Habitat use and reproductive success of waterbirds in the human-dominated landscape of North America's prairies: Using sparse data to inform management

A Dissertation

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Dedication

I dedicate this dissertation to my (younger) brother, Martin “Tino” Specht, who, since the day he was born, has been showing me what it looks like to remain open to opportunities, learn when to say no, and to go after dreams.

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"Don't worry about what you will do next. If you take one step with all the knowledge you have, there is usually just enough light shining to show you the next step."

~ Mardy Murie

HABITAT USE AND REPRODUCTIVE SUCCESS OF WATERBIRDS IN THE HUMAN-DOMINATED LANDSCAPE OF NORTH AMERICA'S PRAIRIES: USING SPARSE DATA TO INFORM MANAGEMENT

Hannah Specht

University of Minnesota, 2018

HISTORICALLY, biodiversity conservation has prioritized protecting large tracts of wilderness. However, alternative strategies are needed to conserve species whose habitat remains as patches within human-dominated landscapes (e.g., farm fields, pastures, development) that now cover more than half of Earth's habitable land. The need for alternative strategies is particularly strong for grassland wildlife, which has experienced greater habitat loss to agriculture and less habitat protection than other biomes worldwide. In North America's grasslands, wildlife conservation happens by facilitating wildlife-compatible use of existing habitat fragments and adoption of wildlife-friendly practices on human-used land (e.g., crops, range, roadsides). Information needed to implement effective management strategies requires an understanding of where, when and how target species use habitats available to them to survive and reproduce. Unfortunately, our increased need to understand the ecology of species of conservation concern often comes too late to easily gather requisite information—We might not have baseline information preceding a population decline, we may lack information that effectively links population processes across the spatial and temporal scales that they occur, or we could be limited by excessive cost to study species (particularly as they become more rare). Here, I present new approaches for field data collection and analysis

for rare and cryptic species, used to improve understanding of how anthropogenic and natural habitat characteristics affect the habitat use and reproductive success of upland-nesting shorebirds and waterfowl, to better inform management in North America's grasslands.

In my first two chapters, I use historical data in new ways to inform today's conservation questions, identifying ecological drivers of upland nesting waterfowl and shorebird fecundity in the Northern Great Plains. In chapter 1, I used 47 years of age data from hundreds of waterfowl banding stations to identify temporally variable habitat and trophic conditions affecting dabbling duck reproductive success throughout the Northern Great Plains. In chapter 2, I used 1,063 nest records of two shorebird species of conservation concern, Willet (*Tringa semipalmata*) and Marbled Godwit (*Limosa fedoa*), collected by more than 20 research projects over the course of 48 years to examine nest habitat selection and its relationship to nest survival. In both chapters, by using historical short-eared owl data as a proxy for population irruptions of voles, the primary prey of predators that eat waterfowl and shorebird eggs (and for which no direct historical data exists), I was able to identify positive relationships between vole populations and metrics of fecundity (age ratios and nest survival). By using regional-scale data, I was able to assess variation in waterfowl productivity across scales and identify range-wide drivers of habitat selection in the studied shorebirds. Throughout their prairie ranges, upland nesting shorebird and waterfowl reproductive success is tightly tied to wetlands, which provide key food resources: increases in wetland inundation improved dabbling duck fecundity and Marbled Godwits experienced higher fecundity in territories with greater

wetland cover. Willets selected nest sites closer to wetlands than expected but experience higher nest survival at locations further from wetlands. Duck species exhibited mixed density dependent effects on fecundity but density of waterfowl or shorebirds did not influence shorebird nest survival. In both chapters, temporal environmental variation accounted for substantial variation in fecundity metrics, indicating that, if not accounted for, temporal variation could mask habitat management effects on fecundity. These chapters demonstrated that data combined across sources and thoughtfully analyzed by accounting for variation attributed to data sourcing can be used to inform basic understanding of species ecology where appropriate data would not be possible to collect in a cost-effective or timely manner.

A substantial portion of the breeding ranges of prairie waterfowl and shorebirds is now additionally being developed for oil. The impacts of habitat alterations on wildlife habitat use are often assessed using baseline data from before habitat alterations took place, but this information does not exist for shorebird species and Northern Pintail (*Anas acuta*) potentially affected by these changes. In chapter 3, I use habitat suitability models to account for the probability of habitat use by shorebird and waterfowl species before oil infrastructure was introduced to the landscape, allowing me to assess differences in waterbird habitat use corresponding to oil infrastructure and vehicle traffic in North Dakota's Bakken oil field. I found reduced habitat use by breeding pairs or broods of all five studied species at sites with higher traffic and that Wilson's phalarope (*Phalaropus tricolor*) breeding pairs avoided habitat with higher well density. A unique survey design

that allowed us to infer brood presence through behavior facilitated identifying effects of traffic on brood habitat use, a situation where data would otherwise have been too sparse.

Occupancy models, used in chapter 3 to assess the probability of habitat use by shorebirds species and Northern Pintail (*Anas acuta*) while accounting for failure to detect the species when present during a survey, are often least accurate when study organisms are present at a minority of sites and difficult to detect. In chapter 4, I use simulations and theoretical analyses to show that a new "conditional" occupancy sampling design improves estimates of habitat use for rare species. This "conditional" occupancy sampling design, which allocates more survey effort to sites where a species is known to be present, improves estimates of the detection probability, in turn, improving estimates of occupancy probability for species that are rare. I explain how this design can be used as a hybrid with other survey designs to assess a suite of species that vary in their expected occupancy and detection probabilities.

Management for upland-nesting waterbirds should continue to prioritize conservation of native grassland and wetlands from conversion and consolidation. In particular, maintaining the capacity of less permanent wetland basins to rehydrate during wetter periods will benefit waterfowl and shorebird fecundity, while active patch management of grassland areas with nearby wetlands can help maintain preferred nesting vegetation for declining Willets and Marbled Godwits. Within areas of rapid landscape development and activity, impacts such as infrastructure and activity should be concentrated within corridors on the landscape while conservation and management of habitat for wildlife should focus on interstitial spaces between development corridors.

Wildlife management will continue to require creative solutions to addressing information needs, particularly for rare and cryptic species. I have demonstrated that careful study design and analysis can often allow us to address information needs by thoughtfully utilizing existing data with modeling approaches that can account for imperfect design and deploying limited resources carefully in field data collection.

Preface

Each chapter of this dissertation has been published, submitted, or is intended for publication; formatting of each chapter thus reflects specifications of the journal for which it is intended for publication. Chapters that are not written in the first person reflect coauthorship, but as first author I am responsible for the content of each chapter. Chapter 1, **'**Banding age ratios reveal that prairie waterfowl fecundity is affected by climate, density dependence and predator-prey dynamics', coauthored by TW Arnold, has been accepted to the *Journal of Applied Ecology*. Chapter 2, 'Using historical nest records to identify habitat characteristics that influence habitat selection and nest survival of willets and marbled godwits in the Northern Great Plains' is being prepared for submission to *Avian Conservation and Ecology*—it will be coauthored by TW Arnold, V St-Louis and data contributors acknowledged in the chapter. I am the sole author of Chapter 3, 'Habitat use by upland-nesting waterbirds is negatively affected by oil well infrastructure and activity', which is intended for submission to Biological Conservation. Finally, a version of Chapter 4 has been published as:

Specht, H.M., H.T. Reich, F. Iannarilli, M. Edwards, M. Johnson, S. Stapleton, M. Weegman, B. Yohannes and T.W. Arnold. 2017. Occupancy surveys with conditional replicates: An alternative sampling design for rare species. Methods in Ecology and Evolution.8: 1725–1734.

A video made to accompany this chapter can be found at: https://youtu.be/mAcXHpljJ2w.

The cumulative bibliography is formatted following guidelines for the journal Biological Conservation.

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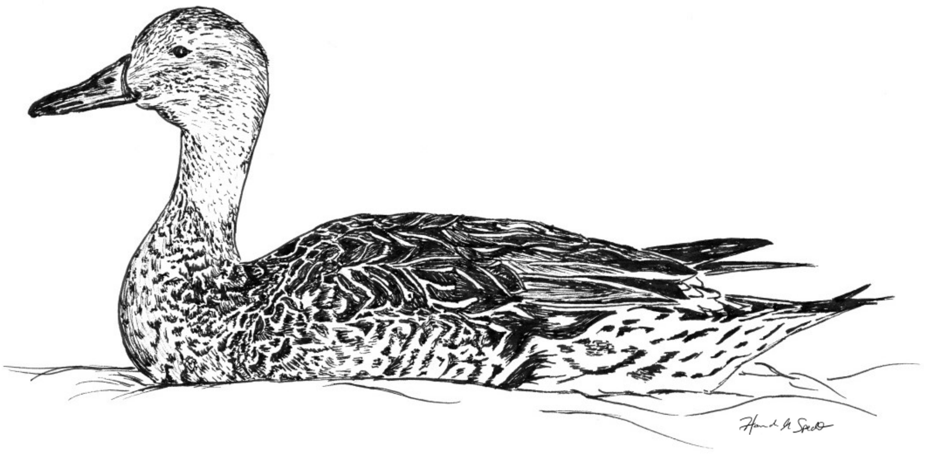
Chapter 1

BANDING AGE RATIOS REVEAL THAT PRAIRIE WATERFOWL FECUNDITY IS AFFECTED BY CLIMATE, DENSITY DEPENDENCE AND PREDATOR-PREY DYNAMICS



SUMMARY

Fecundity estimates for demographic modeling are difficult to acquire at the regional spatial scales that correspond to climate shifts, land use impacts or habitat management programs, yet are important for evaluating such effects. While waterfowl managers have historically used harvest-based age ratios to assess fecundity at continental scales, widely available age ratios from late-summer banding data present an underutilized opportunity to examine a regional fecundity index with broad temporal replication. We used age ratios from banding data and hierarchical mixed-effect models to examine how fecundity of five North American dabbling duck species was affected by temporal variation in hydrological cycles, intra- and inter-specific density dependence and alternate prey availability, and whether those relationships were consistent across a broad geographic area. Model-estimated fecundity was within the range of traditional harvest-based fecundity estimates for each species. Ecological covariates explained between 16 and 53% of the temporal variation in fecundity, dependent on species. Increasing wetland inundation and an indicator of vole population irruptions were consistent predictors of increasing fecundity across all species. Species exhibited mixed positive and negative responses to interspecific and intraspecific breeding pair densities hypothesized to affect nest and brood survival respectively, highlighting the importance of integrating brood survival into fecundity metrics for precocial species. Declines in fecundity over time and across space at more northern latitudes may reflect stronger policies for grassland and wetland protection in the U.S. versus Canadian portions of the prairies over the time period of our study. Maintaining the capacity of less permanent basins to rehydrate in wetter periods through easement protection benefits fecundity, particularly for late-nesting species that acquire a greater proportion of their reproductive energy on the breeding grounds. *Synthesis and applications***.** Age-ratios from banding operations allowed us to attribute variation in fecundity to temporal ecological variables, indicating that effects of habitat management for waterfowl may be masked unless analysts account for this variation. Age ratios at capture could be useful as a fecundity metric in integrated population models and for evaluating population dynamics of extensively banded nongame species, especially if adjusted for capture vulnerability using within-season recapture data.

INTRODUCTION

Understanding how population abundance varies through time and space can help identify potential limiting factors and provide insights to conservationists about when and where to intervene to successfully manage wildlife populations (Brown, Mehlman & Stevens 1995; Conn et al. 2015). However, measuring temporal and spatial variation in survival and fecundity is more difficult, particularly for migratory populations that travel long distances and may cross jurisdictional boundaries (Webster, Marra, Haig, Bensch & Holmes 2002). Research examining vital rates often comes from short-term localized studies that may not adequately represent the long-term dynamics of a regional population. Thus, there is a clear need for reliable data on vital rates collected at large spatiotemporal scales that can be used to identify limiting factors and inform conservation strategies at ecologically meaningful scales (Saracco, Royle, DeSante & Gardner 2010; Nail, Stenoien & Oberhauser 2015).

Avian population dynamics have been extensively studied, yet assessing the effects of climate change, land use or habitat management on fecundity has been hindered by the scale and scope of available fecundity metrics. Age ratios for example, are frequently collected during migration and wintering when birds are congregated, but since this metric inherently captures a mixture of source populations, inference about regional breeding habitat management is limited. Nest survival is a commonly used fecundity metric that is specific to local breeding areas (Walker et al. 2013b); however, it fails to account for breeding effort (Etterson, Bennett, Kershner & Walk 2009) and offspring survival after leaving the nest (Streby & Andersen 2011), which includes the entire brood-rearing period in precocial birds (Amundson, Pieron, Arnold & Beaudoin 2013). Age ratios from late summer banding obtained before birds have initiated extensive post-breeding migration (Mazerolle, Dufour, Hobson & Haan 2005; Nolet et al. 2013) represent an opportunity to examine an integrated fecundity index with broad temporal and spatial replication.

In this study, we demonstrate how female age ratios from late summer banding can be used as a regional fecundity metric. We used this approach to examine whether locally identified factors that affect fecundity in North American dabbling ducks were consistent across species and throughout the Prairie Pothole Region at which scale flyway harvest management is regulated. With this approach we aim to provide conservationists with a new assessment tool that can be used to integrate spatiotemporal fecundity dynamics into full annual cycle models.

Fecundity is an important metric to evaluate at broad scales because it may respond to environmental variation and management in short order, providing a direct measurement of the effectiveness of management, whereas changes in survival or population density may respond more slowly and be confounded by immigration and emigration (Pfister 1998). Fecundity is strongly shaped by trophic interactions, including availability of food resources for breeding adults and offspring (McPeek, Rodenhouse, Holmes & Sherry 2001), intra- and interspecific competition for those resources (Lack 1954; Gurnell, Wauters, Lurz & Tosi 2004), and impacts of nest and brood predators at higher trophic levels (Sinclair & Pech 1996). The effects of these ecological relationships on fecundity components of North American dabbling ducks have been the subject of substantial experimental and observational research (e.g. Stephens, Rotella, Lindberg, Taper & Ringelman 2005; Howerter et al. 2014), yet interactions between fecundity components create an inconsistent picture regarding ecological regulation of fecundity (Amundson & Arnold 2011) and have only rarely been studied with spatial replication (Howerter et al. 2014). Effective integration of habitat and harvest management, as called for by the North American waterfowl management community (Runge et al. 2006; Osnas et al. 2014), therefore requires an improved understanding of how highly variable regional fecundity is affected by temporal ecological variability occurring at spatial scales similar to the scales of ecoregional land-use change, climate change and habitat management (e.g. wetland restoration, predator control, conservation of upland nesting cover), and how these effects aggregate to affect large-scale population dynamics. If the local ecological mechanisms observed or hypothesized to affect components of fecundity operate at broader spatial scales, we would expect to see signals of these relationships repeated across the region. Similarly, we might expect such patterns to be shared across species that share breeding habitats, food resources and predators.

We tested the consistency of ecological relationships related to temporal variation in resource availability, density dependence and predation for five species of dabbling duck: American wigeon (“wigeon”; *Mareca americana*), gadwall (*Mareca strepera*), blue-winged teal (“teal”; *Spatula discors*), mallard (*Anas platyrhynchos*) and northern pintail (“pintail”, *Anas acuta*). Spring wetland inundation drives increases in invertebrate richness (Szalay et al. 2003), which are hypothesized to improve fecundity through higher clutch size, renesting propensity and duckling survival (Cox, Hanson, Roy & Euliss 1998; Krapu, Reynolds, Sargeant & Renner 2004; Arnold, Devries & Howerter 2010). Low summer precipitation and excessive evapotranspiration can lead to loss of flooded wetland habitat, in turn reducing renesting propensity and brood survival (Howerter et al. 2014). In addition to wetland conditions, density dependent effects on fecundity have been identified in North American dabbling ducks at continental scales, although the ecological mechanism remains obscure (Gunnarsson et al. 2013). Foraging theory predicts that higher densities of active nests may increase nest predation intensity, although very high nest densities may reduce predation intensity due to predator satiation (Schmidt 1999), whereas experiments that manipulated brood density indicated that brood survival is negatively affected by density(Amundson & Arnold 2011; Gunnarsson et al. 2013). Foraging theory and the alternate prey hypothesis additionally predict a reduction in predation on nests when primary prey (e.g. microtine rodents) of generalist mammalian predators are more abundant (Schmidt 1999; Ackerman 2002; Brook, Pasitschniak-Arts, Howerter & Messier 2008). Finally, predator populations may exhibit a numerical response to a strong prey base (Schmidt 1999), negatively affecting fecundity of breeding ducks in the following year.

METHODS

Fecundity Index.— We defined fecundity as the proportion of "normal wild" (United States Geological Survey (USGS) Bird Banding Lab status code=3) females captured and banded during late summer (July-Sept) that were aged as juveniles, using data from the USGS Bird Banding Lab:

P_{juv} = Juveniles/(Juveniles+Adults) eq. 1

where Juveniles included banding age codes representing local and hatch-year birds and Adults included codes representing all other known-age birds (<0.001% of banded ducks were of unknown age). Proportion of juveniles can be readily converted into traditional age ratios ($\underline{F}$ = number of juvenile females per adult female) using odds ratios:

$F = \underline{P_{juv}}/(1-P_{juv})$ eq. 2.

However, we preferred the Pjuv parameterization because it is symmetric and bounded between 0 and 1, whereas observed age ratios (F) of small samples are asymmetrically distributed from 0 to infinity. This parameterization facilitated defining the number of juveniles in a banded group as a binomial random variable defined by P_{juv} and weighted by the number of birds in the sample (N_{juv}~Binomial($N_{juvF} + N_{adF}$, P_{juv}) to account for variation in banding effort. In turn, this allowed us to use logistic regression to model P_{juv} as a function of environmental covariates and other fixed and random effects. If capture vulnerability doesn't differ between juveniles and adults, P_{juv} directly estimates fecundity. If capture vulnerability does vary by age, P_{juv} can still function as an index of fecundity, provided that vulnerability varies randomly across years, within the banding season and independently of studied variables, thus permitting systematic variation in capture rates to be modeled with spatial and temporal random intercepts (e.g. banding site, year).

Study Area and Ecological Covariates. – We defined the study area for our analysis as the portions of the prairie pothole region (PPR) that lie within the Waterfowl Breeding Pair and Habitat Survey ("WBPHS"; strata 26-49 totaling 1·1 million km^2; Figure 1), including southern portions of Alberta, Saskatchewan and Manitoba; northeastern Montana; and North and South Dakota. The survey, conducted annually in May since 1955, provides detectability-adjusted estimates of breeding waterfowl populations and the number of wetland basins containing water expected to last at least three weeks beyond the survey date for each stratum (U.S. Fish and Wildlife Service 2016). We used the zones defined in the WBPHS survey (called "strata", 12-109 thousand km^2 each, Fig.1) as the aggregation units for ecological covariate data in our analysis because they reflect combinations of distinct ecological regions and state- or province- based management boundaries and have been the historical survey units for population and habitat evaluation (Nichols, Runge, Johnson & Williams 2007); metrics of ecological drivers are either measured at the stratum level or can be meaningfully aggregated within a stratum for each year. Dabbling ducks are captured on wetlands throughout this region (locations may vary amongst years) in late summer by federal, state and provincial agencies as well as research programs in a targeted effort to deploy bands on mallards and pintail; subsequent recovery of dead birds reported to the Bird Banding Laboratory supports estimation of harvest vulnerability and survival. Other captured species are concurrently banded although their prevalence is influenced by timing of banding efforts and trapping methods (most programs use baited swim-in traps (Dieter, Murano & Galster 2009), and some use rocket nets, but trapping information is not submitted with banding data in North America).

We used banding data from the USGS Bird Banding Lab from 1969-2015 from banding locations within the WBPHS study area, using data from 1 July to 31 August for early fall migrants (teal, pintails and wigeons) and including September bandings for later migrants (gadwalls, mallards). We excluded strata represented by fewer than 10 years of banding data (resulting in inclusion of 14-17 strata, depending on species; Table 1, Appendix S1), reasoning that stratum-specific slopes fit to fewer than 10 years of data were unreliable; many of these excluded strata fell along the eastern boundary of the prairie pothole region and have relatively low densities of waterfowl.

Increases in numbers of inundated ponds that in turn increase invertebrate biomass (Szalay et al. 2003) were represented as the change in flooded wetland density between years (ΔPOND = $D_{s,t}$ - $D_{s,t-1}$, where $D_{s,t}$=inundated basins/ km^2 in stratum s, year t, WBPHS), such that positive values indicate an increase in density. The maintenance of wetland conditions during the renesting and brood-rearing season was represented by the

Dai Palmer Drought Severity Index (PDSI) for July, which incorporates temperature and precipitation of preceding months, normalized to facilitate spatiotemporal comparisons (higher values indicate wetter conditions; NOAA Earth Systems Research Lab, Dai, Trenberth & Qian 2004). Stratum-specific PDSI values were a weighted average of the geographic area of overlap between PDSI cells (2.5 degrees) and each stratum. We hypothesized that wetland re-inundation and maintenance would positively affect fecundity, as nest success and brood density are positively correlated with higher pond counts (Walker et al. 2013a,b).

We represented nesting density in our model as the number of upland nesting duck breeding pairs (seven species) per square kilometer (BPUP) and potential intraspecific brood density as the number of intraspecific breeding pairs per inundated wetland derived from WBPHS population estimates at the strata level. We hypothesized a neutral or positive effect of nesting density on fecundity through predator satiation and a negative effect of intraspecific pair density due to resource competition. Negligible species-specific variation in nest survival (Greenwood, Sargeant, Johnson, Cowardin & Shaffer 1995; Stephens et al. 2005) suggests that nest-driven density dependence is a function of all upland nesting ducks, though we note that densities in most regions were driven by mallards and blue-wings. Intraspecific density per wetland, which accounts for the role of pond density in driving settlement, resource acquisition and brood predation, assumes that intraspecific competition is the most important driver of potential food shortages for ducklings (Elmberg, Nummi, Pöysä & Sjöberg 2003).

The negative effect of generalist predators on waterfowl nest survival and age ratio has been dampened during periods with high abundance of preferred microtine rodent prey (Ackerman 2002; Brook et al. 2008; Nolet et al. 2013); this effect of alternate prey is attributed to predator satiation (Angelstam, Lindström & Widén 1984). Microtine rodent population fluctuations have not been monitored at the landscape scale in North American grasslands. However, short-eared owls (*Asio flammeus*), which also prey on these rodents, exhibit population mobility that allows them to locate high microtine densities on the landscape (Poulin, Wellicome & Todd 2001). We used annual relative abundance of short-eared owls (SEOW; average number of short-eared owls per 40km North American Breeding Bird Survey route within each stratum and year; Sauer et al. 2017) as an indicator of rodent population irruptions in space and time. We hypothesized that vole population irruptions would reduce negative predation effects of generalist predators (e.g. skunk, red fox (*Vulpes vulpes*) and coyote (*Canis latrans*)) on prairie waterfowl fecundity.

Walker et al. (2013b) postulated that reduced waterfowl nest survival in years following wet conditions was driven by higher densities of nest predators resulting from a strong small mammal prey base that was supported by strong primary productivity associated with the wet conditions. We aimed to test this hypothesis more directly by including indicators of small mammal and duck nest food resource availability in the previous year (BPL1 and SOL1), hypothesizing negative effects on fecundity.

Modeling and goodness-of-fit testing.—We modeled Pjuv for each site-year with an a priori logistic mixed effects model for each species using Bayesian Markov chain Monte

Carlo analysis with JAGS (Plummer 2005) in R (Version 3·2·3; R Development Core Team 2015; Appendix S2):

$$logit(Pjuv_{b,t}) = \boldsymbol{\beta_s X'_{s,t}} + \beta_{lat}Lat'_b + \beta_{long}Long'_b + \varepsilon_{s/t/b} \quad \text{eqn. 3}$$

where logit($Pjuv_{b,t}$) is the logarithm of estimated age ratio Pjuv/(1-Pjuv) in at site b (within stratum s) during year t. $\boldsymbol{\beta_s}$ is a vector of 8 stratum-specific regression coefficients (including an intercept) each drawn from a corresponding normal distribution using a vague prior (the prior for the mean of each coefficient in $\boldsymbol{\beta_s}$ is normal with mean=0, σ=2 and the prior for the standard deviation of each coefficient in $\boldsymbol{\beta_s}$ is uniform from 0-1 on the logit scale; Appendix S2). We used stratum-specific regression coefficients in order to examine among-strata variation in ecological relationships with recruitment. $\boldsymbol{X'_{s,t}}$ is a data matrix of covariates for each stratum-year, where ′ indicates that all covariates except the intercept (X_0=1) have been standardized using means and SD from all possible strata-year combinations (24 strata × 47 years= 1 128 strata-year combinations, including those without banding data; Appendix S3) to represent the entire range of spatiotemporal variation. We included fixed effects (β_{lat} and β_{long}) to account for possible clinal effects of standardized banding site (*b*) latitude and longitude. $\mathcal{E}_{s/t/b}$ are residual random effects of year nested within stratum (*s/t*) to account for residual temporal variation (Zhao, Boomer, Silverman & Fleming 2017), and banding site nested with year and stratum (*s/t/b*) to account for fine-scale habitat selection or site-specific variation in capturing methods at different sites (i.e. large molting wetlands that attract a preponderance of adult females, or use of dive-trapping methods that result in higher capture rates of juveniles). Both year and site random effects also reflect the replication of sites and years within strata.

Although ecological drivers of fecundity were of primary interest, we included a stratum-specific year covariate ($\boldsymbol{\beta_8}$ in $\boldsymbol{\beta s X'_{s,t}}$ above) to identify potential long-term trends in fecundity throughout the study area.

We checked covariates in each species data set for collinearity using pair plots and correlation coefficients and included all covariates ($R^2 \leq 0.35$; Appendix S4). Relationships between age ratios and ecological covariates were monotonically increasing/decreasing, indicating that linear logistic regression terms could adequately describe relationships. We implemented 3 MCMC chains in Bayesian models with 20 000 iterations, including a burn-in and adapt periods of 100 and 2000 iterations respectively and a thinning rate of 2, yielding 29 850 samples for each posterior distribution. Gelman-Rubin statistics indicated this was sufficient replication to reach convergence for all parameters and species ($R \leq 1{\cdot}02$; Gelman & Rubin 1992). Use of age ratios as an index of fecundity assumes exclusion of age-specific banding operations ($Pjuv=0$ or $Pjuv=1$). Age-specific banding operations are not identified as part of submitted banding data in North America, so we examined this assumption by evaluating the effects on model fit of single-age records where >1 bird of only juveniles or adults was banded at a site in a year (max=500 birds for mallards, mean=15). These records resulted in under-fit models for teal and mallards (the species for which these cases were most prevalent) due to unnatural variation introduced by these records (Bayesian p-value goodness of fit tests <0.3; Gelman & Rubin 1992); as such, we removed these records from teal and mallard datasets. Single-age records in wigeon, gadwall and pintail (mean=6.5 birds) datasets did not affect model fit and so were retained. As such, final datasets represented 5 900- 400 000 birds (Table 1). We used marginal and conditional R^2 developed for mixed effects models to assess variance explained by fixed and random effects (Johnson 2014; Appendix S2).

RESULTS

Mixed effects models explained 35 to 72% of variation in age ratio, with ecological covariates explaining 16-53% of the identified within-stratum temporal variation in fecundity, depending on species (Table 2; Appendix S2,S5). Site random effects accounted for the greatest proportion of explained spatial variation, with latitude and longitude accounting for modest variation in wigeons, teals and pintails (Table 2).

Models revealed positive recruitment relationships with increasing pond density (ΔPOND) and greater short-eared owl abundances (SEOW) for all five species (Fig. 2, Appendix S1) indicating a consistent effect across strata throughout the region. The increase in estimated proportion of juveniles between the 10th and 90th percentile values for ΔPOND was 0.43 to 0.47 for mallards and 0.53 to 0.80 for wigeons (0.75-0.88 and 1.1-4.0 in traditional fecundity, respectively), the two species showing the weakest and strongest effects, respectively. Increases in the estimated proportion of juveniles corresponding to irruptions of short-eared owls were greatest for wigeon (P_{juv}=0.65-0.76; Fecundity=1.89-3.21; 10th-90th percentile values) and smallest for pintails (P_{juv} =0.56-0.58; Fecundity=1.27-1.38) and occurred above the mean P_{juv} estimates (Table 1) for all species.

Wigeons, gadwalls, mallards and pintails exhibited declines in fecundity over the study period (YEAR; Figs. 2, 3). Wigeons, teals and mallards exhibited positive relationships to upland dabbling duck density (BPUP). Teals and mallards exhibited hypothesized negative effects of intraspecific breeding pairs per pond (BPPO) on fecundity, whereas pintails exhibited a positive relationship (Fig. 2, Appendix S1). Teal exhibited a stronger relationship to BPPO (P_{juv} =0.76-0.43; Fecundity=3.2-0.75; 10th - 90th percentiles) than did mallards (P_{juv} =0.50-0.30; Fecundity=1-0.61) despite similar overall densities of pairs per pond. Teal fecundity was also positively correlated to summer precipitation (PDSI), and short-eared owl density in the previous year (SOL1) but negatively correlated to dabbling duck density in the previous year (BPL1). Stratum-specific random slopes on each covariate were remarkably similar across strata (Fig. 2), even in the absence of strong ecological relationships.

DISCUSSION

Age ratios from late summer banding revealed that temporal patterns in dabbling duck fecundity were related to hydrological cycles, density dependence and alternate prey availability. Many key ecological relationships were shared among all five species and across the entire region—including positive effects of wetland inundation and abundant alternate prey. Substantial variation in fecundity was also explained by site-level random effects, which may reflect smaller site-specific sample sizes, but might also reflect local methodological or environmental variability—such as capture methods or fine-scale habitat variation—that we were unable to model due to lack of data. These effects could be considered in cases where such information is available. Proportions of juveniles estimated from banding data were similar to vulnerability-adjusted age ratios currently derived from harvest-management surveys (Table 2), but because harvest-derived age ratios are collected from birds throughout the flyway, they reflect aggregate fecundity from all potential breeding sources, and cannot be used to infer spatially-specific relationships like those that can be derived using banding data.

The consistent, positive effect of wetland re-inundation on fecundity throughout the region suggests bottom-up food limitation, highlighting the potential importance of wetland-derived foods for duckling growth. Wetland re-inundation may be dually important to later-nesting gadwall and wigeon, which derive most of their energy for egg production on the breeding grounds (Krapu et al. 2004; Raquel et al. 2016) relative to early nesting mallards and pintails that obtain much of their reproductive energy from stored fat reserves (Alisauskas and Ankney 1992). Wetland protection provisions (e.g. Swampbuster in the United States) that maintain the capacity of less permanent basins to rehydrate in wetter periods of hydrologic cycles (Gleason, Euliss, Hubbard & Duffy 2003) will be particularly important to buffer against changes in climate and land use (Johnson et al. 2010; Niemuth, Fleming & Reynolds 2014). Positive effects of wetland inundation might also result from reduced predator abundance following droughts, as hypothesized by Walker et al. (2013b). However, if this were the case we would have expected a negative effect of previous-year prey abundance (BPL1, SOL1) on fecundity, but this effect was only observed in teal. Although within-season precipitation and evapotranspiration, as indexed by PDSI, was a poor predictor of fecundity, local effects of precipitation or temperature on fecundity, such as decreased brood survival during rain events (Krapu et al. 2000; Howerter et al. 2014), are likely dampened by the broad spatial and temporal scale of this metric (Zhao, Boomer & Kendall 2018).

The realized benefits of abundant microtine rodents, as implied by increasing fecundity during short-eared owl irruptions, were smaller than those conferred by increases in wetland inundation, suggesting that microtine abundance only describes a small portion of the predator-prey interactions in this system. Alternate prey relationships may exist between waterfowl and other prey of shared generalist predators, but lack clear population indices due to combined functional and numeric responses of avian predators (Schmutz & Hungle 1989; Poulin et al. 2001) and a paucity of broad monitoring data for mammalian predators. Nevertheless, widely available data on short-eared owl abundances seemingly served as an effective indicator of alternate prey, and these or similar data (e.g. Pan-European Common Bird Monitoring Scheme) might be incorporated into retrospective studies as a proxy for unmonitored vole irruptions in the Northern hemisphere. Gadwalls and wigeons seemed to derive greater benefits from alternate prey (Fig. 2); this may be related to their later nesting behavior (Raquel et al. 2016) at which point in the season generalist nest predators may be specializing on abundant alternate prey, improving nest survival relative to typical seasonal declines (Howerter et al. 2014).

Although density dependence affected fecundity in prairie dabbling ducks, it had both positive and negative effects that varied among species and regions, confirming that density dependent effects on fecundity in waterfowl depends on the life stage and spatial scale examined (Gunnarsson et al. 2013), similar to survival (Zhao et al. 2018). Density dependence is a key component of almost all population models, including continental adaptive harvest management models for waterfowl in North America (Nichols et al. 2007), but variation in how fecundity responds to density within a season and across a region could mask effects at larger scales. We hypothesized positive effects of increasing nest density on fecundity, given little evidence that nest sites themselves are limiting and that many mesopredators likely become satiated after consuming a single duck nest, and we saw indications of this effect for wigeon, teal and mallards. The observed negative response of mallard and teal fecundity to intraspecific pairs per inundated pond was consistent with our predictions that brood survival (or re-nesting effort) would decline at high densities due to competition for limited food resources. Pintail, however, exhibited density-dependent effects that varied with life stage and across the region, exhibiting negative effects of duck pair density in far northern strata where a greater proportion of duck pairs are conspecifics (Appendix S1), while exhibiting positive responses to duck pair density in southern strata and to conspecific pairs per pond throughout the PPR.

We included annual and geographic trends in our models to account for missing ecological or sampling relationships that weren't included in our model (e.g. banding of non-breeders in far northern strata during years with drought-induced overflight of southern portions of the PPR, within-stratum changes in density indices across time). Time trends revealed strata-consistent declines in fecundity for pintail and wigeon, corresponding to population declines (Fig. 2). Declines in gadwall and mallard fecundity across the region were more pronounced in northern strata, which were more consistently sampled across the study period (Appendix S1). Variation in fecundity was lowest in mallards (Fig.2, 3, Appendix S1, S5), the species for which North American waterfowl banding programs are designed, and highest in wigeons and gadwalls, which are often captured incidentally.

Applied Significance.—Fecundity plays a critical role in maintaining North American waterfowl populations; temporal variation in fecundity is strongly affected by environmental heterogeneity, which may mask the effects of habitat management. We suspect that spatial patterns of population declines as well as higher fecundity exhibited by gadwalls, mallards and pintails at more southwestern sites and by teal at more southern sites reflects the earlier pursuit and greater effectiveness of upland and wetland conservation programs in the United States (Reynolds, Shaffer, Renner, Newton & Batt 2001) and the lower rates of upland conversion in the west (Wright & Wimberly 2013). This pattern is corroborated by recent investigations of nest success in parkland Canada (Howerter et al. 2014) and the western U.S. prairies (Stephens et al. 2005). Efforts should be taken to protect wetlands that are inconsistently flooded and most vulnerable to agricultural conversion, because of the positive benefits to fecundity when these wetlands reflood.

Age ratios collected from routine banding operations have great potential for monitoring fecundity and identifying key factors that affect it for widely banded birds. Modelling approaches that account for spatiotemporal variation using random effects could help address biases in fecundity indices derived from long-term, regional banding operations (Peach, Buckland & Baillie 1996; Desante, O’Grady & Pyle 1999), such as variation introduced by methodology or pseudo-replication. Breeding and movement phenology should be used to select appropriate banding intervals for data utilization or intervals should be distinguished with temporal random effects; absent understanding of movement patterns, age ratio indices are most useful for temporal comparisons within a region (Dunn, Hussell & Adams 2004; Hussell 2004). Banding age ratios from mist-netting programs could be corrected for vulnerability to capture using data on within-season recaptures (TW Arnold, unpublished data); we encourage submission and curation of these same-season recapture data. If fecundity is the only vital rate not currently assessed via existing monitoring programs (e.g. apparent survival estimates from constant-effort mist-netting programs and abundance estimates from monitoring), then age ratios at banding could provide information useful in integrated population models (Ahrestani, Saracco, Sauer, Pardieck & Royle 2017). We have demonstrated that the proportion of juveniles provides a useful index of fecundity for North American dabbling ducks, and when combined with proper modelling approaches and ecological monitoring data, can facilitate research into drivers of fecundity over broad temporal and spatial scales.

DATA ACCESSIBILITY & SUPPORTING INFORMATION

Chapter 1.S1: Model coefficients and stratum-specific estimates.

Chapter 1.S2: R Script for JAGS model with code for explained variance (R^2)

Chapter 1.S3: Variable means and standard deviations for normalization

Chapter 1.S4: Covariate correlation plots for each species

Chapter 1.S5: Table 2 expansion, including explained variance derivation

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TABLE 1. Characteristics of banding data sets used to examine ecological relationships to fecundity. See Fig. 1 for map of strata and sites.

	American wigeon	***Blue-winged teal***	***Gadwall***	***Mallard***	***Northern pintail***
Total bands	5 938	283 522	14 385	399 810	71 237
Number of strata included	14	15	14	17	15
Mean Years per Stratum	27.9	34.4	32.5	34.9	33.5
Mean Sites per Stratum	19.3	31.9	25.1	30.6	26.9
Mean bands per site-year	6.0	149.6	11.3	177.6	40.5

Table 2. Estimates of proportion of juveniles (P_{juv}), model fit and explained variance for *a priori* models.

	American wigeon	**Blue-winged teal**	**Gadwall**	**Mallard**	**Northern pintail**
Model estimated Pjuv (se) [a]	0.69(0.14)	0.63(0.07)	0.64(0.12)	0.46(0.09)	0.60(0.12)
Mean Harvest-based Pjuv (1969-2013) [b]	0.67	0.72	0.68	0.57	0.63
Goodness of fit statistic [c]	0.44	0.39	0.50	0.35	0.42
Marginal R^2 (fixed effects)	0.15	0.09	0.07	0.03	0.06
Conditional R^2 (fixed & random effects)	0.72	0.35	0.70	0.47	0.49
Temporal variation explained by ecological variables	53%	39%	16%	34%	17%
Spatial variation explained by site coordinates	16%	16%	8%	6%	12%
Total variation explained by site random effect	36%	26%	50%	35%	43%

[a] Mean P_{juv} estimated from mean values of all variables.

[b] Central Flyway Waterfowl hunting and harvest survey information (Kruse, Sharp, Ladd, Moser & Bublitz 2001; Dubovsky 2017)

[c] Bayesian P-values close to 0.5 (±0.2) were considered to have good fit.

FIGURE 1. The prairie potholes and high plains ecoregions (dark gray) are the most productive area for dabbling ducks in North America. We examined ecological relationships to fecundity across strata (numbered 26-49) defined by the Waterfowl Breeding Pair and Habitat Survey (WBPHS), using data from banding sites throughout the region and ecological variables from WBPHS and the North American Breeding Bird Survey.

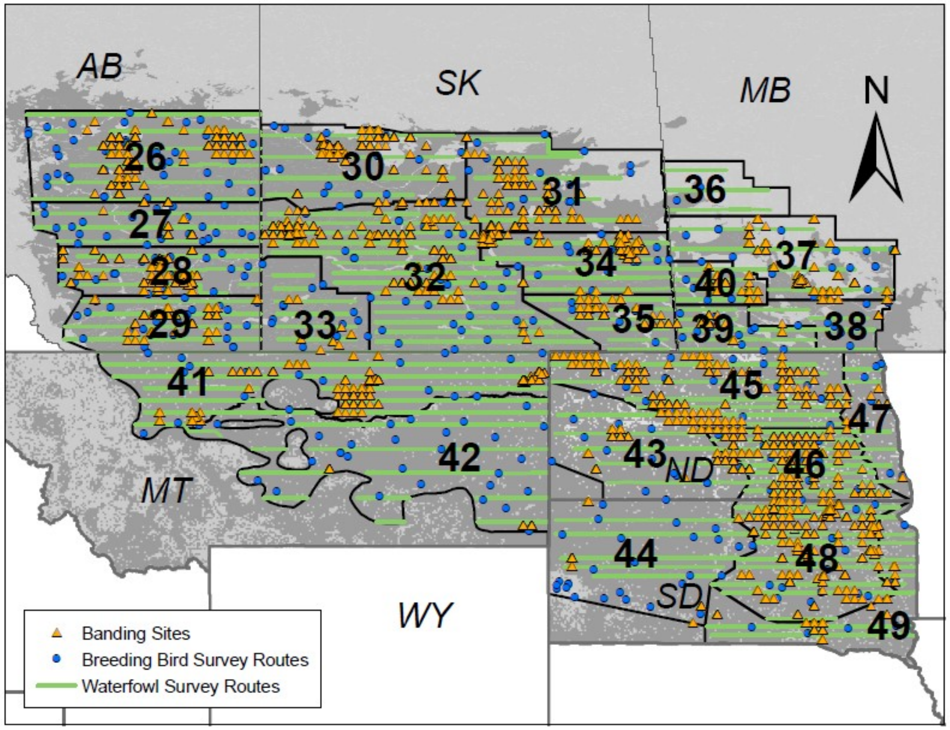


FIGURE 2. Ecological effects on fecundity ($P_{juv}/(1-P_{juv})$) by species from 10th to 90th percentiles of all modeled strata-year combinations; the overall trend (bold line), 80% credible interval (gray band), stratum-specific relationships (orange lines) and relationships for which the 80% CRI excludes zero (*).

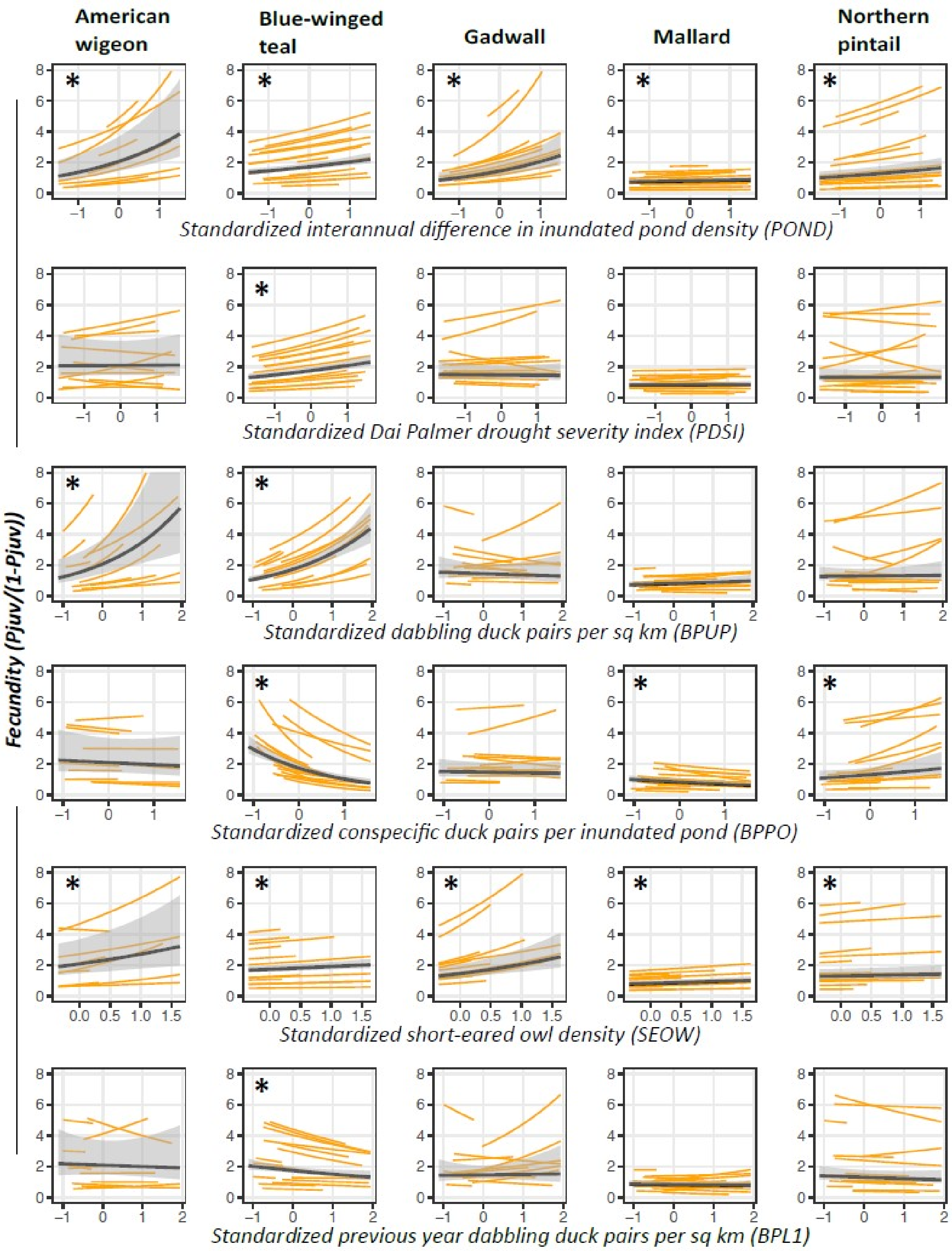
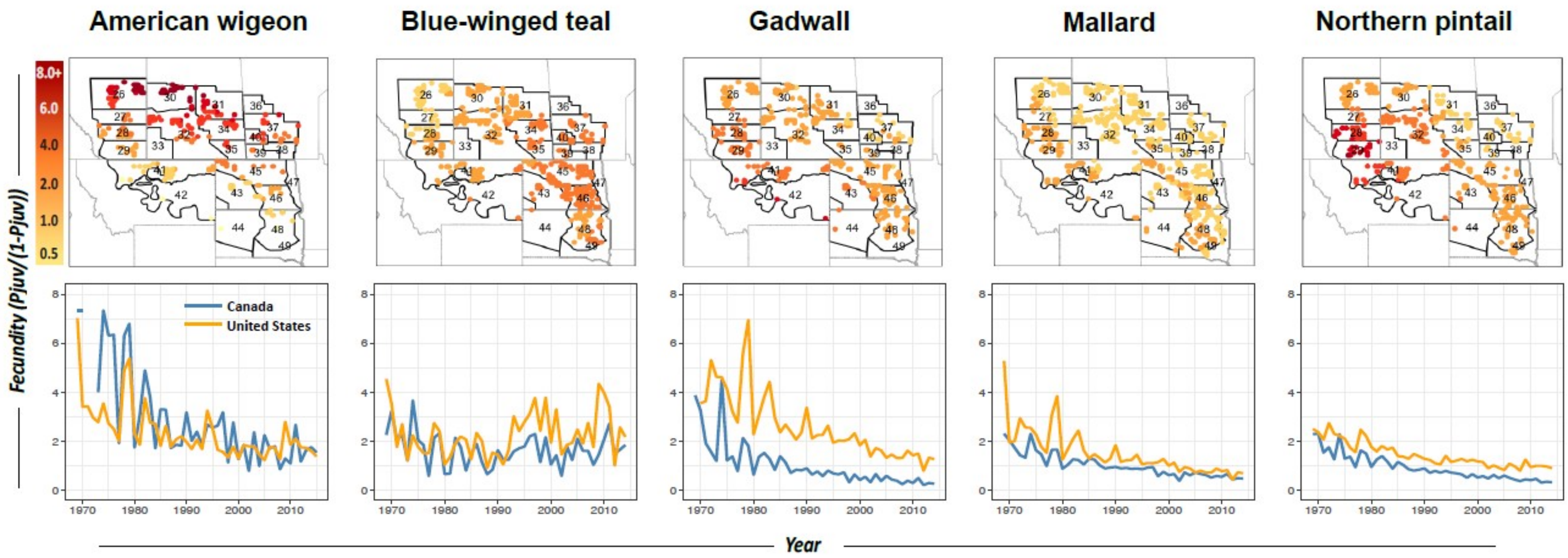
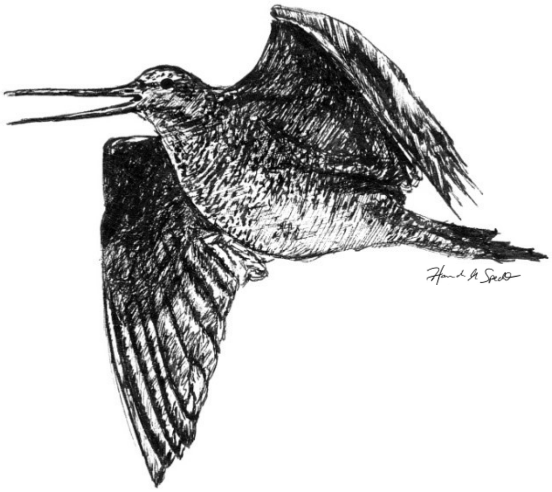

American wigeon
Blue-winged teal
Gadwall
Mallard
Northern pintail
Fecundity (Pjuv/(1-Pjuv))
Standardized interannual difference in inundated pond density (POND)
Standardized Dai Palmer drought severity index (PDSI)
Standardized dabbling duck pairs per sq km (BPUP)
Standardized conspecific duck pairs per inundated pond (BPPO)
Standardized short-eared owl density (SEOW)
Standardized previous year dabbling duck pairs per sq km (BPL1)
*
0
2
4
6
8
−1
0
1
2
0.0
0.5
1.0
1.5

FIGURE 3. Model-predicted fecundity ($P_{juv}/(1-P_{juv})$) across banding sites (top panel) and the time period of the study (bottom panel). In time series figures, year-specific variables and stratum-specific coefficients were averaged across strata within each country.



Chapter 2

USING HISTORICAL NEST RECORDS TO IDENTIFY HABITAT CHARACTERISTICS THAT INFLUENCE HABITAT SELECTION AND NEST SURVIVAL OF WILLETS AND MARBLED GODWITS IN THE NORTHERN GREAT PLAINS



Note: *This chapter is being submitted as a manuscript for publication with multiple other coauthors. Please inquire with the lead author regarding the publication status before citing this chapter.*

SUMMARY

The influence of breeding habitat selection on nest success frequently informs management for species of conservation concern. Yet, conservation delivery for low-density, low-detection species is often limited by inadequate data to assess these relationships. Here, we demonstrate the use of nest location and survival data collated from 1063 intentional and incidental records and 20 data contributors, spanning 1970-2017 from across the Northern Great Plains to examine habitat selection and nest survival of poorly studied Willets (*Tringa semipalmata*) and Marbled Godwits (*Limosa fedoa*). Most nests occurred in grassland within 100m of wetlands, though Willets selected nest sites closer to wetlands and godwits selected territories with greater wetland cover. Marbled godwits nested in cropland more often than Willets and selected nest sites and territories with taller vegetation. We developed a model to estimate daily nest survival regardless of whether nest age was known and estimated nest success of 0.490 (95% credible interval: 0.355-0.626) for Willets and 0.549 (95% credible interval: 0.400-0.686) for Marbled Godwits; this is similar to other upland-nesting shorebirds and higher than waterfowl with which shorebirds share nest predators. Nest survival for both species increased with distance from the nearest wetland edge, with an index of alternate prey abundance, with nest age, and for nests initiated later in the season. Daily nest survival of Willets decreased with territory wetland cover and increased at locations further from wetlands despite selection for nesting sites closer to wetlands, reflecting possible differences in behaviors or predator communities that influence nest survival between these two shorebird species. Despite sampling limited to areas with higher grassland and

wetland cover than points throughout the species' prairie ranges, habitat selection exhibited similar patterns to roadside occurrence surveys conducted throughout the species US prairie range, suggesting habitat suitability models generated from these surveys likely identify preferred nesting habitat. Active patch management of grassland areas with nearby wetlands can help maintain preferred nesting vegetation for these species. Here, we have demonstrated that data combined across sources and thoughtfully analyzed by accounting for variation attributed to data sourcing can be used to inform basic understanding of species ecology where appropriate data would not be possible to collect in a cost- effective or timely manner.

INTRODUCTION

Understanding habitat selection processes in animals and the influence of selection on survival and reproduction is increasingly important to support effective habitat conservation and to understand ecological pressures affecting population growth. In birds, the selection of nesting sites has long been considered to indicate habitat that maximizes fitness outcomes driven by nest failures caused primarily by predation (Clark & Shutler 1999), and in some cases by environmental exposure (Reid et al. 2002) or anthropogenic disturbance (Galbraith 1988). Information on habitat selection and its influence on reproductive success, used for identifying habitat constraints on recruitment as well as habitat management strategies (Battin 2004), often comes from local studies conducted over a few years, and thus results in limited inference (Winter et al. 2005). Identifying range-wide patterns of habitat selection and recruitment is better achieved by conducting studies at sites throughout a species range over time, thereby capturing more temporal and spatial variation in evaluated metrics.

Breeding habitat selection is a hierarchical behavioral process that moves from larger to smaller spatial scales (Johnson 1980). Widely conducted occurrence and abundance surveys (e.g. North American Breeding Bird Survey) provide insight into population range extent and selection of home ranges within a population range (Johnson 1980), but provide limited insight into territory or nest site selection except in cases where behavior indicates territoriality (e.g. singing passerines; Bibby et al. 2000). Nesting data necessary to relate habitat use to reproductive success can be difficult to acquire, particularly for low-density, cryptic species with broad home ranges, such as upland-nesting Willets (*Tringa semipalmata*) and Marbled Godwits (*Limosa fedoa*) in the Northern Great Plains (e.g. low encounter rates of nests and sightings in Garvey et al. 2013 and Niemuth and Solberg 2003). Willets and Marbled Godwits in the Great Plains nest in grassland and cropland (Higgins et al. 1979, Garvey et al. 2013) and populations of both species have declined between 1967 and 2015 (North American Breeding Bird Survey data, Environment and Climate Change Canada 2017, Pardieck et al. 2017). Occurrence and abundance surveys indicate broad habitat selection by Willets and Marbled Godwits for landscapes with greater grassland and wetland cover (N. Niemuth, unpublished data, Ryan and Renken 1987, Ryan et al. 1984), suggesting that declines in both species may be related to ongoing wetland and grassland conversion to agriculture (Stephens et al. 2008, Johnston 2013). Incubating Willets and Marbled Godwits are cryptic and stationary, flushing at <2 meters from observers or remaining on nests until picked up by observers (Gratto-Trevor 2000) and nests are unlikely to be found without the behavioral cue of an incubating bird, due to cryptic coloration of eggs (Gratto-Trevor2000, Lowther et al. 2001). These behaviors make it impractical to conduct nest-based studies at the spatial scales necessary to acquire adequate data for modelling habitat selection processes and identifying habitat management opportunities to benefit these species. Furthermore, few studies have accrued enough nesting data for both species to rigorously assess differences in their nesting habitat selection and nest success (Higgins et al. 1979, Garvey et al 2013, but see Gratto-Trevor 2006), and in some cases investigators have lumped nests from shorebird species together for inference (e.g. McMaster et al. 2005, Ludlow and Davis 2018). Studies based on small sample sizes have found variation in nest success (MAGO: 11-70%, WILL: 3-70%; Higgins et al. 1979, Kantrud and Higgins 1992, Gratto-Trevor 2000, Lowther et al. 2001) but have had little capacity to identify the ecological drivers of variation.

In an effort to gain a better understanding of the influence of habitat selection on nest survival of Willets and Marbled Godwits, we created a unique dataset by compiling 1,063 nest records from different studies from throughout the Northern Great Plains. Nest survival is an important demographic metric, and research that identifies drivers of fecundity metrics in upland nesting shorebirds is rare. Increasingly, data compiled from different sources provide previously inaccessible insight into species ecology and conservation opportunities at broader spatial scales (Weiser et al. 2018). We used our compiled dataset to assess habitat characteristics that influence habitat selection and nest survival for Willets and Marbled Godwits in the Great Plains.

METHODS

Nest record database.—We compiled nest record data from studies that spanned the years 1970-2017 and an area covering Alberta, Saskatchewan, Manitoba, North Dakota and South Dakota (Table 1, Figure 1), including nests from 20 independent data contributors. Nearly all nest records (1053) were collected as part of waterfowl nesting studies (Table 1) where study areas were chain-dragged by vehicles to locate nests (Figure 2) while a small subset of nest records (10) were generated from incidental encounter. The compiled nest record database included 354 godwit nests and 709 Willet nests; 872 records included location data and 745 records included some nest activity and fate information relevant to evaluating nest survival. Location data were provided as either coordinates or hand-drawn on aerial image maps which were subsequently georeferenced. We assumed the spatial precision for mapped nests to be within 30m and all covariates considered in our analyses were thus measured at similar or coarser scales (Table 2). Ninety-nine records included neither location nor sufficient survival data and were therefore excluded from analyses. Most of the recorded nests (88%) occurred in native grassland that still remains, owing in part to corresponding research efforts occurring on protected or managed working grasslands.

Ecological variables.— We derived eleven covariates for inclusion in habitat selection and nest survival models related to vegetation structure (vegetation height and heterogeneity), topography (topographic variation), landscape cover composition (nearest wetland distance and size, wetland cover and annual variation), predator-prey dynamics (density-dependence, alternate prey availability) and other seasonal and behavioral variables (nest age and initiation date; Table 2).

Willets and Marbled Godwits have both been observed to use areas of shorter grass in native grassland and pasture for nesting (Colwell and Oring 1988, Garvey et al. 2013, Ryan et al. 1984, Ryan & Renken 1987) and other behaviors (Higgins et al. 1979, Kantrud and Higgins 1992). Possible selection for specific vegetation structure may reflect selection to improve adult or brood survival (Clark and Shutler 1999). Field measurements of vegetation height at nests were only included in a subset of records (222 nests) and project-specific methodologies were unknown, so we utilized a linear correlation between grassland vegetation height and Band 4 of Landsat-7 Imagery (courtesy of the U.S. Geological Survey) identified by Marsett et al. (2006; see Figure 7) to estimate a grassland *vegetation height index* for the area around the nest (30m cells). Given the imprecision of nest locations, we believe that broad vegetation structure variables were appropriate and assumed that they captured differences in the predominant mixed-grass prairie vegetation structure, which varies more across space than over time owing to complementary productivity of wet and dry adapted species (LaPierre et al. 2016). We selected Landsat images from May to represent typical timing of settlement and nest site selection (mean: 16 May, this dataset). We first selected from a subset of years with Landsat data availability (2000-2016) where inundated May wetland conditions (US Fish and Wildlife Survey, Waterfowl Breeding Pair and Habitat Suitability data) most closely approximated the regional mean for years included in the nesting database (1970-2016); from this subset of years (2001, 2003, 2005, 2012), we selected the image with the least cloud cover. Heterogeneity in vegetation structure is correlated to avian species diversity (St-Louis et al. 2006) and may also identify portions of grassland overgrown with shrubs (Wood et al. 2012). We evaluated *heterogeneity in vegetation structure* as the standard deviation of the estimated *vegetation height index*. *Vegetation height index* was extracted from the cell associated with a nest location while *vegetation heterogeneity* was calculated with a moving window analysis at a radius of 50 meters around a nest location. Both metrics were summarized at the scale of a territory using moving window analyses in ArcMap (ESRI 2018) to examine nest site selection and at the radius of a territory.

Habitat models for Willets and Marbled Godwits have predicted occurrence of both species in areas with low slope or topographic variation (Granfors 2009, Niemuth et al. 2009, Niemuth et al. unpublished data). We were interested in whether this pattern also applied to nest site selection at a local scale. We represented *topographic heterogeneity* using the standard deviation of a digital elevation model derived at nest (50m) and territory scales using moving window analyses (Table 2; Canadian Digital Elevation Data 1.1 2016, US Geological Survey National Elevation Dataset 2013).

Habitat suitability studies for Willets and Marbled Godwits in portions of their breeding range have indicated occurrence in landscapes with high grassland and wetland cover (Niemuth et al. unpublished data, Kantrud and Higgins 1992, Garvey et al. 2013). Ryan et al. (1984) additionally found that Marbled Godwit territories contained a higher number of wetlands with greater diversity of wetland permanence than random locations—these observations likely indicate the importance of wetland-based feeding sites near nests during incubation and brood rearing. However, dabbling duck nest success is reduced close to wetlands, a consequence attributed to generalist nest predators that forage close to wetlands (Phillips et al. 2003, Horn et al. 2005, Thompson et al. 2012). We sought to investigate whether grassland cover, wetland cover and wetland proximity similarly influenced nest survival of Willets and Marbled Godwits. We used North American Land Cover data from 2010 (North American Land Change Monitoring System, Commission for Environmental Cooperation 2016) to assess *proportional wetland and grassland cover* at territory scales around nests and available points, recognizing that these values likely represent minimum coverage due to grassland and wetland loss over the period of the dataset (Stephens et al. 2008, Johnston 2013) as we lacked information related to cover types at the time of searching. We used data from the National Wetland Inventory (US Fish and Wildlife Service), completed portions of the Canadian Wetland Inventory (Alberta Environment and Parks) and additional data from Ducks Unlimited Canada (Institute for Wetlands and Waterfowl Research) to calculate *nest proximity to wetland edge*.

Predation is the primary cause of nest failure of ground nesting birds in the prairies (Johnson et al. 1989, Kantrud and Higgins 1992). The impact of predator-prey interactions on recruitment is driven by interactions between generalist nest predators (striped skunks (*Mephitis mephitis*), red fox (*Vulpes vulpes*) and coyote (*Canis latrans*); Johnson et al. 1989) and two of their food resources, small mammals and upland-nesting bird nests. Nest foraging theory predicts that increasing density of active nests decreases the probability that any individual nest will be encountered by a foraging nest predator and also predicts a reduction in predation on nests when alternate prey is more abundant, attributed to predator satiation (Schmidt 1999). Local studies have revealed a positive relationship between the survival of waterfowl nests and microtine rodent population abundance in North American grasslands (Ackerman 2002, Brook et al 2008); we hypothesized a similar relationship for shorebird nests. Small mammal populations have not been monitored at the temporal or spatial scales requisite to directly include in our nest survival model. However, short-eared owls (SEOW; *Asio flammeus*), which are nomadic specialist predators of voles, exhibit mobility that allows them to track vole population fluctuations across the landscape without time lags (Poulin et al 2001). We used data from the North American Breeding Bird Survey (average number of short-eared owls per 40km route aggregated to the scale of a Waterfowl Breeding Pair and Habitat Survey stratum for each year; Pardieck et al. 2017) to provide a spatio-temporal indicator of microtine rodent irruptions as an *alternate prey index*. We used data from the Waterfowl Breeding Pair and Habitat Survey to examine the effects of waterfowl population density on nest survival and Breeding Bird Survey data to examine effects of conspecific density. The Waterfowl Breeding Pair and Habitat Survey, conducted annually in May since 1955, provides detectability-adjusted estimates of breeding waterfowl populations and the number of wetland basins containing water expected to last at least three weeks beyond the survey date for each survey region across the study area (U.S. Fish and Wildlife Service 2016). We represented *upland waterfowl nesting density* in our model as the number of dabbling duck breeding pairs per square kilometer and *conspecific density* as the number of Willets or Marbled Godwits per breeding bird survey route.

Wetland conditions, highly variable between years and across the prairie region, also shape patterns of waterfowl settlement, predator foraging movements near wetland edges and the availability of wetland-based food resources (Johnson et al. 1987, Phillips et al. 2003, Szalay et al. 2003). We represented *relative pond density* as the proportional density of inundated wetland basins from the Waterfowl Breeding Pair and Habitat Survey within each survey region relative to the maximum observed in that respective region over the period of the dataset (1970-2017). We used this variable as a spatio-temporal index of relative annual wetland conditions at the onset of the breeding season as well as an adjustment factor for wetland cover and proximity variables (Table 2).

Nest survival patterns may also be influenced by the defensive behavior of the incubating pair, leading to higher daily nest survival with nest age, and closer to the middle of the season (Stephens et al. 2005, Smith and Wilson 2010). Based on information provided in nest records, we included variables for both estimated nest age and initiation date.

Habitat selection analyses.— In order to understand sampling biases presented by collated data, we assessed proportional cover by grassland and wetland of 21km cells across the species ranges (as defined by Breeding Bird Survey species-specific predicted densities of greater than 1 bird per Breeding Bird Survey route) relative to cells where nest records occurred (Figure 1). We used a use versus available design to evaluate both nest site and territory selection. The comparison of habitat characteristics at nest sites and territories relative to available habitat allows us to identify habitat that is used disproportionately to its availability, thereby allowing us to examine relationships between environment, behavior and components of fitness (Johnson 1980, Johnson et al. 2006, Beyer et al. 2010, Paton and Matthiopoulos 2016). In order to compare characteristics of nests and territories to areas otherwise available to each nesting pair but not selected by that breeding pair in a given year, we defined a territory as the circular area centered around a nest corresponding to the size of a mean territory for each species (Marbled Godwit: 530m radius corresponding to an 88 ha territory, Ryan et al. 1984; Willet: 375m radius corresponding to a 44.3 ha territory, Ryan and Renken 1987). Similarly, we defined the home range for each species as the circular area centered on a nest corresponding to the size of a mean home range (Marbled Godwits: 2.62km radius corresponding to a 2183 ha home range, Bridget Olsen, USFWS, personal communication). We lacked an estimate for Willet home range radius, and so we assumed the ratio of home range sizes was equal to the ratio of territory sizes between the two species (resulting in a 1.85km Willet home range radius corresponding to a 1080 ha home range). We compared characteristics of territories, such as cover composition and mean vegetation height, to the same metrics assessed at 10 territory-sized circles randomly selected from within the area of the home range that corresponded to each nest. Similarly, we compared characteristics of nest sites (e.g. mean vegetation height index within a 50m radius, distance of the nest to the nearest wetland) to the same metrics assessed at 10 points random ly selected from the non-wetland portions of the circular territory centered on each nest (hereafter nest selection; Table 2). We verified that increasing the number of random availability points for each nest or territory did not affect model inference, as suggested by Northrup et al. (2013).

We modeled selection of territories and nest sites using mixed effects logistic regression (lme4 package; Bates et al. 2015; in R Version 3·2·3; R Development Core Team 2015). We accounted for the conditional structure of use and availability points and clustering of nests on study sites by using a random intercept for territory or nest ID, nested within Study Plot. Territory selection variables included wetland and grassland area, vegetation height and heterogeneity, and topographic variability (Table 2). Nest site-selection models included covariates for proximity to wetland edge, wetland area within 50m, topographic variability within 50m as well as an index of vegetation height, and variation in vegetation height within 50m (Table 2).

Although godwits and Willets have been documented to nest in cropland (particularly grains; Higgins et al. 1979), cropland habitats have not been searched for nests in a proportion representative of their prevalence throughout the species' midcontinent range. As such, we assessed habitat characteristics affecting nest site selection within native grassland and cropland separately. Lacking historical land cover data for the entire study region, we identified nests located within grassland using nest record data where cover was identified, and otherwise used North American Land Cover data to identify nests located in grassland (though not cropland). We reasoned that points that are recently in grassland cover were likely to have been in grassland throughout the duration of the period (all nest records without identified cover were from before 2010). This allowed us to include nests in our analysis for which cover type at the time of the nest record was not provided (44 Marbled Godwit nests, 124 Willet nests). We also examined habitat selection in cropland, as identified by nest records (25 Marbled Godwit and 28 Willet nests). These subsets were also used for models comparing godwit and Willets nest and territory selection (territory covariates were measured at scale 375m scale for both species to facilitate reliable comparison). All continuous covariates were normalized by their means and standard deviations for each analysis and were assessed for absence of excessive collinearity ($r^2<0.35$) before inclusion in models.

Nest Survival Model Development.— Only a subset of nest records (745) included data relevant to the estimation of nest survival: at least two visits to a nest with a nest status recorded for each visit. Existing daily nest survival models utilize an encounter history approach that terminates when either the nest has been found depredated or when the nest is successful (whichever is earlier), requiring knowledge of expected hatch date (Dinsmore and Dinsmore 2007, Royle & Dorazio 2008). In order to utilize data from nest records collected prior to development of shorebird nest aging techniques, we modeled daily nest survival as a draw from a Bernoulli process of the product of two variable-length vectors of daily survival rates for each nest: (1) the period between the day the nest was found and when it was last known active and (2) the period between when the nest was last known active and fated. We used logistic regression to model the effects of nest and group variables on daily nest survival and assumed identical regression relationships applied to both initial and second periods. Though this approach could be used to evaluate day-specific covariates, we did not include any in our analysis. We evaluated this approach with existing datasets against Mayfield estimates, recovering the same daily survival rates out to the fourth decimal place.

Longer intervals between nest monitoring visits increase uncertainty about the timing of nest fate (hatched or failed) particularly when nest age is unknown, and decrease confidence that nest fate can be correctly determined. Further, whereas successful nests of both shorebirds and waterfowl can be identified by small eggshell fragments, depredated shorebird nests often have no trace of eggs (while duck nests will often have evidence of broken or scattered eggs), resulting in possible positive bias in shorebird fating (Klett et al. 1986, Mabee 1997, Mabee et al. 2007). We aimed to include data in our nest survival analyses that represented as much spatial and temporal variation as possible while seeking to avoid biases introduced by differences in data collection methods. Protocols for monitoring nest survival evolved over the time period of the dataset, from an approach where nests were revisited only once to assess fate, often weeks after initial discovery, to an approach where nests were visited every 5-10 days and aged using egg flotation methods (Liebezeit et al. 2007). However, limiting use of nest survival data to the most rigorous protocols (weekly nest checks), limits the spatial and temporal variation included in the analysis (e.g., over 75% of data collected under the most rigorous protocols originated from one study area near Brooks, AB; Gratto-Trevor 2006). Stanley (2004) showed that, in cases where nest fate cannot be evaluated with certainty, one can discard data collected beyond a point where fate can be assessed with reasonable confidence without biasing daily nest survival estimates. We compared nest survival estimates from a null model across data subsets that varied in whether nest age was assessed and in the timing of the final visit relative to expected hatch date (where nest age was known) or to the penultimate visit (Table 4, see code in Appendix S1). We reasoned that nest fate could be confidently determined if nests were fated by the expected hatch date or otherwise had their data truncated (per Stanley 2004) and compared more liberal constraints to estimates produced by this conservative approach (Table 3, subset 1). The null model included a random intercept for project-specific study site to account for similarities in nest monitoring protocols as well as similarities that arise from spatial clustering and pseudo-replication of nests by individual birds within the dataset over time (Thomas & Taylor 2006). We also included a year random intercept in the null model to account for pseudo-replication of years within the dataset. These null-model evaluations were used to inform data inclusion in a full covariate analysis.

We found that datasets with nests that had age estimates produced similar daily nest survival estimates, particularly if nest records were truncated based on the number of days between expected hatch and the fate visit (mean number of days when fated after hatch date: 4.7, range: 1-28). Daily nest survival estimates varied by species around estimates of known-age nests when nests of unknown age were included, suggesting possible bias in fating and that we lacked the ability to address uncertainty in nest fating of unknown age nests with this approach. Given these outcomes, we based inference from full covariate analyses on a dataset of nests with known age, and with truncation of date in cases where the fate visit was >7 days after expected hatch in nest survival analyses (Table 3, subset 3). However, we also ran the full nest survival model on the most and least conservative data subsets (1 and 7, respectively) to understand the effects on inference from different data use approaches.

Full Nest Survival Model.— We modeled the relationships between nest and group variables on daily nest survival with an *a priori* logistic exposure model; we used Bayesian Markov chain Monte Carlo analysis with JAGS (Plummer 2005) in Program R (Version 3·2·3; R Development Core Team 2015; see code in Appendix S2):

$$logit(DSR_{jks}) = \beta_{0jk} + \boldsymbol{\beta_{1S}X_1} + \boldsymbol{\beta_2X_2} \text{eqn. 1}$$

where DSR_{jks} is the daily survival rate for species *s* in year *j* and study plot *k*; β_{0jk} is a year and study plot specific intercept; $\boldsymbol{\beta_{1S}}$ represents a vector of three species-specific coefficients while $\boldsymbol{\beta_2}$ is a vector of 12 coefficients shared across species. Mean DSR was drawn from a uniform (0-1) prior and each coefficient from a normal distribution using a vague prior (mean=0, τ=0.03). We implemented 3 MCMC chains in Bayesian models with 25 000 iterations, including burn-in and adapt periods of 2000 and 5000 iterations respectively and a thinning rate of 2, yielding 34 500 samples for each posterior distribution. We assessed convergence by examining traceplots and r-hat values.

In compiling nest survival data we assumed that the average incubation period was 25 days for Willets and 24 days for Marbled Godwits, that the laying period for a typical 4 egg nest would take 5 days and that there was a least one day of incubation prior to clutch completion (Gratto-Trevor 2000, Lowther et al. 2001). As such, we used nest exposure periods of 29 days for Willets and 28 days for Marbled Godwits. Clutch initiation date was determined based on nest age.

We assumed that Willets and Marbled Godwits experience similar ecological drivers of nest depredation; both species exhibit bi-parental incubation with long incubation bouts and respond similarly when nests are approached. Lacking predator-specific nest predation information, we assumed that nest predation is driven by the same predator community as upland-nesting waterfowl. We specified covariate effects related to predator behavior as shared effects across Marbled Godwit and Willet nests but allowed species-specific variation in nest survival relationships to habitat variables where selection differed in habitat selection models (using the same data subset as for survival analysis Table 5). We parameterized species-specific differences in covariate relationships to nest survival in cases where habitat selection differed between Willets and Marbled Godwits in habitat selection models applied only to data included in the nest survival model. Vegetation height, grassland cover and topographic variation variables were strongly correlated across nest and territory scales within each variable (Appendix S3). We retained vegetation height and topographic variation variables at the scales at which species exhibited differential habitat selection (nest and territory, respectively). For grass cover, we retained the 1000m scale, corresponding to an approximate predator home range (Greenwood et al. 1997) because this scale captures most of the variation at both territory and home-range scales. As with habitat selection analyses, variables were normalized by their means and standard deviations and all pair-wise correlation coefficients of included variables (r^2) were <0.35 (Appendix S3).

RESULTS

Areas that were searched for nests had significantly greater grassland cover than representative of the range of Willets or Marbled Godwits in the Northern Great Plains (Willets: grassland proportional cover: *t*=-4.26, *df*=129, *p-value*<0.001; wetland proportional cover: *t*=-4.70, *df*=129, *p-value*<0.00; Marbled Godwits: grassland proportional cover: *t*=-3.02, *df*=72, *p-value*<0.01; wetland proportional cover: *t*=1.51, *df*=158, *p-value*=0.13). Across their prairie ranges, the ratio of Willet to Marbled Godwit nests reflected the same spatial pattern as population density with relatively more Willet nests located in areas with relatively higher Willet pair density and vice versa (Figure 1). The majority of nests with a cover type identified in the nest record (742 nests) occurred within native grassland (658 nests, 220 godwit and 438 Willet), while a smaller subset were in cropland (25 godwit and 28 Willet) and hayland (13 godwit and 18 Willet). Relative to Willets, Marbled Godwit nests were found in cropland more often than expected (χ^2=4.812, *df*=2, *p-value*=0.09), particularly given that the majority of sites where nests occurred in cropland were in areas with higher Willet population density.

Most nests occurred within 100m of a wetland (Marbled Godwits: mean=91.3m, sd=89.7; Willets mean=65.1m, sd=65.7) and distance to wetland didn't vary by nest cover-type (*ANOVA F-value*=1.20, *df*=2, *p-value*=0.30). Willets placed nests closer to wetlands than godwits, and closer to wetlands than expected within a territory, while godwits selected territories with both greater wetland cover than Willets and more than expected relative to availability within a home range area (Tables 3 & 5). Within a subset of nests where permanence of the nearest wetland was assigned (nearest wetlands corresponding to 395 nests in North and South Dakota, permanence per Cowardin et al.

1979), Marbled Godwits nested by lakes more often the expected and Willets by seasonal wetlands more often than expected (χ^2=26.77, *df*=3, *p-value*=0.007).

Habitat selection.— Willets selected territories with shorter vegetation than available and both species selected territories with greater grass cover than the surrounding landscape (Table 4). Marbled Godwit territories had, taller vegetation, greater vegetation heterogeneity and were flatter than the surrounding landscape, but with lower vegetation heterogeneity than Willet territories (Table 4, Figure 3). Marbled Godwit territories also had greater wetland cover (mean= 0.15, SE=0.01, n=305) than Willet territories (mean=0.08, SE=0.004, n=608) and than other areas within godwit home ranges (mean=0.10, SE=0.001, n=3050).

Marbled Godwits selected flatter nest sites with taller nest vegetation than available points or Willet nests (Table 4, Figure 3). Selection of nest sites with taller vegetation by godwits, compared to Willets, is corroborated by Robel vegetation height measurements taken at 222 nests at the time of data collection, though not in surrounding areas (generalized linear mixed effects model accounting for similarities in measurement methods within studies, p-value=0.044). Both species selected nesting areas with lower heterogeneity in vegetation structure around nests, relative to availability, an effect that was stronger in Willets (Table 4, Figure 3). Cropland subsets of habitat selection models did not reveal differences between nests or territories and available points for either species individually or compared against each other.

The subset of nests included in nest survival analyses showed similar patterns of selection but with variation in strength relative to the full dataset (Tables 4 & 5). At the scale of territories, there were strong differences in selection of vegetation height, heterogeneity, topographic variation and wetland cover, though all differences were changes in effect sizes, not direction. At the scale of nest selection, godwits and Willet habitat selection did not differ from the full dataset. The differences in the two selection models are likely driven by a greater proportion of the data in the smaller subset (>50%) coming from a single study site near Brooks, Alberta (Gratto-Trevor 2006), relative to the full dataset (34%). The inclusion of nests from known cropland cover types in this subset did not affect inference.

Nest survival.—Mean nest initiation date was similar for Marbled Godwits and Willets though Willets had a wider range of nest initiation dates (Marbled Godwit range: 28 April-11 June, mean=16 May; Willet range: 20 April-19 June, mean: 17 May). Initiation was not correlated with year or latitude for either species.

After accounting for similarities in nest survival within years and study plots, mean daily nest survival was estimated to be 0.9753 (95% credible Interval: 0.9649-0.9840) for Willets and 0.9785 (95% credible interval: 0.9677-0.9866) for Marbled Godwits. At mean nest exposure periods of 29 days for Willets and 28 days for Marbled Godwits, this would result in a nest success rate of 0.490 (95% credible interval: 0.355-0.626) for Willets and 0.549 (95% credible interval: 0.400-0.686) for Marbled Godwits.

Nest survival increased with distance from the nearest wetland edge, with an index of alternate prey abundance and with nest age. Nest survival of Willets was lower in in territories with greater wetland cover while Marbled Godwit nest survival increased with territory wetland cover. There was weak evidence of increasing nest survival with initiation date and no evidence to suggest that nest survival in cropland differed from grassland and hayland. Substantial variation in nest survival was explained by both study area and year random effects. More and less conservative data subsets (Table 3, subsets 1 and 7) showed overall similar effects of identified covariates on nest survival. The most conservative data subset (Table 3, subset 1) exhibited an additional positive effect of territory topographic variation on nest survival of Marbled Godwits, while the most inclusive dataset (Table 3, data subset 7) exhibited nest survival-habitat relationships that matched the full model but with greater support for a quadratic relationship between initiation date and nest survival, suggesting a slight decline in nest survival for nests initiated at the end of the season.

DISCUSSION

In this study, we used existing nest data and new analysis approaches to improve understanding of the habitat use and reproductive success of Willets and Marbled Godwits, two species with declining prairie populations. Willets and Marbled Godwits exhibited distinct differences in their selection of habitat at both nest and territory scales. However, only differences in selection related to wetlands translated into differences in nest survival. Similarly, different subsets of nest data exhibited differences in habitat selection and nest survival; however these differences primarily affected the strength and precision of ecological relationships and not the direction of influence on selection or survival (i.e., positive vs. negative), suggesting similarities in patterns of selection and survival throughout the region. We suspect that in the most conservative data subset, differences are driven by the local ecological relationships of the majority of nest records that occurred at a single study area near Brooks, Alberta (Gratto-Trevor 2006, Koper and Schmiegelow 2007; 62% in subsets 1-4, and 53% in subsets 5-7, Table 3).

Estimated daily nest survival rates imply that Willets and Marbled Godwits have overall nest success rates similar to other upland-nesting prairie shorebirds such as upland sandpipers (*Bartramia longicauda,* 67-72%, Kantrud and Higgins 1992, Bowen and Kruse 1993) and long-billed curlews (33-69%, Cochrane and Anderson 1987, Pampush and Anthony 1993) and much higher than dabbling duck species in the same landscape (<20%, Greenwood et al. 1995, Stephens et al. 2005, Howerter et al. 2014). Higher daily survival of upland-nesting shorebird nests relative to waterfowl is attributed to bi-parental incubation and harassment of predators (Smith and Wilson 2010) and cryptic egg coloration (Skrade and Dinsmore 2013); nest success is additionally improved by shorebirds' generally shorter nest exposure period due to smaller clutch sizes. Despite differences in nest success between upland-nesting shorebirds and waterfowl, nest survival of Marbled Godwits and Willets exhibited some similar patterns to dabbling ducks with respect to nest age, wetland cover, and alternate prey availability (Klett and Johnson 1982, Ackerman 2002, Stephens et al. 2005, Specht & Arnold in review), reflecting shared nest predator dynamics. Increased nest survival with nest age is thought to be driven by more defensive parental behavior at older nests; Smith & Wilson (2010) observed that this pattern among arctic nesting shorebirds was driven by shorebird species with biparental incubation, which is true of both Marbled Godwits and Willets. Increased depredation of nests in earlier stages may also be driven by poor habitat selection (Klett and Johnson 1982), where survival improves with age because nests placed in vulnerable locations are quickly found and depredated. A possible down-turn in nest survival for nests initiated late in the season as indicated by the most data-inclusive nest survival model mirrors findings for waterfowl nest survival in managed cover types including hayland and planted cover (Emery et al. 2005).

Similar to prairie nesting waterfowl, Willets and Marbled Godwits experienced higher nest survival further from wetland edges (Phillips et al. 2003, Horn et al. 2005, Thompson et al. 2012), though godwits, which nested further from the nearest wetland than Willets, experienced a greater benefit. Additionally, Marbled Godwits, which selected territories with greater wetland cover than Willets, experienced a positive effect of territory wetland cover on nest survival while territory wetland cover negatively influenced Willet nest survival. These patterns indicate potential differences in the predator community shaping nest survival for each species or in behaviors that mediate differences in daily nest survival patterns. We found no evidence that vegetation structure affected nest survival of either species. However, Willets selected nests with shorter vegetation than Marbled Godwits and similar to the surrounding area while Marbled Godwits selected nest locations with taller vegetation than surrounding areas and Willets and both species selected nesting sites with more homogenous vegetation than surrounding areas. These patterns correspond to findings based on Robel measurements assessing vegetation height around nests and field observations that Willets nest in grazed pasture disproportionate to availability and godwits nest in taller, more homogenous vegetation (Colwell & Oring 1988, Garvey et al. 2013, Ryan and Renken 1987; field observations by Ronningen, Skaggs, Specht).

Willets and Marbled Godwits selected for areas similar to or flatter than those available in the surrounding landscape and with greater grassland and wetland cover. Areas that were searched for nests had significantly greater grassland cover than representative of the range of Marbled Godwits in the Northern Great Plains. Greater grassland and wetland cover has been maintained in areas of the plains with higher topographic variability, such as the morainal belt of the Missouri Coteau, because these areas are more challenging to farm (Johnson et al. 1994). This suggests that Willet and Marbled Godwit selection for flatter habitat might be specific to the ruggedness of the landscape represented in the dataset. However, these patterns of topographic and cover selection are similar to predictions from habitat suitability models based on roadside occurrence survey data that represent a wider range of cover and topography typical of the breeding ranges of these species in North and South Dakota (Niemuth et al. unpublished data). Similarities in selection based on nest locations in this study and broad occurrence data from roadside surveys demonstrating selection for flatter areas with greater wetland and grassland cover indicates the continued importance of wetlands and grassland to breeding season habitat use, despite continued loss throughout the species ranges (Beauchamp et al. 1996, Johnston 2013), additionally suggesting that habitat suitability models generated from occurrence surveys likely identify preferred nesting habitat.

Data combined across sources and thoughtfully analyzed by accounting for variation attributed to data sourcing can be used to inform basic understanding of species ecology and assist in conservation and management of rare and cryptic species. Compiling nest data allowed us to estimate nest survival for two data-poor species as well as assess some habitat-recruitment relationships. Within remaining grassland, Willets and Marbled Godwits selected for different vegetation heights and for patches with less heterogeneity in vegetation height. Without precise nest locations and high quality remotely sensed data that correspond to the year of each nest record, remotely sensed data cannot reflect temporal variation in vegetation structure driven by precipitation, burning and grazing management or fine scale vegetation structure surrounding the nest. However, the observed broad patterns suggest selection by both species for nesting in grasslands that experience and rebound from grazing or burning treatments but are not overgrown with shrubs. These conditions are maintained in remaining grassland through active patch management, creating heterogeneity in grassland structure and continual habitat across the landscape for a diversity of grassland species including upland-nesting shorebirds (Bowen and Kruse 1993, Winter et al. 2005, Fuhlendorf et al. 2006). As the amount of grassland continues to decline throughout the Northern Great Plains, the need to actively maintain grassland conditions that are suitable for a diversity of species may increase.

SUPPORTING INFORMATION

Chapter 2.S1: R, JagsUI code for null daily nest survival model

Chatper 2.S2: R, JagsUI code for full nest survival model

Chapter 2.S3: Variable covariation plots

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Table 1. Sources of Marbled Godwit and Willet nest records compiled to assess habitat selection and nest survival.

Principle Investigators	Institutional Affiliations	Study Location	Study Years	MAGO nests	WILL nests	Associated Publications
Gratto-Trevor	Environment and Climate Change Canada	AB	1995-2000	132	206	Gratto-Trevor (2006, 2011)
Howerter, Garvey, Guyn & Emery	Ducks Unlimited, Canada-Institute for Waterfowl and Wetlands Research	AB, MB, SK	1994,2003, 2005-2009, 2011	57	198	Guyn and Clark (2000), Garvey et al. (2013)
Duebbert,Higgins, Kantrud, Klett, Kruse, Lokemoen	USGS Northern Prairie Wildlife Research Center	ND, SD	1970-1989	78	117	Higgins (1977), Higgins et al. (1979), Duebbert and Kantrud (1987), Kantrud and Higgins (1992), Kruse and Bowen (1996)
Walker, Stephens, Meidinger & Toay	Ducks Unlimited, Inc.	ND	2001, 2003-2009	37	112	Stephens et al. (2005)
Koper	University of Manitoba	AB	2000-2002	34	22	Koper and Schmiegelow (2007)
Ronningen & Skaggs	Delta Waterfowl, Louisiana State University	ND	2015-2017	5	50	Skaggs Thesis (in prep)
Specht and other single incidental finds	University of MN, USFWS, USGS, RMBO, DU	ND	2014-2016	11	4	
TOTAL				**354**	**709**	

Table 2. Covariates included in model selection examining nest and territory selection and corresponding nest survival.

Covariate	Analysis [a]	Spatial resolution of the data [a]	Description
Vegetation height	N, T, S	30m raster	The mean height of vegetation in the area around nesting sites, estimated using reverse NIR from Band 4 of LandSat7 Imagery following the methods of Marsett et al. 2006 (Figure 7).
Vegetation heterogeneity	N, T, S	30m raster	The standard deviation of vegetation height (as measured above) at a 50m or territory length radius.
Grassland Cover	T, S	30m raster	The proportion of an area identified as grassland in 2010 based on the North American Land Cover Dataset
Topographic variation	N, T, S	30m raster	The sd of the 30m merged digital elevation model calculated from Canadian and American Digital Elevation Model Datasets.
Wetland proximity	N, S	Nest	Distance from nest location to the edge of the nearest wetland using wetland polygon data from the National Wetland Inventory (US), Canadian Wetland Inventory (AB) and Ducks Unlimited Canada (AB, SK, MB). Divided by proportional inundation (inundated wetland density index) for the respective region and year to adjust for flooding levels (such that in dry years, wetland edges are further away).
Area of nearest wetland	N, S	ha	Area in ha of wetland nearest to nest.
Wetland Cover	N, T, S	30m raster	Proportion of area within the radius of a home range covered by wetlands based on the 2010 North American Land Cover Dataset. Multiplied by proportional inundation (inundated wetland density index) for the respective region and year to adjust for flooding levels (such that in drier years, there is lower wetland cover).
Inundated wetland density Index	S	Region	Proportional density of inundated wetland basins within the region corresponding to each nest monitored by the USFWS Waterfowl Breeding Pair and Habitat Survey relative to the maximum observed in the respective region over the period of the dataset (1970-2017).
Alternate Prey Index	S	Region	Short-eared owl density, monitored by the North American Breeding Bird Survey, as an index of vole abundance.

Marbled godwit/willet density	S	21mi raster	Estimated density (birds per route) based on North American Breeding Bird Survey data.
Waterfowl nesting density Index	S	Region	Density of upland-nesting dabbling duck breeding pairs as an index of waterfowl nest density based on regional estimates from the USFWS Waterfowl Breeding Pair and Habitat Survey.
Latitude	S	Nest	Decimal degrees, included to account for broad spatial differences in phenology.
Nest Initiation date	S	Nest	Estimated based on nest age information provided in nest records, included as a quadratic effect to account for changes in phenology across the nesting season. Day 1 is the earliest known nest initiation.
Nest age	S	Nest	Estimated from nest record information.
Study Plot	N, T, S		Study areas identified by data contributors and using GIS.

[a] N=Nest site selection, T=Territory selection, S=Nest survival

Table 3. Species-specific nest survival estimates from a nest survival model including only random intercepts effects for year and study plot of a nest for different data subsets that differ in the length of time between when the nest was fated and when it was last seen active and whether nest age was estimated.

Data subset	Age estimated	Days between nest last active and fated [a]	Number of nests/with location [a]	Estimated Daily Survival Rate Marbled Godwit	Estimated Daily Survival Rate Willet	Nest survival Marbled Godwit (28 days)	Nest survival Willet (29 days)
1.	Yes	Truncated if fated >0 days after exp. hatch	595/548 (*240 truncated)	0.9761 (0.0055) 95% CRI: 0.9638-0.9853	0.9774 (0.0046) 95% CRI: 0.9674-0.9856	0.515 (0.077) 95% CRI: 0.3561-0.6609	0.521 (0.070) 95% CRI: 0.3828-0.6561
2.	Yes	Truncated if fated >3 days after exp. hatch	595/548 (*111 truncated)	0.9764 (0.0052)	0.9770 (0.0041)	0.518 (0.074)	0.515 (0.066)
3.	Yes	Truncated if fated >7 days after exp. hatch	595/548 (*47 truncated)	0.9785 (0.0048)	0.9753 (0.0049)	0.549 (0.073)	0.490 (0.070)
4.	Yes	No constraint	595/548	0.9836 (0.0036)	0.9716 (0.0052)	0.632 (0.062)	0.439 (0.066)
5.	No	Truncated if fated >7 days after penult visit	745/653 (#307 truncated)	0.9966 (0.0020)	0.9961 (0.0023)	0.910 (0.049)	0.896 (0.057)
6.	No	Truncated if fated >14 days after penult visit	745/653 (#134 truncated)	0.9863 (0.0064)	0.9856 (0.0065)	0.691 (0.113)	0.667 (0.116)
7.	No	No constraint	745/653	0.983 (0.0038)	0.9728 (0.0051)	0.616 (0.065)	0.454 (0.067)

[a] Nests with a final visit >x days after the expected hatch date (*) or penultimate visit (#) truncated to include only data from when the nest was found until the penultimate visit when it was last seen active (Stanley 2004).

Table 4. Coefficients (sd) from habitat selection mode utilizing all nest records with location data (236 Marbled Godwit and 452 Willet nests). Estimates for which the 95% confidence interval excludes zero are indicated in ***bold italics*** while coefficients with 90% intervals excluding zero are *italicized*.

	Territory Selection			Nest Site Selection		
Covariate	Marbled Godwits	Willets	Species Comparison*	Marbled Godwits	Willets	Species comparison*
Vegetation Structure						
Vegetation Height						
nest				*0.184 (0.094)*	-0.071 (0.065)	***0.566 (0.150)***
territory	0.003 (0.099)	***-0.208 (0.061)***	0.223 (0.179)			
Vegetation Heterogeneity						
50m				*-0.162 (0.096)*	***-0.225 (0.072)***	0.120 (0.121)
territory	0.105 (0.107)	0.083 (0.067)	***-0.294 (0.142)***			
Grass Cover:						
Nest (Nest Record)		(within grassland)			(within grassland)	
Territory (Landsat)	***0.517 (0.129)***	***0.456 (0.077)***	0.164 (0.142)			
Predator (1000m, Landsat)						
Topographic variation						
50m				*-0.246 (0.100)*	0.090 (0.061)	***-0.520 (0.175)***
territory	***-0.168 (0.083)***	-0.093 (0.060)	***-0.405 (0.159)***			

Wetlands						
Wetland proximity (nest)				0.042 (0.075)	-0.106 (0.064)	***0.359 (0.113)***
Area of nearest wetland				-0.010 (0.064)	-0.011 (0.084)	0.061 (0.165)
Wetland cover (territory)	***0.600 (0.073)***	***0.137 (0.055)***	***0.490 (0.191)***			
Wetland Inundation Index (region)						
Random Effects	Territory nested within Study Plot	Territory nested within Study Plot	Study Plot	Nest ID nested within Study Plot	Nest ID nested within Study Plot	Study Plot

* In comparisons between Willet and Marbled Godwit habitat selection, godwits=1 and Willets=0 such that coefficients should be interpreted to reflect habitat selection of Marbled Godwits relative to Willets. At the territory scale in the comparison model, all variables assessed at 375m scale for both species.

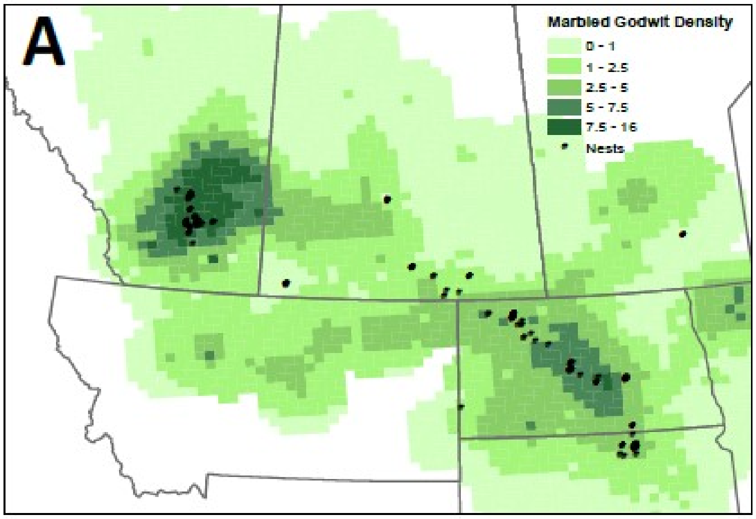
Table 5. Coefficients (sd) from habitat selection and nest survival models using survival data with nest age estimates and location data (Table 4, subset 4; 177 Marbled Godwit, 372 Willet nests). Estimates for which the 95% confidence or credible interval (for habitat selection and survival analysis, respectively) excludes zero are indicated in ***bold italics*** while coefficients with 90% intervals excluding zero are *italicized*.

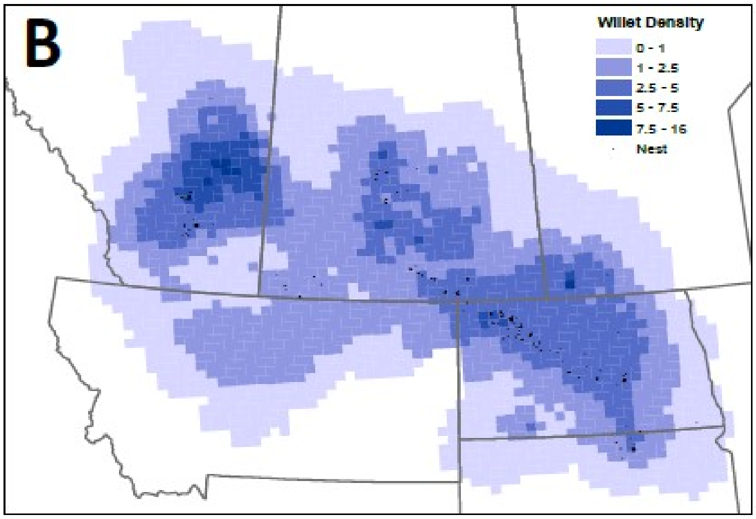
	Territory Selection			**Nest Site Selection**			**Nest Survival**	
	godwits	Willets	comparison*	godwits	Willets	comparison*	godwits	Willets
Vegetation Structure								
Vegetation Height								
nest				***0.189 (0.092)***	-0.021 (0.061)	***0.552 (0.128)***	-0.056 (0.186)	0.066 (0.104)
territory	***0.239 (0.100)***	***-0.192 (0.062)***	***0.404 (0.120)***					
Vegetation Heterogeneity								
50m				-0.168 (0.106)	***-0.289 (0.076)***	0.047 (0.117)		
territory	-0.068 (0.108)	0.046 (0.071)	***-0.443 (0.130)***				-0.082 (0.185)	-0.081 (0.122)
Grass Cover:								
Nest (Nest Record, 1=crop)								
Territory (Landsat)	0.156 (0.105)	***0.348 (0.077)***	-0.178 (0.116)					
Predator (1000m, Landsat)							-0.119 (0.150)	
Topographic variation								
50m				***-0.278 (0.121)***	*0.108 (0.058)*	***-0.598 (0.181)***		
territory	***-0.193 (0.093)***	*-0.116 (0.067)*	***-0.338 (0.120)***				0.197 (0.215)	0.176 (0.147)
Wetlands								
Wetland proximity (nest)				0.027 (0.088)	*-0.133 (0.069)*	***0.258 (0.108)***	***0.505 (0.202)***	***0.249 (0.139)***
Area of Nearest Wetland				-0.155 (1.155)	-0.008 (0.067)	-0.087 (0.174)	-0.091 (0.115)	
Wetland cover (territory)	***0.442 (0.064)***	0.053 (0.060)	***0.332 (0.107)***				***0.294 (0.174)***	***-0.259 (0.118)***
Wetland Inundation Index (region)							0.173 (0.216)	

Alternate Prey Index (region)							***0.271 (0.171)***
Marbled godwit/Willet density							-0.091 (0.105)
Waterfowl nest density Index (region)							-0.168 (0.226)
Nest age (nest record)							***0.449 (0.102)***
Nest Initiation date (nest record)							*0.126 (0.093)*
Nest Initiation date^2							-0.082 (0.077)
Latitude (nest)							0.113 (0.187)
Random Effects	Territory within Study Plot	Territory within Study Plot	Study Plot	Nest ID	Nest ID within Study Plot	Study Plot	Study Plot, Year

* In comparisons between Willet and Marbled Godwit habitat selection, godwits=1 and Willets=0 such that coefficients should be interpreted to reflect habitat selection of Marbled Godwits relative to Willets. At the territory scale in the comparison model, all variables assessed at 375m scale for both species.

Figure 1. Relative breeding season population density of Marbled Godwits (A) and Willets (B) in the prairies based on North American Breeding Bird Survey Data (USGS) where density is represented as the estimated number of birds per 40-km survey route. Black dots in each figure represent nests from each species. More Marbled Godwit nests than Willet nests were located in areas where godwit population density is relatively higher than Willets (C; green shading and black-outlined green cells) and visa-versa (C; blue shading and black-outlined blue cells).


A
Marbled Godwit Density
0 - 1
1 - 2.5
2.5 - 5
5 - 7.5
7.5 - 16
Nests


B
Willet Density
0 - 1
1 - 2.5
2.5 - 5
5 - 7.5
7.5 - 16
Nest

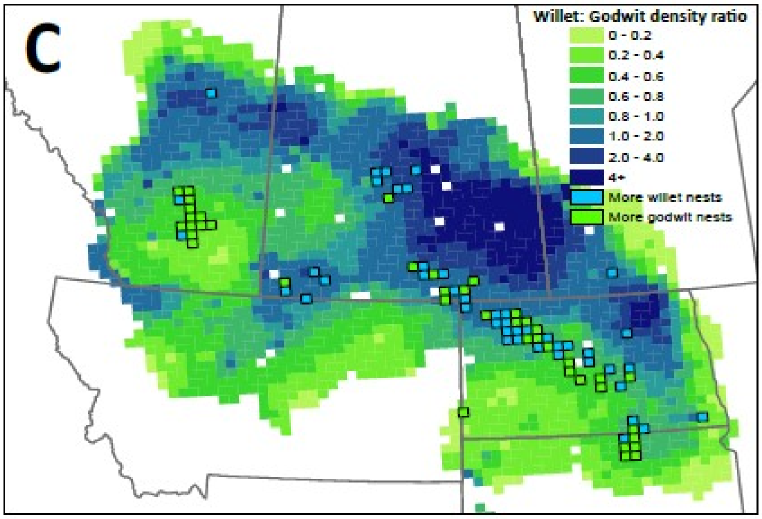

C
Willet: Godwit density ratio
0 - 0.2
0.2 - 0.4
0.4 - 0.6
0.6 - 0.8
0.8 - 1.0
1.0 - 2.0
2.0 - 4.0
4+
More willet nests
More godwit nests

Figure 2. (A) Marbled Godwit and (B) Willet (bird photo credit to J. Kolar), (C) Marbled Godwit nest and (D) Willet nest on Lostwood National Wildlife Refuge in North Dakota (nest photos taken by H. Specht).

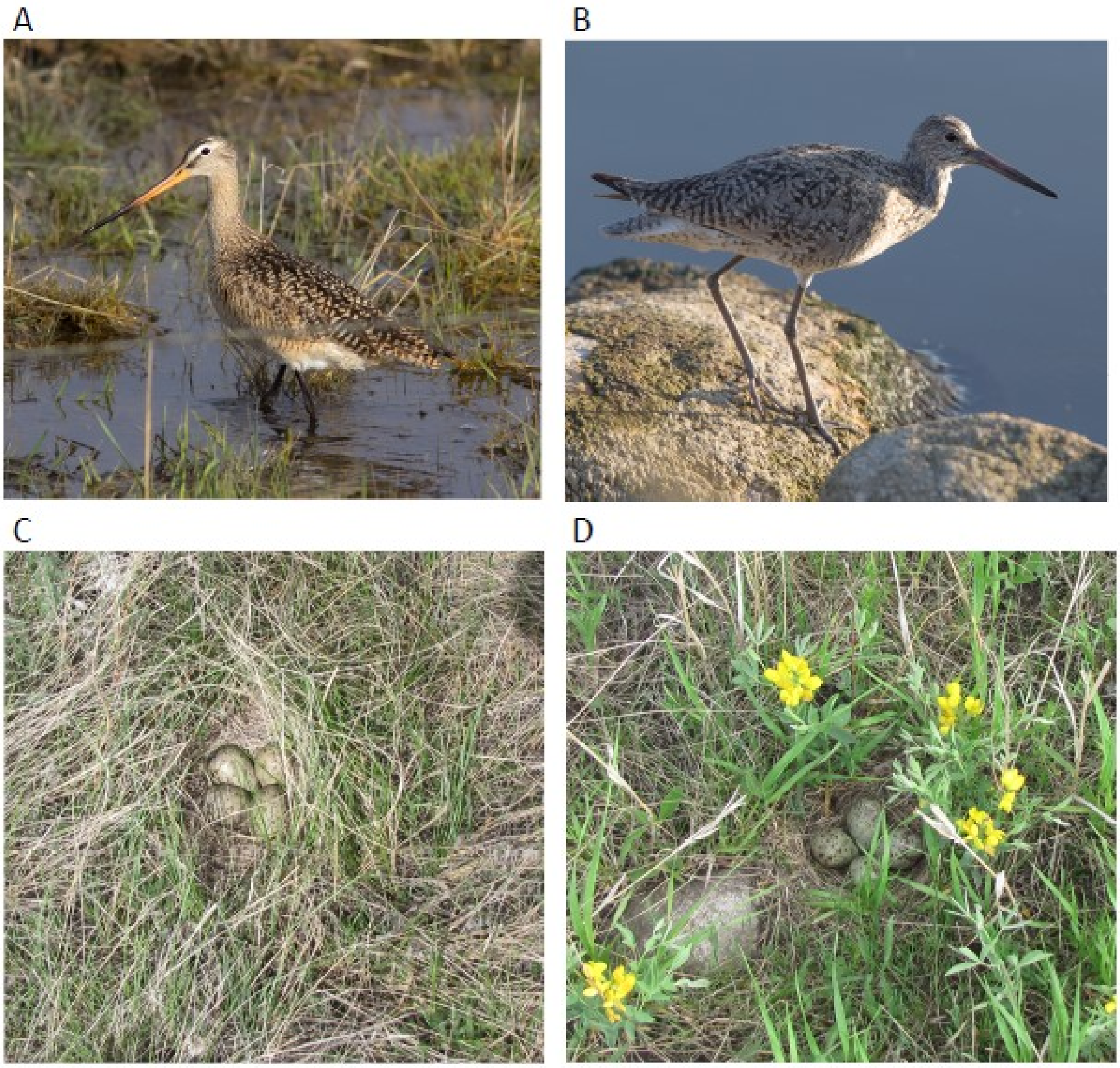
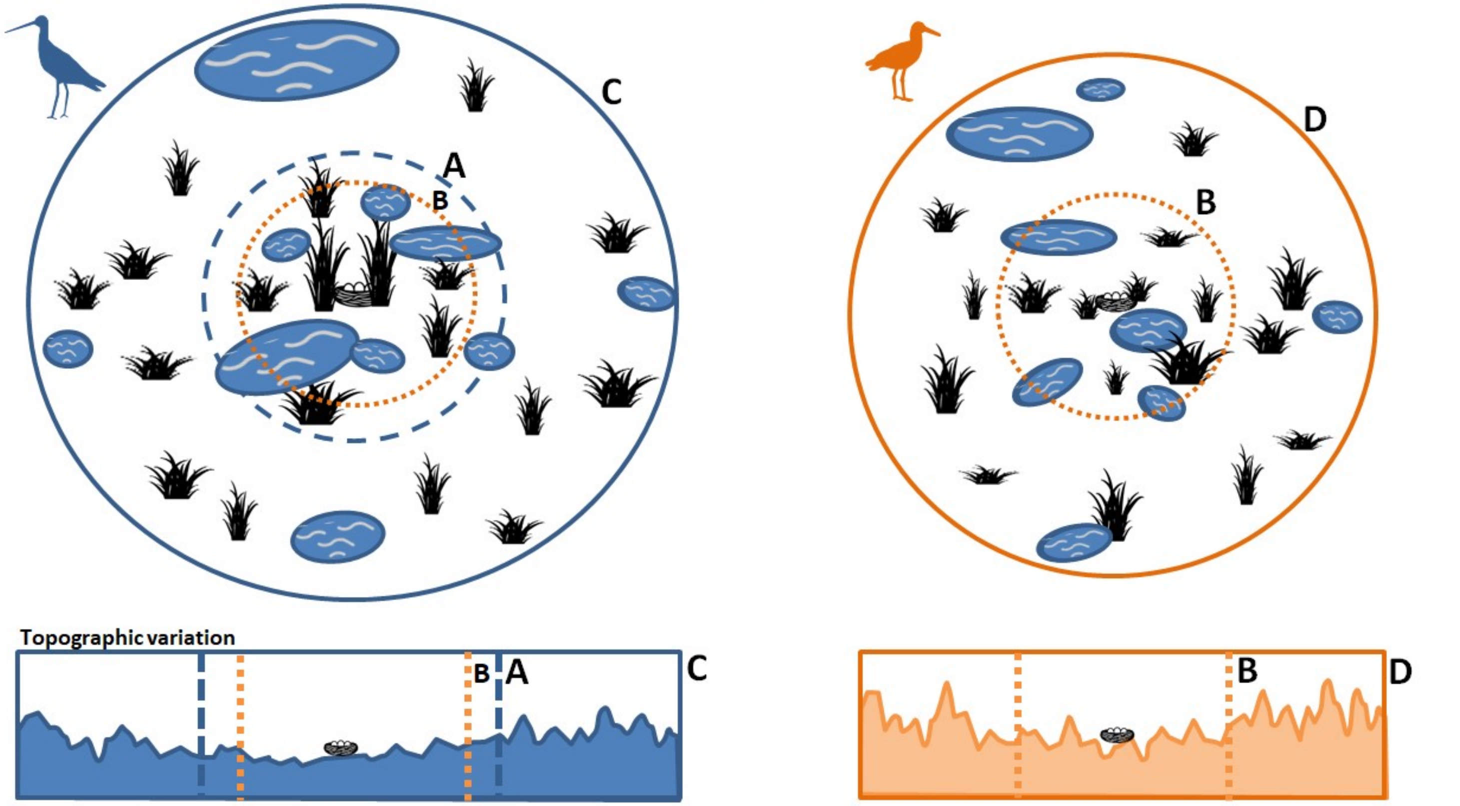


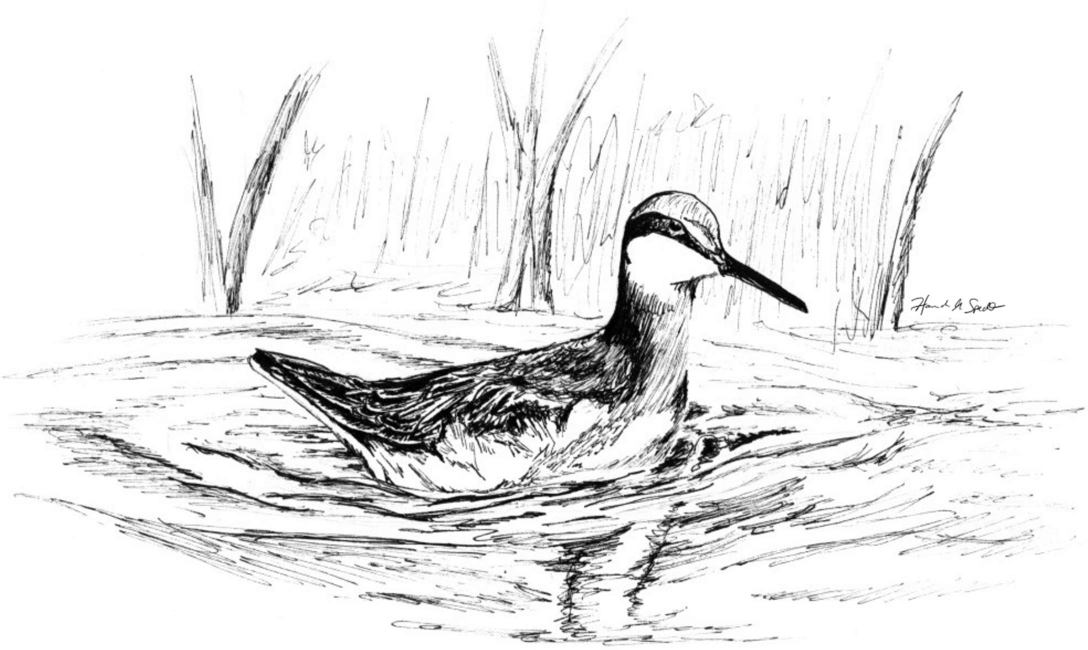
Figure 3. Habitat selection for nest sites and territories by Marbled Godwits and Willets where nest locations were compared to other non-wetland random points within a territory (A for godwits, B for Willets) and territories were compared to territory sized areas within a home range (C for godwits and D for willets). When godwit and willet territories were compared to each other, metrics were assessed at the same scale (B). Territories, home ranges and depicted habitat characteristics are not depicted to scale.

	Marbled Godwits	Willets
Vegetation	Vegetation around nests is taller and more homogenous than other points in territory and taller than willet nests. Territory vegetation and heterogeneity is similar to other possible territories within a home range and is more homogenous than willet territories.	Vegetation around nests is similar in height but more homogenous than other points in territory. Territory vegetation is shorter than other possible territories within a home range but with similar heterogeneity in vegetation height.
Topographic variation	Nests are in flatter places than other points in territory. Territory is flatter than other possible territories within a home range. Both nests and territories are flatter than willets.	Nests are in places with similar topographic variation to other points within a territory. Topographic variation across a territory is similar to other possible territories within a home range.
Wetlands	Godwit nests are located at similar distances to wetlands than other points within a territory and further from wetlands than willet nests (and godwits experience higher nest survival a nest locations further from wetlands). Territories have greater wetland cover than other possible territories within a home range, and than willet territories (and godwits experience higher nest survival in territories with greater wetland cover).	Willet nest closer to wetlands than other points in a territory (but experience higher nest survival at nest locations further from wetlands). Willet territories have similar wetland cover than other possible territories within a home range (and experience a negative effect of territory wetland cover on nest survival).



Chapter 3

HABITAT USE BY UPLAND-NESTING WATERBIRDS IS NEGATIVELY AFFECTED BY OIL WELL INFRASTRUCTURE AND ACTIVITY



SUMMARY

Grassland-nesting wetland-dependent bird populations in North America have declined over the last century due to loss of prairie and wetland habitats to agricultural conversion. Development of the North Dakota Bakken shale for oil is occurring in a portion of the grasslands that supports some of the highest densities of upland-nesting waterbirds in North America. Some of these species' life history characteristics, including microhabitat specialization and declining populations, suggest the birds' vulnerability to habitat fragmentation and development. I used occupancy models to examine the effects of oil extraction activities and associated vehicle traffic on breeding season habitat use by upland-nesting shorebirds and Northern pintail ducks (*Anas acuta*). Data for analyses was collected in 2014 and 2015 using road-side point count and transect surveys at 396, 64-ha sites in northwest North Dakota. Traffic negatively affected breeding pair habitat use of Northern pintails and willets (*Tringa semipalmata*) and broods of shorebird species (> 90% of posterior density < 0) after accounting for habitat suitability and time of year. Oil well density negatively affected occupancy of Wilson's phalaropes (*Phalaropus tricolor*, >99% of posterior density < 0). In combination, these patterns indicate that suitable habitat is being avoided by all species during a portion of the breeding season. A unique survey design that allowed us to infer brood presence through behavior facilitated identification of effects of traffic on brood habitat use where data would otherwise have been too sparse.Conservation goals, including easement acquisition, should focus on maintaining higher quality habitat, especially between development corridors, that addresses not only the birds' physical

requirements, but their tendency to avoid areas with disturbance that accompanies built infrastructure.

INTRODUCTION

North American grassland habitats have declined to ≤20% of their pre-European extent, despite once being the largest vegetative province on the continent (Noss et al. 1995; Samson et al. 2004). Loss of remaining grasslands continues in the US at an annual rate of approximately 0.5% primarily in conversion agricultural production (Stephens et al. 2008). Although most conversion of grasslands to row-crop production took place early in the 20th century (Waisanen & Bliss 2002), declines continue in many grassland species once considered common (Askins et al. 2007), driven by climate change, declining patch size, poor grazing and fire management, wetland consolidation, use of agricultural pesticides, agricultural intensification and development of energy infrastructure (Anteau 2012; Askins et al. 2007; Davis 2004; Mineau & Whiteside 2013; Nenninger & Koper 2018). As a result, grassland bird populations have declined more precipitously than any other subset of North American avifauna (Peterjohn & Sauer 1999; Samson et al. 2004). Approximately one-third of the North American Prairie Pothole Region, which provides core habitat for grassland-nesting waterfowl and shorebirds (Batt et al. 1989; Granfors & Niemuth 2005), overlaps the Bakken shale formation in North Dakota, Montana, Alberta and Saskatchewan (Figure 1). In this region, >10,000 new oil wells were drilled between 2007 and 2017, and up to 40,000 are forecasted (Mason 2012; North Dakota Industrial Commission Well Data 2015). Technological advances in oil extraction techniques, combining hydraulic fracturing and horizontal drilling, have led to rapid change in the Bakken region. Oil infrastructure has added roads and the vehicle traffic required for construction and maintenance of well pads that have pump jacks, storage tanks, power infrastructure, and sometimes gas flares. Nearly half of this development footprint is on native grasslands (Preston & Kim 2016), directly and indirectly impacting grassland habitat through habitat fragmentation and the addition of vertical structures, light and noise, and disturbance from truck traffic and human activity (Nenninger & Koper 2018, Thompson et al. 2015). These changes induce a suite of responses in birds, from avoidance (Francis et al. 2011; Lyon & Anderson 2003; Thompson et al. 2015) to changes in courtship and parental care (Blickley et al. 2012; Francis et al. 2011; Liebeziet et al. 2012; Schroeder et al. 2012). These responses compound direct loss of habitat to further impact sensitive species, ultimately changing bird community composition (Bayne et al. 2008, Thompson et al. 2015).

Characteristics that make a species vulnerable to habitat fragmentation and development, such as declining populations, microhabitat specialization, and ground nesting (Henle et al. 2004; Marzluff 2001), are also those that make species-specific impact assessments difficult, since there is sparse representation of such species in standard monitoring datasets (e.g., roadside bird surveys). These are nevertheless often species of primary interest for monitoring and conservation due to relatively poorer understanding of their habitat use and behavior. Upland-nesting wetland birds exhibit many of these characteristics, making them candidates for further impact assessment in relation to regional habitat changes. Great Plains populations of Northern pintail (*Anas* *acuta*), marbled godwit (*Limosa fedoa*), upland sandpiper (*Bartramia longicauda*), willet (*Tringa semipalmata*) and Wilson's phalarope (*Phalaropus tricolor*) boast single annual broods and microhabitat specialization -- they require both medium grass density typical of historical mixed grass prairies for nesting and, for all but upland sandpipers, shallow, unvegetated wetland edges for feeding. Godwits, willets, phalaropes and pintail additionally exhibit moderate to low and declining population sizes (Andres et al. 2012; Devries 2014).

Previous roadside surveys have found relative local rarity for these species (occurrence at 2-30% of sites or 0.08-0.8 pairs per survey point; Grant et al. 2004; Loesch et al. 2013; Niemuth et al. 2012; Niemuth et al. 2013). Additionally, these species likely exhibit low detection probability in typical roadside survey protocols due to cryptic coloration, infrequent audio cues over short periods (low availability), and common occurrence along wetland edges, which are inherently at topographic low points in the landscape and obscured from many vantage points (Gratto-Trevor 2006; Niemuth et al. 2012; Pagano & Arnold 2009a,b; personal observation). As a result of low density and detection probability, existing long-term monitoring programs (e.g., data from the North American Breeding Bird Survey; Sauer et al. 2017) lack sufficient power to support analyses examining short term changes in populations of these species in relation to habitat changes at local to regional scales .

Within areas of the Bakken oil field that are fully developed, oil wells are constructed along high density corridors spaced by 3.2km (Figure 1), which guarantees human activity within the home ranges of Northern pintails, marbled godwits, and willets (home ranges in Table 1), and fragments habitat used by upland sandpipers and Wilson's phalaropes (Bollinger 1995; Cunningham & Johnson 2006). Previous research has identified a range of effects of energy development on birds with precocial young, including changes in nesting success and habitat use (Blickley et al. 2012; Liebezeit et al. 2009; Loesch et al. 2013; Ludlow & Davis 2018; Lyon & Anderson 2003; Niemuth et al. 2013; Pasitschniak-Arts et al. 1998; Shaffer & Buhl 2016). But only studies of greater sage grouse have examined effects of energy development on habitat use during both nesting and brood rearing stages. I evaluated the effects of oil development infrastructure and activity on habitat use by northern pintails, marbled godwits, upland sandpipers, willets and Wilson's phalaropes. Specifically, I 1) assessed how oil infrastructure and activity affects occupancy during the breeding season while accounting for other components of habitat suitability and seasonality, at scales reflecting the primary unit of land use (64 ha quarter section) and species-specific home ranges (Table 1); 2) assessed how these variables affected occupancy of brood adults as indicated by brood-tending adult behavior at the scale of a study site; and 3) compared differences in detection probability of breeding and brood-rearing adults between two survey approaches, a roadside point count and a walking transect.

MATERIALS AND METHODS

Study Area.—The study area was located in northwestern North Dakota, a region historically dominated by extensive pastured grassland and cropping practices. Development of the Bakken shale as a result of advances combining horizontal drilling and hydraulic fracturing resulted in the addition of 9880 new wells between 2001 and

May 2015 (to the existing 1,900) (North Dakota Industrial Commission Well Data 2015) and an 86% increase in truck traffic between 2008 and 2014 within the region (North Dakota Department of Transportation, 2016). The majority of study sites were located in the Prairie Pothole Region (Figure 1), characterized by mixed-grass prairie and abundant wetlands including the Missouri Coteau which, due to its topography, was not transformed into cropland, thus containing a greater portion of intact grassland than other parts of the region (Johnston 2014; Stephens et al. 2008). To capture the diversity of habitat used by the study species, I also included sites in the badlands and prairies physiographic region, which have shorter grass and wetlands shaped by drainage patterns.

I defined a sample unit as a 64-ha (160 ac) quarter section, the primary unit of land management in the region. Sites were located within Burke, Dunn, Divide, Mountrail and Williams counties, North Dakota (an area covering approximately 22 000km^2), all of which have been extensively developed for oil and gas (Fig.1, Appendix S1). Sites reflected a mix of cropland, and grazed and ungrazed grasslands in public and private ownership. I selected study sites accessible by road that reflected the distribution of relative habitat suitability for Northern pintails, marbled godwits, willets, and Wilson’s phalaropes as well as the presence of active oil and/or gas wells on sites (Appendix S2). Habitat suitability models incorporated variables related to land use, topography, precipitation, and temperature, and wetland cover, type and diversity, at different scales (Table 1). Specifically, these habitat suitability indices did not include variables related to oil development and most informing data were collected outside areas with high density oil development; thus, these models provided a basis for evaluating differences in habitat use driven by oil infrastructure and activity by defining expected habitat value for each species at each study site based on landscape components. Suitability models for marbled godwits, willets and Wilson's phalaropes were based on roadside shorebird monitoring surveys conducted in North and South Dakota's portion of the Prairie Pothole Region from 2004-2014 (N. Niemuth, unpubl. data, details of methodology and habitat variables can be found in Niemuth et al. 2017). I extended the habitat suitability models for these species to Dunn County, ND, across the Missouri River. Habitat suitability for Northern pintails was modeled based on pair numbers and wetland habitat surveys in the Prairie Pothole Region (Reynolds et al. 2006) and suitability for upland sandpipers was modeled using Breeding Bird Survey data with model coverage across all study counties (Niemuth et al. 2017). Although upland sandpipers are not dependent on wetlands, I added them to the study in the second year based on similarities in life history characteristics; although they were not considered in site selection, study sites reflected their habitat suitability distribution (Appendix S2). Only a small number of sites with very high suitability for godwits, willets and phalaropes at the site scale were included in the survey in order for the sample of sites to approximate the distribution of available habitat suitability on the landscape (Appendix S2). However, oil well development was distributed across the landscape irrespective of habitat suitability for all species (nearly identical to distribution of random points) such that the habitat-suitability stratification in site selection also reflected the expected distribution of development impacts.

Roadside occupancy surveys.— I surveyed the occurrence of birds to examine habitat use, and conducted repeat visits to account for imperfect detection of these uncommon and sometimes cryptic species in models of occupancy (MacKenzie et al. 2006). Three surveys were conducted along one 800m road-accessible side of each of 396 sample units, including two 3-minute point count surveys conducted at 200 and 600m, followed by a 30-minute, 800m walking transect survey along the same side of the site (Fig. 1). This approach facilitated a direct comparison of the detection efficiency of point count and transect methods and was designed to achieve a cumulative detection probability >0.75 based on conservative estimates from previous research conducted in similar landscapes (0.25 for point counts and 0.6 for transects; Gratto-Trevor 2006; MacKenzie & Royle 2005; Niemuth et al. 2012; Pagano & Arnold 2009b). Observers were transported by vehicle between point count and transect locations. Counts began immediately when an observer exited the vehicle to minimize behavioral responses from study species. Repeat surveys were separated only by travel time between points to meet the closure assumption of occupancy models.

To identify indicated breeding pairs (definitions in Table1), observers recorded the number and sex of individuals in social groups of each species. Individuals separated by more than 10m were considered independent social groups, unless individuals were directly interacting, i.e. in courtship display (Table 1). Observers additionally recorded distance, detection cue, location, and the observation of “brood tending behavior” (Table 1; previously used to assess juvenile survival; Ruthrauff et al. 2009; Lukacs et al. 2004). Observations included only individuals detected on a wetland or upland portion of the site, or repeatedly displaying over the site—birds flying over the site were not included in the models. Focal species arriving at the site during the survey period were also excluded to maintain the closure assumption and to avoid double-counting. Site visits were conducted between May 15 and July 15 of 2014 and 2015, encompassing both nesting and brood-rearing portions of a breeding cycle (see Table 1 for first brood observations by species). Survey conditions were constrained to hours between 0600 and 1400, temperatures 2-24 degrees centigrade, the absence of strong wind (>32kph), precipitation no more than light scattered showers, and visibility no less than 800m (due to smoke or fog) to improve detection probability (Niemuth et al. 2012; Pagano & Arnold 2009a,b). Observers recorded survey condition covariates that could affect detection and occupancy, including wind speed, temperature, survey time and traffic volume (number of heavy duty tankers and other vehicles traveling along the transect route during the 30 minute transect) to model additional effects on detection probability. Sites where heavy operations were occurring on the well pad (e.g., hydraulic fracturing, drilling, or extensive maintenance) were not surveyed because these local intensive disturbances are ephemeral and therefore not representative of the enduring state of the habitat. Twenty-five percent of sites (99) were visited during both nesting and brood rearing portions of the breeding season (separated by at least five weeks) and/or in both years; these were considered independent visits, since all focal species hatch precocial young that may move distances greater than 1km (Clark et al. 2014; Colwell & Oring 1988; Lowther et al. 2001), and because differences in habitat use have been observed between lone and brood-tending adults (Miller & Duncan 1999; Ryan et al. 1984; Ryan & Renken 1987).

Occupancy modeling of Breeding Pairs: Site level.— To assess effects of oil infrastructure and activity on habitat use by focal species, I modeled the effects of four *a priori* occupancy covariates on site occupancy by focal species (Table 2). To describe the amount of well infrastructure, I summed wells within the 64-ha study site and any additional wells within 200m of the boundary of the site, including those located across roads. I represented local human activity as the number of vehicles that passed along the side of the site where the survey was being conducted during the 30-minute transect survey. In lieu of including a full suite of habitat variables, I controlled for habitat suitability by including a covariate for mean site habitat suitability (described in section 2.1), allowing me to account for key habitat relationships with a single, representative variable. I used Julian survey date to control for an expected seasonal decline in local breeding pair abundance as failed breeders concentrated or departed (Table 2; Niemuth et al. 2012). Finally, I included an indicator variable for species-specific detection of a breeding pair in a previous visit for sites visited more than one time within or across seasons, despite presumption of independence in habitat selection processes within and across seasons.

I modeled differences in survey methodology (point count versus transect) using a dummy variable, resulting in an intercept adjustment in detection probability for transect surveys relative to point count surveys. I considered a suite of detection covariates representing weather, site, and anthropogenic conditions hypothesized to affect detection for one or more species (Table 2). I considered these variables to influence detection in point counts and transects similarly, with the exception of traffic, which was additionally modeled as an interaction with survey type because the short duration of point counts resulted in greater detection consequences of traffic. All continuous occupancy and detection covariates were standardized by the sample mean and standard deviation (Appendix S3) and collinearity was examined using correlation coefficients and plots (Appendix S4). Although the majority of traffic recorded in the study was directly related to oil field activity, it was uncorrelated with well density (r^2=0.003), as many areas with lower well density are travelled for access to other sites and areas with high well densities have less traffic associated with drilling where they are fully developed.

I used a multi-species occupancy model with full species-specific coefficients for all detection and occupancy covariates (Table 2) to evaluate whether detection could be modeled as a shared process across all species (Mackenzie et al. 2004). Models were specified using JAGS (Plummer 2005) in R (Version 3·2·3; R Development Core Team 2015). I used stochastic search variable selection (SSVS) to evaluate support for species-specific detection covariates in the full, species-specific model (O'Hara & Sillanpää 2009). Stochastic search variable selection employs an indicator variable (via a binomial mixture) to summarize the frequency with which an explanatory variable was included in the posterior distribution for each MCMC iteration. I considered variables with indicator values >0.5 as explanatory (median probability model; Barbieri & Berger 2004) which provides similar inference to information-theoretic approaches (Burnham & Anderson 2002) that use a 95% confidence interval to designate variable support (see Appendix S5 for model code and MCMC settings). The full multi-species model indicated species differences in the support for each detection covariate. As such, I proceeded with single-species models retaining only the detection covariates indicated by the full multi-species model for each species (Table 1) and occupancy covariates for habitat suitability, well density, traffic volume, Julian date and previous occupancy; I excluded previous occupancy from the willet model because inclusion prevented model convergence. All site models used three Markov chains for at least 50000 iterations, discarding 5000 values for adaptation and burn in, and thinned by a rate of 2. Convergence of all Bayesian models was assessed using trace plots and R-hat values.

Occupancy modeling of Breeding Pairs: Home Ranges.— The breeding season home ranges for godwits, willets, and pintails are large enough to encompass more than one 64-ha site (Table 1) and research suggests that habitat selection by these species is potentially informed by land use at larger spatial scales (Cunningham & Johnson 2006; Dechant et al. 2001; Naugle et al. 2001). I used Bayesian species-specific conditional auto-regressive (iCAR) occupancy models using R-package hSDM (Vieilledent et al. 2014) to examine the effects of infrastructure at the scale of a home range for godwits, willets, and pintails. Each species-specific model included the detection covariates identified in the site-modeling phase. For these models, habitat suitability and well density (active wells/km^2) were represented at the scale of a home range centered on a site (Table 2). Road density (km/km^2) at this scale represented potential traffic corridors (Table 2). Survey Julian date was also included to account for seasonal changes in occupancy. iCAR occupancy models account for spatial autocorrelation using a neighborhood structure; due to memory intensity of this analytical approach, variables had to be aggregated to the scale of sections (256-ha), thus losing some spatial resolution in the variables I considered. Home range model settings converged using one chain of 20 000 MCMC iterations with 5000 values discarded for burn-in and a thinning rate of 4, with differences between these and other modesl resulting from constraints of hSDM settings.

Occupancy modeling of Brood-Rearing Adults.— Broods were far less dense than breeding pairs, with naïve occupancy low enough (range 0.04-0.06) that species-specific models would be unlikely to converge or estimate occupancy with any useful precision (MacKenzie & Royle 2005). While species-specific detection processes differed for adults (phalaropes were detected primarily by sight while upland sandpipers were often initially detected by sound), identification of brood-tending behavior required audio and visual cues for all shorebird species (only visual cues for pintails), which suggests that the detection process for brood-tending adults should be similar. I used SSVS on a full multi-species brood occupancy model to identify detection covariates for inclusion in a reduced model. The full multi-species brood occupancy model included a shared point count detection estimate as well as shared detection and occupancy covariate structures, while estimating species-specific occupancy and transect-detection probabilities. The reduced model included topography and observer as detection covariates (see Appendix S6 for brood model code).

RESULTS

Six observers conducted a total of 492 sets of surveys across 396 sites in 2014 and 2015. Detection varied among species, with breeding pairs found in 16-52% of surveys

(Table 1). More than one breeding pair of a species was detected at a minority of occupied sites (20-43%, with greater frequency for upland sandpipers and phalaropes, which have smaller home ranges). Detection probabilities estimated from species-specific models were 3- to 4.8-fold higher for the 30-minute transect surveys than for the 3-minute point count surveys (Table 1; Figure 2). Transect surveys resulted in a greater proportion of visual detections than point count surveys across species and 2.7 times as many total detections (Appendix S7). Cumulative detection probabilities across the three surveys ranged between 0.65 (SE 0.09) for willets and 0.85 (SE 0.05) for upland sandpipers. Topography had the most common effect on detection probability, affecting all species except upland sandpipers (Table 1).

Estimated site occupancy of breeding pairs from species-specific models was lowest for godwits (0.21) and highest for upland sandpipers (0.56; Table 1). Phalaropes showed a seasonal decline in the probability of site use (occupancy) by breeding pairs, likely due to less conspicuous behavior during incubation and aggregation during brood-rearing. Both upland sandpipers and phalaropes exhibited strongly increased probability of occupancy at sites with a previously observation of occupancy within the same year or across years (Appendix S7). Suitability exhibited the expected positive relationship to occupancy for pintails, upland sandpipers and phalaropes (Figure 2; 99%, 97% and 91% posterior density > 0, respectively), but not for godwits or willets. Traffic exhibited a negative effect on breeding pair occupancy of pintails and willets (Figure 2; 93% and 97% of posterior density < 0, respectively; Figure 2). Well density negatively affected phalarope occupancy (Figure 2; 98% of posterior density < 0; Figure 2). Spatially explicit analyses did not indicate effects of well or road density on occupancy at the home-range scale (Figure 2); habitat suitability was weakly associated with occupancy for willets but not godwits at this scale (Figure 2, Appendix S7).

Broods were detected at 19% of sites; point count surveys had extremely low detection probability for broods (0.06, se 0.02) while transect detection probability was variable across species (0.49 for pintails and willets to 0.98 for upland sandpipers; Figure 2). After accounting for species-specific habitat suitability, seasonality and previous occupancy, the multi-species model indicated a negative relationship between occupancy by brood-tending adults and traffic (Figure 2; 97% posterior density < 0), and a post-hoc model with species specification of traffic coefficients revealed that this pattern was driven by the shorebird species (Appendix S7; 91%, 85%, 99% and 99% posterior density <0 for godwits, upland sandpipers, willets and phalaropes). Additionally, a post-hoc model with species-specific well coefficients indicated a negative effect of site well density (87% posterior density < 0) on brood occupancy of phalaropes (Appendix S7; >99% posterior density<0).

DISCUSSION

Traffic associated with oil field development and well maintenance negatively affected habitat use by breeding Northern pintails and willets, as well as by brood-tending shorebirds. Noise is implicated as the primary disturbance factor of roads, negatively affecting avian density even when car visibility (motion disturbance) is limited (Kociolek et al. 2011). Noise can cause impaired communication during courtship and brood rearing (Kight et al. 2012), stress responses (Blas et al. 2007), mortality risk (higher for low density species with high movement rates like Northern pintails, marbled godwits and willets; Forman et al. 2003) or diminished roadside habitat quality (Creuzer et al. 2016; Farmer 1993; Ludlow & Davis 2018). Noise and its effects dissipate across space (Blickley et al. 2012); as such, birds that were closer to road-side observers also experienced the highest traffic noise levels. Indicated broods were detected at distances closer to road-side observers than indicated breeding pairs across species, due to less conspicuous behaviors that limited detections at further distances. Therefore, broods may have occupied portions of study sites further from road traffic (and road-side observers), where impacts of traffic noise were dissipated, consequentially making them less available to observer detection. Was this the case, however, it would still support a conclusion of reduced habitat use driven by traffic for indicated broods. In contrast, Northern pintail, marbled godwit, upland sandpiper and willet indicated breeding pairs may have also avoided traffic by moving within a 64 ha site but remained observable due to more conspicuous behavior; any effect of traffic avoidance at this scale would not be identified without surveys that run perpendicular to the road, which were not possible in this survey due to land access restrictions.

This study inferred brood presence using conspicuous parental behavior (Lukacs et al. 2004, Ruthrauff & McCaffery 2005), thereby providing insight into brood-specific habitat use. When indicated broods were evaluated as indicated breeding pairs, traffic avoidance was not detected for marbled godwits, upland sandpipers or Wilson’s phalaropes. The difference in survey type detection probabilities was greater for brood-tending birds than for breeding pairs; I attribute this difference to the longer exposure time of the transect survey, during which observers could witness or be subject to antagonistic interactions exhibited by brood-tending adults. Though short, point-count survey designs might be effective for evaluating home range selection within a broader landscape (second order habitat selection, Johnson 1980), survey designs that increase exposure time and vantage points from which to observe improved availability of species for detection (Pagano & Arnold 2009b) are necessary for local-scale assessments of low-density, low detection species.

There was no evidence that non-phalarope species avoided well infrastructure, despite suitability models indicating they avoid other tall structures, such as tree cover and those present in urbanized areas (Table 1; Kantrud & Higgins 1992; Niemuth et al. 2017; Niemuth unpubl. data). Avoidance of vertical structures by grassland birds is assumed to be driven by an increased risk of predation (for both birds and nests) by perching raptors and corvids, who use visual cues to locate prey and nests (Renfrew et al. 2005; Thompson et al. 2014). While our study was not designed to assess nest site selection or nest survival, Bakken well sites add both vertical structures, and elevated well pads that can provide access into grassland habitat for both visual and olfactory predators (Phillips et al. 2003). In research examining habitat use by all five study species near wind turbines, only pintails exhibited reduced habitat use, yet they maintained sufficient density (change of ≤0.5 breeding pairs) that an occupancy study of the same system may not have detected a difference in habitat use (Loesch et al. 2013; Niemuth et al. 2013, Shaffer & Buhl 2006). In a changing landscape, reproductive success is likely mediated by changes in predator populations and behaviors, vegetation structure (including disrupted vegetation from infrastructure construction) and incubation behavior (Burr et al. 2017; Ludlow & Davis 2018; Smith & Wilson 2010); in cases, animal responses to these changes may result in habitat selection that is not adaptive (Schlaepfer et al. 2002). However, it is not possible to evaluate whether observed habitat use near infrastructure in this study represents an ecological trap without locating and monitoring nests. For example, birds could avoid infrastructure in nest site selection (such as seen with shorebirds nesting in SE Alberta; Ludlow & Davis 2018), while feeding at sites regardless of infrastructure.

The presence of oil wells at a site negatively affected habitat use by Wilson's phalarope breeding pairs, such that the addition of one well to a site or its perimeter decreased the probability of occupancy by 0.08 (95% CRI: 0.01-0.014). While it is not clear whether Wilson's phalaropes avoid infrastructure in nest site selection, phalaropes exhibit short incubation bouts that negatively affect nest predation (Liebezeit et al. 2009, Smith et al. 2012), such that lower occupancy near infrastructure could represent adaptive behavior similar to that exhibited by grassland songbirds (Nenninger & Koper 2017; Thompson et al. 2014; Thompson et al. 2015).

I did not find any effect of predicted suitability on habitat use by willets or marbled godwits at site or home-range scales. However, habitat suitability predicted at 30m resolution already represented habitat variables at spatial scales similar to or larger than study sites (Table 1), such that summarizing the suitability index across a site or home range obscure spatial patterns of habitat quality at more local scales. Indeed, a post-hoc analysis comparing suitability of specific locations where godwits and willets were observed within sites (145 and 167 observations, respectively), relative to 1500 random points suggests that godwits and willets are observed in locations with higher suitability than those available on the landscape (p<0.001, Appendix S9). Marbled godwits also select nest sites with higher suitability than other points within their home range (Specht, unpublished data). The landscape mobility provided by large home ranges and precocial young may afford upland-nesting waterbirds greater flexibility to utilize local high-quality habitat in larger landscapes that are less suitable. This behavior could confer advantages in a changing landscape, as specific habitat requirements related to both upland nesting and wetland feeding are more likely to be available within a larger area. Broods have relatively lower mobility and habitat use than highly mobile breeding pairs (Miller & Duncan 1999; Ryan et al. 1984; Ryan & Renken 1987), reflecting the specific predation threats and high energy demands of precocial offspring (Dreitz 2009), constrained by movement capacity on the landscape (Bloom et al. 2013). Both upland sandpipers and Wilson's phalaropes exhibited strong positive effects of previous site occupancy, suggesting that these species may be nesting and brood rearing in close proximity, and may have less flexibility in habitat selection than Northern pintail, marbled godwits and willets. Despite potential flexibility in habitat use for nesting, feeding and brood rearing, habitat quality may be affected in ways less perceptible to detection by occupancy study designs. For example, key invertebrate food resources could be reduced by chloride-rich brine contamination *(*Preston & Ray 2017), which has the potential to affect up to one-third of Prairie Pothole Region wetlands in the Bakken oil field region (Gleason & Tangen 2014).

Conservation Implications.— While study results show that habitat within oil fields is used for breeding by Northern pintails and upland-nesting shorebirds, they also indicate that some high quality habitat is being avoided due to traffic associated with oil infrastructure installation and maintenance. This study was conducted at the peak of oil development in 2014 and 2015, when traffic associated with drilling wells was high (890-1340 heavy duty vehicle visits for development of pad and drilling of first well (Goodman et al. 2016) with more than 200 drilling rigs in 2014 in Western North Dakota decreasing to 50 in 2017; North Dakota Industrial Commission 2017). Traffic will persist on the landscape as long as wells are being maintained (2-3 heavy duty vehicle visits per well per annum in Goodman et al. 2016, but does not account for hauling of oil from sites where pipeline infrastructure doesn't exist) and re-fracked (adding up to an additional 2000-3000 heavy duty vehicle trips over the life of a well; Goodman et al. 2016). As such, concentration of both wells and traffic along corridors could reduce disturbance and effective habitat loss (Thompson et al. 2015). This could benefit species with lower landscape mobility and may support brood-rearing habitat in the interstitial spaces between corridors within travelable distance from nests for species with precocial young. Additionally, placement of wells on non-grassland cover-types and restoration of large well pads required for drilling to a mixed-grass species assemblage will retain quality grassland habitat on the landscape for grassland obligate species (Ludlow et al. 2015; Ludlow & Davis 2018). Given the development projections of the Bakken oil field and the specific wetland and grassland habitat conditions upland-nesting waterbirds require for successful breeding, ongoing review of the conservation requirements for these species will be needed. Conservation efforts, including easement acquisition, should focus on maintaining higher quality habitat, especially between development corridors, that addresses not only birds' physical requirements, but their tendency to avoid areas with built infrastructure and other disturbances.

SUPPORTING INFORMATION

Chapter 3.S1: Map of oil well development in NW North Dakota 2005-2015.

Chapter 3.S2: Distribution of predicted habitat suitability of study sites relative to randomly selected quarter sections

Chapter 3.S3: Means and standard deviations used to normalize variables for analyses.

Chapter 3.S4: Correlation pair plots of standardized occupancy and detection variables.

Chapter 3.S5: R/JAGSUI model code for full multi-species breeding pair occupancy model with stochastic search variable selection indicators.

Chapter 3.S6: R/JAGSUI model code for full multi-species brood occupancy model.

Chapter 3.S7: Table of model coefficient and standard deviation estimates.

Chapter 3.S8: The proportion of each type of initial detection cue by species and survey type.

Chapter 3.S9: Habitat suitability of observed marbled godwits and willets relative to random points.

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Table 1. Behavioral states for classifying indicated breeding pairs and broods. Breeding pair and brood models included infrastructure variables scaled to home range size, where final included variables differed for each species. Occupancy estimates increased relative to naïve estimates after accounting for detection probability, which was higher in transects (t) than point counts (p) and differed in relationship to covariates for each species. Existing habitat suitability models for each species included and assortment of landscape-scale variables to account for non-infrastructure habitat suitability as a single variable.

Species	Indicated Breeding Pair	Brood Indicator	Earliest Observed Indicated Broods	Home Range Size	Occupancy (bp:breeding pair (se) bt:indicated broods (se))	Detection Probability (p:Point Count (se) t:Transect (se))	Included detection covariates	Landscape variables included in habitat suitability models
Marbled godwit	Social group of < 3 adults	Brood tending: flight circles with alarm calling and diving Brood sighting	June 3	2173 ha [c]	naïve| 0.17 bp| 0.21 (0.03) bt| 0.04 (0.01)	p| 0.200 (0.039) t| 0.627 (0.084)	Topography, date, Observer	800m: crop (-), hay(+), forest(-), development(-), wetland cover(+), wetland diversity(+), topographic variation(-)[g]
Northern pintail	Females and individual males alone or with a female [a]	Brood sighting	June 16	5102 ha [d]	naïve| 0.33 bp| 0.54 (0.08) bt| 0.07 (0.03)	p| 0.144 (0.024) t| 0.700 (0.061)	Topography, Wind, Observer	10.4km blocks: wetland area(+), wetland area^{-2}(+),wetland area^{-2}x easting(-) & northing(-) & E*N(+)[d]
Upland sandpiper	Social group of < 3 adults	Brood tending: Flight circles with alarm call, running along the ground, multi-brood créching[b] Brood sighting	June 19	199 ha [e]	naïve| 0.52 bp| 0.56 (0.04) bt| 0.05 (0.01) (2015 only)	p| 0.247 (0.04) t| 0.749 (0.07)	Wind, Observer	800m: grassland(+), pasture/hay (+), crop(+), forest(-), shrub(+), development(-), open water(-), wetlands(+), topographic variation(-), elevation(-)[h]

Willet	Social group of < 3 adults	Brood tending: flight circles with alarm calling and diving Brood sighting	June 11	1075 ha (estimated based on ratios of MAGO to WILL territory sizes)	naïve| 0.24 bp| 0.39(0.06) bt| 0.07 (0.03)	p| 0.126 (0.026) t| 0.543 (0.081)	Topography, Observer	400m: crop (-), hay(+), WPA & CRP(-), forest(-), development(-), wetland cover(+), wetland diversity(+),wetland count(+),topographic variation(-)[g]
Wilson's phalarope	Up to 5 males and 4 females, or 5 individuals of unknown sex. Loosely colonial nesting patterns.	Brood tending: flight circles with alarm calling and diving Brood sighting	June 13	314 ha [f]	naïve| 0.38 bp| 0.46 (0.05) bt| 0.07 (0.02)	p| 0.206 (0.025) t| 0.720 (0.052)	Topography, Traffic, Time, Observer	400m: crop (-), CRP(-), forest(-), urban(-), wetland cover(+), wetland diversity(+),wetland count(+),topographic variation(-)[g]

[a] Brasher et al. 2002; [b] B. Sandercock, personal communication, June 2015; [c] Bridget Olson, personal communication Aug 2014; [d] Reynolds et al. 2006; [e] Mong 2005; [f] Colwell & Jehl 1994; [g] Niemuth pers.comm. 2017; [h] Niemuth et al. 2017

Table 2. Descriptions of covariates anticipated to explain variation in detection (p) of and occupancy (psi) of breeding pairs and brood-guiding adults of focal species.

Covariate	Parameter	Definition and justification	Source
Observer	detection	Individual who conducted the survey, expected differences in detection across individuals	Recorded
Wind	detection	Wind speed (mph) at start of survey, expected to affect bird activity	Field measurement
Temperature	detection	Temperature at start of survey, expected to affect bird activity	Field measurement
Topography	detection	Standard deviation of elevation across the site, expected to affect visibility at site.	Extracted in ArcMap 10.5 from National Elevation Dataset, USGS
Survey Time	detection	Time of survey, expected to affect bird activity	Recorded
Traffic Volume	detection, occupancy	Number of vehicles that passed the site during 30-minute transect. Expected to affect observation process (potentially differently between survey types) and habitat use by disturbance-avoiding species.	Field observation
Julian Date	detection, occupancy	Julian date of survey, expected to affect the occupancy of incubation and brood-rearing states as well as the visual and audio activity that makes birds available for detection in surveys. Date^2 also included.	Recorded
Previous Occupancy	occupancy	Indicator variable for positive detection of a species at a site in a previous visit. One quarter of sites were visited more than once in two years.	Derived from data.
Suitability	occupancy	Mean habitat suitability of the survey site, expected to be positively correlated with occupancy	Extracted in ArcMap 10.5 from habitat suitability models (Reynolds et al. 2006, Niemuth et al. unpublished data, Niemuth et al. 2017)
Site well density	occupancy	Number of active, oil and/or gas wells within 200m of the site on May 15 of each year. At the scale of home range, derived as wells/km^2 across an area the size of a home range centered on a site.	Extracted in ArcMap 10.5 using well data (North Dakota Oil and Gas Commission 2015)
Home Range road density	occupancy	Meters of road/km^2 across an area the size of a home range centered on a site. Used only in spatially explicit home-range scale models for godwits, pintails and willets to account for habitat fragmentation in densely roaded areas.	Extracted in ArcMap 10.5 from TIGER line road data, US Census Bureau (2015)

Figure 1. Locations of point-count and transect surveys used to assess whether upland-nesting waterbirds avoided habitat due to well density or traffic in the Bakken oil field. Roadside point count surveys (1 and 2) were conducted at 200 and 600m across the 800m length of a 64-ha site, followed by an 800m roadside transect survey (3).

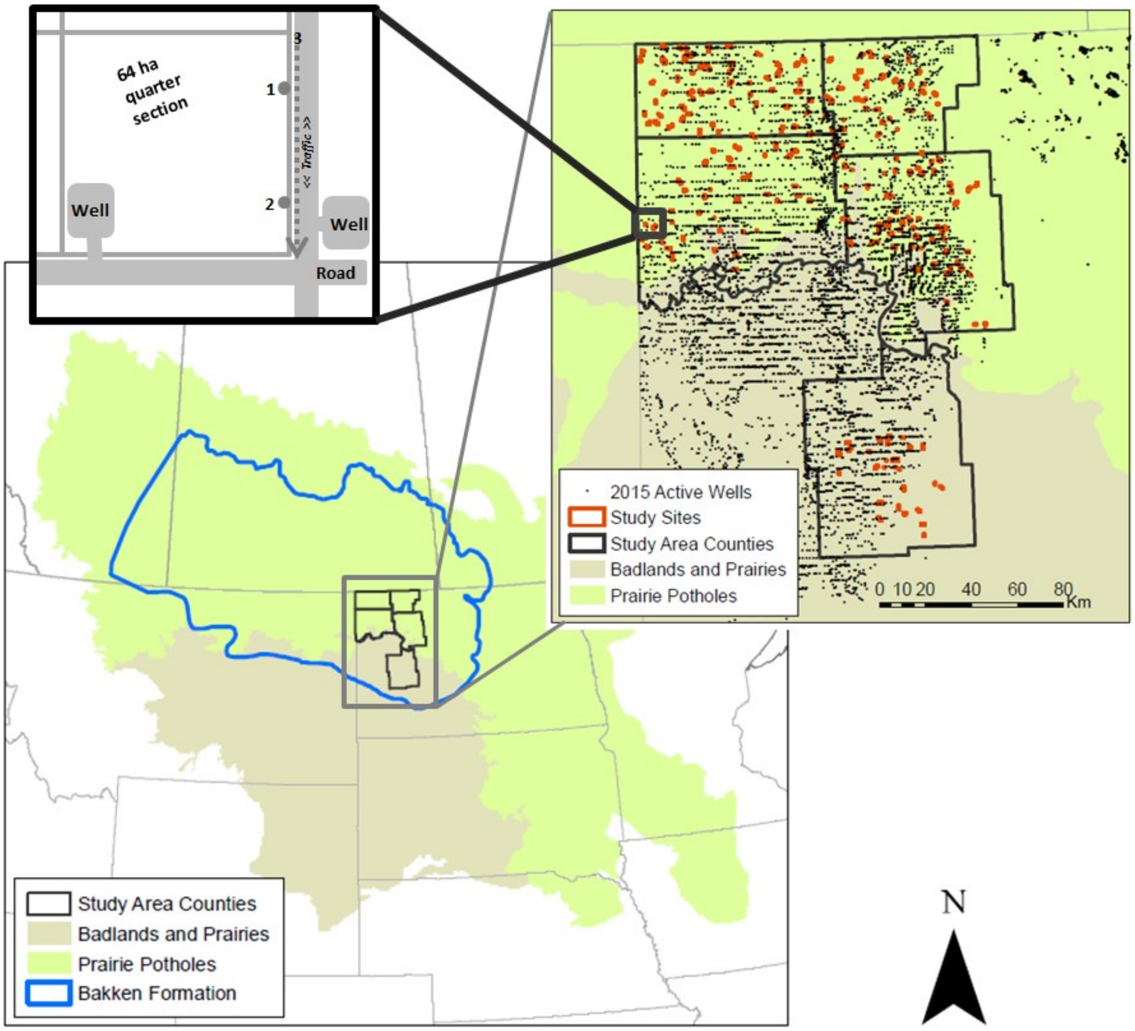
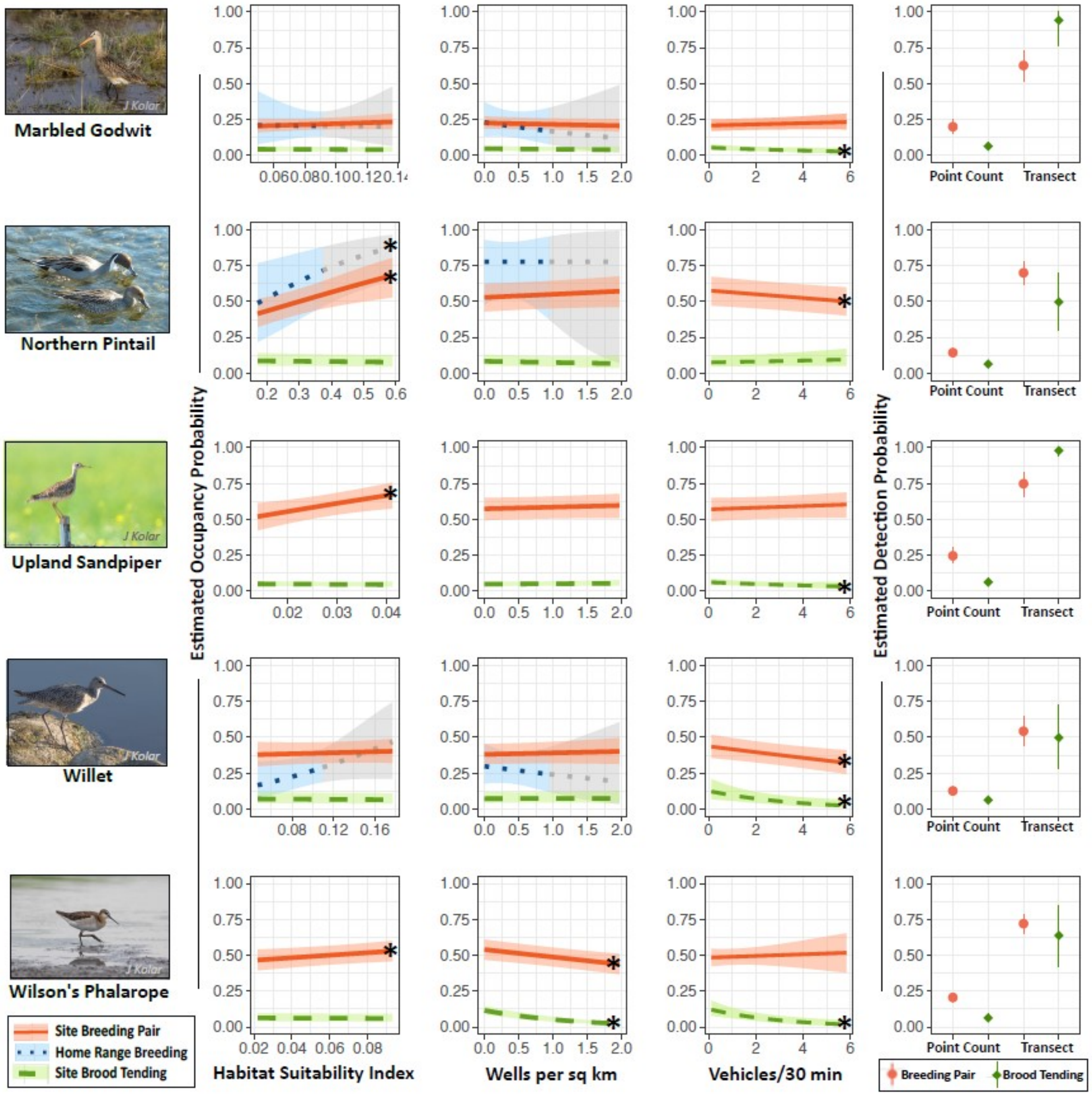


Figure 2. The effects of habitat suitability, oil infrastructure (well density) and activity (traffic) on breeding pair and brood occupancy of five grassland species (with 80% CRI calculated using the delta method, indicated with * when coefficient 80% CRIs don't include 0). Reduced habitat use by breeding pairs was observed in willets and Wilson's phalaropes as well as by brood-tending adults at the scale of 64-ha study sites and by brood-tending shorebirds. The range of species-specific home range well densities was narrower than site well densities due to the greater area represented; estimates extending beyond observed home range well densities are depicted in the lighter gray extension of the dotted line. Thirty-minute transect surveys improved detection probabilities for these cryptic, low-density species 3- to 4.8-fold for breeding pairs and 7- to 15-fold for broods, improving occupancy estimation.



Marbled Godwit
Northern Pintail
Upland Sandpiper
Willet
Wilson's Phalarope
J Kolar
Estimated Occupancy Probability
Estimated Detection Probability
Habitat Suitability Index
Wells per sq km
Vehicles/30 min
Point Count
Transect
Site Breeding Pair
Home Range Breeding
Site Brood Tending
Breeding Pair
Brood Tending
0.00
0.25
0.50
0.75
1.00
0.060.080.100.120.14
0.2 0.3 0.4 0.5 0.6
0.02 0.03 0.04
0.08 0.12 0.16
0.02 0.04 0.06 0.08
0.0 0.5 1.0 1.5 2.0
0 2 4 6
*

Chapter 4

OCCUPANCY SURVEYS WITH CONDITIONAL REPLICATES: AN ALTERNATIVE SAMPLING DESIGN FOR RARE SPECIES

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SUMMARY

1. Occupancy models are widely used to describe the distribution of rare and cryptic species— those that occur on only a small portion of the landscape and cannot be detected reliably during a single survey. However, model estimates of occupancy (ψ) and detection probabilities (p) are often least accurate under these circumstances.
2. Available sampling designs for occupancy surveys include standard design, wherein each of S sites is visited K times, and removal design, wherein S sites are visited K times each or until the species of interest is detected. We propose a new conditional design, wherein each of S sites is visited one time, and sites where the species of interest is encountered during the first survey are visited an additional ($K-1$) times to better estimate detection probability. We used large sample properties of maximum-likelihood estimators and Markov chain Monte Carlo simulations to characterize our proposed conditional design and compare it to standard and removal designs across a wide range of true occupancy and detection probabilities (ψ, $p = 0.1$ to 0.9 by 0.1 increments), maximum visits (K) and total sampling effort (E, the number of surveys accrued across all sites).
3. The conditional design provided more accurate estimates (lower standard or root mean squared error) of occupancy than standard or removal designs in our calculations and simulations when species were rare ($\psi \leq 0.3$) as well as more accurate estimates of detection probability over most combinations of ψ and p. These low-occupancy improvements are achieved by expending a greater

proportion of effort at occupied sites, improving estimates of p and thus ψ. When species are common ($\psi \geq 0.5$) the removal design generally provided the most accurate occupancy estimates, whereas the standard design performed best when ψ was intermediate and during MCMC simulations when p and K were low.

4. We recommend the conditional design for surveys of rare species and pilot studies. For multi-species surveys that include mixtures of rare and common species, a hybrid standard-conditional design with 2-3 replicates at all sites and additional replicates at sites where rare species are detected improves occupancy estimates of rare species.

INTRODUCTION

Understanding the distribution and abundance of species on the landscape is a primary objective of ecological research (Andrewartha & Birch 1954). Occupancy models have become a popular analytical framework for examining the functional relationships between species occurrence and environmental variables through simultaneous estimation of detection (p) and occupancy (ψ) probabilities from replicated surveys (MacKenzie *et al.*2002; Bailey, MacKenzie & Nichols 2014, Guillera-Arroita 2016). Numerous extensions have been developed to expand this framework (e.g., multi-season: MacKenzie *et al* 2003; multi-species: Dorazio *et al.*2010; Richmond, Hines & Beissinger 2010; and multistate: Royle 2004) and overcome violations of traditional model assumptions (e.g., closure: Kendall *et al.*2013; independent replicates: Hines *et al.*2010; heterogenous detection: Royle 2006; and false positives: Royle & Link 2006).

These extensions have increased the versatility of occupancy modeling and allowed researchers to better understand patterns of species occurrence over large spatial scales that cannot be comprehensively inventoried (MacKenzie *et al.*2006; Bailey *et al.*2014).

Occupancy models have been promoted as useful tools for studying rare or cryptic species, whose habitat use, behavior or population dynamics make them less suitable for abundance-based survey methods (Durso, Willson & Winne 2011; Clare, Anderson & MacFarland 2015; Linkie *et al.*2007; MacKenzie & Royle 2005). We define rare species as those that occupy ≤ 30% of sampling units ($\psi \leq 0.3$) and cryptic species as those that have ≤ 30% probability of being detected when present ($p \leq 0.3$). By these definitions, 31% of 182 occupancy estimates from studies that cited MacKenzie *et al.* (2002) or MacKenzie & Royle (2005) reflect rare species, 69% reflect cryptic species and 25% reflect species that were both rare and cryptic (Fig. 1, Appendix S1). Obtaining sufficient data for analyses of rare and cryptic species can be difficult, even when sampling units are well-matched to the spatial ecology of the target species and surveys are conducted using protocols that maximize detection (MacKenzie & Royle 2005; Guillera-Arroita, Ridout & Morgan 2010). Optimal design guidelines for standard and removal sampling for species with $p \leq 0.3$ recommend a large number of visits per survey site (K up to 49; Tables 1 & 3 in MacKenzie & Royle 2005), potentially at the cost of surveying additional sites. If ψ is also low, investigators might visit an insufficient number of occupied sites and expend tremendous effort revisiting unoccupied sites. In these circumstances, occupancy models often provide unstable parameter estimates due to sparse detections (Guillera-Arroita, Ridout & Morgan 2010; Guillera-Arroita *et al.*2014). Nonetheless, rare and cryptic species are arguably the most important subjects for occupancy modeling (MacKenzie *et al.*2005).

Alternatives to standard occupancy designs have not been widely adopted for use with rare or cryptic species. Removal sampling schemes, which survey sites either until the first positive detection or until some maximum number of surveys have been conducted, are efficient when species are common and thus detected at the majority of sites (MacKenzie & Royle 2005). Single survey approaches that concurrently estimate occupancy and detection from unique covariates have appeal due to their simplicity and compatibility with historical data involving unreplicated surveys, but have more restrictive assumptions and potentially lower accuracy (Lele, Moreno & Bayne 2012; Solymos & Lele 2016) and their use is controversial (Knape & Korner-Nievergelt 2016). Two-stage sampling designs can take advantage of site-level covariates to increase sampling intensity of occupied sites, but require prior knowledge of covariate values across all potential sample sites (Pacifici, Dorazio & Conroy 2012).

We propose a new *conditional sampling design* as an alternative approach for rare species. This approach combines elements of single-visit surveys and the standard replicated design. Similar to the single-visit design, all sites are visited once and detection versus non-detection is recorded for species of interest, along with any site- or occasion-specific covariates. Replicate visits are conditional on detection in the first survey, with (K-1) additional visits conducted at sites where the species was detected (Table 1). This is conceptually similar to hybrid sampling designs (MacKenzie *et al.* 2002; MacKenzie & Royle 2005) wherein some randomly selected sites receive single visits, but remaining sites receive replicate visits. However, in our design, replicate visits are not random; they are conditional on a positive detection during the first survey round. This design allows investigators to visit a greater number of sites and expend replicates only at sites where the survey species is known to occur.

In this paper, we compare our proposed conditional sampling design to conventional standard (MacKenzie *et al.*2002) and removal (MacKenzie & Royle 2005) designs. We use large-sample theoretical properties of the maximum likelihood estimators as well as Markov chain Monte Carlo (MCMC) simulations to characterize the conditional sampling design under optimal and literature-based sampling scenarios, respectively. We compare the accuracy of occupancy and detection probability estimates to those from standard and removal designs across true occupancy and detection probabilities ranging from 0.1 to 0.9 and varying cost scenarios. Based on our comparisons, we discuss the most appropriate use of the three designs, with an emphasis on best practices for studying rare and cryptic species.

CHARACTERIZING THE CONDITIONAL OCCUPANCY DESIGN

Standard occupancy sampling employs K_S replicate surveys at each of S_S sites, although missing values can be readily accommodated if some sites are surveyed $<K_S$ times (Table 1; MacKenzie *et al.*2002). Removal sampling involves surveying S_R sites until the focal species is detected or until K_R replicates are conducted (Table 1; MacKenzie & Royle 2005; Bornand *et al.*2014). In our conditional design, S_C sites are each surveyed once, and sites where occupancy is confirmed during the first visit are

resurveyed (K_C-1) additional times (Table 1). Sampling under the conditional design therefore spreads a fixed amount of survey effort across a greater number of sample sites and simultaneously concentrates all replicates on sites known to be occupied to contribute meaningful data for estimating detection probability. This sampling design prevents effort from being wasted on resampling unoccupied sites, but precludes identification of additional occupied sites through replicate surveys. How the different survey designs balance these two factors (effort spent at unoccupied sites versus occupied sites that go undetected) ultimately drives differences in their performances.

For the standard occupancy design, total effort (E) will be distributed predictably across sites and surveys:

$$E_S = S_S K_S \quad \text{(eqn 1)}.$$

In contrast, effort for the conditional and removal designs will vary around their expected values, which are functions of true occupancy (ψ) and detection (p) probabilities of a given study system:

$$E_C = S_C(1+\psi p\,(K_C-1)) \quad \text{(eqn 2)},$$

$$E_R = S_R\left(K_R(1-\psi)+\frac{\psi p^*}{p}\right) \quad \text{(eqn 3)}$$

where p^* represents cumulative detection probability (i.e., the probability of at least one detection at an occupied site) across K surveys, $p^*=1-(1-p)^K$. For the conditional design, replicate surveys only occur at sites where the organism was detected in the first visit, so $p^*=p$ (Appendix S2 Fig.S1 bottom panel).

Because the distribution of survey effort between sites and surveys in conditional and removal designs is affected by the unknown true state of the study system, more sites will be visited under these two designs for a given total effort (*E*) and maximum number of surveys per site (*K*), because some sites will not be revisited *K* times. These differences in the distribution of sampling effort also mean that the three survey designs differ in values of key statistics: expected numbers of sites with positive detections (S_D), total detections (*d*) and supplemental detections ($d_+=d-S_D$) (Guillera-Arroita, Ridout & Morgan 2010).

Assuming that ψ and p are constant across sites and surveys, that occupancy status does not change between replicate surveys (i.e., closure) and that replicate surveys are independent, the conditional design has the following likelihood:

$$L(\psi, p) = \left(\frac{S!}{S_D!(S-S_D)!}(\psi p)^{S_D}(1-\psi p)^{S-S_D}\right)\left(\frac{(S_D(K-1))!}{d_+!(S_D(K-1)-d_+)!}\, p^{d_+}(1-p)^{S_D(K-1)-d_+}\right) \quad \text{(eqn 4).}$$

Likelihoods for the standard and removal designs can be found in MacKenzie *et al.*(2002) and MacKenzie *et al.*(2006).

The maximum likelihood estimate of detection probability for the conditional design is:

$$\hat{p} = \frac{d_+}{(K-1)S_D} \qquad \text{(eqn 5)}$$

and the maximum likelihood estimate of occupancy is:

$$\hat{\psi} = \frac{S_D}{S\hat{p}} = \frac{{S_D}^2(K-1)}{d_+ S} \quad \text{(eqn 6).}$$

Hence, for a given K and S, (S_D, d_+) are sufficient statistics for the conditional occupancy model (with ψ and p constant) and summarize the observed detections without information loss. We note that, like the standard and removal estimators, conditional occupancy can also produce boundary estimates of $\hat{\psi}=1$ if $\hat{p}^*$ is too small (i.e., if there are too few supplemental detections; Guillera-Arroita, Ridout & Morgan 2010; eqns 2-4). However, these sampling scenarios are highly improbable and likely indicative of assumption violations.

The accuracy of parameter estimates is assessed by their bias and precision. To characterize and compare the conditional design with standard and removal designs, we derived the asymptotic variance of occupancy for the conditional design and of detection for conditional and removal designs (Appendix S2, Variance equations) using standard MLE methods (the Fisher information matrix; Williams, Nichols & Conroy 2002). Variances for standard and removal occupancy and standard detection probability were previously derived (MacKenzie & Royle 2005, eqns 4&7; Guillera-Arroita, Ridout & Morgan 2010, eqn 6). Variance is minimized for each design at different values of K depending on the values of true ψ and p, and in all cases variance decreases with increasing effort. A poor choice of K (i.e., from not using the optimal value or incorrectly gauging the true occupancy or detection probability of the study system) can adversely affect the distribution of survey effort and increase variance. The value of K that minimizes Var($\hat{\psi}$) at a given E (equation 2) for the conditional design is:

$$K_{Optimal,C} = Round\left[1 + \sqrt{\frac{1-p}{p^2\psi(1-p\psi)}}\right] \qquad \text{(eqn 7)}$$

Assuming equal costs between initial and replicate surveys, we compared estimates of optimal K for standard, removal and conditional sampling designs for ψ and p=0.1 to 0.9 at 0.1 increments (Table 2). All designs require more visits when p is low to provide more information for estimating detection. At a given effort, the conditional design requires the largest K to achieve an optimal design when occupancy is low, whereas the removal design requires the largest K when occupancy is high. The standard design never requires the most replicates but under conditional or removal designs, most sites will be surveyed fewer than K times so the standard design often averages more visits per site (Appendix 2 Fig. S1). Hence, conditional and removal designs are expected to visit 2.2- and 1.1-fold more sites on average than the standard design while achieving the same total effort. For example, at ψ=0.4 and p=0.3, $K_{optimal,S}$=5, $K_{optimal,R}$=8 and $K_{optimal,C}$=6 (Table 2); at a fixed E=120, representing the 10th percentile of total effort from published occupancy studies (Appendix S1), equations 1-3 give us S_S=24, S_R=25 and S_C=75.

We also calculated the range of K values for each method that would produce a near-optimal variance (±20%; Table 2). This analysis revealed that all sampling designs, and especially removal and conditional designs, were robust to non-optimal choices of K, allowing greater flexibility in study design to accommodate potential constraints in the number of repeat surveys and minimizing the consequences of poor a priori estimates of ψ and p.

COMPARISON OF SAMPLING DESIGNS AT OPTIMAL NUMBER OF SURVEYS

To understand how using conditional, removal and standard designs affects precision of occupancy and detection estimates under ideal sampling scenarios, we compared the SE($\hat{\psi}$), SE($\hat{p}$) and A-optimality (SE($\hat{\psi}$) + SE($\hat{p}$)) of the three designs across values of ψ and p, where variances were calculated using method-specific optimal values of K and S that would result in a total effort of E=120 (Fig. 2). Using these metrics, the conditional design provided the most precise occupancy estimates (SE($\hat{\psi}$)) when occupancy was low ($\psi \leq 0.2$), while the removal design provided the best precision over most of the remaining parameter space ($\psi \geq 0.4$) (Fig. 2). The conditional design provided the most precise estimates for detection (SE($\hat{p}$)) when $\psi \leq 0.5$, but the standard design was superior when ψ or p were high (≥0.7; Fig. 2). When standard errors of both parameter estimates were valued equally (A-optimality), each design outperformed the other designs in approximately one third of the parameter space; the conditional design outperformed when ψ was low and the removal design outperformed when ψ was high (Fig. 2, Appendix S2 Fig. S2). Even with a low level of effort, differences among designs were generally small when effort was distributed optimally between sites and surveys for each design, and differences are expected to diminish further with increasing effort because the variances are inversely proportional to sampling effort.

We also compared the estimation precision of the three designs under scenarios where the cost of initial visits differed from subsequent visits following MacKenzie & Royle (2005), and where each design is implemented at a K optimized to minimize variance (and thus SE) at a given cost ratio. When the cost of establishing new sites is greater than the cost of subsequent visits, standard and removal designs outperformed conditional designs by allocating a greater proportion of effort to cheaper subsequent surveys (Appendix S2 Fig. S3). Perhaps counterintuitively, when designs are optimized for cost ratios >1 (i.e., high initial costs to establish sites), the removal design visits fewer sites than the standard design, improving its performance in these situations. High initial costs might be incurred when there are singular costs associated with establishing sites, such as acquiring access permission or imagery. Consecutive time-to-detection or spatially-adjacent pseudo-replicates might also decrease the cost of replicate surveys by eliminating or reducing travel costs, but they also might require more sophisticated models to deal with spatial or temporal dependence (i.e., effective sample size $<S*K$; Hines *et al.* 2010). Conversely, if initial surveys are cheap but subsequent visits are more expensive (cost ratio <1; e.g., if initial surveys use an existing survey platform, but subsequent visits require additional contracted support), conditional and removal designs are favored over the standard design because a smaller proportion of the total effort is spent revisiting sites.

COMPARISON OF SAMPLING DESIGNS USING LITERATURE-BASED CASE SCENARIOS

Comparisons conducted using optimal study designs presume that investigators are able to select an appropriate study design a priori. Additionally, these assessments exclude bias, which cannot be calculated with MLE methods. Therefore, we used simulated occupancy data to compare parameter estimation of the three designs at sample sizes derived from published occupancy studies (Appendix S1). We generated datasets in a full factorial design with three levels of K, three levels of E, across ψ, p=0.1 to 0.9 in increments of 0.1, resulting in 729 sampling scenarios where both ψ and p were held constant across sites and surveys within each simulation. Our specified levels of replicate visits (K=3, 5 and 15) and total survey effort (E=120, 420 and 1500) approximate the 10th, 50th and 90th percentiles of replication across the reviewed studies.

We calculated the expected number of sampling sites (S_S, S_R, S_C,) that would be required to produce a given value of effort at a given ψ, p and K by solving equations 1-3 for S, reasoning that investigators often implement an approximate a priori sampling scheme of “sample S sites up to K times each” rather than “sample until total effort (E) is reached”. After simulating Bernoulli processes of occupancy and detection, our average simulated effort (mean E_i) was within 1 survey of the targeted values for all methods and effort levels.

For each of the 729 combinations of ψ, p, K and E we simulated 100 data sets in program R (Version 3.2.3; R Development Core Team 2015) with sufficient sites and surveys so that they could be sampled by each method at any given level of E (Appendix S3). Although each data set was sampled using all three designs, conditional and removal designs utilized data from more sites (S), such that naïve occupancy (S_D/S) varied among methods. We adapted existing WinBUGS code for standard design occupancy models (Kéry 2010) that assumed occupancy and detection probability were constant across sites and replicates (i.e., model ψ(.), p(.)) and further modified it for removal and conditional sampling designs (Appendix S3). We implemented Bayesian analyses using MCMC with the R2jags package (Su & Yajima 2015) and retained mean and variance estimates for both $\hat{\psi}$ and $\hat{p}$, the covariance and correlation between $\hat{\psi}$ and $\hat{p}$, realized sampling effort

(E_i) and sampling statistics (S_D, d, d_+). For each analysis, we used vague priors (ψ and $p \sim$ Uniform(0,1)) and implemented 3 MCMC chains with 12 000 iterations, including a burn-in period of 2 000 iterations and a thinning rate of 2, yielding 15 000 samples for each posterior distribution. Preliminary analyses across a wide range of parameter values indicated this was sufficient replication to reach convergence ($\hat{R}$<1.01) on nearly all simulations (Gelman & Rubin 1992).

We compared the estimation accuracy of the three survey designs (Fig. 3) using root mean squared error (RMSE= $\sqrt{SE^2 + Bias^2}$ derived from each posterior distribution and averaged over all 100 replicates) of $\hat{\psi}$ and $\hat{p}$, and A-optimality (RMSE($\hat{\psi}$) + RMSE($\hat{p}$); modified from Guillera-Arroita, Ridout & Morgan 2010). For all occupancy designs, bias decreases with higher detection probability and total effort, and exhibited a similar pattern across combinations of ψ and p for all three designs. Slight improvements of any design over the other two were qualitatively similar to patterns of improvement in standard error which was the main driver of differences between designs. These patterns were corroborated by MLE variances calculated at K=3,5 and 15 (HT Reich, unpubl. data). Full simulation summaries are available as supplemental data (Appendix S4).

Summarizing across all E and K, RMSE($\hat{\psi}$) and A-optimality indicated that the conditional design generally outperformed other methods when ψ was low (≤0.3, Fig. 3), demonstrating that the performance of the conditional design is robust to non-optimal sampling designs at low occupancy. The removal design generally outperformed the other sampling designs for RMSE($\hat{\psi}$) when both ψ and p were ≥0.4. The standard design outperformed the other methods when p≤0.2 or when ψ and p were both intermediate

(Fig. 3). A more detailed inspection of simulation summaries revealed that the standard design performed best at low p when K was limited to 3 or 5, but not 15 (Appendix S4), indicating that the standard design may be more robust to insufficient replication when p is low. However, all three designs performed poorly when p was 0.1, especially if ψ was near 0 or 1, demonstrating the limitations of occupancy models for extremely cryptic species (Appendix S2 Fig. S4, Appendix S4 for data). The conditional design provided the most accurate estimates of detection probability across the majority of parameter space (Fig. 3); but all designs performed well when ψ was high, resulting in negligible pairwise differences in RMSE($\hat{p}$) ($\leq$0.001) across most of the parameter space (Fig. 3).

DISCUSSION

Herein, we propose and assess a new conditional sampling design for occupancy modeling that involves conducting single-visit surveys at a large number of sampling sites, with replicate surveys conducted only at sites where the target species was detected during the initial survey. Due to this different allocation of effort to sites and surveys, the conditional design typically visits more sites (S), detects more occupied sites (S_D), obtains more supplemental detections, ($d+$), and conducts more surveys at occupied sites (K) than the standard design when occupancy is low ($\psi \leq 0.3$) (Appendix S2 Fig. S1). This improves conditional design estimation of detection and occupancy in studies of rare species where a standard design might obtain data too sparse for accurately estimating both parameters. To achieve these improvements, the conditional design deprioritizes identifying occupancy at a majority of occupied sites; in contrast, at optimal distribution of effort, the standard and removal designs both continue sampling sites until >80% of occupied sites are identified through positive detections (Appendix S2, Fig. S1).

Although we only presented models with homogeneous occupancy and detection probabilities, additional unpublished simulations indicated that the conditional design accommodates site-specific covariates on both ψ and p, occasion-specific covariates in p and modeled or unmodeled heterogeneity in p and continues to produce more accurate estimates of occupancy and less biased estimates of covariate coefficients at low ψ, as well as better estimates of site-specific heterogeneity in p using site random effects (HM Specht, TW Arnold, unpubl. data). However, initial surveys must not have a unique detection probability or unique covariates affecting detection probability (i.e., $p_1 \neq p_i$ for i >1 violates model assumptions) or estimation accuracy of ψ decreases (HM Specht, unpubl. data). We also found that when occupancy is low, the conditional design is robust to a wider range of non-optimal choices of K and provides an advantage when subsequent surveys were equally or more expensive than initial surveys because a smaller proportion of the total effort is spent re-visiting sites.

The removal design achieved superior performance when occupancy was high ($\psi \geq 0.5$) by expending more effort identifying occupancy at a greater proportion of occupied sites (Appendix 2 Fig. S1). Under these circumstances, the removal design is a preferable alternative to standard design when both ψ and p are high. However, it performed poorly when ψ was low, which suggests this design is a poor choice for studying rare species (especially in situations involving heterogeneity; HM Specht unpubl. data). It was also the poorest choice for estimating detection probability and performed poorly when detection probability exhibited a monotonic trend across replicate surveys (e.g., $p_1 > p_2 > p_3 \ldots p_k$; HM Specht, unpubl. data).

The standard design benefits from investing effort in estimating detection probability at occupied sites and also in identifying occupancy at a majority of occupied sites, but this becomes a hindrance when ψ approaches 0 or 1. Although it was less frequently the best sampling design for any particular parameter combination, the standard design provided competitive estimates of occupancy and detection probability across most of the parameter space. The standard design provides a uniform distribution of effort across all sites, making it straightforward to use in the field and with readily available adaptations for assumption violations and goodness-of-fit tests for analysis (MacKenzie & Bailey 2004; Warton *et al.*2017). The standard design exhibited a narrower range of acceptable values for near-optimal K (Table 2), but it nevertheless demonstrated the best performance when species were cryptic and simulations included fewer replicates than recommended.

Recommendations for Conditional Design Implementation.— Occupancy surveys are most effective when implemented using a priori estimates of occupancy and detection probabilities to determine appropriate survey designs (e.g., standard, removal or conditional) and optimal numbers of sites and replicates for a given total survey effort. If the target species is rare ($\psi \leq 0.3$), it is necessary to expend a great deal of effort, such that the target species is encountered at multiple sites and in multiple surveys, despite being detected imperfectly. For rare species, the conditional design can provide more accurate estimates of both occupancy and detection probabilities. If the rare species is readily detected at occupied sites ($p>0.3$), then 3 or 4 replicate surveys will provide optimal or near-optimal replication over the entire parameter space; however, if the species is also cryptic ($p\leq0.3$) then 5-10 replicates will be more appropriate (Table 2). The conditional design is also the best choice if estimation of detection probability is an equal or greater priority than occupancy estimation. For example, when field-testing a new survey method (e.g., assessing automatic recording units to survey secretive marsh birds or eDNA samples to detect larval amphibians; Sidie-Slettedahl *et al.*2015; Pilliod *et al.*2013), detection probability might be the parameter of primary interest. When piloting a study design in a new landscape or for a new species, emphasis on detection probability will facilitate assessing the efficacy of the detection method and allow researchers to clarify their approximate location within the ψ by p parameter space and implement an appropriate number of replicates and design for subsequent surveys (e.g., in Table 2, the influence of p on optimal K is 8 times stronger than the influence of ψ or choice of study design). The conditional design could also be used in the first stage of two-stage sampling designs to provide better estimates of ψ and especially p for second-stage sampling (Pacifici, Dorazio & Conroy 2012), and if $\psi\leq0.3$ the conditional design could also be used for second-stage sampling. However, because the conditional design only utilizes replicate surveys when the study organism is detected in the first survey round, the design is not robust to changes in detection probability between initial and subsequent survey rounds, making it critical that subsequent surveys follow initial surveys closely in methodology and time, that surveyed organisms do not exhibit behavioral responses to prior detections (i.e., behave in a trap-happy or trap-shy manner) and that observer performance is not biased by prior knowledge (i.e., observers do not survey more attentively during replicate surveys because they know the site is occupied). We therefore recommend that replicate surveys are implemented by interspersing subsequent visits to sites with positive detections among the initial visits to remaining sites preferentially without observers having knowledge of whether visits represent initial or replicate surveys (Riddle et al. 2010). For example, in a randomized sampling scheme, subsequent visits to occupied sites could be added to the sampling schedule with a probability proportional to the number of visits remaining (i.e., if there are 4 visits remaining at a particular occupied site, a revisit to that site is four times more likely to be selected than a visit to any particular new site).

Data collected under the conditional design can be readily analyzed in a Bayesian framework using JAGS or WinBUGS using code similar to that provided (Appendix S3), or in a maximum likelihood framework using programs such as unmarked (Fiske & Chandler 2011), MARK (White & Burnham 1999) or Presence (Hines & MacKenzie 2004). With missing data coded for visits 2 through K at sites with no detection in the first visit, the standard model implemented in these programs correctly estimates a conditional likelihood for ψ and p. In Appendix S5 we provide worked examples of occupancy analysis in each of these programs for standard, removal and conditional designs with covariates. Goodness-of-fit and violations of independence in detection can be evaluated following goodness-of-fit procedures adapted for the conditional design likelihood (MacKenzie & Bailey 2004; Warton *et al.*2017) whereas models that include a site random effect can be used to detect unexplained heterogeneity across sites.

Due to its flexibility at low occupancy, the conditional design could be used in tandem with the standard design to improve inference on rare species when multi-species standard occupancy surveys have the potential to document rare, conservation-priority species. For example, a standard occupancy survey designed to target more common, observable species could be conducted across all sites using 2-3 replicates at each site, while sites with detections of rare species could be surveyed additional times, thereby improving occupancy estimates for the rare species, without affecting estimates for more common species. In Appendix 2 (Table S5), we demonstrate such an approach for a combined survey of common-conspicuous (ψ 0.6, p 0.6), common-cryptic (ψ 0.6, p 0.3), rare-conspicuous (ψ 0.3, p 0.6), and rare-cryptic (ψ 0.3, p 0.3) species and find that for a given sampling effort, the hybrid model outperformed standard models. If initial surveys are less expensive to conduct than subsequent surveys, which might be the case if initial surveys utilize an existing survey platform, but subsequent surveys would require special targeted effort in addition to the initial survey, the conditional design should be preferred over the standard design for assigning additional effort to improve inference for rare species. For example, the existing North American Breeding Bird Survey (Sauer *et al.* 2017) single-visit survey sites with observed detections of black-billed cuckoos (*Coccyzus erythropthalmu;*$\psi p \approx 0.01$) could be targeted with additional survey effort after the route is completed to provide replicated surveys for estimating $\hat{p}$. Although these survey routes are exhausting, revisiting 1-2 stops on the way home might be cost neutral, and provide sufficient data for estimating $\hat{p}$, and therefore $\hat{\psi}$. However, if initial surveys are more expensive due to travel or start-up costs, then the benefits of the conditional design for rare species decrease relative to the standard design.

In occupancy studies of rare or cryptic species, ideal study design parameters (S,K) change considerably with small changes in occupancy and detection probability. The conditional occupancy design provides efficient and accurate estimates of occupancy for rare species, while allowing flexibility to accommodate suboptimal study designs. This design can be readily implemented in existing software packages and easily combined with existing survey platforms. As such, we believe the conditional design can be a useful tool for studying rare species in an era when financial resources are limiting and conservation is increasingly reliant on quantitative species distribution models.

AUTHORS' CONTRIBUTIONS

TA conceived the initial idea and developed R code for MCMC analysis; HR and HS derived maximum likelihood estimators for variances and optimal sampling effort; HS and TA led the writing effort with significant contributions from HR, FI and ME; and HS led figure and appendix preparation. HS, TA and HR executed additional simulation and theoretical studies. All remaining authors contributed to the literature review and strategic planning, simulated and analyzed data, reviewed manuscript drafts and gave final approval for publication.

DATA ACCESSIBILITY & SUPPORTING INFORMATION

The literature review of occupancy surveys (Appendix S1) as well as additional analyses in Appendix S2 can be found with the published manuscript at: https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/2041-210X.12842
R code for simulating data and comparing methods (Appendix S3), the data resulting from our simulations (Appendix S4) and files to demonstrate the application of the conditional design in other software packages (Appendix S5) can be found at the University of Minnesota digital conservancy: https://doi.org/10.13020/D6BS3K

Chapter 1.S1. Literature review of occupancy surveys

Chapter 1.S2. Variance equations and additional figures presenting the expected sampling efficiency for each method under a scenario of *E*=120 (AS2 Fig. S1), the SE for each method based on the asymptotic variance (AS2 Fig.S2), a comparison of design performance under different cost ratio scenarios (AS2 Fig. S3), RMSE for each method based on simulated data (AS2 Fig. S4) and example implementation of the hybrid standard-conditional design (AS2 Table S5).

Chapter 1.S3. R Code for data generation and Bayesian analysis used in simulations.

Chapter 1.S4. Raw data from simulation study

Chapter 1.S5. Data analysis examples. This includes input and analysis files for analyzing simulated occupancy data in R package unmarked, Program MARK and PRESENCE.

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Table 1. Sample detection histories for occupied and unoccupied sites under standard, removal and conditional occupancy sampling schemes, where 1 indicates a positive detection, 0 indicates non-detection and − represents no survey.

True state	Survey 1	Standard	Removal	Conditional
Occupied	1	10110	1----	10110
Occupied	0	00000	00000	0----
Occupied	0	00110	001--	0----
Occupied	0	00001	00001	0----
Unoccupied	0	00000	00000	0----

Table 2. Optimal number of maximum replicates for given true values of occupancy (*ψ*) and detection probability (*p*) under standard, removal and conditional designs, assuming that replicate and initial surveys bear the same cost. The range of *K* values that will produce a variance within 20% of the minimum variance is in brackets, demonstrating the relative design flexibility of different methods in different areas of the parameter space.

Standard	**ψ**																	
p	0.1		0.2		0.3		0.4		0.5		0.6		0.7		0.8		0.9	
0.1	14	[9-24]	15	[10-25]	16	[10-26]	17	[11-28]	18	[12-30]	20	[12-33]	23	[15-36]	26	[17-41]	34	[23-51]
0.2	7	[5-11]	7	[5-11]	8	[5-12]	8	[6-13]	9	[6-14]	10	[7-15]	11	[7-17]	13	[9-19]	16	[11-24]
0.3	5	[3-7]	5	[4-7]	5	[4-8]	5	[4-8]	6	[4-9]	6	[5-10]	7	[5-11]	8	[6-12]	10	[7-15]
0.4	3	[3-5]	4	[3-5]	4	[3-5]	4	[3-6]	4	[3-6]	5	[3-7]	5	[4-7]	6	[4-8]	7	[5-10]
0.5	3	[2-4]	3	[2-4]	3	[2-4]	3	[3-4]	3	[3-5]	3	[3-5]	4	[3-5]	4	[3-6]	5	[4-7]
0.6	2	[2-3]	2	[2-3]	2	[2-3]	2	[2-3]	3	[2-4]	3	[2-4]	3	[3-4]	3	[3-5]	4	[3-6]
0.7	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-3]	2	[2-3]	2	[2-3]	3	[2-4]	3	[3-4]
0.8	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-3]	2	[2-3]
0.9	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]

Removal	**ψ**																	
p	0.1		0.2		0.3		0.4		0.5		0.6		0.7		0.8		0.9	
0.1	23	[17-34]	24	[17-36]	25	[18-38]	26	[19-40]	28	[21-43]	30	[22-48]	34	[25-54]	39	[28-64]	48	[34-87]
0.2	11	[8-16]	11	[9-17]	12	[9-18]	13	[9-19]	13	[10-20]	15	[11-22]	16	[12-25]	19	[14-30]	23	[17-41]
0.3	7	[5-10]	7	[6-10]	7	[6-11]	8	[6-12]	8	[6-13]	9	[7-14]	10	[8-16]	12	[9-19]	15	[11-26]
0.4	5	[4-7]	5	[4-7]	5	[4-8]	6	[4-8]	6	[5-9]	6	[5-10]	7	[6-11]	8	[6-13]	10	[8-19]
0.5	4	[3-5]	4	[3-5]	4	[3-5]	4	[3-6]	4	[4-7]	5	[4-7]	5	[4-8]	6	[5-10]	8	[6-14]
0.6	3	[3-4]	3	[3-4]	3	[3-4]	3	[3-4]	3	[3-5]	4	[3-5]	4	[3-6]	5	[4-8]	6	[5-11]
0.7	2	[2-3]	2	[2-3]	2	[2-3]	3	[2-4]	3	[2-4]	3	[3-4]	3	[3-5]	4	[3-6]	5	[4-9]
0.8	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-3]	2	[2-3]	3	[2-4]	3	[2-5]	4	[3-7]
0.9	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-3]	2	[2-3]	3	[2-5]

Conditional	**ψ**																	
p	0.1		0.2		0.3		0.4		0.5		0.6		0.7		0.8		0.9	
0.1	31	[12-84]	22	[10-55]	19	[9-44]	16	[8-38]	15	[7-34]	14	[7-31]	13	[6-29]	12	[6-27]	11	[6-25]
0.2	15	[7-40]	11	[5-27]	9	[5-22]	8	[5-19]	8	[4-17]	7	[4-15]	7	[4-14]	6	[4-14]	6	[4-13]
0.3	10	[5-26]	7	[4-17]	6	[4-14]	6	[3-12]	5	[3-11]	5	[3-10]	5	[3-9]	5	[3-9]	4	[3-9]
0.4	7	[4-19]	6	[3-12]	5	[3-12]	4	[3-9]	4	[3-8]	4	[3-7]	4	[3-7]	4	[3-7]	4	[3-7]
0.5	6	[3-14]	4	[3-9]	4	[3-8]	4	[2-7]	3	[2-6]	3	[2-6]	3	[2-6]	3	[2-5]	3	[2-5]
0.6	4	[3-11]	4	[2-7]	3	[2-6]	3	[2-5]	3	[2-5]	3	[2-5]	3	[2-4]	3	[2-4]	3	[2-4]
0.7	4	[2-9]	3	[2-6]	3	[2-5]	2	[2-4]	2	[2-4]	2	[2-4]	2	[2-4]	2	[2-4]	2	[2-4]
0.8	3	[2-7]	2	[2-5]	2	[2-4]	2	[2-3]	2	[2-3]	2	[2-3]	2	[2-3]	2	[2-3]	2	[2-3]
0.9	2	[2-5]	2	[2-3]	2	[2-3]	2	[2-3]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-2]	2	[2-3]

Fig. 1. Estimated occupancy and detection probabilities from 182 occupancy studies (unique combinations of species and/or study areas) from a review of 54 published papers indicate that occupancy models are frequently used to study rare (*ψ*≤0.3) and cryptic (*p*≤0.3) species. See Appendix S1 for full details of our literature review.

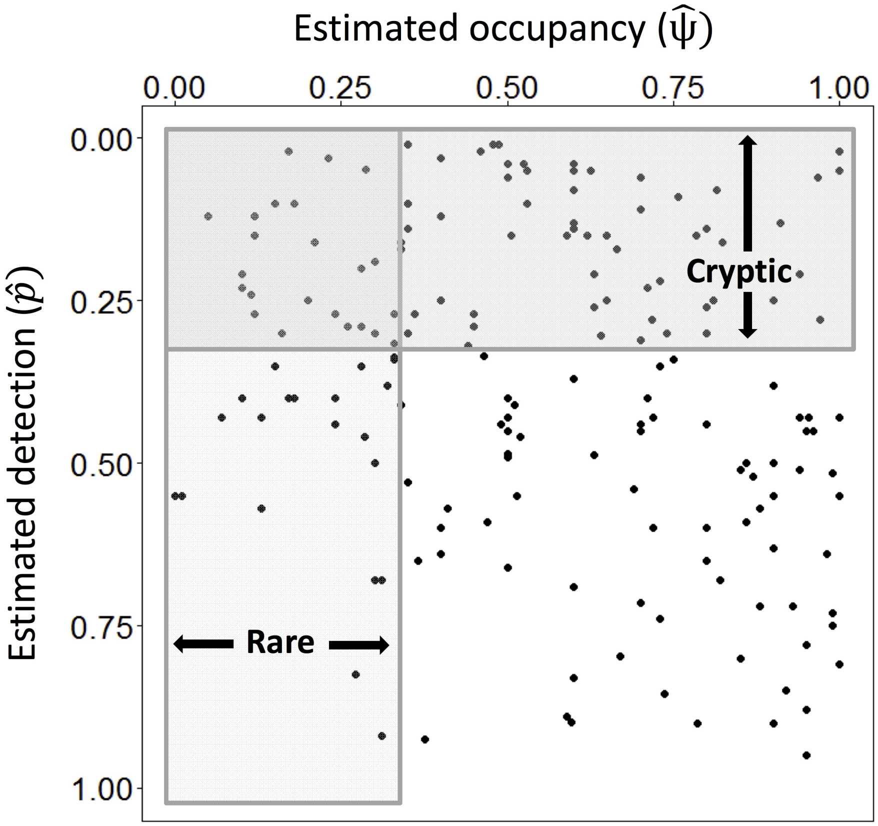
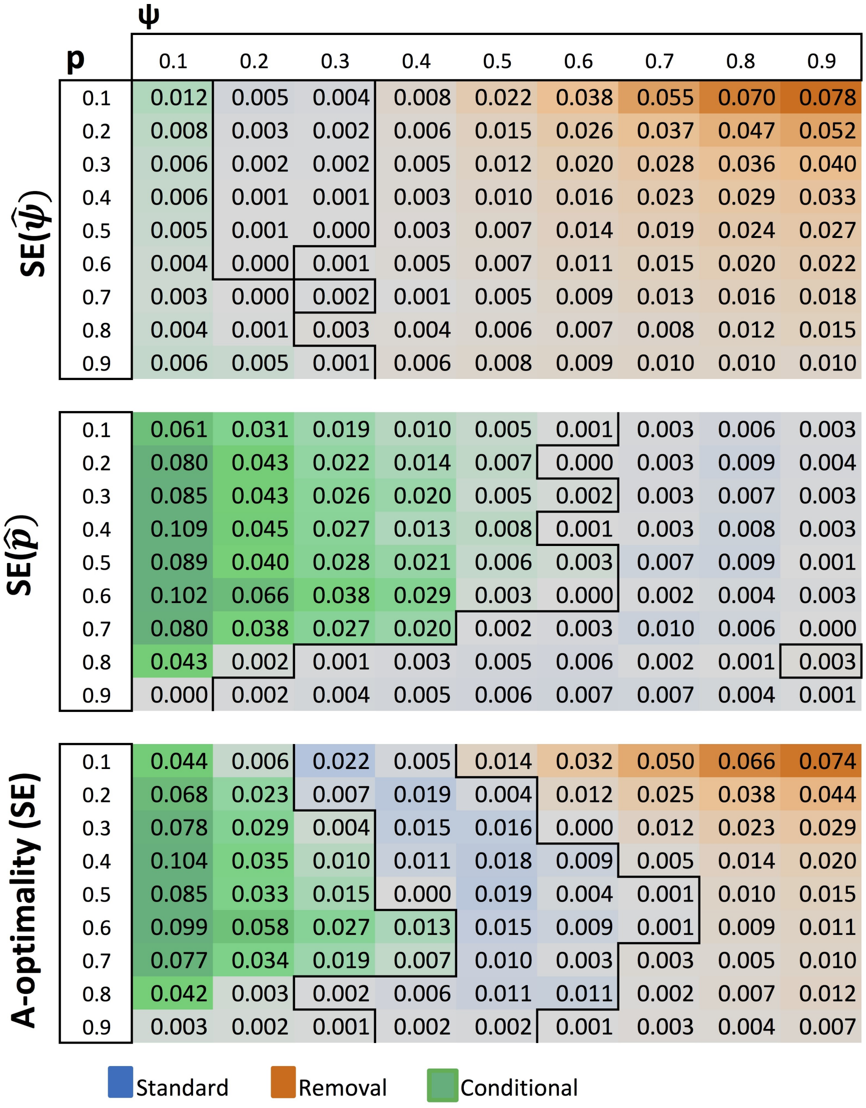


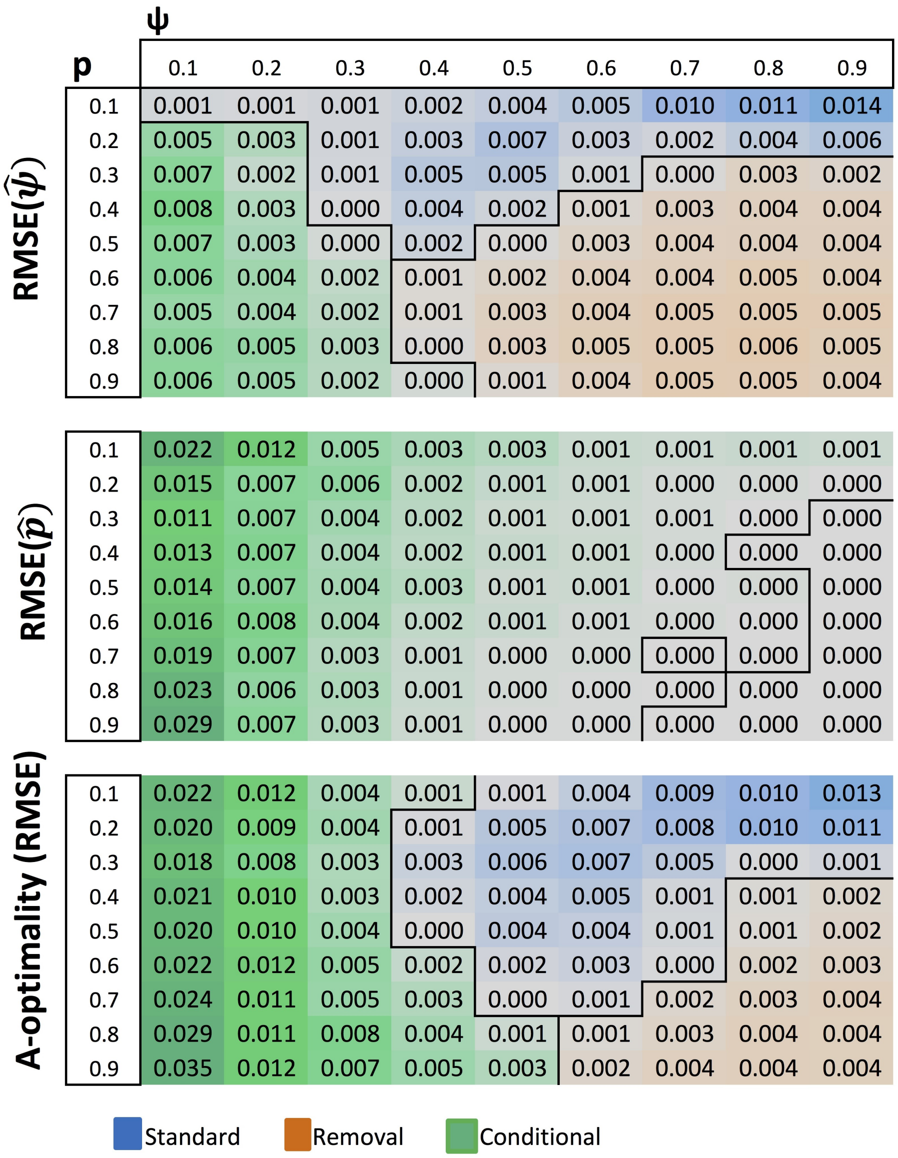
Fig. 2. The best performing method based on standard errors of occupancy estimates (top), detection estimates (middle) and A-optimality (SE($\hat{\psi}$)+SE($\hat{p}$), bottom) when each design was evaluated at its optimal number of visits (*K*) at total effort $E = 120$. Because variance is proportional to $1/E$, absolute differences between methods diminishes as effort increases, though proportional relationships remain constant. Lines delineate the best performing region of each method, but note that many of these differences were small. Colored gradients and values reflect the absolute improvement of the best method over the second best method, SE[1]-SE[2], where [1] is the best method and [2] is the second best method. Stronger shades represent a greater improvement in estimates. SE values for each method are provided in Appendix 2, Fig. S2.



	ψ p	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
SE($\hat{\psi}$)	0.1	0.012	0.005	0.004	0.008	0.022	0.038	0.055	0.070	0.078
	0.2	0.008	0.003	0.002	0.006	0.015	0.026	0.037	0.047	0.052
	0.3	0.006	0.002	0.002	0.005	0.012	0.020	0.028	0.036	0.040
	0.4	0.006	0.001	0.001	0.003	0.010	0.016	0.023	0.029	0.033
	0.5	0.005	0.001	0.000	0.003	0.007	0.014	0.019	0.024	0.027
	0.6	0.004	0.000	0.001	0.005	0.007	0.011	0.015	0.020	0.022
	0.7	0.003	0.000	0.002	0.001	0.005	0.009	0.013	0.016	0.018
	0.8	0.004	0.001	0.003	0.004	0.006	0.007	0.008	0.012	0.015
	0.9	0.006	0.005	0.001	0.006	0.008	0.009	0.010	0.010	0.010
SE($\hat{p}$)	0.1	0.061	0.031	0.019	0.010	0.005	0.001	0.003	0.006	0.003
	0.2	0.080	0.043	0.022	0.014	0.007	0.000	0.003	0.009	0.004
	0.3	0.085	0.043	0.026	0.020	0.005	0.002	0.003	0.007	0.003
	0.4	0.109	0.045	0.027	0.013	0.008	0.001	0.003	0.008	0.003
	0.5	0.089	0.040	0.028	0.021	0.006	0.003	0.007	0.009	0.001
	0.6	0.102	0.066	0.038	0.029	0.003	0.000	0.002	0.004	0.003
	0.7	0.080	0.038	0.027	0.020	0.002	0.003	0.010	0.006	0.000
	0.8	0.043	0.002	0.001	0.003	0.005	0.006	0.002	0.001	0.003
	0.9	0.000	0.002	0.004	0.005	0.006	0.007	0.007	0.004	0.001
A-optimality (SE)	0.1	0.044	0.006	0.022	0.005	0.014	0.032	0.050	0.066	0.074
	0.2	0.068	0.023	0.007	0.019	0.004	0.012	0.025	0.038	0.044
	0.3	0.078	0.029	0.004	0.015	0.016	0.000	0.012	0.023	0.029
	0.4	0.104	0.035	0.010	0.011	0.018	0.009	0.005	0.014	0.020
	0.5	0.085	0.033	0.015	0.000	0.019	0.004	0.001	0.010	0.015
	0.6	0.099	0.058	0.027	0.013	0.015	0.009	0.001	0.009	0.011
	0.7	0.077	0.034	0.019	0.007	0.010	0.003	0.003	0.005	0.010
	0.8	0.042	0.003	0.002	0.006	0.011	0.011	0.002	0.007	0.012
	0.9	0.003	0.002	0.001	0.002	0.002	0.001	0.003	0.004	0.007

🟦 Standard 🟧 Removal 🟩 Conditional

Fig. 3. The best performing method based on root mean squared error (RMSE) of ψ and p and A-optimality (RMSE($\hat{\psi}$)+RMSE($\hat{p}$)) across the parameter space defined by true detection (p) and occupancy (ψ) from simulations analyzed via MCMC. Components were averaged across all nine simulation conditions and replicates for each method (K=3,4 or 15; E=120, 420, or 1500). Lines delineate the best performing region of each method, while colored gradients and values reflect the absolute improvement of the best method over the next best method where stronger shades represent a greater improvement in estimates. RMSE values for each method are provided in Appendix 2, Fig. S4.



	ψ								
p	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
RMSE($\widehat{\psi}$)									
0.1	0.001	0.001	0.001	0.002	0.004	0.005	0.010	0.011	0.014
0.2	0.005	0.003	0.001	0.003	0.007	0.003	0.002	0.004	0.006
0.3	0.007	0.002	0.001	0.005	0.005	0.001	0.000	0.003	0.002
0.4	0.008	0.003	0.000	0.004	0.002	0.001	0.003	0.004	0.004
0.5	0.007	0.003	0.000	0.002	0.000	0.003	0.004	0.004	0.004
0.6	0.006	0.004	0.002	0.001	0.002	0.004	0.004	0.005	0.004
0.7	0.005	0.004	0.002	0.001	0.003	0.004	0.005	0.005	0.005
0.8	0.006	0.005	0.003	0.000	0.003	0.005	0.005	0.006	0.005
0.9	0.006	0.005	0.002	0.000	0.001	0.004	0.005	0.005	0.004
RMSE($\widehat{p}$)									
0.1	0.022	0.012	0.005	0.003	0.003	0.001	0.001	0.001	0.001
0.2	0.015	0.007	0.006	0.002	0.001	0.001	0.000	0.000	0.000
0.3	0.011	0.007	0.004	0.002	0.001	0.001	0.001	0.000	0.000
0.4	0.013	0.007	0.004	0.002	0.001	0.001	0.000	0.000	0.000
0.5	0.014	0.007	0.004	0.003	0.001	0.001	0.000	0.000	0.000
0.6	0.016	0.008	0.004	0.002	0.001	0.001	0.000	0.000	0.000
0.7	0.019	0.007	0.003	0.001	0.000	0.000	0.000	0.000	0.000
0.8	0.023	0.006	0.003	0.001	0.000	0.000	0.000	0.000	0.000
0.9	0.029	0.007	0.003	0.001	0.000	0.000	0.000	0.000	0.000
A-optimality (RMSE)									
0.1	0.022	0.012	0.004	0.001	0.001	0.004	0.009	0.010	0.013
0.2	0.020	0.009	0.004	0.001	0.005	0.007	0.008	0.010	0.011
0.3	0.018	0.008	0.003	0.003	0.006	0.007	0.005	0.000	0.001
0.4	0.021	0.010	0.003	0.002	0.004	0.005	0.001	0.001	0.002
0.5	0.020	0.010	0.004	0.000	0.004	0.004	0.001	0.001	0.002
0.6	0.022	0.012	0.005	0.002	0.002	0.003	0.000	0.002	0.003
0.7	0.024	0.011	0.005	0.003	0.000	0.001	0.002	0.003	0.004
0.8	0.029	0.011	0.008	0.004	0.001	0.001	0.003	0.004	0.004
0.9	0.035	0.012	0.007	0.005	0.003	0.002	0.004	0.004	0.004

🟦 Standard 🟧 Removal 🟩 Conditional

Literature Cited

Ackerman, J.T., 2002. Of mice and mallards: positive indirect effects of coexisting prey on waterfowl nest success. Oikos 99, 469–480.

Ahrestani, F.S., Saracco, J.F., Sauer, J.R., Pardieck, K.L., Royle, J.A., 2017. An integrated population model for bird monitoring in North America. Ecol. Appl. 27, 916–924.

Alisauskas, R.T., Ankney, C., 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl, in: Batt, B.D.., Afton, A., Anderson, M.G., Ankney, C., Johnson D, Kaldec, J., Krapu, G.L. (Eds.), The Ecology and Management of Breeding Waterfowl. University of Minnesota Press.

Amundson, C.L., Arnold, T.W., 2011. The role of predator removal, density-dependence, and environmental factors on mallard duckling survival in North Dakota. J. Wildl. Manage. 75, 1330–1339.

Amundson, C.L., Pieron, M.R., Arnold, T.W., Beaudoin, L.A., 2013. The effects of predator removal on mallard production and population change in northeastern North Dakota. J. Wildl. Manage. 77, 143–152.

Andres, B.A., Smith, P.A., Morrison, R.I.G., Gratto-Trevor, C.L., Brown, S.C., Friis, C.A., 2012. Population estimates of North American shorebirds, 2012. Wader Study Gr. Bull. 119, 178–194.

Andrewartha, H.G., Birch, C., 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.

Angelstam, P., Lindström, E., Widén, P., 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. Oecologia 62, 199–208. https://doi.org/10.1007/BF00379014

Anteau, M.J., 2012. Do interactions of land use and climate affect productivity of waterbirds and prairie-pothole wetlands? Wetlands 32, 1–9.

Arnold, T.W., Devries, J.H., Howerter, D.W., 2010. Factors that affect renesting in Mallards (Anas platyrhynchos). Auk 127, 212–221.

Askins, R.A., Chávez-Ramírez, F., Dale, B.C., Haas, C.A., Herkert, J.R., Knopf, F.L., Vickery, P., 2007. Conservation of Grassland Birds in North America : Understanding Ecological Processes in Different Regions. Ornithol. Monogr. 64, 1–46.

Bailey, L.L., Mackenzie, D.I., Nichols, J.D., 2014. Advances and applications of occupancy models. Methods Ecol. Evol. 5, 1269–1279.

Barbieri, M.M., Berger, J.O., 2004. Optimal predictive model selection. Ann. Stat. 32, 870–897.

Batt, B.D., Anderson, M.G., Anderson, C.D., Caswell, F.D., 1989. The use of prairie potholes by North American ducks, in: van der Valk, A. (Ed.), Northern Prairie Wetlands. Iowa State University Press, Ames, Iowa, USA, pp. 201–227.

Bates, D., Machler, M., Bolker, B.M., Walker, S.C., 2015. Fitting Linear Mixed-Effects Models using lme4. J. Stat. Softw. 67, 1–48.

Battin, J., 2004. When good animals love bad habitats: Ecological traps and the conservation of animal populations. Conserv. Biol.

Bayne, E.M., Habib, L., Boutin, S., 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. Conserv. Biol. 22, 1186–1193. Beauchamp, W.D., Koford, R.R., Nudds, T.D., Clark, R.G., Johnson, D.H., 1996. Long-Term Declines in Nest Success of Prairie Ducks. J. Wildl. Manage. 60, 247–257.

Beyer, H.L., Haydon, D.T., Morales, J.M., Frair, J.L., Hebblewhite, M., Mitchell, M., Matthiopoulos, J., 2010. The interpretation of habitat preference metrics under use-availability designs. Philos. Trans. R. Soc. B Biol. Sci. 365, 2245–2254.

Bibby, C.J., Burgess, N.D., Hill, D.A., 2000. Bird census techniques. 2nd Edition, Academic Press, London, UK.

Blas, J., Bortolotti, G.R., Tella, J.L., Baos, R., Marchant, T.A., 2007. Stress response during development predicts fitness in a wild, long lived vertebrate. Proc. Natl. Acad. Sci. 104, 8880–8884.

Blickley, J.L., Blackwood, D., Patricelli, G.L., 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of Greater Sage-Grouse at leks. Conserv. Biol. 26, 461–471.

Bloom, P.M., Clark, R.G., Howerter, D.W., Armstrong, L.M., 2013. Multi-scale habitat selection affects offspring survival in a precocial species. Oecologia 173, 1249–1259.

Bollinger, E.K., 1995. Succesional changes and habitat selection in successional hayfield bird communities. Auk 112, 720–730.

Bornand, C.N., Kéry, M., Bueche, L., Fischer, M., 2014. Hide-and-seek in vegetation: time-to-detection is an efficient design for estimating detectability and occurrence. Methods Ecol. Evol. 5, 433–442.

Bowen, B.S., Kruse, A.D., 1993. Effects of grazing on nesting by Upland Sandpipers in South-Central North-Dakota. J Wildl. Manag. 57, 291–301.

Brasher, M.G., Kaminski, R.M., Burger, L.W., 2002. Evaluation of indicated breeding pair criteria to estimate mallard breeding populations. J. Wildl. Manage. 66, 985–992.

Brook, R.W., Pasitschniak-Arts, M., Howerter, D.W., Messier, F., 2008. Influence of rodent abundance on nesting success of prairie waterfowl. Can. J. Zool. 86, 497–506.

Brown, J.H., Mehlman, D.W., Stevens, G.C., 1995. Spatial variation in abundance. Ecology 76, 2028–2043.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach, Ecological Modelling. Springer, Fort Collins, USA.

Burr, P.C., Robinson, A.C., Larsen, R.T., Newman, R.A., Ellis-Felege, S.N., 2017. Sharp-tailed grouse nest survival and nest predator habitat use in North Dakota's Bakken oil field. PLoS One 12.

Clark, R. G., Fleskes, J. P., Guyn, K. L., Haukos, D. A., Austin, J. E., Miller, M. R., 2014. Northern Pintail (Anas acuta), version 2.0. In The Birds of North America (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi-org.ezp1.lib.umn.edu/10.2173/bna.163

Clare, J.D.J., Anderson, E.M., MacFarland, D.M., 2015. Predicting bobcat abundance at a landscape scale and evaluating occupancy as a density index in central Wisconsin. J. Wildl. Manage. 79, 469–480.

Clark, R.G., Shutler, D., 1999. Avian habitat selection: Pattern from process in nest-site use by ducks? Ecology 80, 272–287.

Cochran, J.F., Anderson, S.H., 1987. Comparison of habitat attributes at sites of stable and declining long-billed curlew populations. Gt. Basin Nat. 47, 459–466.

Colwell, M. A., Jehl Jr., J. R., 1994. Wilson's Phalarope (Phalaropus tricolor), version 2.0. In The Birds of North America (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi-org.ezp1.lib.umn.edu/10.2173/bna.83

Colwell, M.A., Oring, L.W., 1988. Breeding biology of Wilson's phalarope in southcentral Saskatchewan. Wilson Bull. 100, 567–582.

Colwell, M.A., Oring, L.W., 1988. Habitat use by breeding and migrating shorebirds in southcentral Saskatchewan. Wilson Bull. 100, 554–566.

Conn, P.B., Johnson, D.S., Ver Hoef, J.M., Hooten, M.B., London, J.M., Boveng, P.L., 2015. Using spatiotemporal statistical models to estimate animal abundance and infer ecological dynamics from survey counts. Ecol. Monogr. 85, 235-252.

Cowardin, L.M., Carter, V., Golet, F.C., LaRoe, E.T., 1979. Classification of wetlands and deepwater habitats of the United States, FGDC-STD-004-2013. Second Edition.

Cox, R.R., Hanson, M.A., Roy, C.C., Euliss, N.H., Johnson, D.H., Butler, M.G., 1998. Mallard duckling growth and survival in relation to aquatic invertebrates. J. Wildl. Manage. 62, 124-133.

Creuzer, J., Hargiss, C.L.M., Norland, J.E., DeSutter, T., Casey, F.X., DeKeyser, E.S., Ell, M., 2016. Does increased road dust due to energy development impact wetlands in the Bakken Region? Water, Air, Soil Pollut. 227, 39.

Cunningham, M.A., Johnson, D.H., 2006. Proximate and landscape factors influence grassland bird distributions. Ecol. Appl. 16, 1062–1075.

Dai, A., Trenberth, K.E., Qian, T., 2004. A global dataset of Palmer Drought Severity Index for 1870–2002: Relationship with soil moisture and effects of surface warming. J. Hydrometeorol. 5, 1117–1130.

Davis, S.K., 2004. Area sensitivity in grassland passerines: Effects of patch size, patch shape, and vegetation structure on bird abundance and occurrence in Southern Saskatchewan. Auk 121, 1130–1145.

Dechant, J., Sondreal, M., Johnson, D., Igl, L., Goldade, C., Nenneman, M., Euliss, B., 2001. Effects of management practices on grassland birds: Marbled Godwit. Northern Prairie Wildlife Research Center, Jamestown, ND, USA.

Desante, D.F., O'grady, D.R., Pyle, P., 1999. Measures of productivity and survival derived from standardized mist-netting are consistent with observed population changes. Bird Study 46, S178–S188.

Devries, J.H., 2014. Fitness consequences of avian habitat selection in dynamic landscapes: multi-scale evalutations in Northern Pintails. PhD Dissertation, University of Saskatchewan. https://ecommons.usask.ca/handle/10388/ETD-2014-10-1788.

Dieter, C., Murano, R. & Galster, D., 2009. Capture and mortality rates of ducks in selected trap types. J. Wildl. Manage.73, 1223–1228.

Dinsmore, S.J., Dinsmore, J.J., 2007. Modeling avian nest survival in Program MARK. Stud. Avian Biol. 34, 73–83.

Dorazio, R.M., Kéry, M., Royle, J.A., Plattner, M., 2010. Models for inference in dynamic metacommunity systems. Ecology 91, 2466–2475.

Dreitz, V.J., 2009. Parental behaviour of a precocial species: Implications for juvenile survival. J. Appl. Ecol. 46, 870–878.

Dubovsky, J.A., 2017. Central Flyway harvest and population survey data book 2017. U.S. Fish and Wildlife Service, Lakewood CO.

Duebbert, H.F., Kantrud, H.A., 1987. Use of no-till winter wheat by nesting ducks in North Dakota. J. Soil Water Conserv. 42, 50–53.

Dunn, E., Hussell, D., Adams, R., 2004. An investigation of productivity indices derived from banding of fall migrants. Stud. Avian Biol. 29, 92–96.

Durso, A.M., Willson, J.D., Winne, C.T., 2011. Needles in haystacks: Estimating detection probability and occupancy of rare and cryptic snakes. Biol. Conserv. 144, 1508–1515.

Elmberg, J., Nummi, P., Pöysä, H., Sjöberg, K., 2003. Breeding success of sympatric dabbling ducks in relation to population density and food resources. Oikos 100, 333–341.

Emery, R.B., Howerter, D.W., Armstrong, L.M., Anderson, M.G., Devries, J.H., Joynt, B.L., 2005. Seasonal variation in waterfowl nesting success and its relation to cover management in the Canadian prairies. J. Wildl. Manage. 69, 1181–1193.

Environmental Systems Research Institute (ESRI). 2018. ArcGIS Release 10.6. Redlands, CA.

Etterson, M.A., Bennett, R.S., Kershner, E.L, & Walk, J.W. 2009., Markov chain estimation of avian seasonal fecundity. Ecological Applications, 19, 622-630.

Farmer, A.M., 1993. The effects of dust on vegetation - a review. Environ. Pollut. 79, 63–75.

Fiske, I., Chandler, R., 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software. J. Stat. Softw. 43, 1–23.

Forman, R., Sperling, D., Bissonette, J., Clevenger, A.P., Cutshall, C., Dale, V., Fahrig, L., France, R., Goldman, C., Heanue, K., Jones, J., Swanson, F., Turrentine, T., Winter, T., 2003. Road ecology: science and solutions. Island Press, Washington, DC.

Francis, C.D., Paritsis, J., Ortega, C.P., Cruz, A., 2011. Landscape patterns of avian habitat use and nest success are affected by chronic gas well compressor noise. Landsc. Ecol. 26, 1269–1280.

Fuhlendorf, S.D., Harrell, W.C., Engle, D.M., Hamilton, R.G., Davis, C.A., Leslie, D.M., 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecol. Appl. 16, 1706–1716.

Galbraith, H., 1988. Effects of agriculture on the breeding ecology of Lapwings Vanellus vanellus. J. Appl. Ecol. 25, 487–503.

Garvey, M.E., Nol, E., Howerter, D.W., Armstrong, L.M., 2013. A spatial analysis of factors affecting nesting success of shorebirds in the Canadian prairies. Condor 115, 58–66.

Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. Stat. Sci. 7, 457–511.

Gleason, R., Euliss, N.H., Hubbard, D.E., Duffy, W.G., 2003. Effects of sediment load on emergence of aquatic invertebrates and plants from wetland soil egg and seed banks. Wetlands 23, 26–34.

Gleason, R., Tangen, B.A., 2014. Brine contamination to aquatic resources from oil and gas development in the Williston Basin, United States: U.S. Geological Survey Scientific Investigations Report 2014–5017, 127 p., http://dx.doi.org/10.3133/sir20145017.

Goodman, P.S., Galatioto, F., Thorpe, N., Namdeo, A.K., Davies, R.J., Bird, R.N., 2016. Investigating the traffic-related environmental impacts of hydraulic-fracturing (fracking) operations. Environ. Int. 89–90, 248–260.

Granfors, D.., 2009. Expert Model for Marbled Godwit Landscapes (v.2) [WWW Document]. USFWS Habitat Popul. Eval. Team. URL <http://www.fws.gov/midwest/hapet/GodwitModel.htm

Granfors, D., Niemuth, N.D., 2005. Prairie Potholes Joint Venture 2005 Implementation Plan Section III- Shorebird Plan.

Grant, T. a, Madden, E., Berkey, G.B., 2004. Tree and shrub invasion in northern mixed grass prairie: implications for breeding grassland birds. Wildl. Soc. Bull. 32, 807–818.

Gratto-Trevor, C. L., 2000. Marbled Godwit (Limosa fedoa), version 2.0. In The Birds of North America (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi-org.ezp1.lib.umn.edu/10.2173/bna.492

Gratto-Trevor, C.L., 2006. Upland nesting Prairie shorebirds: use of managed wetland basins and accuracy of breeding surveys. Avian Conserv. Ecol. Conserv. des oiseaux 1, 2.

Gratto-Trevor, C.L., 2011. Connectivity in Willets and Marbled Godwits breeding in western Canada. Wader Study Gr. Bull. 118, 55–57.

Greenwood, R., Newton, W., Pearson, G., Schamber, G., 1997. Population and movement characteristics of radio-collared striped skunks in North Dakota during an epizootic of rabies. J. Wildl. Dis. 33, 226–241.

Greenwood, R.J., Sargeant, A.B., Johnson, D.H., Cowardin, L.M., Shaffer, T.L., 1995. Factors associated with duck nest success in the Prairie Pothole Region of Canada. Wildl. Monogr. 128, 1–57.

Guillera-Arroita, G., 2016. Modelling of species distributions, range dynamics and communities under imperfect detection: Advances, challenges and opportunities. Ecography. 40, 281–295.

Guillera-Arroita, G., Lahoz-Monfort, J.J., MacKenzie, D.I., Wintle, B.A., McCarthy, M.A., 2014. Ignoring imperfect detection in biological surveys is dangerous: A response to "fitting and interpreting occupancy models." PLoS One 9, e99571.

Guillera-Arroita, G., Ridout, M.S., Morgan, B.J.T., 2010. Design of occupancy studies with imperfect detection. Methods Ecol. Evol. 1, 131–139.

Gunnarsson, G., Elmberg, J., Pöysä, H., Nummi, P., Sjöberg, K., Dessborn, L., Arzel, C., 2013. Density dependence in ducks: A review of the evidence. Eur. J. Wildl. Res. 3, 305-321.

Gurnell, J., Wauters, L.A., Lurz, P.W.W., Tosi, G., 2004. Alien species and interspecific competition: Effects of introduced eastern grey squirrels on red squirrel population dynamics. J. Anim. Ecol. 73, 26–35.

Guyn, K.L., Clark, R.G., 2000. Nesting effort of Northern Pintails in Alberta. Condor 102, 619–628.

Henle, K., Davies, K.F., Kleyer, M., Margules, C., Settele, J., 2004. Predictors of species sensitivity to fragmentation. Biodivers. Conserv. 13, 207–251.

Higgins, K.F., 1977. Duck nesting in intensively farmed areas of North Dakota. J. Wildl. Manage. 41, 232–242.

Higgins, K.F., Kirsch, L.M., Ryan, M.R., Renken, R.B., 1979. Some ecological aspects of Marbled Godwits and Willets in North Dakota. Prairie Nat. 11, 115–118.

Hines, J.E. & Mackenzie, D.I., 2004. Presence. USGS Patuxent Wildlife Research Center, Patuxent, Maryland. URL http://www.mbr-pwrc.usgs.gov/software/presence.html [accessed 24 October 2016]

Hines, J.E., Nichols, J.D., Royle, J.A., Mackenzie, D.I., Gopalaswamy, A.M., Kumar, N.S., Karanth, K.U., 2010. Tigers on trails: Occupancy modeling for cluster sampling. Ecol. Appl. 20, 1456–1466.

Horn, D.J., Phillips, M.L., Koford, R.R., Clark, W.R., Sovada, M.A., Greenwood, R.J., 2005. Landscape composition, patch size, and distance to edges: Interactions affecting duck reproductive success. Ecol. Appl. 15, 1367–1376.

Howerter, D.W., Anderson, M.G., Devries, J.H., Joynt, B.L., Armstrong, L.M., Emery, R.B., Arnold, T.W., 2014. Variation in mallard vital rates in Canadian Aspen Parklands: The Prairie Habitat Joint Venture assessment. Wildl. Monogr. 188,1-37.

Hussell, D., 2004. Determining productivity indices from age composition of migrants captured for banding: problems and possible solutions. Stud. Avian Biol. 29, 82–91.

Johnson, C.J., Nielsen, S.E., Merrill, E.H., McDonald, T.L., Boyce, M.S., 2006. Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. J. Wildl. Manage. 70, 347–357.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71.

Johnson, D.H., Haseltine, S.D., Cowardin, L.M., 1994. Wildlife habitat management on the Northern prairie landscape. Landsc. Urban Plan. 28, 5–21.

Johnson, D.H., Sparling, D.W., Cowardin, L.M., 1987. A model of the productivity of the mallard duck. Ecol. Modell. 38, 257–275.

Johnson, P.C.D., 2014. Extension of Nakagawa & Schielzeth's R2GLMM to random slopes models. Methods Ecol. Evol. 5, 944–946.

Johnson, W.C., Werner, B., Guntenspergen, G.R., Voldseth, R. a., Millett, B., Naugle, D.E., Tulbure, M., Carroll, R.W.H., Tracy, J., Olawsky, C., 2010. Prairie wetland complexes as landscape functional units in a changing climate. Bioscience 60, 128–140.

Johnston, C.A., 2013. Wetland losses due to row crop expansion in the Dakota prairie pothole region. Wetlands 33, 175–182.

Johnston, C.A., 2014. Agricultural expansion: Land use shell game in the U.S. Northern Plains. Landsc. Ecol. 29, 81–95.

Kantrud, H.A., Higgins, K.F., 1992. Nest and nest site characteristics of same ground-nesting, non-passerine birds of Northern Grasslands. Prairie Nat. 24, 67–84.

Kendall, W.L., Hines, J.E., Nichols, J.D. & Grant, E.H.C., 2013. Relaxing the closure assumption in occupancy models: Staggered arrival and departure times. Ecology 94, 610–617.

Kéry, M., 2010. Introduction to WinBUGS for Ecologists. pp.237-251. Elsevier, Amsterdam.

Kight, C.R., Saha, M.S., Swaddle, J.P., 2012. Anthropogenic noise is associated with reductions in the productivity of breeding Eastern Bluebirds (Sialia sialis). Ecol. Appl. 22, 1989–1996.

Klett, A.T., Duebbert, H.F., Faanes, C.A., Higgins, K.F., 1986. Techniques for studying nest success in upland habitats in the Prairie Pothole Region. United States Dep. Inter. Fish Wildl. Serv. Resour. Publ. 158, 1–24.

Klett, A.T., Johnson, D.H., 1982. Variability in nest survival rates and implications to nesting studies. Auk 99, 77–87.

Knape, J., Korner-Nievergelt, F., 2016. On assumptions behind estimates of abundance from counts at multiple sites. Methods Ecol. Evol. 7, 206–209.

Kociolek, A. V., Clevenger, A.P., St. Clair, C.C., Proppe, D.S., 2011. Effects of road networks on bird populations. Conserv. Biol. 25, 241–249.

Koper, N., Schmiegelow, F., 2007. Does management for duck productivity affect songbird nesting success? J. Wildl. Manage. 71, 2249-2257.

Krapu, G.L., Pietz, P.J., Brandt, D.A., Cox, R.R., 2000. Factors limiting mallard brood survival in prairie pothole landscapes. J. Wildl. Manage. 64, 553–561.

Krapu, G.L., Pietz, P.J., Brandt, D., Cox Jr, R.R., 2004. Does presence of permanent fresh water affect recruitment in prairie-nesting dabbling ducks? J. Wildl. Manage. 68, 332–341.

Krapu, G.L., Reynolds, R.E., Sargeant, A.B., Renner, R.W., 2004. Patterns of variation in clutch sizes in a guild of temperate nesting dabbling ducks. Auk 121, 695–706.

Kruse, A.D., Bowen, B.S., 1996. Effects of grazing and burning on densities and habitats of breeding ducks in North Dakota. J. Wildl. Manage. 60, 233–246.

Kruse, K.L., Sharp, D.E., Ladd, W.N., Moser, T.J., Bublitz, E.A., 2004. Central Flyway waterfowl hunting and harvest survey information, 1961-2001. Denver, CO.

La Pierre, K.J., Blumenthal, D.M., Brown, C.S., Klein, J.A., Smith, M.D., 2016. Drivers of Variation in Aboveground Net Primary Productivity and Plant Community Composition Differ Across a Broad Precipitation Gradient. Ecosystems 19, 521–533.

Lack, D., 1954. The Significance of Migration in: The natural regulation of animal numbers. Oxford Clarenden Press.

Lele, S.R., Moreno, M., Bayne, E., 2012. Dealing with detection error in site occupancy surveys: What can we do with a single survey? J. Plant Ecol. 5, 22–31.

Liebezeit, J.R., Kendall, S.J., Brown, S., Johnson, C.B., Martin, P., McDonald, T.L., Payer, D.C., Rea, C.L., Streever, B., Wildman, A.M., Zack, S., 2009. Influence of human development and predators on nest survival of tundra birds, Arctic Coastal Plain, Alaska. Ecol. Appl. 19, 1628–1644.

Liebezeit, J.R., Smith, P.A., Lanctot, R.B., Schekkerman, H., Kendall, S.J., Tracy, D.M., Rodrigues, R.J., Meltofte, H., Robinson, J.A., Gratto-Trevor, C., McCaffery, B.J., Morse, J., Zack, S.W., 2007. Assessing the development of shorebird eggs using the flotation method: species-specific and generalized regression models. Condor 109, 32–47.

Linkie, M., Dinata, Y., Nugroho, A., Haidir, I.A., 2007. Estimating occupancy of a data deficient mammalian species living in tropical rainforests: Sun bears in the Kerinci Seblat region, Sumatra. Biol. Conserv. 137, 20–27.

Loesch, C.R., Walker, J.A., Reynolds, R.E., Gleason, J.S., Niemuth, N.D., Stephens, S.E., Erickson, M.A., 2013. Effect of wind energy development on breeding duck densities in the Prairie Pothole Region. J. Wildl. Manage. 77, 587–598.

Lowther, P. E., H. D. Douglas III, and C. L. Gratto-Trevor, 2001. Willet (Tringa semipalmata), version 2.0. In The Birds of North America (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi-org.ezp1.lib.umn.edu/10.2173/bna.579

Ludlow, S.M., Brigham, R.M., Davis, S.K., 2015. Oil and natural gas development has mixed effects on the density and reproductive success of grassland songbirds. Condor 117, 64–75.

Ludlow, S.M., Davis, S.K., 2018. Oil and natural gas development influence nest-site selection and nest survival of upland-nesting waterfowl and shorebirds. Wildl. Soc. Bull. doi: 10.1002/wsb.849.

Lukacs, P.M., Dreitz, V.J., Knopf, F.L., Burnham, K.P., 2004. Estimating survival probabilities of unmarked dependent young when detection is imperfect. Condor 106, 926–931.

Lyon, A.G., Anderson, S.H., 2003. Potential gas development impacts on sage grouse nest initiation and movement. Wildl. Soc. Bull. 31, 486–491.

Mabee, T.J., 1997. Using eggshell evidence to determine nest fate of shorebirds. Wilson Bull. 109, 307–313.

Mabee, T.J., Wildman, A.M., Johnson, C.B., 2006. Using egg flotation and eggshell evidence to determine age and fate of Arctic shorebird nests. J. F. Ornithol. 77, 163–172.

MacKenzie, D.I., Bailey, L.L., 2004. Assessing the fit of site-occupancy models. J. Agric. Biol. Environ. Stat. 9, 300–318.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84, 2200–2207.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, A.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248–2255.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollack, K.H., Bailey, L.L., Hines, J.E., 2006. Occupancy Estimation and Modeling. pp. 324. Elsevier Science, London, UK.

MacKenzie, D.I., Nichols, J.D., Sutton, N., Kawanishi, K., Bailey, L.L., 2005. Improving inferences in population studies of rare species that are detected imperfectly. Ecology 86, 1101–1113.

Mackenzie, D.I., Royle, J.A., 2005. Designing occupancy studies: General advice and allocating survey effort. J. Appl. Ecol. 45, 1105-1114.

Marsett, R.C., Qi, J., Heilman, P., Biedenbender, S.H., Watson, M.C., Amer, S., Weltz, M., Goodrich, D., Marsett, R., 2006. Remote sensing for grassland management in the arid Southwest. Rangel. Ecol. Manag. 59, 530–540.

Marzluff, J.M., 2001. Worldwide urbanization and its effects on birds, in: Avian Ecology and Conservation in an Urbanizing World. pp. 19–47. Springer Science, New York, USA.

Mason, J., 2012. Bakken's maximum potential oil production explored. Oil Gas J. 110, i4.

Mazerolle, D.F., Dufour, K.W., Hobson, K.A., Den Haan, H.E., 2005. Effects of large-scale climatic fluctuations on survival and production of young in a Neotropical migrant songbird, the yellow warbler Dendroica petechia. J. Avian Biol. 36, 155–163.

McMaster, D.G., Devries, J.H., Davis, S.K., 2005. Grassland birds nesting in haylands of southern Saskatchewan: landscape influences and conservation priorities. J. Wildl. Manage. 69, 211–221.

McPeek, M.A., Rodenhouse, N.L., Holmes, R.T., Sherry, T.W., 2001. A general model of site-dependent population regulation: population-level regulation without individual-level interactions. Oikos 94, 417–424.

Miller, M., Duncan, D., 1999. The Northern Pintail in North America: Status and conservation needs of a struggling population. Wildl. Soc. Bull. 27, 788–800.

Mineau, P., Whiteside, M., 2013. Pesticide acute toxicity is a better correlate of U.S. grassland bird declines than agricultural intensification. PLoS One 8, e57457.

Mong, T.W., 2005. Using radio-telemetry to determine range and resource requirements of upland sandpipers at an experimentally managed prairie landscape. Kansas State University.

Nail, K.R., Stenoien, C., Oberhauser, K.S., 2015. Immature monarch survival: Effects of site characteristics, density, and time. Ann. Entomol. Soc. Am. 108, 680–690.

Naugle, D.E., Johnson, R.R., Estey, M.E., Higgins, K.F., 2001. A landscape approach to conserving wetland bird habitat in the prairie pothole region of eastern South Dakota. Wetlands. 20, 588-604.

Nenninger, H., Koper, N., 2018. Effects of conventional oil wells on grassland songbird abundance are caused by presence of infrastructure, not noise. Biol. Conserv. 218, 124–133.

Nichols, J.D., Runge, M.C., Johnson, F.A., Williams, B.K., 2007. Adaptive harvest management of North American waterfowl populations: A brief history and future prospects. J. Ornithol. 148, 343-349.

Niemuth, N.D., Estey, M.E., Fields, S.P., Wangler, B., Bishop, A.A., Moore, P.J., Grosse, R.C., Ryba, A.J., 2017. Developing spatial models to guide conservation of grassland birds in the U.S. Northern Great Plains. Condor 119, 506–525.

Niemuth, N.D., Estey, M.E., Reynolds, R.E., 2012. Factors influencing presence and detection of breeding shorebirds in the Prairie Pothole Region of North Dakota, South Dakota, and Montana, USA. Wader Study Gr. Bull. 119, 37–45.

Niemuth, N.D., Fleming, K.K., Reynolds, R.E., 2014. Waterfowl conservation in the US prairie pothole region: Confronting the complexities of climate change. PLoS One 9, e100034.

Niemuth, N.D., Reynolds, R.E., Granfors, D.A., Johnson, R.R., Wangler, B., Estey, M.E., 2009. Landscape-level planning for conservation of wetland birds in the U.S. Prairie Pothole Region, in: Models for Planning Wildlife Conservation in Large Landscapes. pp. 533–560. Academic Press, London, UK.

Niemuth, N.D., Solberg, J.W., 2003. Response of waterbirds to number of wetlands in the Prairie Pothole Region of North Dakota , U.S.A. Waterbirds 26, 233–238.

Niemuth, N.D., Walker, J., Gleason, J.S., Loesch, C.R., Reynolds, R.E., Stephens, S.E., Erickson, M. ., 2013. Influence of wind turbines on presence of Willet, Marbled

Godwit, Wilson’s Phalarope and Black Tern on wetlands in the Prairie Pothole Region of North Dakota and South Dakota. Waterbirds 36, 263–276.

Nolet, B.A., Bauer, S., Feige, N., Kokorev, Y.I., Popov, I.Y., Ebbinge, B.S., 2013. Faltering lemming cycles reduce productivity and population size of a migratory Arctic goose species. J. Anim. Ecol. 82, 804–813.

North American Breeding Bird Survey - Canadian Trends Website, Data-version 2015, 2017. Gatineau, Quebec, K1A 0H3.

North Dakota Department of Transportation, 2016. North Dakota Transportation Handbook.

North Dakota Industrial Commission, 2015. Well Data. Accessed 16 May 2015. https://www.dmr.nd.gov/OaGIMS/viewer.htm

North Dakota Industrial Commission, 2017. Monthly statistical update. Accessed 15 Dec 2017. https://www.dmr.nd.gov/oilgas/stats/statisticsvw.asp

Northrup, J.M., Hooten, M.B., Anderson, C.R., Wittemyer, G., 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. Ecology 94, 1456–1463.

Noss, R.F., LaRoe III, E.T., Scott, J.M., 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Biol. Rep. 28, pp. 83.

O’Hara, R.B., Sillanpää, M.J., 2009. A review of Bayesian variable selection methods: what, how and which. Bayesian Anal. 4, 85–117.

Osnas, E.E., Runge, M.C., Mattsson, B.J., Austin, J., Boomer, G.S., Clark, R.G., Devers, P., Eadie, J.M., Lonsdorf, E. V., Tavernia, B.G., 2014. Managing harvest and habitat as integrated components. Wildfowl. Ecol. Modell. 225, 146-158.

Pacifici, K., Dorazio, R.M., Conroy, M.J., 2012. A two-phase sampling design for increasing detections of rare species in occupancy surveys. Methods Ecol. Evol. 3, 721–730.

Pagano, A.M., Arnold, T.W., 2009a. Detection probabilities for ground-based breeding waterfowl surveys. J. Wildl. Manage. 73, 392–398.

Pagano, A.M., Arnold, T.W., 2009b. Estimating detection probabilities of waterfowl broods from ground-based surveys. J. Wildl. Manage. 73, 686–694.

Pampush, G.J., Anthony, R.G., 1993. Nest success, habitat utilization and nest-site selection of long-billed Curlews in the Columbia Basin, Oregon. Condor 95, 957–967.

Pardieck, K.L., Ziolkowski Jr., D.J., Lutmerding, M., Campbell, K., Hudson, M.-A.R., 2017. North American Breeding Bird Survey Dataset 1966 - 2016, version 2016.

Pasitschniak-Arts, M., Clark, R.G., Messier, F., 1998. Duck nesting success in a fragmented prairie landscape: Is edge effect important? Biol. Conserv. 85, 55–62.

Paton, R.S., Matthiopoulos, J., 2016. Defining the scale of habitat availability for models of habitat selection. Ecology 97, 1113–1122.

Peach, W.J., Buckland, S.T., Baillie, S.R., 1996. The use of constant effort mist-netting to measure between-year changes in the abundance and productivity of common passerines. Bird Study 43, 142–156.

Peterjohn, B.G., Sauer, J.R., 1999. Population status of North American grassland birds from the North American Breeding Bird Survey, 1966-1996. Stud. Avian Biol. 19, 27–44.

Pfister, C.A., 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. Proc. Natl. Acad. Sci. 95, 213–218.

Phillips, M.M.L., Clark, W.R.W., Sovada, M.A., Horn, D.J., Koford, R.R., Greenwood, R.J., 2003. Predator selection of prairie landscape features and its relation to duck nest success. J. Wildl. Manage. 67, 104–114.

Pilliod, D.S., Goldberg, C.S., Arkle, R.S., Waits, L.P., Richardson, J., 2013. Estimating occupancy and abundance of stream amphibians using environmental DNA from filtered water samples. Can. J. Fish. Aquat. Sci. 70, 1123–1130.

Plummer, M., 2005. JAGS: just another Gibbs sampler, in: Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003).

Poulin, R., Wellicome, T., Todd, L., 2001. Synchronous and delayed numerical responses of a predatory bird community to a vole outbreak on the Canadian prairies. J. Raptor Res. 35, 288–295.

Preston, T.M., Kim, K., 2016. Land cover changes associated with recent energy development in the Williston Basin; Northern Great Plains, USA. Sci. Total Environ. 566–567, 1511–1518.

Preston, T.M., Ray, A.M., 2016. Effects of energy development on wetland plants and macroinvertebrate communities in Prairie Pothole Region wetlands. J. Freshw. Ecol. 1–6.

R Development Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna. URL http://www.R-project.org [accessed 24 October 2016]

Raquel, A.J., Devries, J.H., Howerter, D.W., Alisauskas, R.T., Leach, S.W., Clark, R.G., 2016. Timing of nesting of upland-nesting ducks in the Canadian prairies and its relation to spring wetland conditions. Can. J. Zool. 94, 575-581.

Reid, J.M., Cresswell, W., Holt, S., Mellanby, R.J., Whitfield, D.P., Ruxton, G.D., 2002. Nest scrape design and clutch heat loss in Pectoral Sandpipers (Calidris melanotos). Funct. Ecol. 16, 305–312.

Renfrew, R.B., Ribic, C. a, Nack, J.L., 2005. Edge avoidance by nesting grassland birds: a futile strategy in a fragmented landscape. Auk 122, 618–636.

Reynolds, R.E., Shaffer, T.L., Loesch, C.R., Cox Jr., R.R., 2006. The Farm Bill and duck production in the Prairie Pothole Region: Increasing the benefits. Wildl. Soc. Bull. 34, 963–974.

Reynolds, R.E., Shaffer, T.L., Renner, R.W., Newton, W.E., Batt, B.D., 2001. Impact of the Conservation Reserve Program on duck recruitment in the U.S. Prairie Pothole Region. J. Wildl. Manage. 65, 765–780.

Richmond, O.M.W., Hines, J.E., Beissinger, S.R., 2010. Two-species occupancy models: A new parameterization applied to co-occurrence of secretive rails. Ecol. Appl. 20, 2036–2046.

Riddle, J.D., Mordecai, R.S., Pollock, K.H., Simons, T.R., 2010. Effects of prior detections on estimates of detection probability, abundance, and occupancy. Auk 127, 94–99.

Royle, J.A., 2006. Site occupancy models with heterogeneous detection probabilities. Biometrics 62, 97–102.

Royle, J.A., 2004. Modeling abundance index data from anuran calling surveys. Conserv. Biol. 18, 1378-1385.

Royle, J., Dorazio, R., 2009. Hierarchical modeling and inference in ecology, hierarchical modeling and inference in ecology. pp.808 Academic Press, London, UK.

Royle, J.A., Link, W.A., 2006. Generalized site occupancy models allowing for false positive and false negative errors. Ecology 87, 835–841.

Runge, M.C., Johnson, F. a, Anderson, M.G., Koneff, M.D., Reed, E.T., Mott, S.E., 2006. The need for coherence between waterfowl harvest and habitat management. Wildl. Soc. Bull. 34, 1231–1237.

Ruthrauff, D.R., McCaffery, B.J., 2005. Survival of Western Sandpiper broods on the Yukon-Kuskokwim Delta, Alaska. Condor 107, 597–604.

Ryan, M., Renken, R.B., 1987. Habitat use by breeding Willets in the Northern Great Plains. Wilson Bull 99, 175–189.

Ryan, M.R., Renken, R.B., Dinsmore, J., 1984. Marbled Godwit habitat selection in the Northern Prairie Region. J. Wildl. Manage. 48, 1206–1218.

Samson, F.B., Knopf, F.L., Ostlie, W.R., 2004. Great Plains ecosystems: past, present, and future. Wildl. Soc. Bull. 32, 6–15.

Saracco, J.F., Andrew Royle, J., DeSante, D.F., Gardner, B., 2010. Modeling spatial variation in avian survival and residency probabilities. Ecology 91, 1885–1891.

Sauer, J.R., Niven, D.K., Hines, J.E., Fallon, J.E., Pardieck, K.L., Ziolkowski Jr., D.J., Link, W.A., 2017. The North American Breeding Bird Survey, Results and Analysis 1966 -2015. Version 2.07.2017, USGS Patuxent Wildlife Research Center, Laurel, MD.

Schlaepfer, M.A., Runge, M.C., Sherman, P.W., 2002. Ecological and evolutionary traps. Trends Ecol. Evol. 17, 474-480.

Schmidt, K.A., 1999. Foraging theory as a conceptual framework for studying nest predation. Oikos 85, 151–160.

Schmutz, J.K., Hungle, D.J., 1989. Populations of ferruginous and Swainson's hawks increase in synchrony with ground squirrels. Can. J. Zool. 67, 2596–2601.

Schroeder, J., Nakagawa, S., Cleasby, I.R., Burke, T., 2012. Passerine birds breeding under chronic noise experience reduced fitness. PLoS One 7, e39200.

Shaffer, J.A., Buhl, D.A., 2016. Effects of wind-energy facilities on breeding grassland bird distributions. Conserv. Biol. 30, 59–71.

Sidie-Slettedahl, A.M., Jensen, K.C., Johnson, R.R., Arnold, T.W., Austin, J.E., Stafford, J.D., 2015. Evaluation of autonomous recording units for detecting three species of secretive marsh birds. Wildl. Soc. Bull. 39, 626–634.

Sinclair, A.R.E., Pech, R.P., 1996. Density dependence, stochasticity, compensation and predator regulation. Oikos 75, 164–173.

Skrade, P.D.B., Dinsmore, S.J., 2013. Egg crypsis in a ground-nesting shorebird influences nest survival. Ecosphere 4, 1-9.

Smith, P.A., Tulp, I., Schekkerman, H., Gilchrist, H.G., Forbes, M.R., 2012. Shorebird incubation behaviour and its influence on the risk of nest predation. Anim. Behav. 84, 835–842.

Smith, P.A., Wilson, S., 2010. Intraseasonal patterns in shorebird nest survival are related to nest age and defence behaviour. Oecologia 163, 613–624.

Sólymos, P., Lele, S.R., 2016. Revisiting resource selection probability functions and single-visit methods: Clarification and extensions. Methods Ecol. Evol. 7, 196–205.

St-Louis, V., Pidgeon, A.M., Radeloff, V.C., Hawbaker, T.J., Clayton, M.K., 2006. High-resolution image texture as a predictor of bird species richness. Remote Sens. Environ. 105, 299–312.

Stanley, T.R., 2004. When should Mayfield model data be discarded? Wilson Bull. 116, 267–269.

Stephens, S.E., Rotella, J.J., Lindberg, M.S., Taper, M.L., Ringelman, J.K., 2005. Duck nest survival in the Missouri Coteau of North Dakota: Landscape effects at multiple spatial scales. Ecol. Appl. 15, 2137–2149.

Stephens, S.E., Walker, J.A., Blunck, D.R., Jayaraman, A., Naugle, D.E., Ringelman, J.K., Smith, A.J., 2008. Predicting risk of habitat conversion in native temperate grasslands. Conserv. Biol. 22, 1320–1330.

Streby, H.M., & Andersen, D.E., 2011. Seasonal productivity in a population of migratory songbirds: why nest data are not enough. Ecosphere 2, 1-15.

Su, Y., Yajima, M., 2015. R2jags: Using R to Run “JAGS.”

Szalay, F.A. De, Carroll, L.C., Beam, J.A., Resh, V.H., Henry, W., Avenue, M., Banos, L., Chantelle Carroll, L., Beam, J.A., Resh, V.H., 2003. Temporal overlap of nesting duck and aquatic invertebrate abundances in the Grasslands Ecological Area, California, USA. Wetlands 23, 739–749.

Thomas, D., Taylor, E., 2006. Study Designs and Tests for Comparing Resource Use and Availability II. J. Wildl. Manage. 70, 324–336.

Thompson, S.J., Arnold, T.W., Amundson, C.L., 2014. A multiscale assessment of tree avoidance by prairie birds. Condor 116, 303–315.

Thompson, S.J., Arnold, T.W., Vacek, S., 2012. Impact of encroaching woody vegetation on nest success of upland nesting waterfowl. J. Wildl. Manage. 76, 1635–1642.

Thompson, S.J., Johnson, D.H., Niemuth, N.D., Ribic, C.A., 2015. Avoidance of unconventional oil wells and roads exacerbates habitat loss for grassland birds in the North American great plains. Biol. Conserv. 192, 82–90.

U.S. Fish and Wildlife Service, 2016. Waterfowl Population Status, 2016. Washington D.C., USA.

Vieilledent, G., Merow, C., Guelat, J., Latimer, A., Kery, M., Gelfand, A., Wilson, A., Mortier, F., Silander, J., 2014. hSDM: hierarchical Bayesian species distribution models.

Walker, J., Rotella, J.J., Schmidt, J.H., Loesch, C.R., Reynolds, R.E., Lindberg, M.S., Ringelman, J.K., Stephens, S.E., 2013a. Distribution of duck broods relative to habitat characteristics in the Prairie Pothole Region. J. Wildl. Manage. 77, 392-404.

Walker, J., Rotella, J.J., Stephens, S.E., Lindberg, M.S., Ringelman, J.K., Hunter, C., Smith, A.J., 2013b. Time-lagged variation in pond density and primary productivity affects duck nest survival in the Prairie Pothole Region. Ecol. Appl. 23, 1061–1074.

Waisanen, P.J., Bliss, N.B., 2002. Changes in population and agricultural land in conterminous United States counties, 1790 to 1997. Global Biogeochem. Cycles 16, 84-1-84–19.

Warton, D.I., Stoklosa, J., Guillera-Arroita, G., MacKenzie, D.I., Welsh, A.H., 2017. Graphical diagnostics for occupancy models with imperfect detection. Methods Ecol. Evol. 8, 408–419.

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S., Holmes, R.T., 2002. Links between worlds: Unraveling migratory connectivity. Trends Ecol. Evol. 17, 76-83.

Weiser, E.L., Brown, S.C., Lanctot, R.B., Gates, H.R., Abraham, K.F., Bentzen, R.L., Bêty, J., Boldenow, M.L., Brook, R.W., Donnelly, T.F., English, W.B., Flemming, S.A., Franks, S.E., Gilchrist, H.G., Giroux, M.A., Johnson, A., Kendall, S., Kennedy, L. V., Koloski, L., Kwon, E., Lamarre, J.F., Lank, D.B., Latty, C.J., Lecomte, N., Liebezeit, J.R., Mckinnon, L., Nol, E., Perz, J., Rausch, J., Robards, M., Saalfeld, S.T., Senner, N.R., Smith, P.A., Soloviev, M., Solovyeva, D., Ward, D.H., Woodard, P.F., Sandercock, B.K., 2018. Effects of environmental conditions on reproductive effort and nest success of Arctic-breeding shorebirds. Ibis. doi: 10.1111/ibi.12571

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46, S120–S139.

Winter, M., Johnson, D.H., Shaffer, J.A., 2005. Variability in vegetation effects on density and nesting success of grassland birds. J. Wildl. Manage. 69, 185–197.

Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. Analysis and management of animal populations. Academic Press, New York, USA.

Wood, E.M., Pidgeon, A.M., Radeloff, V.C., Keuler, N.S., 2012. Image texture as a remotely sensed measure of vegetation structure. Remote Sens. Environ. 121, 516–526.

Wright, C.K., Wimberly, M.C., 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. Proc. Natl. Acad. Sci. U. S. A. 110, 4134–9.

Wright, W.J., Irvine, K.M., Rodhouse, T.J., 2016. A goodness-of-fit test for occupancy models with correlated within-season revisits. Ecol. Evol. 6, 5404–5415.

Zhao, Q., Boomer, G.S., Kendall, W.L., 2018. The non-linear, interactive effects of population density and climate drive the geographical patterns of waterfowl survival. Biol. Conserv. 221, 1–9.

Zhao, Q., Boomer, G.S., Silverman, E., Fleming, K., 2017. Accounting for the temporal variation of spatial effect improves inference and projection of population dynamics models. Ecol. Modell. 360, 252–259.

Appendices

CHAPTER 1 APPENDICES

Chapter 1. S1. Model coefficients and stratum-specific estimates. Strata were excluded from species models if there were fewer than 10 years of data (strata 27, 33, 35, 36, 38, 40, 42, 44, 47 and 49, depending on species). Model output from missing strata is noted as an "NA" in the table below.

						Stratum																
Spp.	**Variable**	**coef**	**sd**	**80L**	**80H**	**26**	**28**	**29**	**30**	**31**	**32**	**34**	**35**	**37**	**39**	**40**	**41**	**43**	**45**	**46**	**48**	**49**
AMWI	int	0.644	0.47	0.05	1.23	-0	1.4	1.58	-0	-0.9	0.44	-0.4	NA	-0.1	-0.9	2.14	2.49	3.71	0.7	NA	-0.7	NA
AMWI	PDD1	**0.412**	0.16	0.21	0.61	0.43	0.53	0.45	0.27	0.38	0.5	0.4	NA	0.44	0.33	0.38	0.44	0.42	0.34	NA	0.48	NA
AMWI	PDSI	0.006	0.17	-0.2	0.21	0.35	0.28	-0	0.11	0.02	0.03	-0.1	NA	0.01	-0.1	-0.1	0.09	-0.1	-0.3	NA	-0	NA
AMWI	BPUP	**0.517**	0.29	0.17	0.88	0.43	0.7	0.68	0.74	0.25	0.38	0.26	NA	0.64	0.39	0.68	0.59	0.31	0.58	NA	0.64	NA
AMWI	BPPO	-0.067	0.2	-0.3	0.19	-0	-0.1	-0	-0.1	-0.2	-0.1	-0.1	NA	-0	0.01	-0	0.04	-0.2	-0.1	NA	-0.1	NA
AMWI	SEOW	**0.265**	0.19	0.05	0.5	0.43	0.49	0.61	-0.1	0.18	0.12	0.38	NA	0.13	0.16	0.21	0.31	-0	0.46	NA	0.33	NA
AMWI	SOL1	0.018	0.14	-0.2	0.19	0.05	0.03	0.05	0.03	0.02	-0.1	0.05	NA	0.06	0.01	0.01	0.03	0.01	-0	NA	0.03	NA
AMWI	BPL1	-0.044	0.28	-0.4	0.31	-0.1	0.08	-0.1	0.19	-0.1	-0.2	-0.2	NA	0.01	-0	-0	-0.1	-0.2	0.17	NA	-0.1	NA
AMWI	TIME	**-0.468**	0.19	-0.7	-0.2	-0.7	-0.6	-0.4	-0.4	-0.4	-0.5	-0.4	NA	-0.5	-0.4	-0.6	-0.6	-0.4	-0.4	NA	-0.4	NA
AMWI	Lat	**1.099**	0.48	0.48	1.72	1.1	1.1	1.1	1.1	1.1	1.1	1.1	NA	1.1	1.1	1.1	1.1	1.1	1.1	NA	1.1	NA
AMWI	Long	**0.458**	0.28	0.09	0.82	0.46	0.46	0.46	0.46	0.46	0.46	0.46	NA	0.46	0.46	0.46	0.46	0.46	0.46	NA	0.46	NA

BWTE	int	0.611	0.11	0.48	0.74	0.57	0.72	0.54	0.51	0.36	0.57	0.45	NA	0.85	0.49	0.68	0.6	0.84	0.51	0.74	0.75	NA
BWTE	PDD1	**0.162**	0.06	0.09	0.23	0.15	0.18	0.16	0.2	0.18	0.18	0.17	NA	0.15	0.13	0.16	0.17	0.16	0.13	0.16	0.16	NA
BWTE	PDSI	**0.172**	0.06	0.1	0.24	0.19	0.21	0.17	0.21	0.22	0.16	0.15	NA	0.16	0.18	0.17	0.16	0.18	0.14	0.17	0.1	NA
BWTE	BPUP	**0.474**	0.11	0.33	0.61	0.48	0.64	0.54	0.51	0.48	0.53	0.46	NA	0.37	0.36	0.45	0.57	0.44	0.45	0.44	0.41	NA
BWTE	BPPO	**-0.529**	0.13	-0.7	-0.4	-0.7	-0.5	-0.3	-0.9	-0.6	-0.6	-0.6	NA	-0.8	-0.6	-0.4	-0.7	-0.2	-0.5	-0.4	-0.2	NA
BWTE	SEOW	**0.095**	0.05	0.03	0.16	0.08	0.11	0.08	0.09	0.12	0.09	0.1	NA	0.08	0.08	0.09	0.12	0.09	0.12	0.08	0.09	NA
BWTE	SOL1	**0.089**	0.06	0.01	0.17	0.19	0.05	0.02	0.16	0.11	0	0.12	NA	0.09	0.09	0.08	0.06	0.11	0.06	0.13	0.07	NA
BWTE	BPL1	**-0.146**	0.1	-0.3	-0	-0.1	-0.1	-0.1	-0.2	-0.1	-0.2	-0.2	NA	-0.2	-0.2	-0.1	-0.1	-0.2	-0.1	-0.2	-0.1	NA
BWTE	TIME	0.034	0.08	-0.1	0.13	-0.1	0.03	0.06	0.27	0.24	0.04	0.13	NA	0.14	-0	-0.1	-0.1	0.18	0.06	-0.2	-0.2	NA
BWTE	Lat	**-0.216**	0.12	-0.4	-0.1	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	NA	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	NA
BWTE	Long	**0.366**	0.07	0.27	0.46	0.37	0.37	0.37	0.37	0.37	0.37	0.37	NA	0.37	0.37	0.37	0.37	0.37	0.37	0.37	0.37	NA
GADW	int	0.529	0.28	0.18	0.87	0.48	-0.2	0.33	1.02	0.54	0.43	0.24	NA	0.72	-0.4	NA	1.19	1.21	0.74	0.12	1.16	NA
GADW	PDD1	**0.359**	0.16	0.16	0.55	0.43	0.39	0.34	0.33	0.36	0.37	0.28	NA	0.37	0.41	NA	0.4	0.35	0.34	0.31	0.38	NA
GADW	PDSI	-0.013	0.14	-0.2	0.16	0.05	0.03	-0	0.02	-0.1	-0.1	-0.1	NA	0.02	-0	NA	0.09	0.08	-0.2	0.05	0.03	NA
GADW	BPUP	-0.06	0.26	-0.4	0.27	-0.1	0.08	0.05	-0.1	-0.2	-0.1	-0.2	NA	-0.1	-0.2	NA	-0.1	-0.2	0.03	0.14	0.07	NA
GADW	BPPO	-0.03	0.16	-0.2	0.17	-0.1	-0.2	-0	0.03	-0.1	-0.1	-0	NA	-0.1	0.04	NA	0.03	-0	-0.1	0.11	0.07	NA
GADW	SEOW	**0.348**	0.15	0.16	0.54	0.23	0.44	0.19	0.26	0.38	0.26	0.34	NA	0.3	0.39	NA	0.42	0.44	0.48	0.46	0.28	NA
GADW	SOL1	-0.018	0.15	-0.2	0.16	-0	0.03	0.09	-0.1	-0.1	-0.1	-0	NA	0.02	0.02	NA	-0	0.01	-0.1	-0.1	-0	NA
GADW	BPL1	0.025	0.29	-0.3	0.39	0.07	0.02	0.3	0.13	0.21	-0.2	-0.2	NA	-0.1	-0.3	NA	-0.2	-0.1	0.17	0.38	0.18	NA
GADW	TIME	**-0.537**	0.26	-0.9	-0.2	-0.9	-0.2	-1.2	-0.2	-1	-1.3	-0.4	NA	0.44	-0.7	NA	-1.2	0.44	-0.3	-0.4	-0.7	NA
GADW	Lat	**-0.428**	0.3	-0.8	-0	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	NA	-0.4	-0.4	NA	-0.4	-0.4	-0.4	-0.4	-0.4	NA
GADW	Long	**-0.359**	0.21	-0.6	-0.1	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	NA	-0.4	-0.4	NA	-0.4	-0.4	-0.4	-0.4	-0.4	NA
MALL	int	-0.134	0.15	-0.3	0.06	0.31	-0.5	-0.6	0.38	-0	-0.1	-0.6	-0.5	-0.1	-1	0.43	-0.2	0.33	-0.5	0.01	-0.3	0.7
MALL	PDD1	**0.053**	0.04	0.00	0.11	0.07	0.07	0.05	0.06	0.05	0.04	0.06	0.05	0.05	0.06	0.02	0.05	0.04	0.06	0.05	0.06	0.05
MALL	PDSI	0.009	0.05	-0.1	0.07	0.08	0.03	-0	0.16	0.02	-0	-0.1	-0	-0	0.02	0.02	0.04	0.02	-0.1	0.01	-0.1	0.02
MALL	BPUP	**0.097**	0.11	-0	0.23	-0.1	0.32	0.33	0.07	-0	-0.1	0	0.29	0.11	-0.2	0.07	0.37	0.08	0.11	0.06	0.14	0.03
MALL	BPPO	**-0.183**	0.08	-0.3	-0.1	-0.4	-0.3	-0.1	-0.2	-0.1	-0.4	-0.3	-0	-0.1	-0.3	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1
MALL	SEOW	**0.133**	0.04	0.08	0.19	0.13	0.14	0.12	0.14	0.14	0.13	0.14	0.14	0.13	0.14	0.13	0.13	0.13	0.13	0.13	0.13	0.13
MALL	SOL1	-0.005	0.05	-0.1	0.05	0.01	-0	-0	0.02	-0	-0	0.03	0.02	-0	-0	-0	-0	-0	-0	0.01	-0	-0
MALL	BPL1	-0.033	0.12	-0.2	0.12	-0.1	-0.2	0.41	-0.1	0.05	-0.1	-0.2	-0.2	0.23	-0.3	-0	0.06	0.05	-0.1	0.22	-0.1	-0.1
MALL	TIME	-0.144	0.16	-0.3	0.05	-1	-0.5	-0.7	0.17	-0.1	-0.4	0.02	-0.7	-0.2	-0.6	-0.5	-0.2	0.55	0.28	0.2	0.83	0.43
MALL	Lat	-0.305	0.12	-0.5	-0.1	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3
MALL	Long	-0.186	0.08	-0.3	-0.1	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2

NOPI	int	0.39	0.24	0.09	0.69	0.54	-0.4	-0.6	0.96	0	0.25	0.17	NA	0.33	-0.3	1.24	0.12	1.69	0.16	1.13	0.68	NA
NOPI	PDD1	**0.163**	0.06	0.09	0.24	0.17	0.16	0.17	0.15	0.16	0.18	0.13	NA	0.14	0.19	0.19	0.16	0.16	0.16	0.16	0.17	NA
NOPI	PDSI	0.00	0.09	-0.1	0.11	0.27	0.19	-0.1	0.18	-0.1	0.1	-0.1	NA	-0.1	-0.1	-0	0.01	-0	-0.3	0.05	-0.2	NA
NOPI	BPUP	0.021	0.17	-0.2	0.23	-0.3	0.01	0.14	-0.1	-0	0.01	-0.2	NA	-0.1	-0.3	0.04	-0	0.05	0.47	0.16	0.38	NA
NOPI	BPPO	**0.174**	0.17	-0	0.39	0.26	0.13	0.03	0.21	0.2	0.05	0.15	NA	0.2	0.13	0.05	-0	0.1	0.41	0.2	0.51	NA
NOPI	SEOW	**0.053**	0.07	-0	0.14	0.06	0.03	0.01	0.07	0.07	0.04	0.08	NA	0.01	0.05	0.05	0.04	0.09	0.1	0.05	0.05	NA
NOPI	SOL1	0.026	0.1	-0.1	0.14	0.17	-0	0.07	0.09	0.02	-0	0.1	NA	0	-0	0	0.08	-0	-0.1	0.01	0.03	NA
NOPI	BPL1	-0.068	0.13	-0.2	0.09	-0	-0.1	-0.1	-0.1	0.01	-0.1	-0	NA	-0.1	-0.1	-0.1	-0	-0.1	-0.1	-0	-0.1	NA
NOPI	TIME	**-0.398**	0.13	-0.6	-0.2	-0.8	-0	-0.5	-0.1	-0.3	-0.4	-0.3	NA	-1	-0.6	-0.5	-0.4	-0	-0.2	-0.4	-0.4	NA
NOPI	Lat	**-0.378**	0.21	-0.7	-0.1	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	NA	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	NA
NOPI	Long	**-0.265**	0.14	-0.4	-0.1	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	NA	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	NA

Chapter 1.S2. R Script for JAGS model with code for explained variance (R^2)

```
sink("full_model.jags")
cat("
   model {

 # Priors and constraints
   # mean parameter values (regression coefficients
   # note: JAGS uses precision (1/var), precision = 0.25, variance = 4, SD = 2
   b0.mu ~ dnorm(0,0.25)  # intercepts
   b1.mu ~ dnorm(0,0.25)  # POND-change in pond density between Year_T and Year _T-1
   b2.mu ~ dnorm(0,0.25)  # PDSI- Palmer Drought Severity Index
   b3.mu ~ dnorm(0,0.25)  # upland pair density (BPUP)
   b4.mu ~ dnorm(0,0.25)  # intraspecific breeding pairs per pond (BPPO)
   b5.mu ~ dnorm(0,0.25)  # SEOW-Short-eared owls per BBS route (vole index)
   b6.mu ~ dnorm(0, 0.25)  # SEOW density in previous year (SOL1)
   b7.mu ~ dnorm(0, 0.25)  # upland pair density in previous year (BPL1)
   b8.mu ~ dnorm(0, 0.25)  # Year (linear trend)
   b9.mu ~ dnorm(0, 0.25)  # Site Latitude
   b10.mu ~ dnorm(0, 0.25)  #Site Longitude

   # Priors for SD to describe stratum-specific variation in regression coefficients
   b0.sigma ~ dunif(0,5)  # numerically indexed as above
   b1.sigma ~ dunif(0,5)
   b2.sigma ~ dunif(0,5)
   b3.sigma ~ dunif(0,5)
   b4.sigma ~ dunif(0,5)
   b5.sigma ~ dunif(0,5)
   b6.sigma ~ dunif(0,5)
   b7.sigma ~ dunif(0,5)
   b8.sigma ~ dunif(0,5)

   # convert SD to precision (tau) by inverting and squaring
   b0.tau <- pow(b0.sigma,-2)
   b1.tau <- pow(b1.sigma,-2)
   b2.tau <- pow(b2.sigma,-2)
   b3.tau <- pow(b3.sigma,-2)
   b4.tau <- pow(b4.sigma,-2)
   b5.tau <- pow(b5.sigma,-2)
   b6.tau <- pow(b6.sigma,-2)
   b7.tau <- pow(b7.sigma,-2)
   b8.tau <- pow(b8.sigma,-2)

   # priors for random year and banding location (site) effects
   eta.yr.sigma ~ dunif(0,5)
```

```
  eta.site.sigma ~ dunif(0,5)

  eta.yr.tau <- pow(eta.yr.sigma,-2)
  eta.site.tau <- pow(eta.site.sigma,-2)

 # Likelihood
  for (i in 1:strata){                    # where i indexes to the maximum number of strata
    b0[i] ~ dnorm(b0.mu,b0.tau)           # generate strata specific regression coefficients
    b1[i] ~ dnorm(b1.mu,b1.tau)
    b2[i] ~ dnorm(b2.mu,b2.tau)
    b3[i] ~ dnorm(b3.mu,b3.tau)
    b4[i] ~ dnorm(b4.mu,b4.tau)
    b5[i] ~ dnorm(b5.mu,b5.tau)
    b6[i] ~ dnorm(b6.mu,b6.tau)
    b7[i] ~ dnorm(b7.mu,b7.tau)
    b8[i]~ dnorm(b8.mu,b8.tau)

    for (j in 1:maxyrs){                  # where j indexes to number of years surveyed in each
stratum
      eta.yr[i,j] ~ dnorm(0,eta.yr.tau)   # generate random year effects within each stratum

      for (k in 1:maxsites){              # where k indexes to the maximum number of banding
sites
         eta.site[i,j,k] ~ dnorm(0,eta.site.tau)   # generate random banding site effects
      }  # close sites loop
    }  # close years loop
  }  # close strata loop

 # Observation model
  for (k in 1:nrows){     # k indexes each line of data (from a banding site within a year within a
stratum)
    # predict proportion of juveniles (Pjuv) based on stratum-specific random covariates,
      # fixed effects (lat, long), and random effects of year/stratum and site/year/stratum
    logit(Pjuv[k]) <- b0[stratum[k]] + b1[stratum[k]]*POND[k] + b2[stratum[k]]*PDSI[k] +
      b3[stratum[k]]*BPUP[k] + b4[stratum[k]]*BPPO[k]+
      b5[stratum[k]]*SEOW[k] + b6[stratum[k]]*SOL1[k] +
      b7[stratum[k]]*BPL1[k] + b8[stratum[i]]*YEAR[i]+ b9.mu*Lat[k] + b9.mu*Long[k] +
      eta.yr[stratum[k],yr[k]] +  eta.site[stratum[k],yr[k],site[k]]

   # compare observed juveniles to predicted juveniles based on above model
   HY_bands[k] ~ dbinom(Pjuv[k],bands[k])       # Juv ~ Binomial(P=Pjuv, N=Juv+Ad)

  #Fit assessments: Residuals
    predicted[k]<-Pjuv [k]    #Age ratio predicted from data based on estimated coefficients
      resid[k]<-(HY_bands[k]/bands[k])-predicted[k] # Residuals: observed-predicted
```

```
  #Gelman-Rubin Fit statistic derivation
  chi2[k]<-pow(((HY_bands[k]/bands[k])-Pjuv[k]),2)/sqrt(Pjuv[k]+0.00001)      # Chi squared:
  (Observed-predicted)^2/sqrt(predicted + a very small number to make it non-zero)
   HYBands_new[k]~dbinom(Pjuv[k],bands[k])  # new dataset based on predicted age ratio and
  observed number of bands
   new.Age.rat[k]<-HYBands_new[k]/bands[k] # New age ratios

   chi2.new[k]<-pow(((HYBands_new[k]/bands[k])-Pjuv[k]),2)/sqrt(Pjuv[k]+0.00001) #Chi
squared for new data
    }

   # Add discrepancy measures for dataset
   fit<-sum(chi2[]) # cumulative discrepancy for model relative to data.
   fit.new<-sum(chi2.new[])# cumulative discrepancy for model relative to new data.

   }   # end bugs model
   ",fill=TRUE)
sink()



# Data
bugs.data <- list(strata=max(dat$Strata_fac), stratum=dat$Strata_fac, yr=dat $Year_fac,
     maxyrs=max(dat $Year_fac), site=dat$Site_fac, maxsites=max(dat$Site_fac),
     PDSI=dat$ST_wPDSI, PDdiff=dat$ST_PD1Diff,  UplandDD=dat$ST_BPDenUP,
     PondDD=dat$ST_BPDenPond, SEOW=dat$ST_SEOWT, SEOWTM1=dat$ST_SEOWTL1,
     UplandDDTM1=dat$ST_TPop.Den.TM1, Lat=dat$ST.Lat,
     Long=dat$ST.Long,YEAR=dat$ST_Year, HY_bands=dat$HY_bands, bands=dat$Bands,
     nrows=nrow(dat))


# Parameters to save.

parameters <- c("b0.mu","b0.sigma", "b1.mu", "b1.sigma", "b2.mu", "b2.sigma", "b3.mu",
"b3.sigma", "b4.mu", "b4.sigma", "b5.mu", "b5.sigma", "b6.mu", "b6.sigma", "b7.mu",
"b7.sigma", "b8.mu", "b8.sigma", "b9.mu","b10.mu","eta.yr.sigma", "eta.site.sigma","eta.yr",
"eta.site", "resid", "b0", "b1", "b2", "b3", "b4", "b5", "b6", "b7","b8","fit","fit.new")

out.model <- jagsUI(bugs.data, inits=NULL, parameters, "full.model.jags", n.chains=3,
                n.thin=2,n.iter=20000,n.burnin=100, n.adapt=2000)

##Bayesian p value good if close to 0.5, bad if close to 0 or 1
mean(out.model$sims.list$fit.new>out.model$sims.list$fit)

# #====================================================
#  Partitioning variance using the mallard model as an example
```

Marginal and Conditional R2GLMM per Johnson (2014) Methods in Ecology and Evolution 5 (944-946)
and Nakagawa & Schielzeth (2013) Methods in Ecology and Evolution 4 (133-142)
Their approach was designed to estimate a pseudo-R2 for generalized models with random intercepts   and slopes and can be adapted for our bayesian modelling approach. Marginal and conditional R2 (Table 2 in Nakagawa and Schielzeth (2013) are calculated based on 4 variance components and distribution-specific adjustment ($\pi^2/3$ in the case of a logit model). The four components are:
σ^2f= variance of fixed effects components,
$\sigma^2\gamma$= variance of group-specific effects,
$\sigma^2\alpha$ = variance of individual-specific effects,
σ^2e = variance of residual

#1. Calculate random effects variance ($\sigma^2\gamma + \sigma^2\alpha$) based on the estimated random effect sigmas saved by the model. This is a simplification of the covariance-matrix-based method for finding the total random effects covariance provided by Johnson (2014) eqns 10-11. The simple sum of the random effects variance was cross validated against Johnson's variance-covariance matrix approach for all species.

List of random effect sigma objects from coda object

```
vars.sigl<-list(out.model$sims.list$b0.sigma,
          out.model$sims.list$eta.yr.sigma,
          out.model$sims.list$eta.site.sigma,
          out.model$sims.list$b1.sigma,
          out.model$sims.list$b2.sigma,
          out.model$sims.list$b3.sigma,
          out.model$sims.list$b4.sigma,
          out.model$sims.list$b5.sigma,
          out.model$sims.list$b6.sigma,
          out.model$sims.list$b7.sigma,
          out.model$sims.list$b8.sigma

)
```

create empty matrix for each random effect to hold variance (sigma^2) with one row for each random effect (three intercept random effects (for strata, year within strata and banding site within year and stratum) and 8 slopes)

```
RE.s2mat<-matrix(NA,ncol=1, nrow=11)
rownames(RE.s2mat)<-c("x.S", "x.SY","x.SYB", "x.PDD1",  "x.PDSI",
                 "x.BPUP",  "x.BPPO",
                 "x.SEOW", "x.SOL1",
                 "x.BPL1", “x.YEAR”)
```

create list of variance (sigma^2) of each random effect in matrix so that can be used in matrix multiplication later:

```
for(i in 1:nrow(RE.s2mat)){
  RE.s2mat[i,1]<-(mean(vars.sigl[[i]]))^2

}


Sl<-colSums(RE.s2mat)  # Total Random Effect variance- same result as eqn 11 in Johnson 2014
                                                #can be achieved with var-cov matrix as well
# We can also look at subsets of the random effects variance
Sl.t<-sum(RE.s2mat[c(2),])                #only year random effect
Sl.s<-sum(RE.s2mat[c(1,3:10),])           #leave out year random effect
Sl.site<-RE.s2mat[3,]                     #only site random effect

#-------------------------------------------------------
# 2. Mean fixed effects variance(σ2f):

# save coefficients
out.coef<-c(out.BWTE.year$mean$b0.mu,
            out.BWTE.year$mean$b1.mu,
            out.BWTE.year$mean$b2.mu,
            out.BWTE.year$mean$b3.mu,
            out.BWTE.year$mean$b4.mu,
            out.BWTE.year$mean$b5.mu,
            out.BWTE.year$mean$b6.mu,
            out.BWTE.year$mean$b7.mu,
            out.BWTE.year$mean$b8.mu,
            out.BWTE.year$mean$b9.mu,
            out.BWTE.year$mean$b10.mu
    )

#Matrix of 1s of length data to provide intercepts for matrix algebra below
x<-matrix(1, ncol=1, nrow=nrow(dat))

# covariate data matrix
xmat.FE<-cbind(x[,1], dat$ST_PD1Diff, dat$ST_wPDSI,dat$ST_BPDenUP,dat$ST_BPDenPond,
dat$ST_SEOWT,dat$ST_SEOWTL1,dat$ST_TPop.Den.TM1, dat$ST.Lat, dat$ST.Long)

# Fixed effects variance following code from Johnson is the variance of product of coefficient
matrix and data matrix
Sf <- var(xmat.FE %*% out.model$coef)
Sf.t<-var(xmat.FE[,1:7]%*%out.model$coef[1:7]) # Fixed effects var without lat long or year
Sf.t2<-var(Y.xmat.FE[,1:8]%*%out.coef[1:8]) # Fixed effects var with year but not lat long

# 3. Variance of the residuals (σ2e):

Se<- var(colMeans(out$sims.list$resid))
```

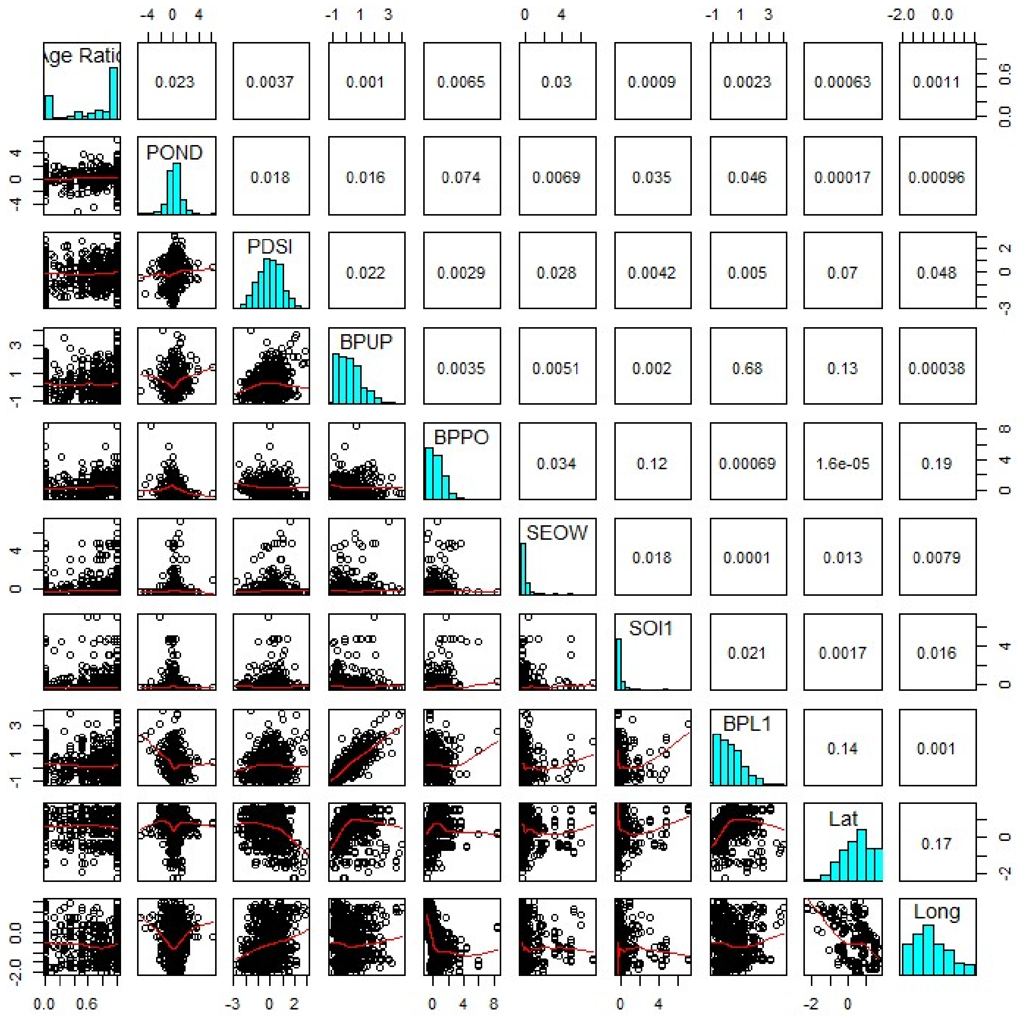
```
# Distribution-specific variance for binomial following Nakagawa & Schielzeth (2013) Table 2
Sd<-(3.14159^2)/3

# Total variance (denominator in Marginal and Conditional R2GLMM equations)
Tvar<-Sl+Se+Sf+Sd
# Marginal R2 (Just fixed effects in numerator); Johnson(2014) eqn 1
R2M<-Sf/Tvar
# Conditional R2 (fixed and random effects in numerator); Johnson(2014) eqn 2
R2C<-(Sf+Sl)/Tvar

#==========================
#We can further partition the variance and look at specific portions relative to each other.

# How much of the identified temporal variation was explained by ecological fixed effects?
(Sf.t)/Tvar;   # Ecological fixed effects (no lat long)
(Sf.t2+Sl.t)/Tvar; # Ecological fixed effects + strata and year random effects and year fixed effects
((Sf.t)/Tvar)/((Sf.t2+Sl.t)/Tvar)

#How much of the spatial variation is explained by lat-long?
((Sf-Sf.t))/Tvar  # Lat-Long FE
((Sf-Sf.t)+Sl.s)/Tvar  # Lat long FE and strata, site REs
(((Sf-Sf.t))/Tvar)/(((Sf-Sf.t)+Sl.s)/Tvar)

# How much of the explained variation is explained by site REs?
(Sl.site)/Tvar  # variation explained by by site RE
((Sl.site)/Tvar)/R2C
```

Chapter 1.S3. Standardization table

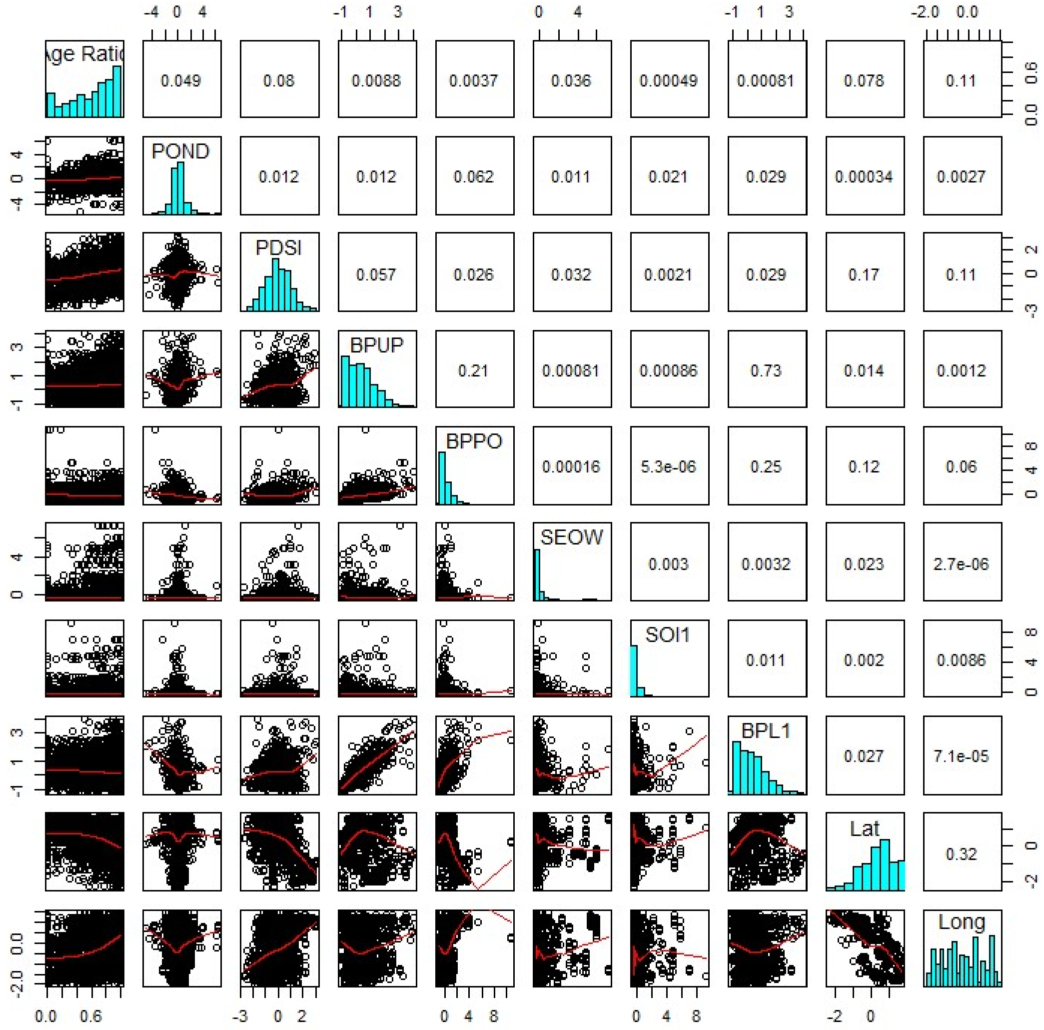
	Mean	**SD**
ΔPOND	-0.012	3.435
PDSI	-0.209	2.351
BPPO	AMWI: 0.172 BWTE: 0.883 GADW: 0.406 MALL : 1.057 NOPI: 0.460	AMWI: 0.192 BWTE: 0.757 GADW: 0.350 MALL: 0.693 NOPI: 0.559
BPUP	16.113	12.643
SEOW	0.198	0.571
SOL1	0.202	0.583
BPL1	15.944	12.520
Lat	49.49	2.60
Long	-104.77	4.94
Year	1992	13.7

Chapter 1.S4. Covariation Plots of covariate values for each species. Numbers to the right of the diagonal are r^2 values.

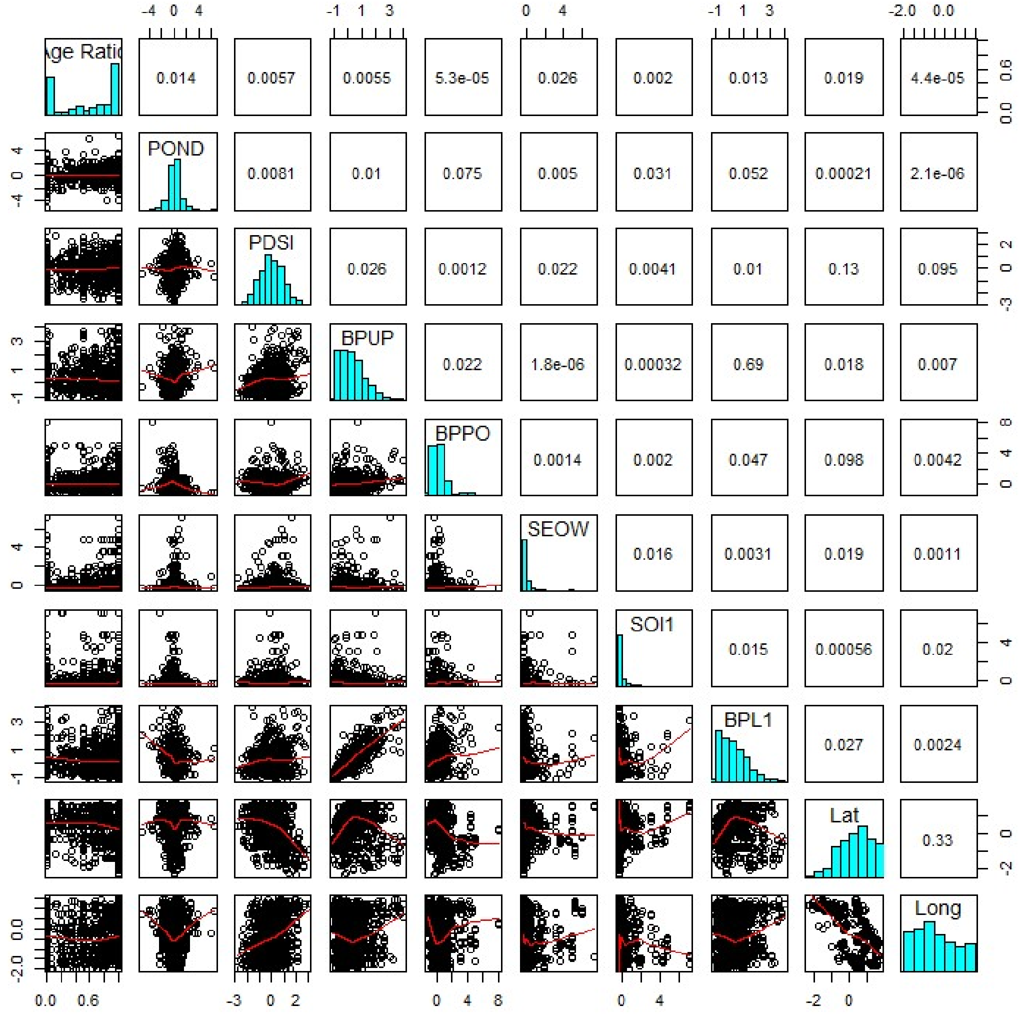
American wigeon



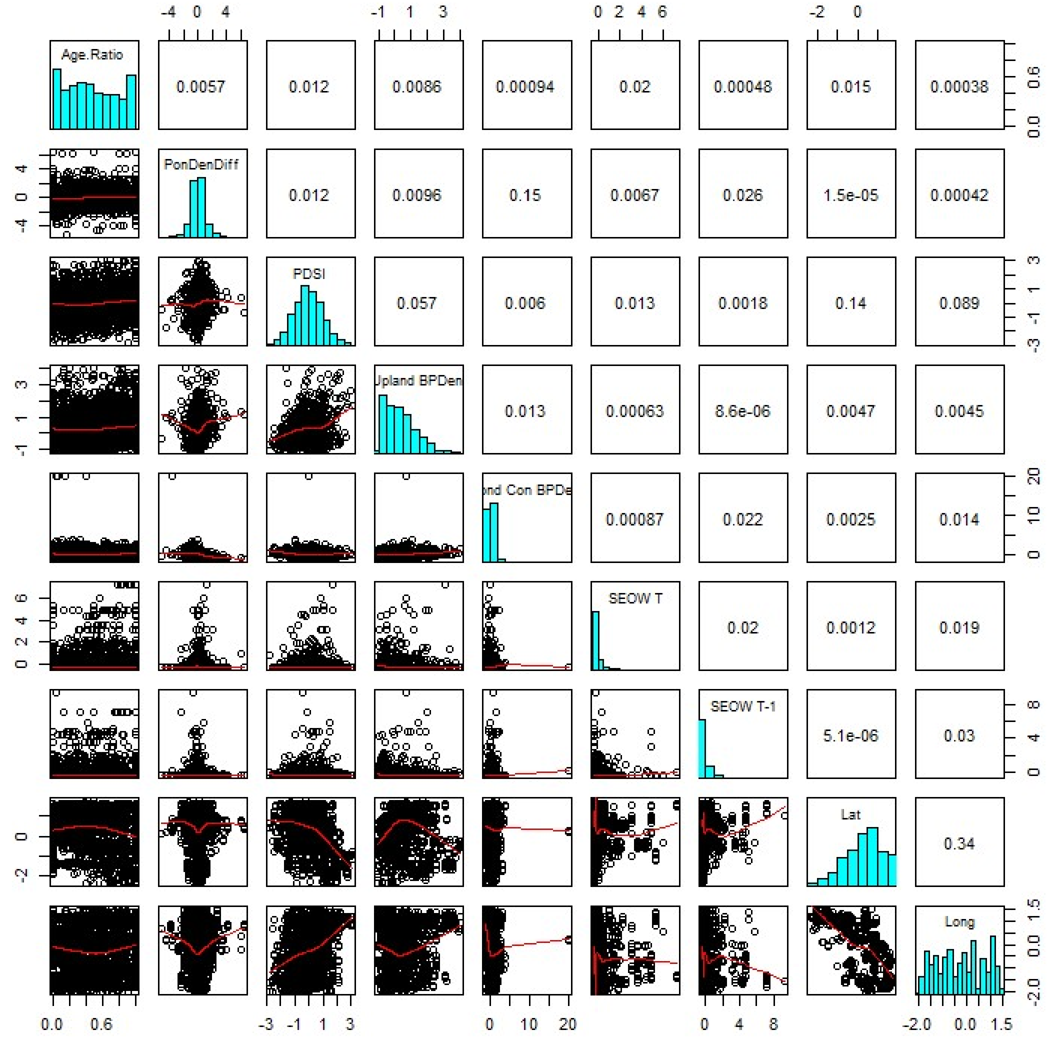
Blue-winged teal



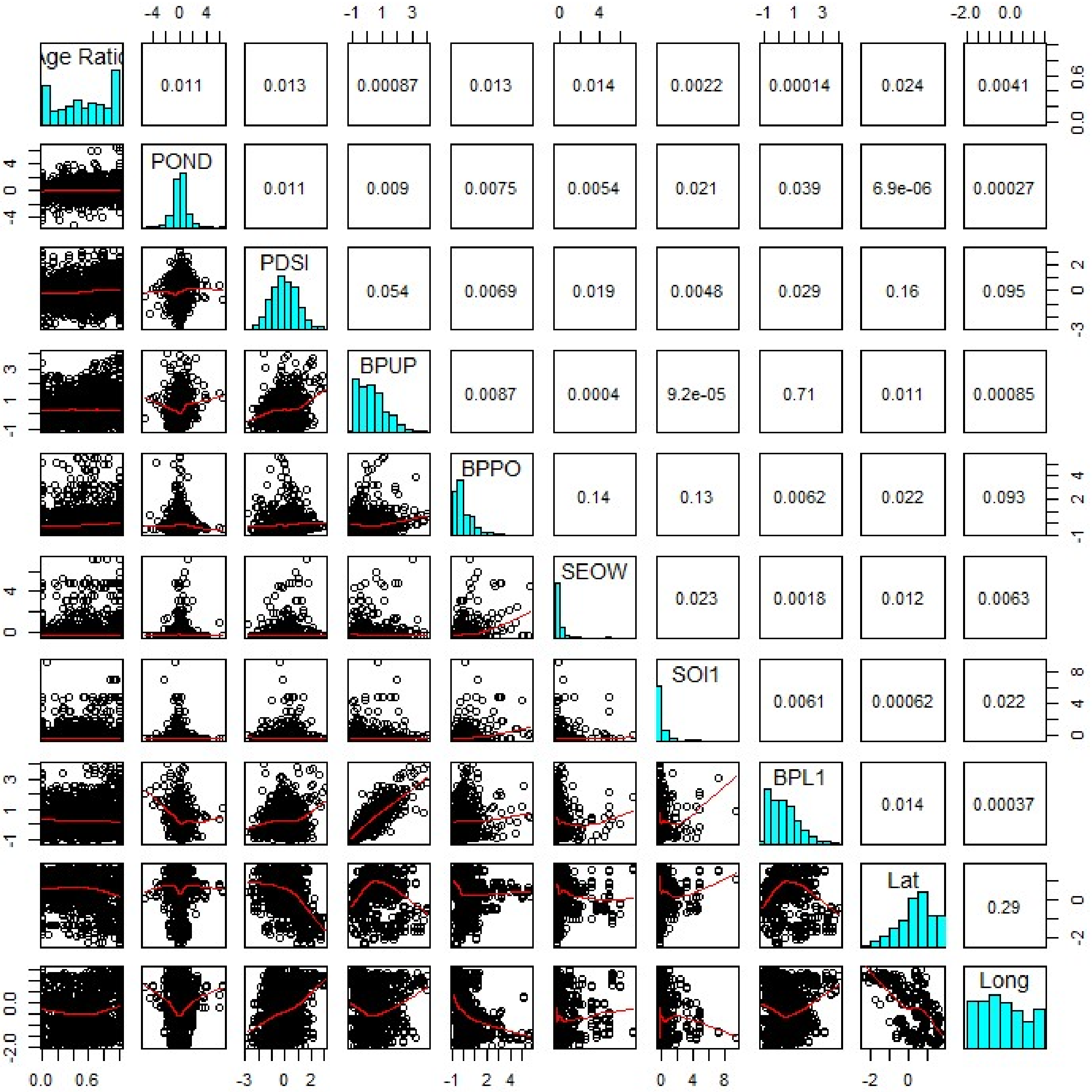
Gadwall


Age Ratio
POND
PDSI
BPUP
BPPO
SEOW
SOI1
BPL1
Lat
Long
0.014
0.0057
0.0055
5.3e-05
0.026
0.002
0.013
0.019
4.4e-05
0.0081
0.01
0.075
0.005
0.031
0.052
0.00021
2.1e-06
0.026
0.0012
0.022
0.0041
0.01
0.13
0.095
0.022
1.8e-06
0.00032
0.69
0.018
0.007
0.0014
0.002
0.047
0.098
0.0042
0.016
0.0031
0.019
0.0011
0.015
0.00056
0.02
0.027
0.0024
0.33
-4 0 4
-1 1 3
0 4
-1 1 3
-2.0 0.0
0.0 0.6
-3 0 2
0 4 8
0 4
-2 0

Mallard


-4 0 4
-1 1 3
0 2 4 6
-2 0
Age.Ratio
0.0057
0.012
0.0086
0.00094
0.02
0.00048
0.015
0.00038
0.0 0.6
PonDenDiff
0.012
0.0096
0.15
0.0067
0.026
1.5e-05
0.00042
-4 0 4
PDSI
0.057
0.006
0.013
0.0018
0.14
0.089
-3 -1 1 3
Upland BPDen
0.013
0.00063
8.6e-06
0.0047
0.0045
-1 1 3
Pond Con BPDe
0.00087
0.022
0.0025
0.014
0 10 20
SEOW T
0.02
0.0012
0.019
0 2 4 6
SEOW T-1
5.1e-06
0.03
0 4 8
Lat
0.34
-2 0
Long
-2.0 0.0 1.5
0.0 0.6
-3 -1 1 3
0 10 20
0 4 8
-2.0 0.0 1.5

Northern pintail



Chapter 1. S5. Expansion of Table 2 including details on derivation of explained variance calculations.

	American wigeon	Blue-winged teal	Gadwall	Mallard	Northern pintail
Model estimated mean Proportion of Juveniles (se)	0.69 (0.14)	0.63 (0.07)	0.64 (0.12)	0.46 (0.09)	0.60 (0.12)
Mean Harvest-based Proportion of Juveniles (1969-2013)[a]	0.67	0.72	0.68	0.57	0.63
Goodness of fit statistic[b]	0.44	0.39	0.5	0.35	0.42
Marginal R2 [c]	0.15	0.09	0.07	0.03	0.06
Conditional R2 [d]	0.72	0.35	0.70	0.47	0.49
a. Numerator= Temporal Fixed effects only (no year, lat, long or random effects), Denominator=Total Variance	*0.05*	*0.07*	*0.03*	*0.01*	*0.01*
b. Numerator= Ecological Fixed effects, year and year random effects, Denominator=Total Variance	*0.09*	*0.17*	*0.15*	*0.04*	*0.06*
Proportion of temporal variation explained by Ecological Fixed Effects (a/b)	0.53	0.39	0.16	0.34	0.17
c. Numerator= LatLong Fixed Effects, Denominator=Total Variance	*0.10*	*0.03*	*0.04*	*0.02*	*0.05*
d. Numerator=LatLong Fixed Effects & strata&Site Random Effects (spatial variation), Denominator=Total Variance	*0.62*	*0.16*	*0.49*	*0.26*	*0.41*
Prop of spatial variation explained by site Lat & Long (c/d)	0.16	0.16	0.08	0.06	0.12
e. Numerator= site random effects, Denominator=Total Variance	*0.26*	*0.09*	*0.35*	*0.16*	*0.21*
Proportion of variance explained by site random effects (e/Conditional R^2)	0.36	0.26	0.50	0.35	0.43

[a] Central Flyway parts survey data, USFWS

[b] Bayesian P-values close to 0.5 (±0.2) were considered to have good fit.

[c] var(fixed effects)/Σ(var(fixed effects), var(random effects), var(residuals), distribution specific adjustment (see Nakagawa & Schielzeth 2013, Johnson 2014).

[d] (var(fixed effects)+var(random effects))/Σ(var(fixed effects), var(random effects), var(residuals), distribution specific adjustment) (see Nakagawa & Schielzeth 2013, Johnson 2014).

CHAPTER 2 APPENDICES:

Chapter 2. S1. R, JagsUI code for null daily nest survival model

```
# Jags version
   sink("dsr.jags.null")
   cat("
     model {

#Priors==============
     #Random Effects

     for (r in 1:nYears){
     eta.Study_Yr[r] ~ dnorm(0, tau.Study_Yr)  # Prior for random effect of year
     }

     sigma.Study_Yr ~ dunif(0,5) #residual standard deviation for rand effect of year
     tau.Study_Yr <- pow(sigma.Study_Yr, -2) #precision param for rand effect of year

     for (s in 1:nPlot){
     eta.Study_Plot[s] ~ dnorm(0, tau.Study_Plot)  # Prior for random effect of Plot
     }
     sigma.Study_Plot ~ dunif(0,5) #residual standard deviation for rand effect of plot
     tau.Study_Plot <- pow(sigma.Study_Plot, -2) #precision param for rand effect of plot
```

```
    #Fixed Effects================
        dsr ~ dunif(0, 1) # Prior for daily nest survival rate
        beta.mu <- logit(dsr) # logit prior for intercept

# Likelihood=================
    for (i in 1:no.nests){
    for (j in found[i]:penult[i]){
    logit(S1[i,j]) <- beta.mu + eta.Study_Yr[Study_Year[i]] + eta.Study_Plot[Study_Plot[i]]
    + beta.spp * spp[i]
     } # replace dsr with linear function of nest covariates [i], age [i,j]

    for (k in penult[i]:last[i]){    # Same as first period
    logit(S2[i,k]) <- beta.mu + eta.Study_Yr[Study_Year[i]] + eta.Study_Plot[Study_Plot[i]]
    + beta.spp * spp[i]
     } # ditto

    SS1[i] <- prod(S1[i,found[i]:penult[i]]) # prob of surviving found to penult give dsr
    SS2[i] <- prod(S2[i,penult[i]:last[i]])
    ISR[i] <- SS1[i] * SS2[i]
    fate[i] ~ dbern(ISR[i])
    }

    # Derived quantities =============

    dsr.mago<-exp(beta.mu)/(1+exp(beta.mu)) # Daily survival rate godwits
    dsr.will<-exp(beta.mu+beta.spp)/(1+exp(beta.mu+beta.spp)) # daily survival rate Willets
```

```
        ns.mago<-dsr.mago^28 # nest success  godwits
        ns.will<-dsr.will^29  # nest success Willets

        } # end jags model
        ",fill = TRUE)
      sink()

# data=====
      dsr.data.null <- list(no.nests=no.nests, found=dat$Jd_found, fate=1-dat$UMN_fate_coded,
                        penult=dat$LA.HA, last=dat$FD,nYears=max(dat$Year_fac),Study_Year=dat$Year_fac,
                        spp=Spp_code, nPlot=max(dat$Plot_fac),Study_Plot=dat$Plot_fac)

     # Parameters to save========
      dsr.parms.null <- c("dsr", "beta.mu", "beta.spp", "dsr.mago", "dsr.will", "ns.mago", "ns.will","eta.Study_Yr", "eta.Study_Plot")

      dsr.inits <- function(){list(ISR = runif(1, 0.9, 1))}

      # MCMC settings
      na <- 5000 ;      ni <- 25000;      nt <- 2;      nb <- 2000;      nc <- 3

      out.null <- jagsUI(dsr.data.null, inits=NULL, dsr.parms.null, "dsr.jags.null", n.adapt = na, n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb,
parallel=TRUE)
```

Chapter 2. S2. R, JagsUI code for Full Nest Survival model

```
sink("dsr.jags.full ")
   cat("
     model {

#======= PRIORS========#

 #Random Effects========

     for (r in 1:nYears){
     eta.Study_Yr[r] ~ dnorm(0, tau.Study_Yr)  # Prior for random effect of year
     }

     sigma.Study_Yr ~ dunif(0,5) #residual standard deviation for random effect of year
     tau.Study_Yr <- pow(sigma.Study_Yr, -2) #precision specification for random effect of year

     for (s in 1:nPlot){
     eta.Study_Plot[s] ~ dnorm(0, tau.Study_Plot)  # Prior for random effect of PI
     }
     sigma.Study_Plot ~ dunif(0,5) #residual standard deviation for random effect of study plot
     tau.Study_Plot <- pow(sigma.Study_Plot, -2) #precision specification for random effect of study plot
 #Fixed Effects ========

      dsr ~ dunif(0, 1) # prior for daily nest survival rate
```

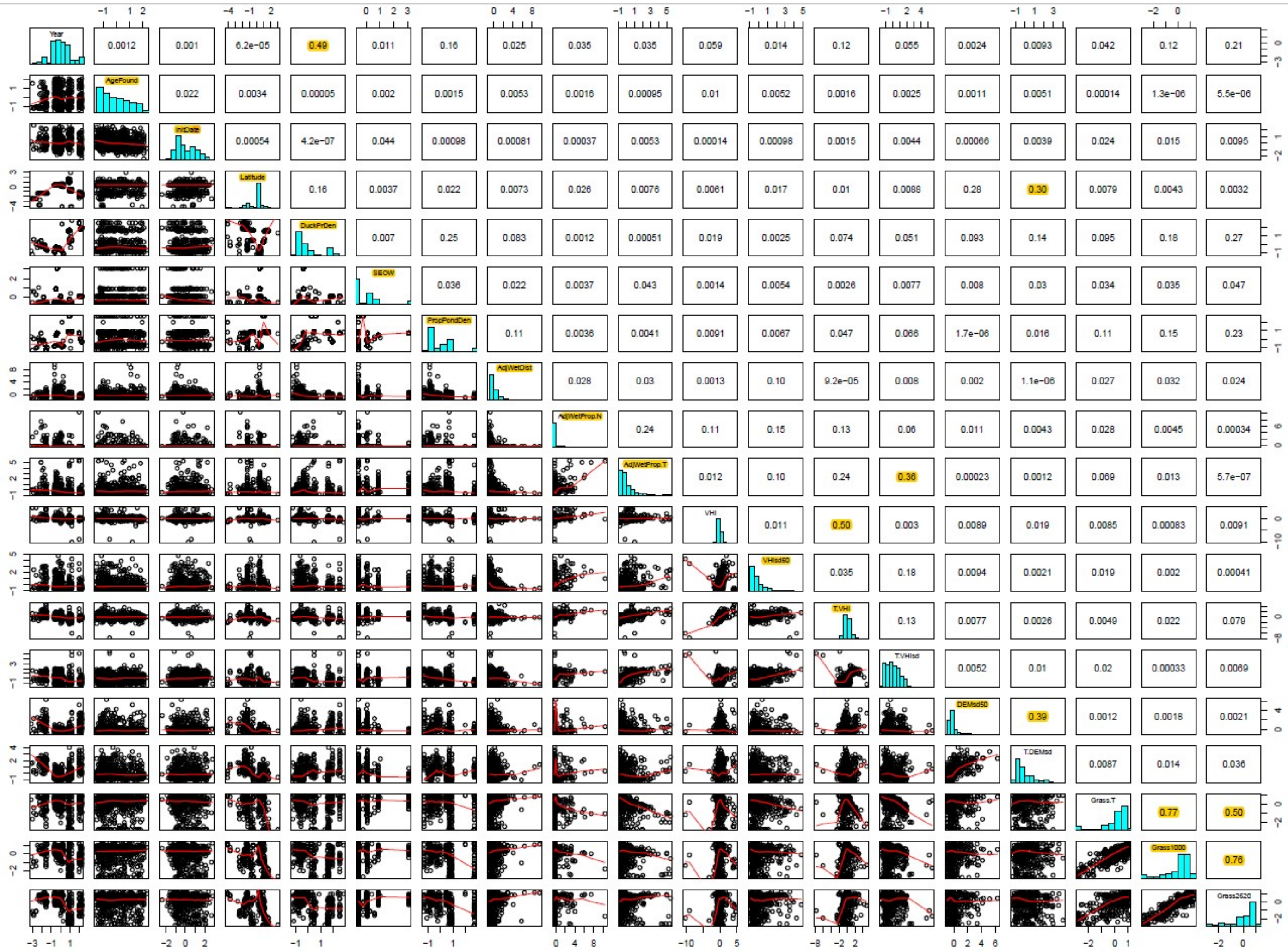
```
beta.mu <- logit(dsr) # logit for intercept
beta.age ~ dnorm(0,0.3) #prior for nest age
beta.init ~ dnorm(0,0.3) #prior date of nest initiation
beta.init2 ~ dnorm(0,0.3) #prior date of nest initiation quadratic term

beta.Lat ~ dnorm(0,0.3) #prior for latitude
beta.BPUP ~ dnorm(0,0.3) # prior for dabbling duck density
beta.CDen ~ dnorm(0,0.3) # prior for conspecific shorebird density
beta.SEOW ~ dnorm(0, 0.3) # prior for short-eared owl density

# Vegetation variables
beta.VHI.N.WILL ~ dnorm(0,0.3) # prior for veg height index (willet)
beta.VHI.N.MAGO ~ dnorm(0,0.3) # prior for veg height index (godwit)
beta.VHI.sdT.MAGO~ dnorm(0,0.3) # prior for veg height index (godwit)
beta.VHI.sdT.WILL~ dnorm(0,0.3) # prior for veg height index (willet)
beta.Grass1000 ~ dnorm(0,0.3) # prior for relative grass cover at scale of skunk home range
beta.GrassI ~ dnorm(0,0.3) # prior for  location of nest in cropland (Indicator that Not in grass)

# Topography variables
beta.DEM.T.MAGO ~ dnorm(0,0.3) # prior for topographic variability (godwit)
beta.DEM.T.WILL ~ dnorm(0,0.3) # prior for topographic variability (willet)

# Wetland variables
beta.P.PDen ~ dnorm(0,0.3) # prior for relative pond pond density
beta.IWetD.MAGO ~ dnorm(0,0.3) # prior for Distance to the nearest wetland adjusted by PondDensity (godwit)
beta.IWetD.WILL ~ dnorm(0,0.3) # prior for Distance to the nearest wetland adjusted by PondDensity (willet)
```

```
    beta.N.IWetSize ~dnorm(0,0.3) # prior for proportion of home range adjusted by pond density
    beta.T.IWetProp.MAGO ~dnorm(0,0.3) # prior for proportion of home range adjusted by pond density (godwit)
    beta.T.IWetProp.WILL ~dnorm(0,0.3) # prior for proportion of home range adjusted by pond density (willet)

# Likelihood:

    for (i in 1:no.nests){  # For each nest
        for (j in found[i]:penult[i]){  # from the day the nest was found to when it was last seen active
   # linear function of nest covariates [i], age [i,j]- only nest used here:
    logit(S1[i,j]) <-  beta.mu +eta.Study_Yr[Study_Year[i]]+ eta.Study_Plot[Study_Plot[i]]
    + beta.init * Init.date[i] + beta.init2 * Init.date2[i] + beta.age*A.found[i]
    + beta.Lat * Latitude[i] + beta.BPUP * BPUP[i] + beta.CDen *CDen[i] +beta.SEOW * SEOW[i]
    + beta.VHI.N.WILL *VHI.N[i]*WILL[i] + beta.VHI.N.MAGO *VHI.N[i]*MAGO[i]
    + beta.VHI.sdT.MAGO *VHI.sd.T[i]*MAGO[i] + beta.VHI.sdT.WILL *VHI.sd.T[i]*WILL[i]
    + beta.Grass1000* Grass1000[i] + beta.GrassI*GrassI[i]
    + beta.DEM.T.MAGO * DEM.T[i]* MAGO[i] + beta.DEM.T.WILL * DEM.T[i] * WILL[i]
    + beta.P.PDen* P.PDen[i]
    + beta.IWetD.MAGO*IWetD[i]*MAGO[i] + beta.IWetD.WILL*IWetD[i]*WILL[i]
    + beta.N.IWetSize*IWetSize[i]
    + beta.T.IWetProp.MAGO*IWetProp[i]*MAGO[i] + beta.T.IWetProp.WILL*IWetProp[i]*WILL[i]

    }

    for (k in penult[i]:last[i]){    # from the day the nest was last seen active until the earlier of fate or expected hatch date
   # linear function of nest covariates [i], age [i,j]- SAME AS ABOVE- WE DON'T EXPECT DIFFERENCES IN DSR THAT AREN'T EXPLAINED BY OUR
COVARIATES!:
```

```
        logit(S2[i,j]) <-  beta.mu +eta.Study_Yr[Study_Year[i]]+ eta.Study_Plot[Study_Plot[i]]
        + beta.init * Init.date[i] + beta.init2 * Init.date2[i] + beta.age*A.found[i]
        + beta.Lat * Latitude[i] + beta.BPUP * BPUP[i] + beta.CDen *CDen[i] +beta.SEOW * SEOW[i]
        + beta.VHI.N.WILL *VHI.N[i]*WILL[i] + beta.VHI.N.MAGO *VHI.N[i]*MAGO[i]
        + beta.VHI.sdT.MAGO *VHI.sd.T[i]*MAGO[i] + beta.VHI.sdT.WILL *VHI.sd.T[i]*WILL[i]
        + beta.Grass1000* Grass1000[i] + beta.GrassI*GrassI[i]
        + beta.DEM.T.MAGO * DEM.T[i]* MAGO[i] + beta.DEM.T.WILL * DEM.T[i] * WILL[i]
        + beta.P.PDen* P.PDen[i]
        + beta.IWetD.MAGO*IWetD[i]*MAGO[i] + beta.IWetD.WILL*IWetD[i]*WILL[i]
        + beta.N.IWetSize*IWetSize[i]
        + beta.T.IWetProp.MAGO*IWetProp[i]*MAGO[i] + beta.T.IWetProp.WILL*IWetProp[i]*WILL[i]
                }

# Specify relationships between S1, S2 and DSR:
        SS1[i] <- prod(S1[i,found[i]:penult[i]]) # prob of surviving found to penult give dsr
        SS2[i] <- prod(S2[i,penult[i]:last[i]])
        ISR[i] <- SS1[i] * SS2[i]
        fate[i] ~ dbern(ISR[i])

        } # End likelihood
             } # end jags model
        ",fill = TRUE)
    sink()
     # Specify data
    dsr.data <- list(no.nests=no.nests, found=dat$Jd_found, fate=1-dat$UMN_fate_coded,
                        penult=dat$LA.HA, last=dat$FD,nYears=max(dat$Year_fac),Study_Year=dat$Year_fac,
```

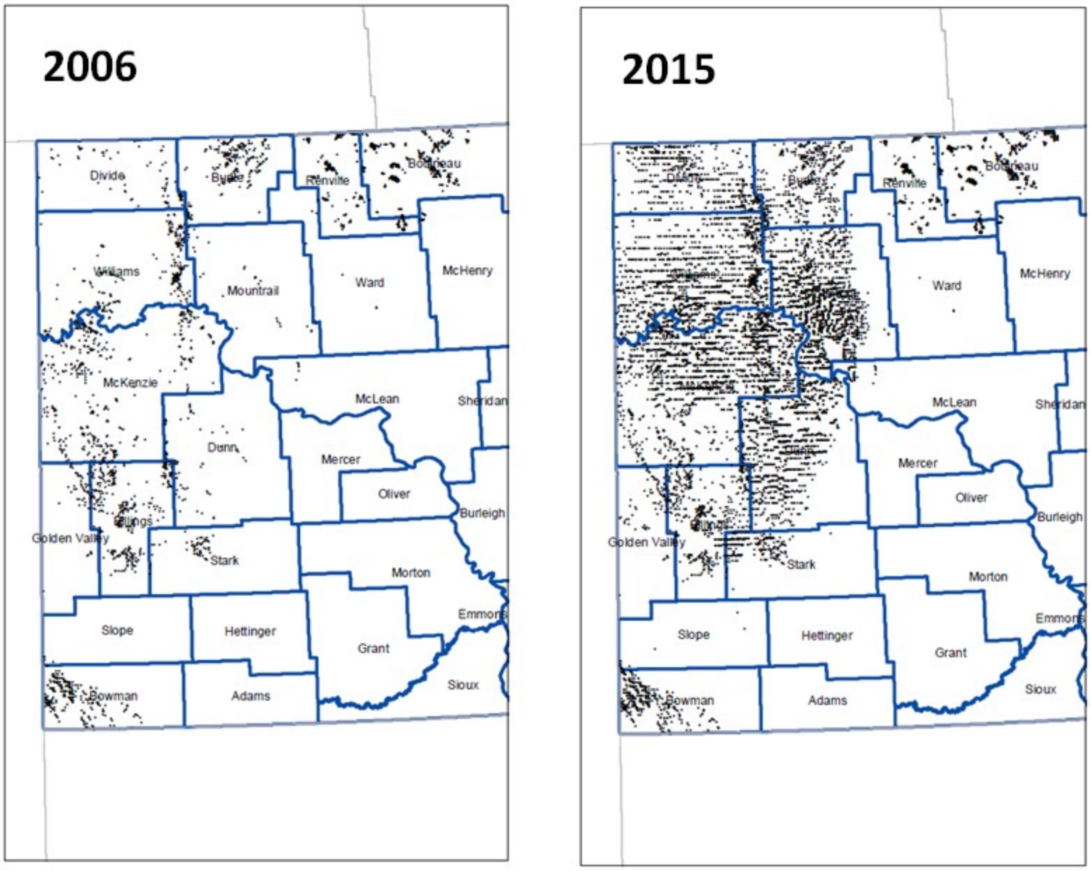
```
                        nPlot=max(dat$Plot_fac),Study_Plot=dat$Plot_fac,
                        Init.date=dat$c.init, Init.date2=dat$c.init^2, Latitude=dat$c.Lat, WILL=dat$WILL,MAGO=dat$MAGO,
                          A.found=dat$c.AFound,
                        SEOW=as.vector(dat$c.SEOW), BPUP=as.vector(dat$c.BPUP), CDen=dat$c.ConDen,
                        VHI.N=dat$c.VHI, VHI.sd.T=dat$c.T.VHIsd,
                        P.PDen=dat$c.P.PondDen, IWetD=as.vector(dat$c.I.WetDist), IWetProp=as.vector(dat$c.I.T.WetProp),
                             IWetSize=as.vector(dat$c.I.N.WetSize),
                        DEM.T=dat$c.T.DEM, Grass1000=dat$c.grass1000,GrassI=dat$NotGrass )
# Specify parameters to save
    dsr.parms.full <- c( "beta.mu", "beta.init", "beta.init2", "beta.age","beta.Lat",#"beta.WILL", "beta.MAGO","beta.year",
                "beta.BPUP","beta.CDen","beta.SEOW",
                "beta.P.PDen",  "beta.IWetD.MAGO",  "beta.IWetD.WILL",
                  "beta.N.IWetSize","beta.T.IWetProp.MAGO","beta.T.IWetProp.WILL",
                "beta.DEM.T.MAGO", "beta.DEM.T.WILL",
                "beta.VHI.N.MAGO", "beta.VHI.N.WILL",
                "beta.VHI.sdT.MAGO", "beta.VHI.sdT.WILL",
                "beta.Grass1000","beta.GrassI",
                "sigma.Study_Yr","sigma.Study_Plot","eta.Study_Yr", "eta.Study_Plot")
     # MCMC settings
        na <- 5000
         ni <- 25000
          nt <- 2
         nb <- 2000
          nc <- 3

     dsr.out <- jagsUI(dsr.data, inits=NULL, dsr.parms.full, "dsr.jags.full", n.adapt = na, n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb)
```

Chapter 2.S3. Correlation plot of standardized variables included in nest survival and habitat selection analyses. Values represent r^2 and those highlighted in yellow exhibit $r^2 \geq 0.3$. Variables highlighted in yellow were included in full nest survival analyses.

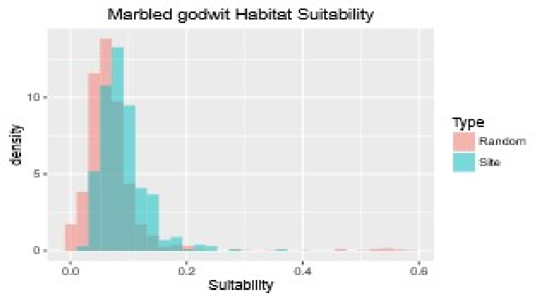

Year
AgeFound
InitDate
Latitude
DuckPrDen
SEOW
PropPondDen
AdjWetDist
AdjWetProp.N
AdjWetProp.T
VHI
VHIsd50
T.VHI
T.VHIsd
DEMsd50
T.DEMsd
Grass.T
Grass1000
Grass2620
0.0012 0.001 6.2e-05 0.49 0.011 0.16 0.025 0.035 0.035 0.059 0.014 0.12 0.055 0.0024 0.0093 0.042 0.12 0.21
0.022 0.0034 0.00005 0.002 0.0015 0.0053 0.0016 0.00095 0.01 0.0052 0.0016 0.0025 0.0011 0.0051 0.00014 1.3e-06 5.5e-06
0.00054 4.2e-07 0.044 0.00098 0.00081 0.00037 0.0053 0.00014 0.00098 0.0015 0.0044 0.00066 0.0039 0.024 0.015 0.0095
0.16 0.0037 0.022 0.0073 0.026 0.0076 0.0061 0.017 0.01 0.0088 0.28 0.30 0.0079 0.0043 0.0032
0.007 0.25 0.083 0.0012 0.00051 0.019 0.0025 0.074 0.051 0.093 0.14 0.095 0.18 0.27
0.036 0.022 0.0037 0.043 0.0014 0.0054 0.0026 0.0077 0.008 0.03 0.034 0.035 0.047
0.11 0.0036 0.0041 0.0091 0.0067 0.047 0.066 1.7e-06 0.016 0.11 0.15 0.23
0.028 0.03 0.0013 0.10 9.2e-05 0.008 0.002 1.1e-06 0.027 0.032 0.024
0.24 0.11 0.15 0.13 0.06 0.011 0.0043 0.028 0.0045 0.00034
0.012 0.10 0.24 0.36 0.00023 0.0012 0.069 0.013 5.7e-07
0.011 0.50 0.003 0.0089 0.019 0.0085 0.00083 0.0091
0.035 0.18 0.0094 0.0021 0.019 0.002 0.00041
0.13 0.0077 0.0026 0.0049 0.022 0.079
0.0052 0.01 0.02 0.00033 0.0069
0.39 0.0012 0.0018 0.0021
0.0087 0.014 0.036
0.77 0.50
0.76
-1 1 2
-4 -1 2
0 1 2 3
0 4 8
-1 1 3 5
-1 1 3 5
-1 2 4
-1 1 3
-2 0
-3 -1 1
-2 0 2
-1 1
-1 1
0 4 8
-10 0 5
-8 -2 2
0 2 4 6
-2 0 1
-2 0

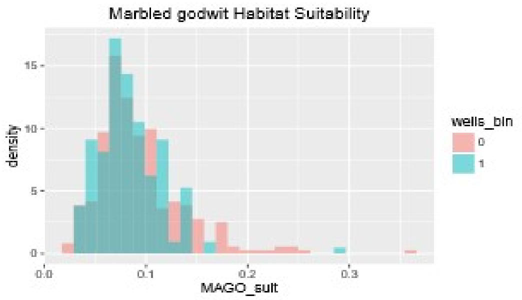
CHAPTER 3 APPENDICES:

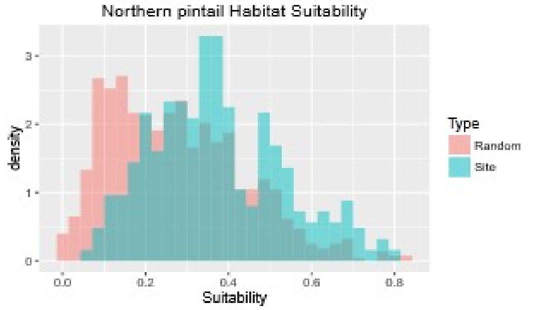
Chapter 3. S1. Oil and gas have been extensively developed in Northwest North Dakota starting in 2007, when the combination of hydraulic fracturing and horizontal drilling made previously tight reserves economically accessible for extraction. Between 2007 and 2015, 9366 wells have been added to the landscape.

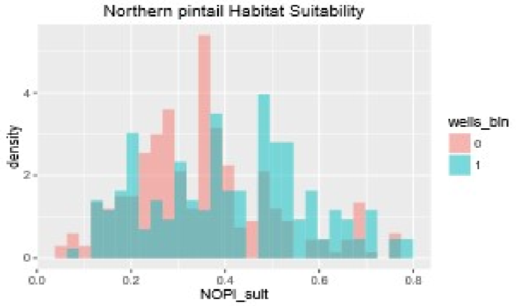


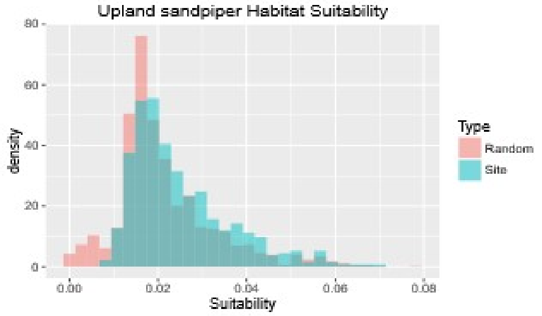
Chapter 3.S2: Distribution of predicted habitat suitability of study sites relative to >1200 randomly selected quarter sections within the study area and between study sites with and without wells by species. Habitat suitability of random and study sites is derived from species-specific habitat suitability models (Niemuth et al. 2017 and Reynolds et al. 2006). Suitability of study sites tended to be fairly similar to random sites (albeit slightly more suitable) and between sites with and without wells.

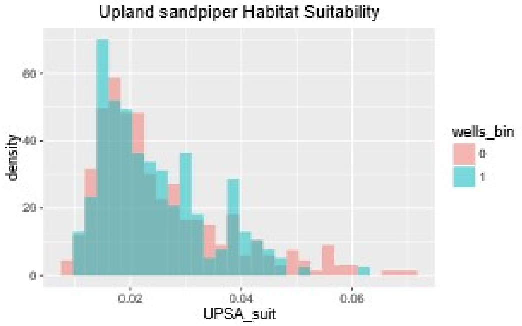

Marbled godwit Habitat Suitability
density
0
5
10
0.0
0.2
0.4
0.6
Suitability
Type
Random
Site

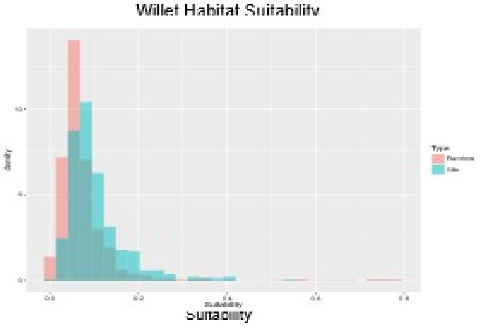

Marbled godwit Habitat Suitability
density
0
5
10
15
0.0
0.1
0.2
0.3
MAGO_suit
wells_bin
0
1

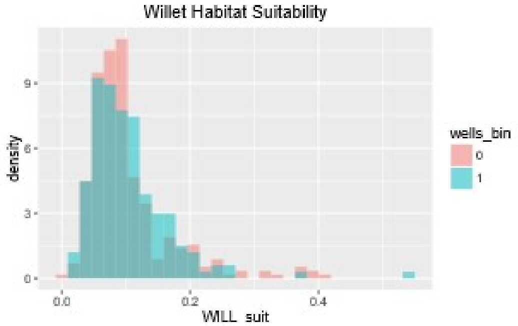

Northern pintail Habitat Suitability
density
0
1
2
3
0.0
0.2
0.4
0.6
0.8
Suitability
Type
Random
Site

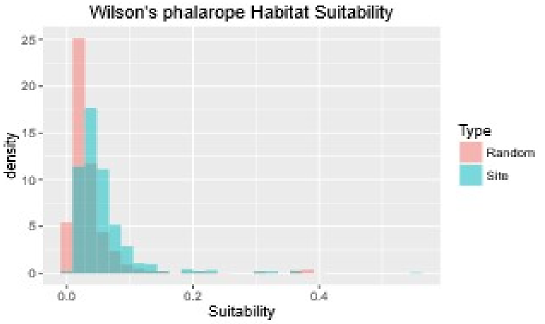

Northern pintail Habitat Suitability
density
0
2
4
0.0
0.2
0.4
0.6
0.8
NOPI_suit
wells_bin
0
1

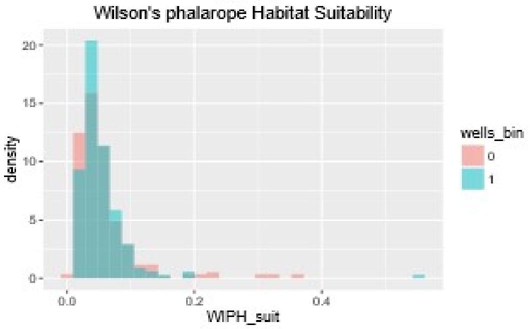

Upland sandpiper Habitat Suitability
density
0
20
40
60
80
0.00
0.02
0.04
0.06
0.08
Suitability
Type
Random
Site


Upland sandpiper Habitat Suitability
density
0
20
40
60
0.02
0.04
0.06
UPSA_suit
wells_bin
0
1


Willet Habitat Suitability
Suitability


Willet Habitat Suitability
density
0
3
6
9
0.0
0.2
0.4
WILL_suit
wells_bin
0
1

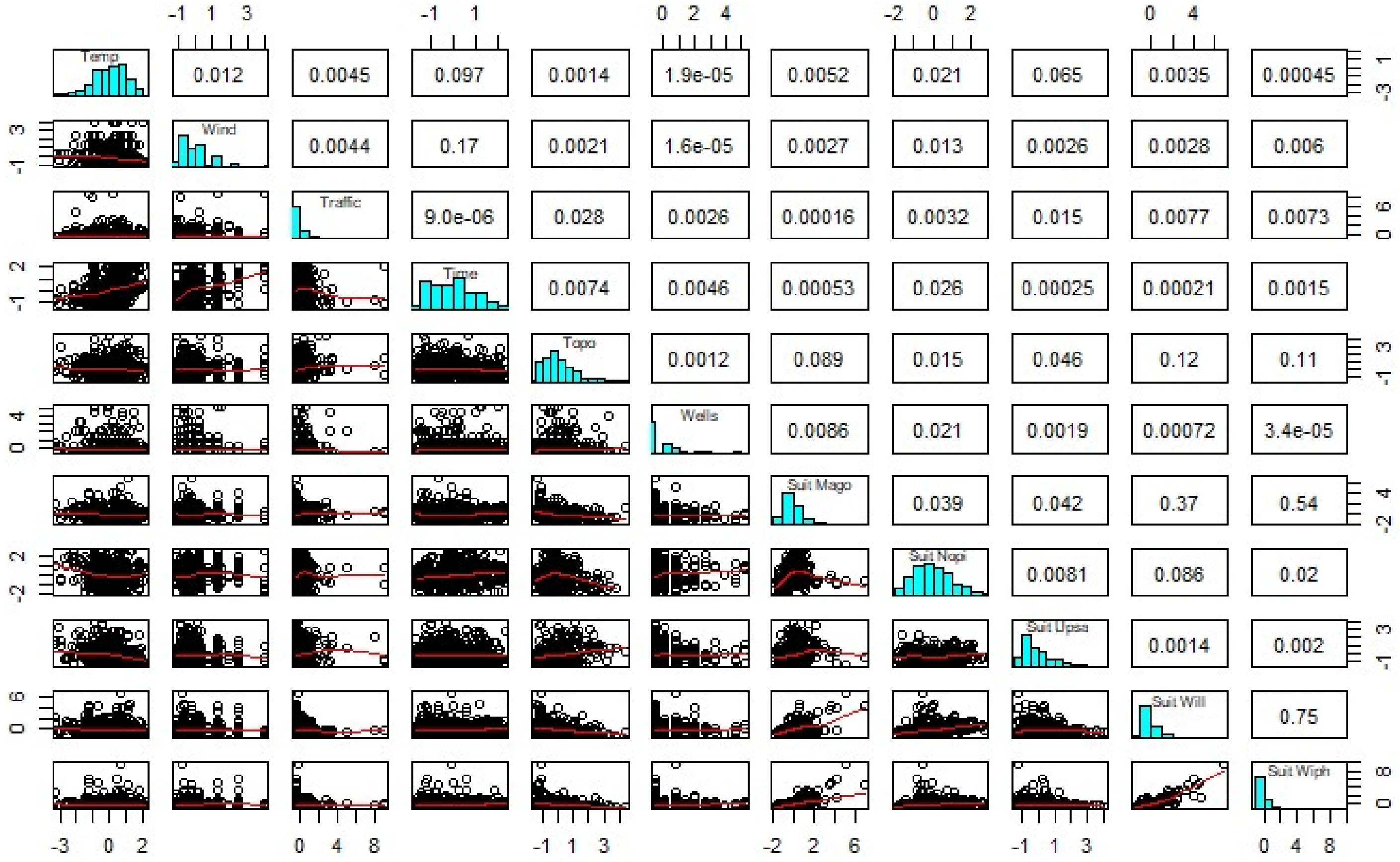

Wilson's phalarope Habitat Suitability
density
0
5
10
15
20
25
0.0
0.2
0.4
Suitability
Type
Random
Site


Wilson's phalarope Habitat Suitability
density
0
5
10
15
20
0.0
0.2
0.4
WIPH_suit
wells_bin
0
1

Chapter 3.S3. Normalization values for variables in breeding pair and brood datasets.

	Breeding Pairs		**Broods**	
	mean	sd	mean	sd
Jdate	171.562	17.145	177.321	12.214
Temp	61.821	7.676	62.946	7.009
Wind	4.789	4.160	4.649	4.251
Traffic	2.350	4.688	2.216	4.435
Time	574.805	116.935	571.443	118.884
Topo	3.648	2.108	3.647	2.113
Wells Site	0.817	1.574	0.779	1.520
Suitability_MAGO	0.090	0.039	0.086	0.038
Suitability_NOPI	0.371	0.159	0.355	0.150
Suitability_UPSA	0.025	0.011	0.023	0.011
Suitability_WILL	0.103	0.065	0.099	0.064
Suitability_WIPH	0.056	0.051	0.054	0.050
MAGO_Home Range Wells	7.710	7.858	7.282	7.829
NOPI_Home Range Wells	17.615	15.846	16.540	15.681
WILL_Home Range Wells	4.229	4.878	4.049	4.884

Chapter 3.S4: Correlation (R-squared) value and pair plots of standardized occupancy and detection variables.



Chapter 3.S5. Multi-species SSVS occupancy code. Model code for full multi-species breeding pair occupancy model with stochastic search variable selection indicators.

```
sink("ms_FULL_ind.txt")
cat("
  model {

  # Uniform priors (logit scale) for across species means
          psi.mean ~ dunif(-4, 4)  # mean occupancy across species
          psi.SD ~ dunif(0.05, 2) # mean sd of occupancy across species
          psi.tau <- pow(psi.SD, -2)

          p.mean ~ dunif(-4, 4)  # mean detection probability across species
          p.SD ~ dunif(0.05, 2)  # mean sd of detection probability across species
          p.tau <- pow(p.SD, -2)

  # generate species specific means on logit scale
          for (j in 1:spp){ # for each species
          logit.psi.spp[j] ~ dnorm(psi.mean,psi.tau)
          logit.p.spp[j] ~ dnorm(p.mean,p.tau)

  # Species-specific Covariate Priors
    #Occupancy Priors
          alpha0[j]<-logit.psi.spp[j]  # Intercept
          alpha.Suit[j]~dunif(-20,20)  # Habitat Suitability (Species specific varible)
          alpha.Traffic[j]~dunif(-20,20) # Traffic volume (site specific variable)
          alpha.Wells200[j]~dunif(-20,20) # Number of wells (site specific variable)
          alpha.Jdate[j]~dunif(-20,20) # Date to account for progression of breeding season
        behaviors
         alpha.PrecOcc[j] ~dunif(-20,20) # Previous known occupancy by that species at a site
  #Detection Priors without indicators
        beta0[j]<-logit.p.spp[j]  # intercept
        beta.Survey[j]~dunif(-20,20) # indicator for transect survey type
   #Indicators on detection priors. The “gamma.___” terms indicate that a variable should be
included if >0.5, functioning as a similar metric to p-values based on alpha=0.5
           beta.Traffic[j]~dnorm(0,tau[ind.Traffic[j]]) # traffic volume
            gamma.Traffic[j]<-ind.Traffic[j]-1
            ind.Traffic[j]~ dcat(p_ind[ ])
```

```
 beta.Topo[j]~dnorm(0,tau[ind.Topo[j]])  #Topography of site
   gamma.Topo[j]<-ind.Topo[j]-1
   ind.Topo[j]~ dcat(p_ind[ ])

beta.Wind[j]~dnorm(0,tau[ind.Wind[j]]) # ~Wind speed during survey
   gamma.Wind[j]<-ind.Wind[j]-1
ind.Wind[j]~ dcat(p_ind[ ])

beta.Temp[j]~dnorm(0,tau[ind.Temp[j]]) # Temperature at start of survey
   gamma.Temp[j]<-ind.Temp[j]-1
ind.Temp[j]~ dcat(p_ind[ ])

beta.Jdate[j]~dnorm(0,tau[ind.Jdate[j]]) # Date, to account for phenology, behavior
   gamma.Jdate[j]<-ind.Jdate[j]-1
ind.Jdate[j]~ dcat(p_ind[ ])

beta.Jdate2[j]~dnorm(0,tau[ind.Jdate2[j]]) # Date, quadratic term
   gamma.Jdate2[j]<-ind.Jdate2[j]-1
ind.Jdate2[j]~ dcat(p_ind[ ])

beta.Survey.Traffic[j]~dnorm(0,tau[ind.Survey.Traffic[j]]) #Survey type-traffic interaction
   gamma.Survey.Traffic[j]<-ind.Survey.Traffic[j]-1
ind.Survey.Traffic[j]~ dcat(p_ind[ ])

beta.ASM[j]~dnorm(0,tau[ind.ASM[j]]) # Observer
gamma.ASM[j]<-ind.ASM[j]-1
ind.ASM[j]~ dcat(p_ind[ ])

beta.LRL[j]~dnorm(0,tau[ind.LRL[j]]) # Observer
gamma.LRL[j]<-ind.LRL[j]-1
ind.LRL[j]~ dcat(p_ind[ ])

beta.MEW[j]~dnorm(0,tau[ind.MEW[j]]) # Observer
gamma.MEW[j]<-ind.MEW[j]-1
ind.MEW[j]~ dcat(p_ind[ ])

beta.SMC[j]~dnorm(0,tau[ind.SMC[j]]) # Observer
gamma.SMC[j]<-ind.SMC[j]-1
ind.SMC[j]~ dcat(p_ind[ ])
```

```
              }
   # Indicator priors
     p_ind[1]<-1/2
     p_ind[2]<-1-p_ind[1]
          tau[1]<-tau_in
          tau[2]<-tau_in/1000
          tau_in<-pow(sd_beta,-2)
          sd_beta~dunif(0,100)

  # Likelihood ==============================================
         for (i in 1:S) { # sites
         for (j in 1:spp){ # species
    # Occupancy Function (species specific): is site i occupied by spp j?
          z[i,j] ~ dbern(psi[i,j])
          logit(psi[i,j])<-alpha0[j] + alpha.Suit[j]*suit[i,j] + alpha.Traffic[j]*Traffic[i]
                         + alpha.Wells200[j]*Wells200[i]
                         + alpha.Jdate[j]*Jdate[i]+beta.Jdate2[j]*(Jdate[i]*Jdate[i])
                         + alpha.PrevOcc[j]*PrevOcc[i,j]

   # Detection Function (species specific)
  for (r in 1:3) {  # Surveys
          y[i,(j-1)*3+r] ~ dbern(z[i,j]*p1[i,(j-1)*3+r]) # prob of detecting spp
          logit(p1[i,(j-1)*3+r])<-beta0[j] + beta.Survey[j]*survey.type[r] +
            beta.ASM[j]*ASM[i] + beta.LRL[j]*LRL[i] + beta.MEW[j]*MEW[i] +
        beta.SMC[j]*SMC[i] +
            beta.Traffic[j]*Traffic[i] +
            beta.Topo[j]*Topo[i] + beta.Wind[j]*Wind[i] + beta.Temp[j]*Temp[i] +
            beta.Survey.Traffic[j]*survey.type[r]*Traffic[i]
    } # end r= Surveys
          } # end j= Species
          } # end S= Sites
    # Derived Quantities (back transformed occupancy and detection estimates)
          for(l in 1:spp){
          logit(psi.spp.pred[l])<- logit.psi.spp[l] #occupancy
          logit(p.spp.pred.pc[l])<-logit.p.spp[l]  # detection- point count
          logit(p.spp.pred.tr[l])<-logit.p.spp[l]+beta.Survey[l] # detection- transect
          }
    } # end jags model
  ",fill = TRUE)
sink()
```

Chapter 3.S6. Multi-species brood occupancy model code. Model code for full multi-species brood occupancy model with shared detection and occupancy covariates retained after stochastic search variable selection.

```
sink("ms_FULL_Broods_redb2.txt")
cat("
  model {

  # Uniform priors (logit scale)
 #Mean occupancy and detection estimates across species
  psi.mean ~ dunif(-4, 4)
  psi.SD ~ dunif(0.05, 2)
  psi.tau <- pow(psi.SD, -2)

  p.mean ~ dunif(-4, 4)
  p.SD ~ dunif(0.05, 2)
  p.tau <- pow(p.SD, -2)

  # generate species specific means on logit scale
  for (j in 1:spp){
  logit.psi.spp[j] ~ dnorm(psi.mean,psi.tau)
   # ===Species-specific Covariate Priors ==============
  #Occupancy
        alpha0[j]<-logit.psi.spp[j] # Intercept
    #Detection
         beta.Survey[j]~dunif(-20,20) # indicator for transect survey type
         }
         logit.p~ dnorm(p.mean,p.tau)
         beta0<-logit.p
# == Non species specific priors==
         alpha.Suit~dunif(-20,20) # suitability- species specific variable, shared coefficient
         alpha.Traffic~dunif(-20,20)  # Traffic volume
         alpha.Wells200~dunif(-20,20) # number of wells
         alpha.Jdate~dunif(-20,20) # date
         alpha.PrevOcc~dunif(-20,20) # PrevOcc
         beta.Topo~dunif(-20,20) # topography
         beta.LRL~dunif(-20,20) # observe
 # Likelihood====================================
  for (i in 1:S) { # sites
```

```
  for (j in 1:spp){ # species
    # Occupancy
          z[i,j] ~ dbern(psi[i,j]) # is site occupied by spp j?
          logit(psi[i,j])<-alpha0[j] + alpha.Suit*suit[i,j] + alpha.Traffic*Traffic[i] +
          alpha.Wells200*Wells200[i] + alpha.Jdate*Jdate[i] + alpha.PrevOcc*PrevOcc[i,j]
    # Detection
        for (r in 1:3) {  # Surveys
          y[i,(j-1)*3+r] ~ dbern(z[i,j]*p1[i,(j-1)*3+r]) # prob of detecting spp
          logit(p1[i,(j-1)*3+r])<-beta0 + beta.Survey[j]*survey.type[r] +
          beta.Topo*Topo[i] + beta.LRL*LRL[i]

          } # end r= Surveys
          } # end j= Species
          } # end S= Sites
# Derived Quantities
        for(l in 1:spp){
          logit(psi.spp.pred[l])<- logit.psi.spp[l] #back-transformed occupancy
          logit(p.spp.pred.tr[l])<-logit.p+beta.Survey[l] #back-transformed transect detection
          }
            logit(p.pred.pc)<-logit.p #back-transformed point count detection
          } # end jags model
          ",fill = TRUE)
       sink()
# MCMC settings
       ni <- 50000  # total iterations
       nt <- 2     # thinning rate (save every nth simulation)
       nb <- 5000  # discard first 2000 as burn-in (crappy estimates prior to convergence)
       nc <- 3     # replicate chains (to assess convergence)
       na <- 1000  # n.adapt
#Initial values
       zst <- matrix(NA, nrow = nrow(DM.b), ncol = spp)    # create matrix for initial values
       for (i in 1:nrow(DM.b)){
        for (j in 1:spp){
          zst[i,j] <- ifelse(is.infinite(max(DM.b[i,((j-1)*3+1):((j-1)*3+3)], na.rm=T)),NA,
                    max(DM.b[i,((j-1)*3+1):((j-1)*3+3)], na.rm=T))# if seen, set initial value for
       z[i,j] to 1
        }
       }
       inits <- function() list(z=zst, psi.mean=runif(1,-4,4), p.mean=runif(1,-4,4),
                     psi.SD=runif(1,0.05,2), p.SD=runif(1,0.05,2))
```

Chapter 3.S7. Table of model coefficient and standard deviation estimates. Gray shading indicates 80% credible intervals that do not include zero.

		Coefficient					SD				
Model	**Variables**	**MAGO**	**NOPI**	**UPSA**	**WILL**	**WIPH**	**MAGO**	**NOPI**	**UPSA**	**WILL**	**WIPH**
Site Breeding Pair	Intercept	-1.311	0.157	0.229	-0.449	-0.181	0.185	0.315	0.156	0.241	0.202
	Suit	0.075	0.421	0.266	0.049	0.181	0.134	0.218	0.156	0.141	0.139
	Traffic	0.111	-0.247	0.111	-0.394	0.11	0.177	0.176	0.197	0.221	0.397
	Wells	-0.092	0.142	0.077	0.07	-0.328	0.143	0.185	0.143	0.172	0.146
	Julian date	-0.307	-1.309	0.196	-0.102	-0.84	0.167	0.288	0.179	0.153	0.164
	Previous Occupancy	0.679	0.253	2.721	-		0.6	0.456	4.321	-	0.43
Home Range Breeding Pair	Intercept	-1.294	1.217	-	-1.035	-	0.461	0.849	-	0.438	-
	Suit	-0.013	0.674	-	0.466	-	0.468	0.386	-	0.439	-
	Roads	-0.091	-0.33	-	-0.203	-	0.306	0.49	-	0.333	-
	Wells	-0.137	0.001	-	-0.114	-	0.218	0.33	-	0.212	-
	Julian date	-0.096	-2.659	-	-0.277	-	0.255	0.487	-	0.244	-
	Previous Occupancy	-0.592	-0.972	-	-	-	0.802	0.676	-	-	-
Site Brood Tending (Traffic)	Intercept	-3.213	-2.587	-3.035	-2.725	-2.915	0.291	0.411	0.258	0.432	0.359
	Suit	-0.041	-0.041	-0.041	-0.041	-0.041	0.107	0.107	0.107	0.107	0.107
	Traffic	-0.568	0.2	-0.518	-1.347	-1.57	0.467	0.302	0.517	0.751	0.705
	Wells	-0.096	-0.096	-0.096	-0.096	-0.096	0.131	0.131	0.131	0.131	0.131
	Julian date	0.229	0.229	0.229	0.229	0.229	0.123	0.123	0.123	0.123	0.123
	Previous Occupancy	1.323	1.323	1.323	1.323	1.323	0.296	0.296	0.296	0.296	0.296
Site Brood Tending (Wells)	Intercept	-3.168	-2.663	-2.987	-2.651	-2.901	0.291	0.411	0.258	0.432	0.359
	Suit	-0.02	-0.02	-0.02	-0.02	-0.02	0.107	0.107	0.107	0.107	0.107
	Traffic	-0.354	-0.354	-0.354	-0.354	-0.354	0.467	0.302	0.517	0.751	0.705
	Wells	-0.135	-0.184	0.098	0.02	-1.326	0.131	0.131	0.131	0.131	0.131
	Julian date	0.225	0.225	0.225	0.225	0.225	0.123	0.123	0.123	0.123	0.123
	Previous Occupancy	1.328	1.328	1.328	1.328	1.328	0.296	0.296	0.296	0.296	0.296

Chapter 3.S8. The proportion of each type of initial detection cue by species and survey type.

Point Count	Audio	Visual	Total detections
MAGO	0.61	0.39	109
NOPI	0	1	204
UPSA	0.83	0.17	246
WILL	0.51	0.49	109
WIPH	0.08	0.92	246

Transect	Audio	Visual	Total detections
MAGO	0.56	0.44	146
NOPI	0	1	295
UPSA	0.7	0.3	312
WILL	0.44	0.56	167
WIPH	0.03	0.97	1577

Chapter 3.S9. Habitat suitability of observed marbled godwits (MAGO) and willets (WILL) (dark gray) relative to suitability of 1500 random points drawn from the study landscape (light gray). Two sample t-tests indicated differences between observation and random points with $p<0.001$.