the last 100 yr, while Blue-gray Gnatcatcher,

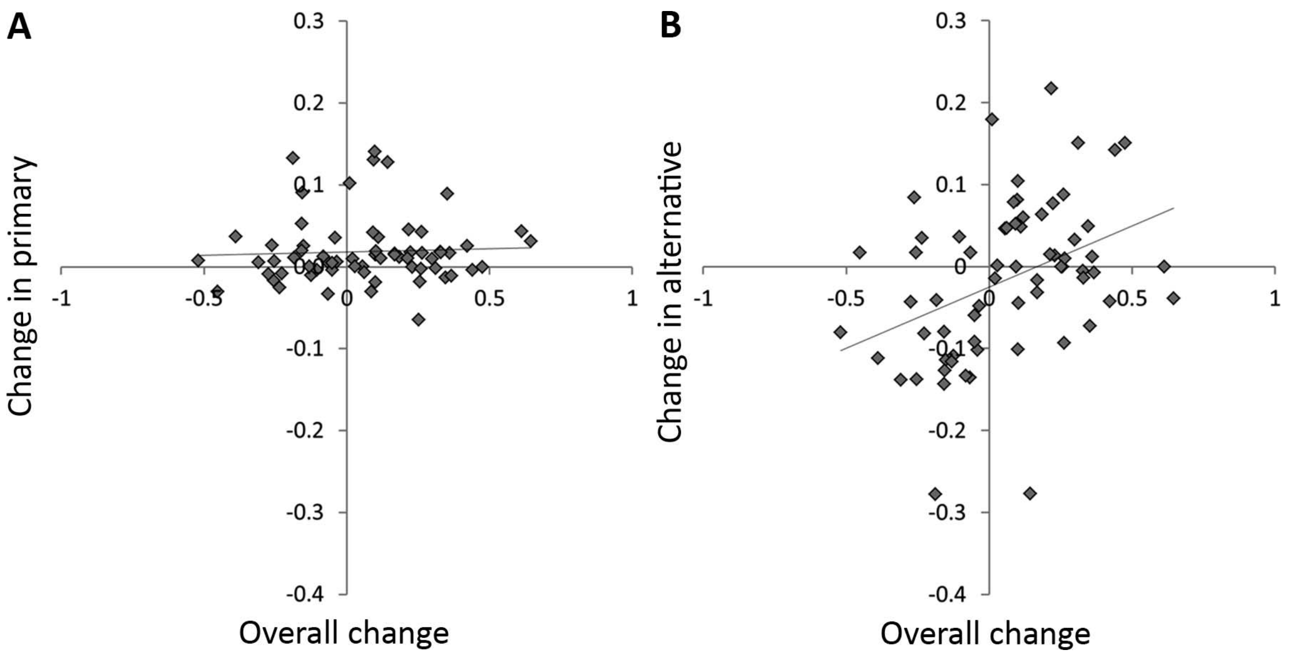


FIGURE 1. Correlation between changes in overall occupancy and changes in occupancy of primary (**A**) and alternative (**B**) habitats between 1900s and 2000s surveys. Each point is an individual species.

Barn Swallow, and Northern Rough-winged Swallow increased the most (Table 1). Species changed their use of alternative habitats (min: –0.28 change; max: 0.22 change) to a greater degree than they changed their use of primary habitats (min: –0.06 change; max: 0.14 change). Furthermore, changes in the overall occupancy of species were not correlated with changes in the use of their primary habitat types (Pearson's correlation coefficient: 0.05, $P = 0.687$; Figure 1A, Table 2), but were correlated with changes in the use of alternative habitat (Pearson's correlation coefficient: 0.37, $P = 0.003$; Figure 1B). Finally, species that increased in overall occupancy did so by utilizing particular land cover types and not generally increasing in all land covers ($F_{4,195} = 8.89$, $P < 0.001$); a similar pattern was observed for species that decreased in occupancy ($F_{4,125} = 13.76$, $P < 0.001$). Specifically, species whose occupancy increased did so by increasing their use of urban, forest, and other habitats (Figure 2A), while those species whose occupancy decreased utilized agricultural and grassland habitats (Figure 2B).

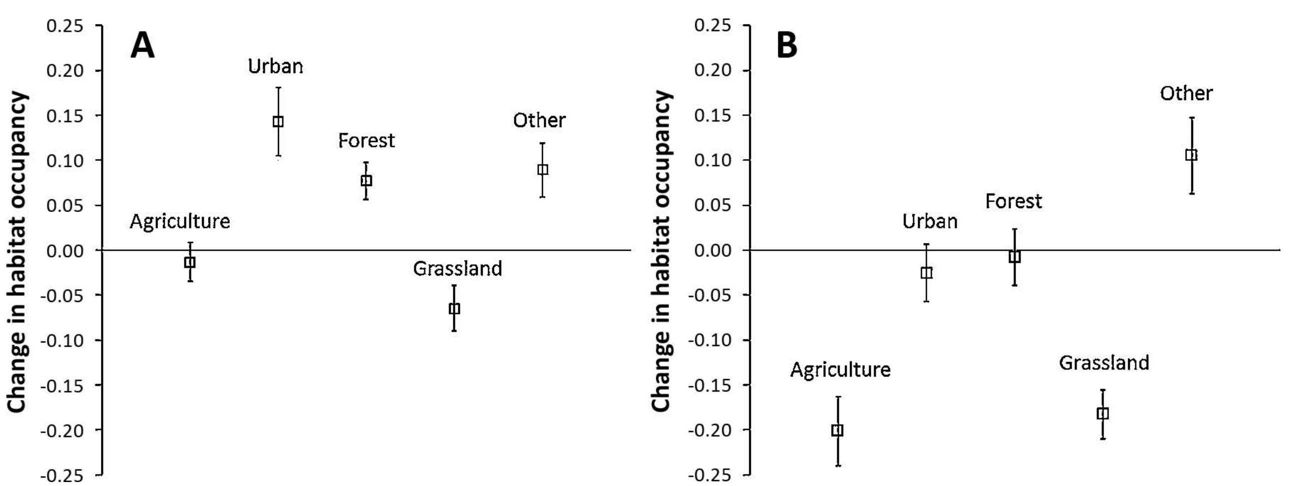


FIGURE 2. Changes in use of specific habitats (mean ± 95% CI) for species that increased in overall distribution (**A**) and decreased in overall distribution (**B**).

TABLE 2. List of the top 10 species by habitat-specific occupancies in the 1900s and 2000s.

Agriculture		Urban	
1900s	2000s	1900s	2000s
Eastern Meadowlark (0.92)	Red-winged Blackbird (0.92)	Eastern Kingbird (0.66)	Common Grackle (0.93)
Mourning Dove (0.89)	Common Grackle (0.91)	Northern Flicker (0.64)	American Robin (0.92)
Common Grackle (0.81)	Brown-headed Cowbird (0.90)	Northern Mockingbird (0.62)	Mourning Dove (0.89)
Dickcissel (0.81)	Horned Lark (0.89)	Purple Martin (0.51)	Chimney Swift (0.87)
Eastern Kingbird (0.80)	Mourning Dove (0.88)	Gray Catbird (0.47)	Chipping Sparrow (0.81)
American Robin (0.76)	Barn Swallow (0.87)	American Goldfinch (0.44)	Northern Cardinal (0.78)
Red-headed Woodpecker (0.75)	American Robin (0.82)	Blue Jay (0.44)	Brown-headed Cowbird (0.78)
Red-winged Blackbird (0.73)	Eastern Meadowlark (0.72)	Brown Thrasher (0.43)	Barn Swallow (0.76)
Loggerhead Shrike (0.73)	Chipping Sparrow (0.68)	American Robin (0.41)	American Goldfinch (0.75)
Horned Lark (0.73)	Killdeer (0.66)	Eastern Phoebe (0.40)	Cedar Waxwing (0.59)
Forest		**Grassland**	
1900s	2000s	1900s	2000s
Blue Jay (0.84)	Eastern Wood-Pewee (0.87)	Eastern Meadowlark (0.93)	Red-winged Blackbird (0.92)
Red-headed Woodpecker (0.75)	Indigo Bunting (0.83)	Mourning Dove (0.88)	Eastern Meadowlark (0.85)
Eastern Towhee (0.73)	American Robin (0.82)	Brown Thrasher (0.86)	Barn Swallow (0.85)
Great Crested Flycatcher (0.72)	Brown-headed Cowbird (0.80)	Eastern Kingbird (0.83)	Mourning Dove (0.83)
Northern Flicker (0.69)	Blue-gray Gnatcatcher (0.80)	Red-headed Woodpecker (0.82)	Brown-headed Cowbird (0.77)
Northern Cardinal (0.69)	Gray Catbird (0.78)	American Robin (0.81)	Common Grackle (0.77)
Orchard Oriole (0.68)	Chimney Swift (0.75)	Common Grackle (0.81)	American Goldfinch (0.71)
Indigo Bunting (0.68)	Barn Swallow (0.73)	Dickcissel (0.81)	Dickcissel (0.70)
American Robin (0.64)	Northern Cardinal (0.70)	Red-winged Blackbird (0.80)	Chipping Sparrow (0.67)
Yellow-billed Cuckoo (0.62)	Blue Jay (0.68)	Common Yellowthroat (0.78)	Field Sparrow (0.66)
Shrub/Wetland			
1900s	2000s		
Red-winged Blackbird (0.76)	Red-winged Blackbird (0.91)		
Field Sparrow (0.73)	Brown-headed Cowbird (0.91)		
Eastern Towhee (0.70)	American Robin (0.88)		
Common Yellowthroat (0.68)	Common Grackle (0.88)		
Orchard Oriole (0.68)	Mourning Dove (0.84)		
Northern Cardinal (0.67)	Indigo Bunting (0.82)		
Yellow-billed Cuckoo (0.63)	American Goldfinch (0.80)		
Loggerhead Shrike (0.60)	Chipping Sparrow (0.79)		
Eastern Meadowlark (0.58)	Gray Catbird (0.78)		
American Crow (0.57)	Northern Cardinal (076)		

DISCUSSION

Over the 20th century, we estimated that a little over half of the 66 species we investigated increased in occupancy. However, these changes were not related to the use of a species' primary habitat, but instead appeared to be driven by changes in the use of alternative habitat. A species' primary habitat is the highest quality for that species and should be the first to be colonized and the last to go extinct (Fretwell and Lucas 1970), resulting in relatively stable use (e.g., Sergio and Newton 2003, Gadenne et al. 2014). In accordance with this expectation, we observed less variation in the use of a species' primary habitat relative to what we observed in alternative habitats. Alternative habitats may provide novel opportunities to allow a species to increase in occupancy. For instance, Chipping Sparrows and Northern Cardinals increased dramatically over the past 100 yr by using urban habitats, which they did not use 100 yr ago. Conversely, species that declined contracted into primary habitat and became extirpated from alternative habitats. For instance, Red-headed Woodpeckers, whose primary habitat is forest, exhibited much reduced occupancy in urban, agriculture, and grassland habitats accompanying their population decline over the past century. Consequently, species appear to use alternative habitats as populations grow, but withdraw into primary habitats as populations contract.

Urban habitats represented one of the greatest opportunities for species to increase over the last 100 yr. Urban areas have increased dramatically in recent decades (Brown et al. 2005, Foley et al. 2005), and species taking advantage of this newly created habitat may have benefited. We found that increased use of urban habitats was associated with increased overall occupancy. While urban habitats have been present for hundreds of years in Illinois, their suitability for birds has changed drastically. In the early 1900s, the majority of urban areas in Illinois were relative new, with few trees and shrubs. Over the last 100 yr, the vegetation of many of these urban centers has matured and become more structurally heterogeneous. Moreover, human persecution of birds in urban areas has decreased. A. O. Gross, one of the 1900s surveyors, reported that granivores and raptors were actively harassed or killed in towns and cities to protect gardens and poultry (Forbes and Gross 1922). Ridgway (1915) described how species in southern Illinois declined between 1900 and 1910 due to human persecution, with most examples being from urban habitats. In contrast, granivorous species are now actively encouraged in urban areas via supplemental feeding (i.e. bird feeders, which are most common in urban habitats), and laws prohibit the harassment and killing of most species, including raptors.

In sharp contrast to urban habitats, changes in suitability of agricultural habitats may have driven population declines of the species that used them. In the early 1900s, agricultural habitats had attributes more attractive to grassland and shrubland birds, compared to the intensive row-crop agriculture that is now ubiquitous throughout Illinois and most of the midwestern United States. Agriculture in the early 1900s was more diverse than today, including crops like wheat, oats, and alfalfa that provided large areas of habitat for grassland species. Fields were weedy, considerably smaller, and often bordered by wooded or shrubby edges. By the 2000s, most grassland-like small grain and hay crops had been replaced by corn and soybean monocultures. Coupled with the proliferation of herbicides and insecticides, nesting and foraging conditions in agricultural habitats have changed significantly (VanBeek et al. 2014). Consequently, species that once used agricultural fields, even marginally, no longer do so, hastening their declines.

We had the unique opportunity to use one of the first systematic bird surveys to investigate how long-term changes in land use influence bird species. While we provide insight into the importance of alternative habitats over a long interval, there are many challenges associated with using 100-year-old data, and our results should be viewed with caution. For instance, we had to use spatial rather than temporal replicates in an attempt to account for imperfect detection, which may lead to a positive bias in our occupancy estimates (Kendall and White 2009). Furthermore, we were unable to survey the same amount of area per transect in the 2000s as surveyors did in the 1900s. Surveying smaller areas could potentially lead to a negative bias in overall changes in occupancy. However, we attain similar results when relaxing the criterion for which species were increasing or decreasing (i.e. incorporating species with slight increases together with decreasing species). Another challenge we faced was lack of data for some species in one time period, which leads to low detection probabilities. As a result, estimates for the use of low-affinity habitats appeared to be unreasonably high (e.g., Acadian Flycatchers using agricultural fields within an occupied transect at a probability of 23%). We attempted to correct for this shortcoming by using slightly informed priors, which influenced the posterior distribution of our estimates when we did not have access to abundant data. However, we investigated the effects of the informative priors on a few species and found that estimates for use of high-affinity habitat was slightly greater on average (0.08), similar for medium-affinity habitat (0.01), and much lower for low-affinity habitat (–0.18). We have no reason to believe these changes would significantly influence our results. Consequently, we believe it was important to include biological realism into our modelling approach through use of informed priors.

Conservation Implications

Changes in species' populations within alternative habitats may be the key to understanding the current status of a species and predicting its future. For example, both urban and agricultural habitat increased in Illinois over the last 100 yr. However, intensification of agricultural lands has made them less suitable for most species (VanBeek et al. 2014), while urban areas have become much more wildlife friendly (Fischer et al. 2012). These fundamental changes may have led to the differential response we observed for species that were increasing in occupancy vs. those that were decreasing. The implications of this result are that if we work to make agricultural practices more wildlife friendly, we may see a new suite of species increasing and taking advantage of this opportunity or an increase in populations of species that were detrimentally affected in agricultural areas between 1900s and 2000s.

At the conclusion of the early 1900s survey, A. O. Gross gave a lecture to scientists at the University of Illinois in which he stated the following about Northern Flickers: "The Yellow Hammer is the most versatile of our American birds. If all our other birds should disappear, the Flicker would be the last to go for he is the hardiest of all our feathered residents. He hammers the borers out of the bark with the Red-heads. He confiscates cherries, in season, with the Catbird. He is found digging grubs in the fields with the Meadowlarks. If it ever comes to the survival of the fittest, the Yellow Hammer is bound to stay with us because of his ability to change with surrounding conditions." At the time, flickers were among the most abundant species, and likely the most abundant woodpecker in Illinois. However, after the early 1900s, the species experienced a dramatic reduction in distribution within Illinois (Walk et al. 2010), which was driven by changes in its alternative habitat (agricultural lands). The flicker is now listed as a Species in Greatest Conservation Need in Illinois (IDNR 2016).

ACKNOWLEDGMENTS

We thank Steve Bailey, Tara Beveroth, Mark Alessi, Kevin Sierzega, Courtney McCusker, Misty Barron, Heather Fraser, Jessica Cochran, and Stephanie Wright for their assistance. Dr. Jean Graber, one of the 1950s surveyors, was extremely helpful in providing information necessary for repeating this survey. We thank reviewers, particularly Jim Nichols, for comments on the manuscript. Finally, we thank the many private landowners on whose property the surveys were conducted.

Funding statement: This study was funded by the State Wildlife Grant Program (T-16-P-1).

Ethics statement: We followed the research ethics protocol of the University of Illinois. No IACUC permit was needed for this research.

Author contributions: M. P. Ward, J. D. Brawn, and J. W. Walk conceived the idea, design, experiment (supervised research, formulated questions or hypothesis). M. P. Ward, J. D. Brawn, and J. W. Walk performed the experiments (collected data, conducted the research). M. P. Ward, K. Stodola, and T. J. Benson wrote paper. M. P. Ward, K. Stodola, J. Walk, J. Deppe, T. J. Benson, and J. Brawn developed or designed the methods. K. Stodola and T. J. Benson analyzed the data. M. P. Ward and J. Walk contributed substantial materials, resources, or funding.

LITERATURE CITED

Blackburn, T. M., P. Cassey, R. P. Duncan, K. L. Evans, and K. J. Gaston (2004). Avian extinction and mammalian introductions on oceanic islands. Science 305:1955–1958.

Brown, D. G., K. M. Johnson, T. R. Loveland, and D. M. Theobald (2005). Rural land-use trends in the conterminous United States, 1950–2000. Ecological Applications 15:1851–1863.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Fischer, J. D., S. H. Cleeton, T. P. Lyons, and J. R. Miller (2012). Urbanization and the predation paradox: The role of trophic dynamics in structuring vertebrate communities. Bioscience 62:809–818.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, et al. (2005). Global consequences of land use. Science 309:570–574.

Forbes, S. A. (1907). An ornithological cross-section of Illinois in autumn. Illinois Natural History Survey Bulletin 7:305–335.

Forbes, S. A., and A. O. Gross (1922). The number and local distribution in summer of Illinois land birds of the open country. Illinois Natural History Survey Bulletin 14:187–218.

Ford, E. R., C. C. Sanborn, and C. B. Coursen (1934). Birds of the Chicago Region. Chicago Academy of Sciences, Chicago, IL, USA.

Fretwell, S. D., and H. L. Lucas (1970). On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19:16–36.

Gadenne, H., T. Cornulier, C. E. Eraud, J-C. Barbraud, and C. Barbraud (2014). Evidence for density-dependent habitat occupancy at varying scales in an expanding bird population. Population Ecology 56:493–506.

Gaston, K. J. (2009). Geographic range limits: Achieving synthesis. Proceedings of the Royal Society B-Biological Sciences 276: 1395–1406.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin (2003). Bayesian Data Analysis. Chapman and Hall, Boca Raton, FL, USA.

Howell, A. H. (1911). Birds of Arkansas. U.S. Department of Agriculture, Biological Survey Bulletin 38.

[IDNR] Illinois Department of Natural Resources (2016). 2015 Implementation Guide to the Illinois Wildlife Action Plan. https://www.dnr.illinois.gov/conservation/IWAP/Documents/FinalDraft2015_FINAL_Revision%204-18-16.pdf

Jetz, W., D. S. Wilcove, and A. P. Dobson (2007). Projected impacts of climate and land-use change on the global diversity of birds. PLOS Biology 5(6):e157.

Kendall, W. L., and G. C. White (2009). A cautionary note on substituting spatial subunits for repeated temporal sampling in studies of site occupancy. Journal of Applied Ecology 46: 1182–1188.

Lunn, D., D. Spiegelhalter, A. Thomas, and N. Best (2009). The BUGS project: Evolution, critique and future directions (with discussion). Statistics in Medicine 28:3049–3082.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines (2006). Occupancy Estimation and Modeling. Academic Press, London, UK.

Mordecai, R. S., B. J. Mattsson, C. J. Tzilkowski, and R. J. Cooper (2011). Addressing challenges when studying mobile or episodic species: Hierarchical Bayes estimation of occupancy and use. Journal of Applied Ecology 48:56–66.

Musselman, T. E. (1921). A history of birds of Illinois. Journal of the Illinois State Historical Society 14:1–73.

Parmesan, C., and G. Yohe (2003). A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37–42.

Ridgway, R. (1889). The Ornithology of Illinois, Volume 1. State Laboratory of Natural History, Champaign, IL, USA.

Ridgway, R. (1915). Bird-life in southern Illinois: Changes which have taken place in half a century. Bird-Lore 17:191–198.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosensweig, and J. A. Pounds (2003). Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

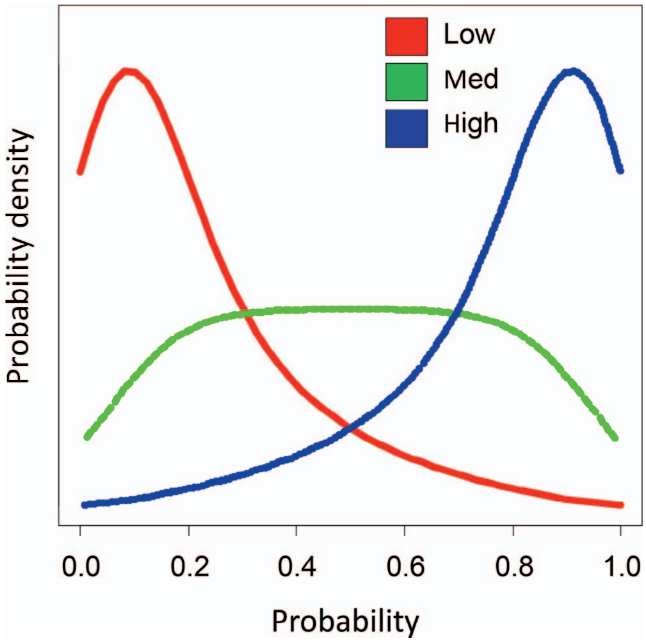
Sergio, F., and I. Newton (2003). Occupancy as a measure of territory quality. Journal of Animal Ecology 72:857–865.

Stralberg, D., D. Jongsomjit, C. A. Howell, M. A. Synder, J. D. Alexander, J. A. Wiens, and T. L. Root (2009). Re-shuffling of species with climate disruption: A no-analog future for California Birds? PLOS One 4(9):e6825.

VanBeek, K. J., J. D. Brawn, and M. P. Ward (2014). Avian nesting ecology in soybean fields: Does no-till provide any benefits? Agriculture, Ecosystems, and Environment 185:59–64.

Vitousek, P. M., C. M. Dantonio, L. L. Loope, and R. Westbrooks (1996). Biological invasions as global environmental change. American Scientist 84:468–478.

Walk, J. W., M. P. Ward, T. J. Benson, J. L. Deppe, S. A. Lischka, S. D. Bailey, and J. D. Brawn (2010). Illinois Birds: A century of change. Illinois Natural History Survey Special Publication 31.



APPENDIX FIGURE 3. Probability density plot for the 3 possible informative priors of "high," "med," and "low" habitat affinity covariates for the estimation of habitat specific use (θ).