

SHOREBIRD MIGRATORY STOPOVER RESPONSES TO LOCAL AND
REGIONAL CHANGE: HABITAT DECISIONS IN A VANISHING LANDSCAPE

by

Caitlyn Gillespie

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Caitlyn Gillespie, M.S.

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Adviser: Joseph J. Fontaine

Understanding the consequences of anthropogenic change for migratory species is challenging because although they have evolved to cope with environmental uncertainty, migrants still rely on predictable relationships within and among habitats to make informed decisions. *Calidris* shorebirds rely on ephemeral wetlands during northward migration through mid-continental North America, where favorable habitat conditions are annually and regionally unpredictable and increasingly altered by land-use change. During spring 2013 and 2014, we assessed *Calidris* habitat use in the Rainwater Basin (RWB) and the Prairie Pothole Region (PPR) at both local and landscape scales. Although anthropogenic change has altered the wetland landscape in both regions, the scope and scale of anthropogenic change is more pronounced in the RWB. Our results indicate that invertebrate abundance predicted occupancy, but not abundance, of *Calidris* shorebirds at wetlands in the RWB. Regionally, we find that habitat structure which predicts shorebird occupancy and abundance is similar in both regions, but wetlands in the PPR supported a higher abundance of *Calidris* shorebirds than wetlands in the RWB. Our results suggest that the overall availability of wetlands on the landscape limits shorebird abundance independent of individual wetland quality, thus management efforts

should consider not only the structure and function of individual wetlands, but also entire networks of managed habitat across the landscape.

We also tested for variance in abundance estimates within and among wetlands by employing both visual point and flush surveys. We find considerable variation in predicted relationships between shorebird abundance and habitat attributes depending on method, observer, and site; variance also increased with area and vegetative characteristics of wetlands. Our results draw attention to potential weaknesses associated with traditional shorebird sampling approaches, as it is unclear whether errors in detection or shifts in habitat use account for variation among surveys. We urge further examination of sources of error in shorebird surveys in order to establish meaningful patterns relevant for the management of wetland habitat and the conservation of migratory populations.

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Table of Contents

Acknowledgements.....	iv
Table of Contents	vi
List of Tables and Figures.....	viii
 Chapter 1: Shorebird Migratory Stopover Responses to Local and Regional	
Change: Habitat Decisions in a Vanishing Landscape	1
Abstract	1
Introduction	2
Methods	6
Study sites.....	6
Survey methods	7
Local use.....	8
Landscape use.....	10
Results	12
Local use.....	12
Landscape use.....	13
Discussion	14
Tables and Figures	25
Literature Cited	33
Appendix 1	40

Chapter 2: Are Our Survey Methods Adequate for Changing Landscapes? An	
Assessment of Repeatability of Shorebird Surveys in Heterogeneous Wetland	
Habitats	41
Abstract	41
Introduction	42
Methods	44
Study sites	44
Survey methods	45
Analysis	45
Results	47
Discussion	49
Tables and Figures	56
Literature Cited	61

List of Tables and Figures

Chapter 1

Table 1.	Species and total numbers of all <i>Calidris</i> observed in both study regions in 2013 and 2014	25
Table 2.	Results of models predicting <i>Calidris</i> occupancy and abundance in wetlands in the RWB and the PPR	26
Table 3.	Results of models predicting <i>Calidris</i> occupancy and abundance in relation to invertebrate abundance in wetlands in the RWB and results of the model predicting cover types associated with invertebrate abundance in plots	27
Table 4.	Results of models predicting <i>Calidris</i> occupancy and abundance at wetlands between the RWB and the PPR in both years	27
Figure 1.	Relationships between wetland attributes and <i>Calidris</i> occupancy at wetlands in the RWB (a-c) and the PPR (d)	28
Figure 2.	Relationships between wetland attributes and <i>Calidris</i> abundance at wetlands in the RWB (a-b) and the PPR (c-f)	29
Figure 3.	<i>Calidris</i> occupancy (a) and abundance (b) in relationship with invertebrate abundance at wetlands in the RWB	30
Figure 4.	<i>Calidris</i> abundance at wetlands by year in the RWB and the PPR	31
Figure 5.	Predicted <i>Calidris</i> occupancy (a) and abundance (b) at wetlands across years between the RWB and the PPR	32

Chapter 2

- Table 1. Results of models predicting *Calidris* abundance at wetlands according to point and perimeter surveys in relation to observed wetland cover types56
- Figure 1. Count estimates of *Calidris* shorebirds differed between observers independent of survey method, and differences between counts were not predicted by any habitat attributes.....57
- Figure 2. Predicted relationships between habitat characteristics and *Calidris* abundance at wetlands according to point surveys versus perimeter surveys based on our original models with site ID included as a random effect.....58
- Figure 3. Predicted relationships between habitat characteristics and *Calidris* abundance according to point surveys versus perimeter surveys based on our second set of models which did not include site ID as a random effect59
- Figure 4. Variance in the residuals of the model comparing estimates of *Calidris* abundance among the four surveys at each wetland60

Chapter 1

Shorebird Migratory Stopover Responses to Local and Regional Change: Habitat Decisions in a Vanishing Landscape

Abstract

Understanding the consequences of anthropogenic change to stopover habitat for migratory species is challenging because while selection has favored the evolution of plastic responses to environmental change, migratory species still rely on predictable relationships within and among habitats to make informed decisions. The inland populations of *Calidris* shorebird species rely on ephemeral wetlands during northward migration through mid-continental North America, where favorable habitat conditions are annually and regionally unpredictable and increasingly altered by land-use change. To establish how landscape alteration influences *Calidris* habitat selection during spring migration, we assessed migratory bird abundance in response to both local habitat attributes and intra- and inter- annual landscape-scale habitat availability. During spring 2013 and 2014, we documented *Calidris* habitat use in the Rainwater Basin (RWB) and the Prairie Pothole Region (PPR) at both local and landscape scales. Although anthropogenic change has altered the wetland landscape in both regions, the scope and scale of anthropogenic change is more pronounced in the RWB. Our results indicate that invertebrate abundance predicted occupancy, but not abundance, of *Calidris* shorebirds at wetlands in the RWB. Regionally, we find that habitat structure which predicts shorebird occupancy and abundance is similar in both regions, but wetlands in the PPR supported a

higher abundance of *Calidris* shorebirds than wetlands in the RWB. Our results suggest that the overall availability of wetlands on the landscape limits shorebird abundance independent of individual wetland quality, thus management efforts should consider not only the structure and function of individual wetlands, but also entire networks of managed habitat across the landscape.

Introduction

Long-distance migration is an energetically demanding period in the annual cycle of many migratory species, and represents a strong source of mortality in bird populations (Sillet & Holmes 2002; Newton 2006). Finding and taking advantage of stopover habitat for rest and refueling *en route* is essential for the success of migratory journeys; yet individuals must frequently make habitat decisions in unfamiliar environments under severe time and energetic constraints (Hutto 1985; Loria & Moore 1990; Moore & Aborn 2000; Petit 2000). Selection has thus favored the evolution of migratory strategies which minimize risk associated with environmental uncertainty; for example, many populations time migratory movements to coincide with regional and seasonal peaks in resource abundance (Moore *et al* 1995), and use local habitat cues, rather than sampling habitats directly, to quickly assess resource availability and overall suitability of unfamiliar habitats (Hutto 1985; Moore & Aborn 2000). Thus while migratory species have evolved plasticity which allows for quick and effective selection of habitat in unfamiliar locations, they still rely on predictable relationships within and among habitats to make informed decisions (e.g., McGrath, Van Riper III & Fontaine 2009). Anthropogenic disturbance

which alters the availability, distribution, and phenology of stopover habitat can therefore strain migratory populations accustomed to historically predictable peaks in resource abundance during migratory stopover through habitat loss (Moore *et al* 1995; Weber, Houston & Ens 1999), and mismatches in resource and migratory phenology (Both *et al* 2006; Both *et al* 2010; Jones & Cresswell 2010). Nevertheless, it often remains unclear how migratory species may respond to anthropogenic alterations to stopover habitat conditions because selection has favored the evolution of plastic responses to environmental change, allowing migratory species to make stopover decisions despite environmental uncertainty (Moore *et al* 1995; Moore & Aborn 2000; Parrish 2000; Petit 2000).

The inland populations of *Calidris* shorebirds rely on highly dynamic and unpredictable ephemeral wetland systems during northward migration. Because wetland habitat conditions are subject to local weather and climate conditions, the availability, distribution, and quality of suitable wetland habitat in the Great Plains is unpredictable (Skagen, Granfors & Melcher 2008). Favorable habitat conditions for *Calidris* are often fleeting, as shallow-water habitat, invertebrate abundance, and vegetation structure change rapidly in response to local weather events and the ensuing onset of spring (Kantrud *et al* 1989; Albanese & Davis 2012). Moreover, physical and biotic conditions such as soil type, hydrology, and vegetative cover all influence local habitat conditions and wetland suitability for *Calidris* and vary considerably across the midcontinent (Davis & Smith 1998; Anderson & Smith 2000; Euliss *et al* 2004). The dynamics of heterogeneity in weather and climate conditions overlaid across a landscape that varies in

physical and biotic communities together create a heterogeneous and diverse landscape that changes annually and seasonally. In response, *Calidris* have evolved highly flexible migratory behaviors which allow for changes in habitat decisions across multiple spatial and temporal scales (Skagen & Knopf 1994b; Skagen 2006). So although *Calidris* prefer shallow wetlands with abundant mudflat (Colwell & Oring 1988; Skagen & Knopf 1994b; Davis & Smith 1998) and generally time migratory movements to coincide with seasonal peaks in invertebrate abundance (Stutzman & Fontaine 2015), *Calidris* are highly plastic in the timing of migratory events (Skagen & Knopf 1994a), the habitats they occupy (Skagen & Knopf 1994b), the foods they exploit (Skagen & Omen 1996; Davis & Smith 2001), and the foraging behaviors they express (Davis & Smith 1998, Stutzman 2012). However, as anthropogenic change has altered wetland conditions throughout the central plains (Dahl 2000; Dahl 2014), it remains unclear if behavioral flexibility is sufficient to overcome the costs of limited habitat availability, reduced habitat quality, and alterations in resource and migratory phenology.

Although local habitat conditions clearly affect stopover decisions (Moore, Kerlinger & Simons 1990; Moore & Aborn 2000; Petit 2000), theory (e.g., Hutto 1985), and recent empirical studies (e.g., Buler, Moore & Woltmann 2007; Jorgenson *et al* 2014) suggest that factors acting at larger spatial scales may influence the distribution of species on the landscape. Thus the availability of wetlands within a region may act to affect habitat decisions independent of the local conditions. Because habitat availability changes both annually and within a single migratory season, ephemeral wetlands are an ideal system for examining how changing landscape conditions influence habitat

decisions, as *Calidris* shorebirds may alter stopover decisions as wetland availability changes. Indeed, shorebirds are known to respond to dense networks of wetland habitat (Skagen & Knopf 1994b; Farmer & Parent 1997; Neimuth & Solberg 2003; Taft & Haig 2006), and it is likely that wetland abundance on the landscape functions as an important cue of local habitat suitability in a spatio-temporally variable system (Webb *et al* 2010; Albanese & Davis 2012; Albanese & Davis 2013). However, within highly altered landscapes, the availability and distribution of wetlands with appropriate habitat characteristics are highly constrained by total wetland availability, likely increasing the severity of the requisite trade-offs dictating shorebird occupancy and abundance. Still, without consideration of the trade-offs expressed in response to both local and landscape-level resource availability, it remains unclear to what extent management may mitigate the consequences of escalating change because it is yet unknown how shorebirds make habitat decisions in response to the simultaneous pressure of overall limitation in habitat availability, alterations in key attributes of the remaining habitat, and variation in resource or migratory phenology.

Here, we take advantage of regional and annual variation in wetland availability to examine the stopover decisions of migratory *Calidris* shorebirds in response to resource availability at both local and landscape scales. While *Calidris* habitat preferences are well established (Colwell & Oring 1988; Skagen & Knopf 1994b; Davis & Smith 1998), alteration of key wetland habitat attributes may force trade-offs in habitat decisions to mediate the costs of limited resource availability in highly altered landscapes. Our goals were thus to assess: 1) the local wetland attributes predicting

Calidris habitat use and 2) the importance of landscape-level habitat availability on stopover decisions and habitat use during spring migration.

Methods

Study sites

We monitored *Calidris* spring migratory stopover ecology in two regions: the Rainwater Basin (RWB) in south-central Nebraska (Hall, Adams, Clay, Seward, Franklin, Kearney, Hamilton, Saline, York, Fillmore, Phelps, and Gosper counties) and a portion of the Prairie Pothole Region (PPR) (Charles Mix, Brule, Aurora, and Douglas counties). The RWB historically consisted of a network of over 200,000 acres of temporary playa wetlands stretching across much of south-central Nebraska (Bishop & Vrtiska 2008). Large-scale conversion to agriculture has left fewer than 10% of the historical wetland basins intact, most of which have compromised hydrological regimes (Bishop & Vrtiska 2008). As such wetland habitat in the RWB is fragmented and concentrated in a few actively managed public areas (Bishop & Vrtiska 2008). Located 300km north of the RWB, the southern PPR is another ephemeral wetland system which acts as an important stopover habitat for migratory *Calidris* shorebirds. While land-use change has also diminished and altered the function of wetlands in the PPR (Dahl 2000; Dahl 2014) wetland function more closely resembles historical conditions as anthropogenic change is considerably less advanced in the PPR when compared to the RWB (Bishop & Vrtiska 2008; Dahl 2014).

Survey methods

We conducted visual surveys of *Calidris* shorebirds from late March through mid-June of 2013 and 2014, encompassing the entire spring migratory period for *Calidris* species in both regions (Skagen, Grandfors & Melcher 2008; Webb *et al* 2010). In the RWB, we focused our sampling on public management areas, which comprised the majority of the water available during the study period (Gillespie per. obs.). Because of the abundance of wetlands in the PPR, we were able to conduct road-side surveys of wetlands along transects 25km long that were selected based on a systematic random sampling protocol (following Stutzman & Fontaine 2015). We conducted surveys in both regions every 7-10 days, a sampling period that exceeds the typical stopover duration of *Calidris* (Skagen & Knopf 1994a), minimizing our chances of recounting individuals while allowing us to assess changes in the migratory population. We used binoculars and a spotting scope to count and identify all shorebirds at each wetland within a 10-minute sampling window, which allowed us to control for sampling effort and detection probability (following Stutzman 2012, but see Chapter 2). To ensure we were able to detect birds that were present, 95% of surveys were conducted within 200m of the wetland and surveyed wetlands were separated by at least 0.8km to minimize recounting of the same individuals at multiple wetlands. Migratory periods overlap, but do not coincide among *Calidris* species (Skagen, Grandfors & Melcher 2008); therefore, to widen our scope and inference and to control for any possible observer errors in species identification we grouped *Calidris* species together for analyses.

Local use

Habitat attributes

The availability and height of vegetation relative to shallow water and mudflat often predicts *Calidris* occupancy and abundance (Colwell & Oring 1988; Skagen & Knopf 1994b; Davis & Smith 1998; Stutzman 2012), so we recorded wetland attributes by visually estimating the proportion of each of four cover types at the wetland (water, mud, green vegetation, and brown vegetation or litter) and the percentage of vegetation in each of three height classes (less than 15cm, between 15 and 60 cm, and greater than 60 cm). In the RWB, we estimated wetland size using a handheld GPS to record the edge of the inundated wetland habitat at four points around the wetland parameter and recorded the distance to the edge of the open water from each to define the edge of the habitat. Due to logistical constraints associated with access to private lands in the PPR we used a rangefinder to visually estimate the total ponded area of the wetland basin and the distance between the open water and edge of the inundated habitat (following Stutzman 2012). Although less precise, visual estimates of wetland area are widely adopted and known to correlate with habitat decisions of a range of waterbirds, including *Calidris* (e.g., Niemuth *et al* 2006).

In the RWB, we also assessed food availability for migratory *Calidris* by measuring invertebrate abundance at a subset of focal wetlands. Following a bird survey, we randomly placed three to five 3m x 3m sample plots within the inundated wetland area, each separated by at least 20m. Using a 5cm diameter soil core we took three samples from each plot which we washed through a 0.5mm soil sieve. We counted

benthic invertebrates from each core and weighed the total wet invertebrate sample on a digital scale accurate to 0.001g. *Calidris* shorebirds express high dietary plasticity (Skagen & Omen 1996), so we deemed classification to species unnecessary. In each plot we visually estimated vegetative cover (litter, water, dry soil, wet soil, and vegetation) and measured vegetation height (following Stutzman 2012) at three random locations (Daubinmire 1959) as well as soil conditions (pH, moisture content, temperature, compactness) at a 5cm depth in the center of each plot using a Kelway soil meter, standard soil thermometer, and a soil penetrometer. We calculated the slope of the shorebird foraging habitat by measuring water depth both 1 meter and 5 meters towards the water from the edge of each sample plot.

We identified relevant local wetland habitat attributes associated with shorebird occupancy and abundance using generalized linear mixed models (GLMMs) with either a binomial or Poisson distribution. We identified separate models for each region to explore for unique habitat decisions between regions. We examined the probability of occupancy after converting all observations to simple presence/absence; wetlands with at least one bird present were considered “occupied.” Due to a high number of unoccupied wetlands, we only analyzed abundance at wetlands with at least one bird present. We used a global model that originally included day and site as random effects, year as a fixed effect, and all biologically relevant variables and interactions; we identified and removed highly correlated terms and interactions with a variance inflation factor (VIF) greater than 2 (Zuur, Ieno & Smith 2007). We identified a global model to test for occupancy and abundance within each region that included percent mud, percent total

vegetation, wetland size, a wetland size by percent mud interaction, percent of vegetation between 15cm- 60cm, and year, with the survey site and day included as random effects. We then used backwards selection from the global model to identify final GLMMs explaining occupancy and abundance at wetlands in each region and used a Wald χ^2 test for significance of the fixed effects in the final models (Bolker *et al* 2009). We developed models using program R (R Core Team 2014), package ‘lme4’ (Bates *et al* 2014). We used estimates calculated using package ‘effects’ (Fox 2003) to graph predictions from the final models.

To assess whether food abundance predicted shorebird occupancy and abundance, we used GLMMs with a binomial or a Poisson distribution, with percent mud and year as fixed effects and day and site as random effects. We then used GLMMs with a Poisson distribution to explore which factors predicted invertebrate abundance within plots using the same approach described above, removing highly correlated variables and performing backwards selection from a global model. After removing correlated terms, our global model predicting invertebrate abundance within plots included percent vegetation, percent dry soil, percent water, percent litter, maximum vegetation height, soil temperatures, soil pH, slope, and year, with the unique wetland survey ID and the date included as random effects. We then performed backwards selection and used a Wald χ^2 test for significance of the fixed effects in the final model.

Landscape use

We tested for variation in wetland abundance between years using a combination of agency monitoring data (e.g., Rainwater Basin Joint Venture, unpublished), and the

area calculated from our wetland surveys (described above). Although interannual variation in wetland availability in any one region may offer opportunities to explore how landscape conditions influence stopover decisions, many other aspects of migratory biology also vary seasonally and annually, including *Calidris* population size. Thus, to increase the validity of our assessment, we also compared annual differences in habitat use between regions. While there are subtle differences in the wetland attributes characterizing the habitat in each region, the discrepancy between current and historical availability of wetland basins contrasts sharply between the two regions giving us an opportunity to gauge how birds may respond to escalating anthropogenic change and increasingly sparse habitat distribution.

We tested for annual variation in *Calidris* occupancy and abundance at wetlands within each landscape using a GLMM with either a binomial or a Poisson distribution, respectively. To account for difference in available shorebird habitat we included percent mudflat, size, and year as fixed effects, with site and sampling period specified as random effects. Due to a high number of unoccupied wetlands, we analyzed flock size at occupied wetlands only, as occupied wetlands were more likely to contain attractive habitat cues allowing us to more effectively evaluate the relative importance of the landscape context for shorebird stopover decisions while controlling for locally preferable habitat conditions (e.g., Elphick and Oring 1998).

Results

In the RWB, we sampled 48 wetlands in 2013 and 43 in 2014 for a total of 437 shorebird surveys and 320 microhabitat assessments. Due to annual variation in wetland inundation, 28 of 48 sites were surveyed in both years. In the PPR, the number of wetlands along each transect varied by sampling period due to local weather events; we surveyed a maximum of 43 wetlands per sampling period in 2013 and a maximum of 27 in 2014, for a total of 369 shorebird surveys in two years; 19 of 43 wetlands were surveyed in both years. Over the course of two years we counted 9300 shorebirds, representing 7 *Calidris* species in both locations (Table 1).

Local use

Because vegetative characteristics are inherently correlated with local phenology and each other, we included the total percentage of vegetation (i.e., green plus brown) in our models to explore for local habitat preferences in each region. In both regions there was significant inter-annual variation in the *Calidris* population, as occupancy and abundance were higher in 2014. Not surprisingly, the availability of mudflat was the primary determinant of *Calidris* occupancy and abundance in both regions; however there were subtle differences between regions as *Calidris* occupancy was greater at larger wetlands in the PPR, but shorebirds were less likely to be present at larger wetlands in the RWB (Table 2; Fig. 1 & 2). Moreover, while *Calidris* abundance at wetlands in the PPR clearly increased as wetlands became larger and had more mudflat and less tall vegetation, the relationship was more complicated in the RWB as the weak effect of the

interaction between wetland size and percent mudflat is only apparent on the largest wetlands, and the negative relationship between shorebird abundance and vegetation height was not significant (Table 2; Fig. 2).

Invertebrate abundance was significantly associated with invertebrate sample mass ($R^2=0.77$, $F_{1,145} = 498.8$, $p<0.001$), indicating that abundance is a meaningful proxy of macroinvertebrate biomass. Invertebrate abundance was higher in 2014, and positively associated with soil temperature, vegetation, and dry soil, and negatively with litter (Table 3). Invertebrate abundance in both years predicted *Calidris* occupancy, but not abundance, with invertebrate abundance exhibiting a significant negative relationship with bird abundance at used wetlands (Table 3; Fig. 3).

Landscape Use

Occupancy and abundance were higher in 2014 in both the RWB and the PPR (Table 2; Fig. 4). The increase in *Calidris* occupancy and abundance coincided with an increase in wetland availability in the RWB which was 64% higher in March 2014 than in March 2013 (Rainwater Basin Joint Venture, unpublished data), and total inundated wetland habitat within our sites was 54% higher at the beginning of the season in 2014 than in 2013. The change in wetland conditions in the landscape was reflected in a change in climatic conditions between years as the Palmer Drought Severity Index (PDSI) averaged -1.93 across the RWB March 2014, compared to -3.37 in March 2013 (NOAA National Climate Data Center 2014). In the PPR, the PDSI was -3.86 for our study region in the PPR in 2013 and 1.69 in 2014 (NOAA National Climate Data Center

2014), although local wetland conditions were drier in 2014, as 54% of the wetlands we sampled at the beginning of the season in April 2013 were dry in April 2014.

After controlling for year, sampling period, and percent mudflat of wetlands, we found occupancy did not differ between regions, but there were significantly more birds per occupied wetland in the PPR than in the RWB (Table 4; Fig. 5). The interaction of region and wetland size was not related to mudflat ($F_{3,270} = 3.267$, $p=0.069$), suggesting that used wetlands in each region had comparable availability of shorebird habitat.

Discussion

It is increasingly evident that stopover wetlands do not operate as isolated units, but instead represent a complex and integrated landscape for migratory species accustomed to ephemeral and unpredictable habitat suitability (Skagen & Knopf 1994b; Farmer & Parent 1997; Webb *et al* 2010; Albanese & Davis 2012). By examining both local and landscape use of wetland habitat between two regions that vary in wetland availability, we observed that although *Calidris* exhibit similar habitat preferences across regions, importantly wetlands in the PPR support more birds than wetlands in the RWB. Thus our results are consistent with recent findings that wetland abundance on the landscape functions both as a heterogeneous network of potential stopover sites and as a critical cue driving stopover decisions (Skagen & Knopf 1993; Skagen, Grandfors & Melcher 2008; Albanese & Davis 2013). Still, while theory (e.g., Hutto 1985) and more recently empirical evidence (e.g., Buler, Moore & Woltmann 2007; Jorgenson *et al* 2014) increasingly suggest that the landscape context is important in determining migratory bird

abundance at stopover sites, *Calidris* abundance within wetlands are ultimately a consequence of many concurrent processes and complex interactions, making it important to examine the sources of variation at local and landscape scales which may have contributed to the patterns we observed.

Consistent with our existing understanding of *Calidris* habitat preferences (Colwell & Oring 1988; Skagen & Knopf 1994b; Davis & Smith 1998), occupancy was higher on wetlands with a higher proportion of mudflat and there was a positive relationship between bird abundance and mudflat in the PPR (Fig. 2c), but the relationship in the RWB was weaker (Fig. 2a). Moreover, while we find a positive interaction between mudflat and wetland size in the PPR, we failed to find a similar pattern in the RWB. A possible explanation for our incongruent findings may be based on differences in wetland structure between regions. Although mudflat is clearly important shorebird habitat, when there is sufficient available shallow-water habitat, shorebirds also congregated in vegetated wetlands (Fig. 2b & 2d; Webb *et al* 2010). In the RWB, where nearly all wetlands are shallow, the presence or absence of vegetation may have little bearing on habitat decisions; in the PPR, where vegetated wetlands are more often associated with deeper water, it is not surprising that we see a negative relationship between vegetation height and shorebird abundance (Fig. 2f). Still, while it is possible that our results indicate *Calidris* favor different habitat characteristics within each region because of structural differences in wetland types, given what we know about shorebird habitat preferences across a variety of landscapes (Colwell & Oring 1988; Skagen & Knopf 1994b; Davis & Smith 1998, Elphick & Oring 1998; Neimuth *et al* 2006; Webb *et*

al 2010), a more parsimonious explanation may be regional differences in the remaining available wetlands. Land-use change differences between regions not only led to differences in the number of wetlands, but also the sizes of wetlands. So while the PPR continues to have a diversity of wetland sizes, most of the larger wetlands in the RWB are drained and those that remain are actively managed to maintain water for migratory ducks, leaving little mudflat and subsequently few opportunities for *Calidris* to choose what is presumably more favorable habitat. Ultimately, despite inherent differences in wetland availability and wetland characteristics between regions, our data suggest that shorebirds assess local wetland conditions within each region and make predictable habitat decisions consistent with established understanding of *Calidris* habitat preferences (Colwell & Oring 1988; Skagen & Knopf 1994b; Davis & Smith 1998).

Presumably the habitat preferences of *Calidris* have intrinsic fitness benefits (Krebs & Davies 2012), and given the energetic demands of migration, food availability is often identified as the primary determinant of migratory success (reviewed in Moore *et al* 1995). Indeed, migratory routes and migratory timing evolve to take advantage of local peaks in resource abundance and phenology (e.g., Rodewald *et al* 2007; McGrath, Van Riper III & Fontaine 2009; Strode 2009; Fontaine, Stutzman & Gannes 2015) and in systems where resource distribution may be unpredictable, individuals may buffer against uncertainty by timing movements to coincide with resource peaks (e.g., Stutzman & Fontaine 2015, also see Appendix 1). Still, whether food availability is truly limiting during migration and how it shapes stopover decisions is challenging to ascertain and remains largely unknown despite the importance to migratory theory and species

management (Smith *et al* 1989; Moore *et al* 2005; Newton 2006; Colwell 2010). After accounting for phenology, we did find that occupancy was higher on wetlands with more invertebrates; however, food abundance did not predict bird abundance, and indeed, our models for *Calidris* occupancy predict a 40% probability of occupancy on wetlands with what would seem to be very limited invertebrate abundance (Fig. 3a). Given the importance ascribed to food abundance in shaping habitat decisions for energetically-stressed migratory birds (Moore *et al* 1995), that we fail to find a positive relationship between food and bird abundance is surprising especially in 2013, when both water on the landscape and food resources within wetlands were less abundant and presumably competition for resources higher (Moore & Yong 1991). Thus our results may suggest that food is not limiting during stopover, at least not at the level we were able to measure it.

While our inability to find a strong relationship between food and shorebird abundance may indicate that food is not limiting, it does not mean that energy is not limiting. Although it is generally assumed that the primary factor limiting energy uptake during migration is food availability (reviewed in Moore *et al* 1995) considering the specialized foraging behavior of *Calidris* requires shallow water for wading, it is possible that suitable foraging habitat may more severely limit foraging success than food abundance per se. Still, even after accounting for the availability of suitable shorebird foraging habitat within a wetland we failed to find a relationship between food and bird abundance (Fig. 3b). Although food depletion may in part account for the patterns we found, ecological conditions other than food are clearly important in shaping habitat

decisions, but are often undervalued in assessments of stopover decisions (Moore *et al* 1995; Moore *et al* 2005; Newton 2006; but see Ydenburg *et al* 2002). Vegetation, which is associated with macroinvertebrate abundance (Table 3), also increases predation risk for ground-foraging birds such as *Calidris* (Whitingham & Evans 2004), and thus requires increased vigilance and reduced activity to avoid detection by predators (Lima & Dill 1990). It is not surprising then that shorebirds not only avoid heavily vegetated wetlands, but appear to forage more actively in open habitats, even when food is less abundant (Stutzman 2012). So while other studies have found that food abundance predicts habitat decisions (Davis & Smith 1998; Johnson & Sherry 2001; Andrei *et al* 2008), our findings suggest ecological conditions which limit energy assimilation, including but not limited to food abundance (Moore & Yong 1991; Moore *et al* 1995; Kelly *et al* 2002; Ydenburg *et al* 2002; Moore *et al* 2005), ultimately determine stopover decisions. Future examinations of migratory stopover decisions may do well to consider the multitude of ecological conditions that affect foraging efficiency beyond food availability, as the factors constraining foraging efficiency are likely species and habitat dependent.

In migratory systems many interacting processes ultimately shape patterns of observed bird abundance, and differentiating among ecological factors that predict migratory behaviors is challenging. For example, the difference in abundance we detected between 2014 than 2013 (Table 4; Fig. 4) may reflect annual changes in *Calidris* population size, but it may also reflect large-scale changes in the ecological conditions present. Spring temperatures in April 2013 were colder than normal throughout the mid-

continent (NOAA National Climatic Data Center, 2013), which may have prevented many individuals from advancing migration at historically appropriate times.

Constrained by the need to arrive at the breeding grounds when local conditions were appropriate, individuals may have shortened stopover duration or altogether skipped stopover in the RWB and PPR. Indeed, while the annual onset of spring migration may be triggered by endogenous factors (i.e., photoperiod), many migratory populations are known to adjust stopover duration and the speed of migratory progression in response to local environmental conditions and phenology (e.g., Marra *et al* 2005; Tøttrup *et al* 2008; Tøttrup *et al* 2010). Alternatively, limited habitat availability in the region may have also contributed to the annual differences we observed. The dry conditions that were pervasive in the Great Plains in 2013 may have caused shorebird populations to adjust migratory routes to take advantage of more suitable conditions outside of our study area. Although mid-continental *Calidris* populations are typically only observed between 90° W and 100° W longitude during annual spring migration (Skagen *et al* 1999), the annual variation in wetland ponding in prairie wetland complexes create a shifting mosaic of habitat which often results in large inter-annual fluctuations in the total numbers of birds observed on any individual survey location, as individuals take advantage of appropriate habitat conditions across the landscape opportunistically (Skagen 2008). Indeed, increasing evidence suggests that large-scale habitat conditions are important in predicting local animal populations (e.g., Buler, Moore & Woltmann 2007; Albanese & Davis 2013; Jorgenson *et al* 2014). That there were more birds in 2014 may be indicative

of the availability of wetland habitat constraining stopover decisions in 2013, particularly in the RWB where habitat is already limited.

The differences we found in flock sizes of *Calidris* between the PPR and the RWB is potentially further evidence that landscape conditions may drive changes in *Calidris* stopover decisions. Even after accounting for local habitat attributes on individual wetlands, there was a discrepancy in the number of birds using wetlands in landscapes which contrasted in surrounding habitat availability (Fig. 5). Admittedly, the PPR has always contained more permanent wetlands than the RWB, and it is possible that shorebirds have always used the RWB more opportunistically. While we cannot dismiss the possibility that our observations may reflect some of the inherent intrinsic differences in our two study regions, it nevertheless remains that shorebirds overwhelmingly prefer temporary and seasonal wetlands when they are available (Neimuth *et al* 2006), presumably because habitat conditions (shallow water and mudflat) and invertebrate productivity in ephemeral wetlands make them ideal habitat for the energetic demands of migratory stopover (Davis & Smith 1998; Euliss *et al* 1999). That we find more birds per wetland in the PPR is thus unlikely to be solely the result of the presence of more permanent bodies of water, as shorebirds still exhibit preferences for wetlands with inherently less predictable water regimes. Indeed, if the predictability of water resources was the primary determinant of *Calidris* stopover ecology, we may expect prairie river systems, such as the Missouri, to be the most important stopover habitat in the Great Plains. Instead, populations of migratory shorebirds are repeatedly documented using extremely unpredictable wetland systems such as the playas of Texas

and Oklahoma (e.g. Davis & Smith 1998) or even agrarian wetlands in the Dakotas (Neimuth *et al* 2006, Stutzman 2012).

So although our study design limits our inference due to possible intrinsic difference between regions, and in isolation the observed difference in migratory bird abundance at wetland may be the result of annual differences in migratory populations or longitudinal variation in migratory routes (Fig. 2; Morrison *et al* 2006), because our survey method allowed us to also detect intra-annual variation in habitat use we are more confident in concluding that the patterns we see in wetland use are at least in part the result of overall habitat availability on the landscape. Moreover, our results are consistent with theoretical predictions of habitat selection for migratory species *en route* (e.g., Hutto 1985), and many other studies have observed the importance of dense networks of stopover habitat for *Calidris* shorebirds (Skagen & Knopf 1994b; Farmer & Parent 1997; Neimuth & Solberg 2003). Even at very local scales the regional availability of shallow-water habitat predicts both migratory bird abundance and species richness in dynamic and unpredictable ephemeral wetland landscapes (Webb *et al* 2010; Albanese & Davis 2012; Albanese & Davis 2013). So even though shorebirds may time migratory arrival to coincide with food abundance (Appendix 1; Stutzman & Fontaine 2015), suitable habitat is highly ephemeral and unpredictable (Skagen and Knopf 1994b; Albanese & Davis 2013), and accessibility to sufficient food resources for migratory refueling is constrained by multiple sources of selection (Petit 2000; Kelly *et al* 2002; Ydenburg *et al* 2002; Moore *et al* 2005). The unpredictability of suitable wetland habitat likely favored the evolution of a risk-adverse response to water scarcity in any one

location—for example, *Calidris* may respond to wetland scarcity by skipping over available habitat or shortening stopover duration when wetlands are less available. While historically such a strategy may have allowed migratory birds to take advantage of wetland habitat that was more abundant elsewhere, land-use change increasingly limits wetland habitat throughout the Great Plains, potentially decreasing the benefits of this opportunistic stopover strategy (Higgins, Naugle & Forman 2002; Skagen 2006).

While we cannot point to specific costs associated with apparent trade-offs in response to altered landscapes, as trade-offs may be manifested in subsequent stopover events or alternative stages of the annual cycle (Moore *et al* 1995; Moore *et al* 2005; Norris & Marra 2007; Small-Lorenz *et al* 2013), we can hypothesize that as land-use and climate change escalate to further diminish wetland landscapes (Dahl 2000; Johnson *et al* 2005; Dahl 2011) apparent alteration in either stopover frequency or duration may lead to repercussions for individuals and populations (Newton 2006). Less frequent stopover may require birds to extend stopover duration at other sites or to delay migratory progression, which may result in fitness consequences by delaying arrival at the breeding grounds, perhaps decoupling breeding phenology from optimal ecological conditions resulting in cascading consequences for individuals and their offspring which may resonate throughout the annual cycle (Baker *et al* 2004; Smith & Moore 2005; Catry *et al* 2013). Alternatively, birds may shorten stopover duration when habitat is limited, departing with fewer energy reserves, which may result in costs to individual condition and physiology, or even death (Pfister, Kasprzyk & Harrington 1998; Moore *et al* 2005; Morrison 2006). In this scenario, even if migrants arrive at breeding grounds on time,

they are likely to require longer recovery time prior to the onset of breeding or be physiologically constrained in reproductive investment (Bêty, Gauthier, & Giroux 2003; Smith & Moore 2003; Newton 2004). While the specific carry-over effects of trade-offs in response to landscape change may yet be unknown, periods in the annual cycle of migratory birds are inherently linked (Small-Lorenz *et al* 2013), and therefore the consequences of anthropogenic perturbations may be impossible to detect without consideration of the broader geographic scales at which species must make trade-offs in habitat decisions (Hutto 1985; Farmer & Wiens 1998; Haig, Mehlman & Oring 1998). Our study underscores the need to understand how species respond to anthropogenic change across multiple scales, and ideally throughout the annual cycle.

Given the complexity of the necessary trade-offs migratory species exhibit in response to highly altered landscapes, it may be necessary to focus habitat management efforts so as to maximize the value of the remaining wetland habitat for migratory shorebirds. Although models of habitat conservation traditionally focus on improving the resource availability within existing habitats, studies increasingly suggest that even the best local habitat conditions are ultimately constrained by the surrounding landscape (e.g., Buler, Moore & Woltmann 2007; Jorgensen *et al* 2014). In wetland complexes, management practices frequently involve manipulation of water levels or other actions such as grazing or burning which manipulate habitat conditions (i.e., mud flat), food availability, or vegetation within individual wetlands (USFWS 2007; Davis & Bidwell 2008); however, while it is seemingly possible to manage a wetland for preferred shorebird habitats our results suggest that the overall availability of wetlands on the

landscape limits shorebird abundance during migration independent of individual wetland quality. Thus, it becomes relevant to understand not only the structure and function of individually-managed wetlands, but entire networks of managed wetlands on the landscape. The consequences of anthropogenic change for migratory species in highly altered landscapes are ultimately the result of a complex integration of local, phenological, and landscape-scale processes, and thus the future of migratory species conservation will depend heavily on our ability to mitigate the consequences of habitat loss while considering the full scale at which migratory species make habitat decisions.

Tables and Figures

Table 1. Species and total number of individuals of all *Calidris* shorebirds observed in both study locations in 2013 and 2014.

<i>Species</i>	<i>Rainwater Basin</i>		<i>Prairie Pothole Region</i>	
	2013	2014	2013	2014
Baird's Sandpiper (<i>Calidris bairdii</i>)	161	295	15	614
Dunlin (<i>Calidris alpina</i>)	0	67	4	1
Least Sandpiper (<i>Calidris minutilla</i>)	5	116	86	22
Pectoral Sandpiper (<i>Calidris melanotos</i>)	19	56	6	33
Semipalmated Sandpiper (<i>Calidris pusilla</i>)	46	240	87	497
Stilt Sandpiper (<i>Calidris himantopus</i>)	45	147	291	1109
White-rumped Sandpiper (<i>Calidris fuscicollis</i>)	179	700	297	2435
Unidentified <i>Calidris</i> spp.	237	817	571	102
TOTAL	692	2438	1357	4813

Table 2. Coefficients, standard error, and significance of the fixed effects in each of the final GLMMs predicting occupancy and abundance of *Caldris* shorebirds on wetlands in the RWB and the PPR; all models included site and day as random effects. Due to a high number of unoccupied wetlands, we only analyzed abundance at wetlands with at least one bird present. Terms that were removed during backwards selection and were not tested in the final models are designated ‘NA.’

<i>Parameter</i>	β	<i>SE</i>	<i>Wald</i> χ^2	<i>p</i>	β	<i>SE</i>	<i>Wald</i> χ^2	<i>p</i>
RWB Occupancy					PPR Occupancy			
Size (ha)	-0.007	0.002	20.206	<0.001	-0.038	0.036	3.250	0.07
Mud (%)	0.017	0.002	108.125	<0.001	0.023	0.016	7.307	<0.01
Size x Mud	NA	NA	NA	NA	0.011	0.004	9.236	<0.01
Total Vegetation (%)	-0.017	0.002	115.165	<0.001	NA	NA	NA	NA
Vegetation 15cm-60cm (%)	-0.003	0.002	3.018	0.082	NA	NA	NA	NA
Year	0.353	0.002	46163.4 50	<0.001	1.738	0.793	4.809	<0.01
RWB Abundance					PPR Abundance			
Size (ha)	-0.055	0.008	43.403	<0.001	0.024	0.007	11.807	<0.001
Mud (%)	-0.013	0.003	10.197	<0.01	0.082	0.004	389.832	<0.001
Size x Mud	0.002	0.000	10.093	<0.01	NA	NA	NA	NA
Total Vegetation (%)	0.006	0.003	4.705	<0.05	0.030	0.003	86,970	<0.001
Vegetation 15cm-60cm (%)	-0.001	0.003	0.236	0.627	-0.017	0.002	58.647	<0.001
Year	1.376	0.000	83.468	<0.001	1.500	0.720	4.340	<0.05

Table 3. Results of GLMMs predicting *Calidris* occupancy and abundance in the RWB in relation to food abundance in wetlands, and the final model predicting invertebrate abundance in sample plots. Site and day were included in all models as random effects.

<i>Parameter</i>	β	<i>St. Error</i>	<i>Wald χ^2</i>	<i>p</i>
<i>Calidris</i> Occupancy				
Percent Mud	0.017	0.009	4.089	0.043
Wetland Size	-0.003	0.013	0.053	0.817
Invertebrates	0.020	0.009	5.469	<0.05
Year	0.235	0.280	0.703	0.402
<i>Calidris</i> Abundance				
Percent Mud	-0.010	0.003	11.611	<0.001
Wetland Size	-0.054	0.007	58.067	<0.001
Invertebrates	-0.006	0.002	10.531	<0.01
Year	1.630	0.153	112.880	<0.001
Invertebrate abundance within plots				
Vegetation (%)	0.005	0.002	4.94	<0.05
Dry Soil (%)	0.017	0.005	9.47	<0.01
Litter (%)	-0.006	0.003	4.87	<0.05
Soil Temp (C)	0.040	0.012	11.43	<0.001
Soil pH	-0.057	0.042	1.84	0.174
Year	1.200	0.315	14.48	<0.001

Table 4. Results of GLMMs predicting occupancy and abundance at wetlands between the RWB and the PPR across both years. Due to a high number of unoccupied wetlands, we only analyzed abundance at wetlands with at least one bird present. Site and sampling period were included as random effects in both models.

<i>Parameter</i>	β	<i>St. Error</i>	<i>Wald χ^2</i>	<i>p</i>
Occupancy				
Region	-0.025	0.259	0.009	0.922
Percent Mud	0.023	0.006	14.198	<0.001
Year	0.682	0.210	10.553	<0.01
Abundance				
Region	-0.821	0.365	9.555	<0.01
Percent Mud	0.003	0.001	5.334	<0.05
Year	0.951	0.055	295.817	<0.001

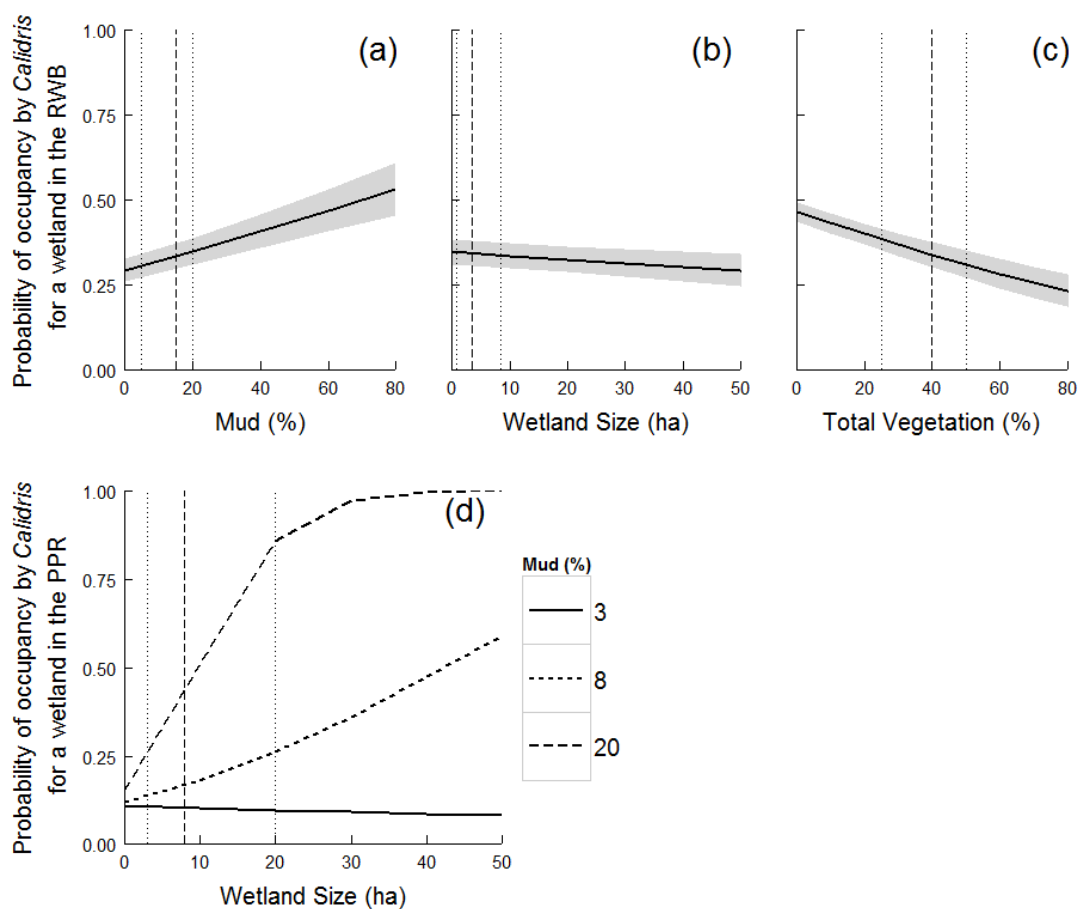


Figure 1. *Calidris* occupancy at wetlands in the RWB was predicted by percent mud (a), wetland size (b), and percent total vegetation (c), while occupancy at wetlands in the PPR was predicted by an interaction of percent mudflat and wetland size (d) (Table 2). Lines and shaded areas represent predicted probability of occupancy with 95% confidence intervals; for ease of comparison, confidence intervals are not included on (d). Vertical lines represent the median and 1st and 3rd quartile for the parameter across sampled wetlands.

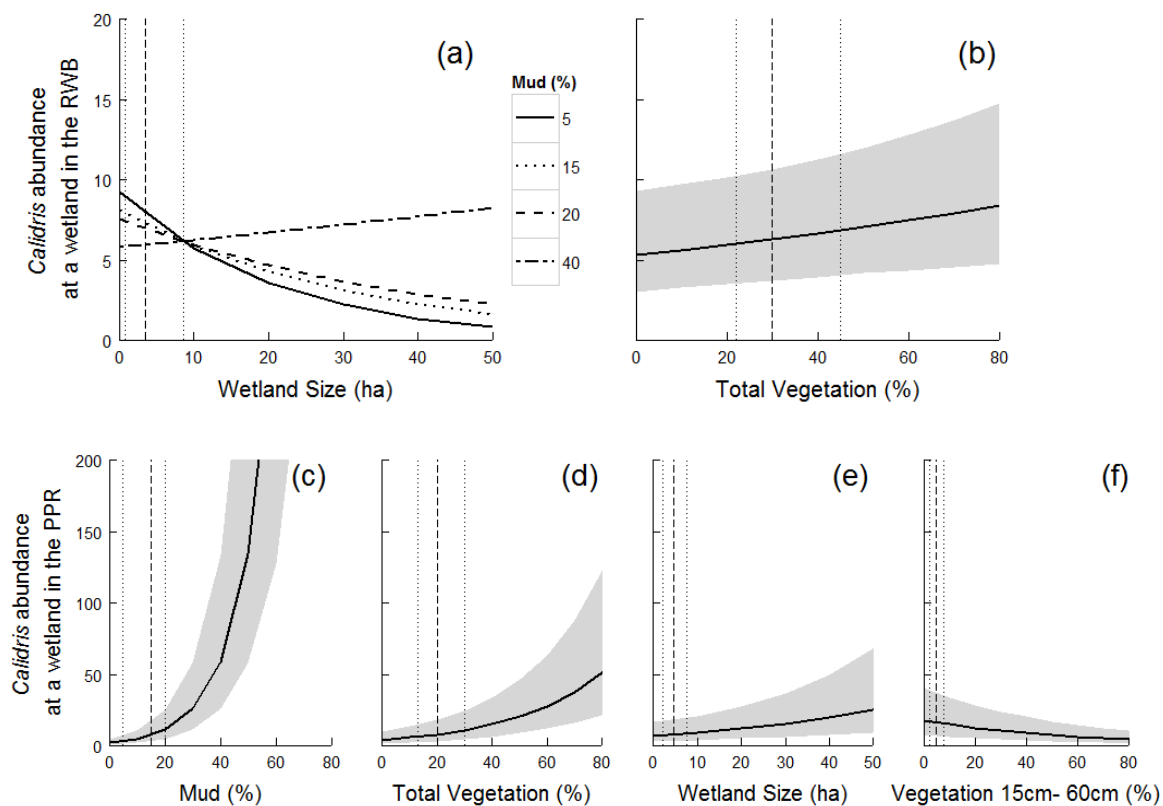


Figure 2. *Calidris* abundance at wetlands in the RWB was predicted by an interaction of percent mud and wetland size (a) and the total percent vegetation (b) (Table 2). Abundance in the PPR was predicted by percent mud (c), percent vegetation (d), wetland size (e), and percent of vegetation between 15cm-60cm (f) (Table 2). Lines and shaded areas represent predicted probability of occupancy with 95% confidence intervals; for ease of comparison, confidence intervals are not included on (a). Vertical lines represent the median and 1st and 3rd quartile for the parameter across sampled wetlands.

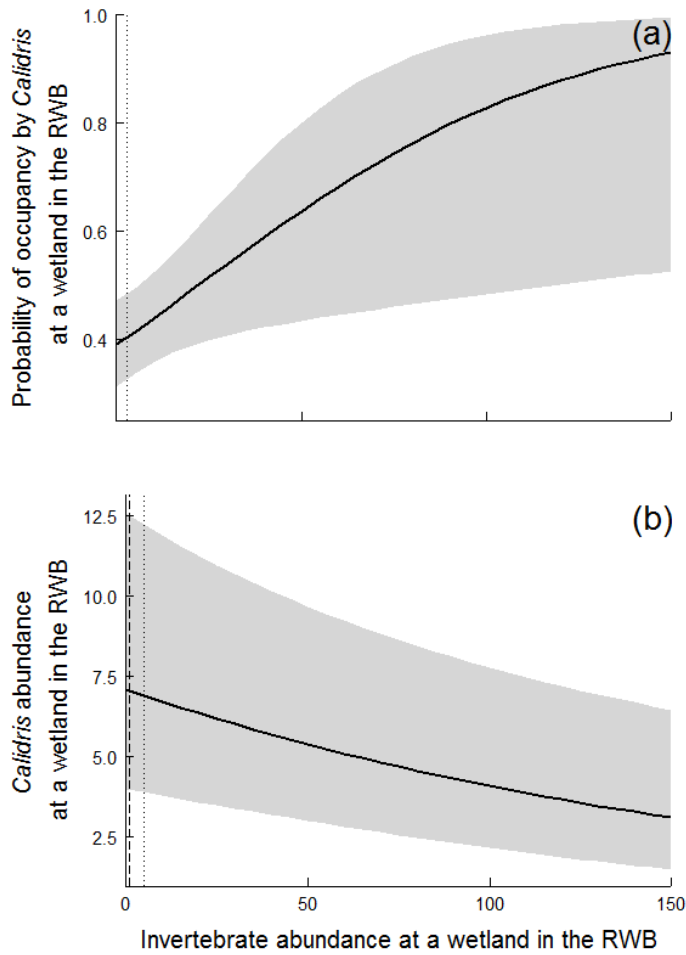


Figure 3. Invertebrate abundance predicts occupancy (a), but not abundance (b) of *Calidris* shorebirds in the RWB (Table 3). Lines and shaded areas represent predicted probability of occupancy with 95% confidence intervals. Vertical lines represent the median and 1st and 3rd quartile for the parameter across all sampled wetlands.

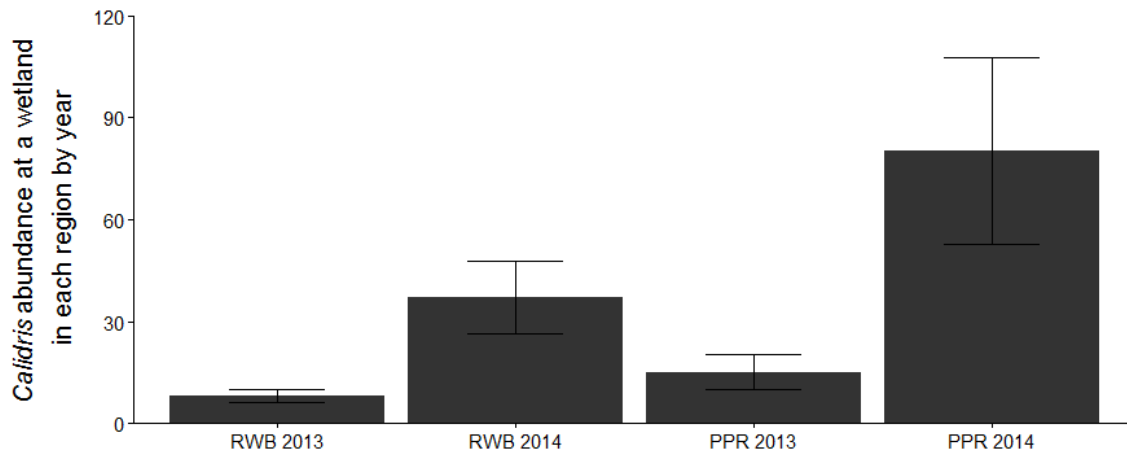


Figure 4. Abundance of *Calidris* individuals at wetlands was higher in 2014 in both the RWB and the PPR (Table 2). Columns represent predicted means and standard error after controlling for covariates and random effects.

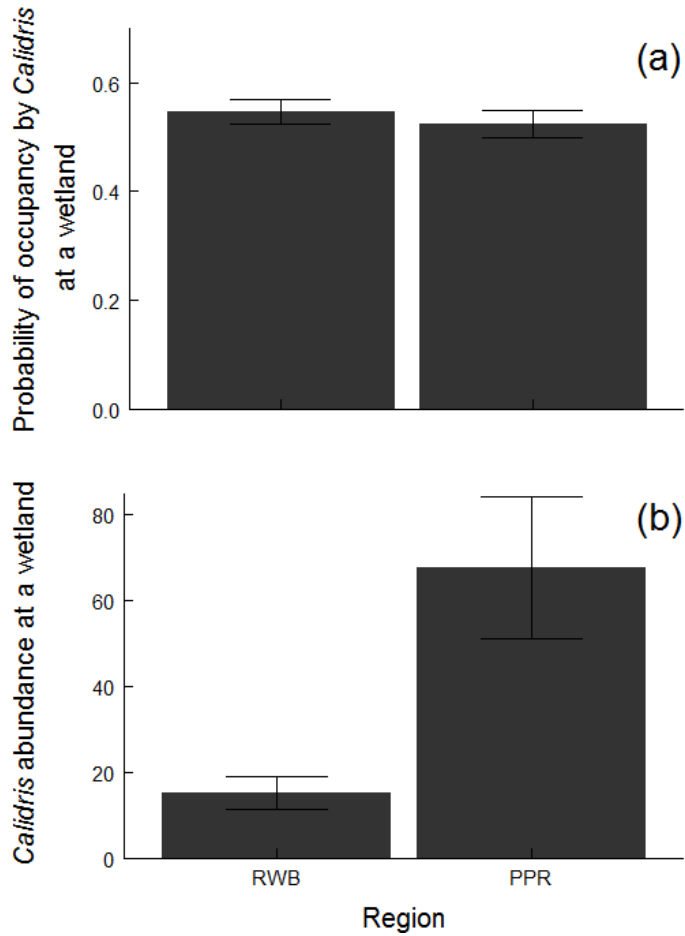


Figure 5. Probability of *Calidris* occupancy did not differ between regions (a), but *Calidris* abundance at wetlands with at least one individual present was significantly higher in the PPR than in the RWB (b) (Table 4). Columns represent predicted means and standard error after controlling for covariates and random effects.

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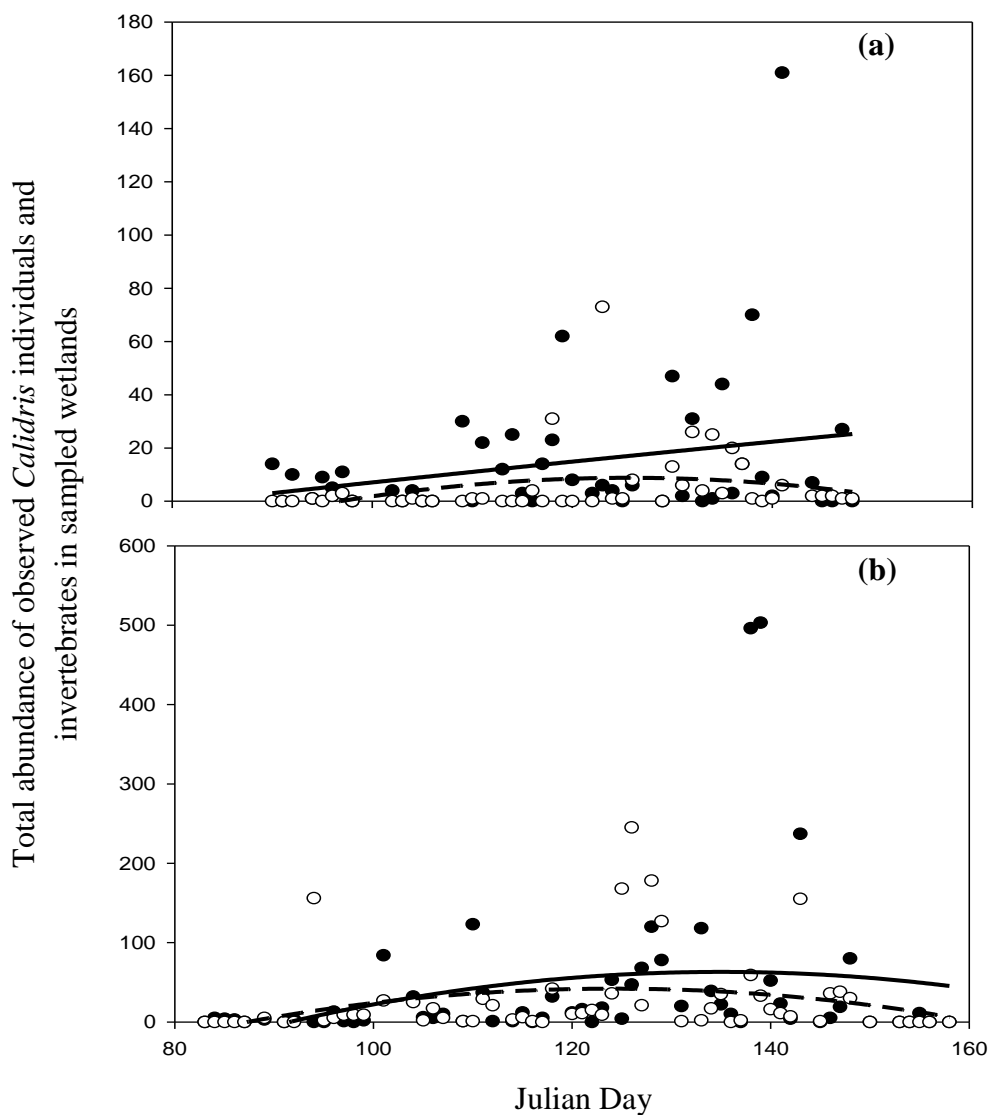
Appendix 1.

Figure 1. In the RWB, migration phenology (solid lines) and invertebrate phenology (dotted lines) were highly correlated in both 2013 (a) and 2014 (b). Black dots represent the total observed *Calidris* individuals observed on the day surveyed; white dots represent the sum of invertebrates observed in sample plots on the survey date.

Chapter 2

Are Our Survey Methods Adequate for Changing Landscapes? An Assessment of Repeatability of Shorebird Surveys in Heterogeneous Wetland Habitats

Abstract

Shorebird surveys are key for monitoring populations and for understanding how to best manage and conserve species; yet there is little understanding of the repeatability of survey approaches in highly heterogeneous wetland habitat. During migration, *Calidris* shorebird species may be particularly vulnerable to sampling errors as detection probability and habitat use at stopover sites may interact unpredictably, making annual estimations of migratory populations difficult. Here we tested for variance in survey estimates of migratory *Calidris* shorebird species within and among habitats by employing both visual point surveys and flush surveys at managed wetland complexes in the Rainwater Basin of south-central Nebraska. We find considerable variation in predicted relationships between shorebird abundance and habitat attributes depending on method, observer, location, and site; total variance among surveys within wetlands also increased with wetland area and vegetative characteristics of wetland habitats. Our results draw attention to potential weaknesses associated with traditional sampling approaches for estimating shorebird abundance across an array of wetland habitat types, as it is unclear whether habitat use or detection accounts for disproportionately distributed variance across wetland habitats. We urge further examination of ambiguity in shorebird abundance estimates at migratory stopover sites, as a failure to distinguish

between errors in detection and shifts in habitat use will severely impair our ability to establish patterns in habitat use relevant for management of wetland complexes and the conservation of migratory waterbird populations.

Introduction

Wildlife surveys are central to our understanding of population dynamics and habitat use and ultimately determine how we manage and conserve wildlife species; however, sampling methods vary widely among species, habitats, and investigators, creating challenges for comparing and repeating studies (Cochran 1977; Sutherland *et al* 2004). Visual surveys are a common sampling method for species such as shorebirds, which typically occupy open habitat, are active diurnally, and tend to forage in large groups (Davis and Smith 1998a). However, visual surveys of ground-foraging birds, especially small species, are subject to error in detection resulting from variation in vegetation structure, sampling distance, weather conditions, and even time of day (Thompson 2002). To account for detection errors in visual surveys of waterbirds, some studies employ alternative sampling methods to accompany traditional visual point-count or road-side survey estimates. For example, studies sometimes use “double sampling,” where rapid sampling is accompanied by more intensive surveys on a subsample of surveyed plots to determine actual abundance (e.g., Bart and Earnst 2002) or “flush counts,” where observers walk through waterbird habitat to provoke the movement and thus easier detection of birds otherwise hidden from initial observations (e.g., Farmer and Durbian 2006). Not all studies utilize multiple sampling methods, however, which could

result in ambiguity within and among studies if imperfect detection interferes with estimates of species abundance, distribution, and habitat use (Farmer and Dubian 2006; Mackenzie 2006; Morrison *et al* 2007). Additionally, there is surprisingly little understanding of the repeatability of estimates among alternative sampling methods in shorebird surveys.

Given that shorebird distribution and habitat selection are highly subject to naturally unpredictable and heterogeneous wetland habitats, variables such as flock size and vegetation potentially covary or interact with habitat use making inference about what is driving patterns in population estimates challenging. For example, it is well established that small shorebird species prefer open mudflat and avoid habitats with abundant vegetation (Colwell and Oring 1988; Skagen and Knopf 1994a; Davis and Smith 1998b); however, standard visual surveys are also better equipped to detect individuals in open areas, as birds are less obstructed by vegetation and are also typically more active in sparsely vegetated habitats (Stutzman 2012). Equally challenging, individuals are easier to detect in large groups, but group size can vary annually, within and across seasons, and by habitat (Deleon and Smith 1999; Neimuth 2003; Stutzman 2012). Moreover, larger groups are more difficult to count within a standardized sampling window, resulting in increasing precision errors with increasing flock size (Rapoldt *et al* 1985). As monitoring efforts are often concerned with changes in population size or distribution, sampling biases that vary inconsistently among habitats, across seasons, or among years may severely inhibit inferences important for management. Although modeling efforts can help alleviate some sampling biases,

detection probability models generally assume covariates such as vegetation or group size only influence detection, not abundance (Nichols *et al* 2000). Given the potential interactions of detection with habitat use and group size in surveys of shorebirds in particular, it is increasingly important that biologists evaluate inconsistent biases in sampling methods, as accurate demographic and habitat use information is vital for establishment of effective conservation strategies.

Here we tested for variance in survey estimates of migratory *Calidris* shorebird species both within and among wetland habitats. We employed both visual point-count and flush surveys for shorebird abundance at publically-managed wetland habitats in the Rainwater Basin (RWB) wetland complex in south-central Nebraska during spring migration. We then modeled differences in survey estimates within wetland habitats to determine whether covariates such as flock size and vegetation influenced variation in detection, and whether detection and habitat use covariates interact disproportionately among wetlands to bias abundance estimates of *Calidris* shorebird species in ephemeral wetland habitats during spring migration.

Methods

Study sites

We completed 210 two-person shorebird surveys at wetlands from March-June 2013 and 2014 at a total of 38 sites in the RWB in south-central Nebraska. The region is defined by a playa wetland system within a predominantly agricultural landscape; wetlands are subject to highly variable seasonal and annual inundation due to a naturally

variable climate and active wetland management. Due to annual variation in climate conditions, management, and subsequently hydroperiod, 24 of our sites were surveyed in both years. Surveys were conducted as a subset of a study of shorebird habitat selection in managed wetlands in this region (Chapter 1), in which sites across the RWB were surveyed for shorebird habitat use once every 7-10 days, excluding sampling periods when the wetland was dry. Our sampling periods exceed the typical stopover duration of *Calidris* species in this region (Skagen and Knopf 1994b) and thus minimized the likelihood of recounting individuals allowing us the opportunity to assess changes in the migratory population over time.

Survey methods

Wetland visits consisted of two surveys conducted by each of two observers, for a total of four surveys during a single wetland observation day. Upon arrival at the site, observers conducted simultaneous visual point-count surveys (hereafter referred to as “point surveys”) from opposite sides of the wetland using a spotting scope and binoculars. Depending on the structure and size of the wetland, observers positioned point surveys at elevations and distances which maximized wetland visibility while simultaneously minimizing bird disturbance, with 95% of all visual point surveys conducted within 200m of the nearest wetland edge. During a ten-minute sampling window, observers recorded the number and species of all shorebirds visible from the observation location. When both observers had completed their respective point-surveys, they immediately commenced a second survey, walking towards the water from the

observation point and continuing around the water's edge for $\frac{1}{4}$ of the wetland perimeter (e.g. one observer walking from the North point of the wetland to the East and the other observer walking from the South point to the West) each traveling the same direction (i.e., clockwise or counter-clockwise). This partial wetland-edge survey (hereafter referred to as "perimeter surveys") was done to minimize re-counting of individuals moving in response to observer presence and to ensure independence in survey estimates between observers. We treated the perimeter survey as entirely separate from the initial point survey, and recorded the number and species of all shorebirds visible during the walk towards and around the wetland. Each observer also estimated wetland habitat attributes by visually estimating the proportion of the entire wetland covered in each of four cover types (water, mud, green vegetation, and brown vegetation or litter) and estimated the percentage of the vegetation in each of three height classes (less than 15cm, between 15cm and 60cm, and greater than 60cm). Using a handheld Garmin GPS unit observers recorded the location of the point surveys and four points (N, S, E, W) around the wetland indicating the edge of the inundated wetland habitat. We used these UTM locations to calculate the distance from the observer to the wetland during point surveys and to calculate an estimate of the ponded area on the survey date.

Analysis

We tested for patterns predicting shorebird abundance in relation to key habitat attributes using generalized linear mixed models with a Poisson distribution which included year as a covariate and site and day as random effects. We modeled predictions

from point surveys and perimeter surveys separately. To evaluate the importance of individual sites to our analyses, we also tested a second set of generalized linear mixed effects models for each habitat attribute without including site as a random effect, essentially treating each wetland visit as a unique individual replicate.

We then tested for variation in total *Calidris* abundance among the four surveys at each wetland using a generalized linear mixed-effects model with a Poisson distribution which included observer number and method as fixed effects and the wetland survey as a random effect. Vegetation characteristics, flock size, and wetland size all have the potential to contribute to visual obstruction and observer error associated with waterbird surveys, so because we were interested in whether variance among surveys at each wetland covaried with key wetland habitat attributes, we examined the residuals from our model and plotted them against each relevant wetland attribute to look for patterns. We then used the absolute value of the residuals from the model in a series of linear regression models to test whether variance in *Calidris* abundance estimates on a single survey date within each wetland covaried with wetland habitat attributes (percent mud, water, vegetation, green vegetation, brown vegetation, vegetation height, and wetland area), flock size, or observer distance from the water.

Results

Estimates of *Calidris* abundance did not vary among all the individual observers participating in data collection ($F_{11,198}=1.427$, $p=0.163$), but did vary between observers at each wetland (Figure 1: $\chi^2_1=20.71$, $p<0.001$), and was higher in perimeter surveys than

in point surveys ($\chi_1^2 = 222.93$, $p < 0.001$). Observer estimates of wetland habitat attributes were highly positively correlated (Total vegetation: $r(205) = 0.61$, $p < 0.001$; Green vegetation: $r(206) = 0.80$, $p < 0.001$; Brown vegetation: $r(205) = 0.65$, $p < 0.001$; Mud: $r(205) = 0.61$, $p < 0.001$; Water: $r(205) = 0.60$, $p < 0.001$; Short vegetation: $r(203) = 0.53$, $p < 0.001$).

Estimates of shorebird abundance were sensitive to changes in habitat attributes, but the direction and magnitude of the effect varied by wetland characteristic and was not predictable between approaches (Table 1; Figure 2). After removing site from the model to evaluate whether repeated visits to individual sites influenced our results, we found that the relationship between abundance and habitat shifted in magnitude and direction for several key wetland attributes (Table 1; Figure 3).

Variance among all four survey estimates at each wetland (Figure 4) was not significantly related to percent water ($r^2 = 0.001$, $F_{1,832} = 1.85$, $p = 0.17$), mud ($r^2 = -0.001$, $F_{1,832} = 0.005$, $p = 0.942$), or total vegetation ($r^2 = 0.001$, $F_{1,832} = 2.12$, $p = 0.15$); but did increase with increasing percentages of short vegetation ($r^2 = 0.01$, $F_{1,828} = 9.95$, $p < 0.01$), green vegetation ($r^2 = 0.02$, $F_{1,834} = 18.46$, $p < 0.001$), and decreased with increasing percentage of brown vegetation ($r^2 = 0.03$, $F_{1,832} = 28.09$, $p < 0.001$). There was no relationship in variance between survey estimates depending on the distance of the observer from the edge of the water ($r^2 = 0.001$, $F_{1,824} = 0.025$, $p = 0.87$). Variance in survey estimates did increase significantly with wetland area ($r^2 = 0.012$, $F_{1,806} = 10.81$, $p < 0.01$) and flock size ($r^2 = 0.12$, $F_{1,838} = 110.6$, $p < 0.001$).

Discussion

The assumption of repeatability among survey estimates in wildlife studies has important implications both for scientific inference and ultimately for management decisions. While variation in detection probabilities for bird surveys are widely discussed among wildlife professionals (Thompson 2002, Nichols *et al* 2000), it still remains necessary to understand the interaction between detectability and habitat use, especially for species such as shorebirds which may be particularly vulnerable to detection errors imposed by heterogeneous habitat structure. We find that not only do abundance estimates vary by observer, location and sampling method, but that several key wetland habitat attributes predict variation in both abundance of birds and detection probability.

It is well established that shorebirds prefer open, sparsely vegetated habitat (Colwell and Oring 1988; Skagen and Knopf 1994a; Davis and Smith 1998b); yet it is less clear to what extent detection probability interacts with habitat use to drive estimates in less open habitats. By utilizing two different survey techniques, we demonstrate considerable ambiguity surrounding the relationship between shorebird abundance and wetland structure. Total vegetation, for example, positively predicts shorebird abundance in point surveys, but negatively predicts abundance in perimeter surveys, making it impossible to infer the distinct mechanisms independently driving habitat preferences and detection. The fact that we also find positive relationships between bird abundance and brown vegetation, but negative relationships with mudflat also suggests that there may be important structural differences associated with our sites which predict bird abundance

and detection beyond the habitat attributes we measured. Traditional modeling approaches dictate that we include site as a random effect when using repeated sampling at sites over time to model predicted abundance in relation to habitat characteristics, which allows the intercept to vary among sites while calculating the overall patterns describing bird-habitat relationships. However, when we ignore the potential intrinsic variation within sites and instead treat each survey as a unique replicate in order to evaluate relationships between bird abundance and habitat attributes, we find that our predictions change in both magnitude and direction. The fact that the relationships change so dramatically suggests that there may be important variation associated with specific sites which predict shorebird abundance beyond the habitat attributes we measured. We find a strong site effect unsurprising for two reasons. First, as shorebirds are known to respond to landscape-level cues of habitat availability, it is likely that the extent of surrounding water on the landscape plays a role in the likelihood of bird abundance on any given wetland within our study area (Chapter 1). Second, shallow wetland habitat can change rapidly within a sampling season as local weather conditions inundate or desiccate wetlands and vegetative phenology advances with warming spring conditions. Repeated samples at sites over time may thus arguably be treated as unique observations, as the variation within wetland habitat over time may be equal to or be even greater than the variation among wetlands (Gillespie pers. obs.).

We employed two different survey methods in an attempt to determine whether alternative survey methods may be appropriate for habitat with a high probability of imperfect detection; however, our results demonstrate that inherent difficulties in

separating habitat preferences from detection probability may be more difficult to mediate than a simple change in sampling method. Point surveys and perimeter surveys provided very similar estimates of shorebird abundance in relation to green vegetation, short vegetation, and wetland area, but our two survey methods differed in predicted abundance in relation to mudflat, water, brown vegetation, and total vegetation. Still, even when alternative methods provide similar results, we still find distinct differences in estimates between observers in both point and perimeter surveys, suggesting that survey method alone is not responsible for all the variation in abundance estimates. Although flush counts are typically employed to ease assessment of flocks in heavily vegetated areas, our results suggest that these assessments are still vulnerable to unpredictable error, and thus may not be any more reliable than point surveys. Indeed, as the median percent vegetation on our wetlands was relatively high (40%), it is likely that a combination of limited open shorebird habitat and reduced detection probability may simultaneously account for most of the variation in our estimates among methods and observers. Our results highlight the heightened potential for interactions between habitat use and detection probability especially in highly-altered landscapes where landscape conditions are no longer favorable or in dry years when open mudflat habitat is limited and sparsely distributed.

Diagnosing the specific mechanisms driving variance among survey methods and among wetlands is challenging. For instance, total variance among all four surveys within any single wetland visit increased significantly with flock size; yet we would expect any number of important habitat attributes to covary with bird abundance in

wetland habitats. Of course, heightened variance is much more likely when birds are present than when they are absent, and it appears that our survey methods are fairly consistent when flock sizes are small—i.e., it is likely that all survey methods accurately predict wetland occupancy. However, as flock size is often a more informative metric than occupancy for monitoring migratory populations (Morrison *et al* 2007, Chapter 1), and *Calidris* shorebirds tend to congregate in large flocks during migratory stopover (Davis and Smith 1998a), the heightened potential for error when counting large groups of birds is troubling. We emphasize that it is important to evaluate the potential sources of error contributing to amplified variance in larger groups, and suggest two possible explanations. First, novice observers tend to underestimate large flocks of birds (Rapoldt *et al* 1985); however, given that the maximum abundance of birds within our study sites was only a few hundred, we find this explanation unlikely. Alternatively, it is possible that variation in our survey estimates resulted from variation in detection among observers and methods, and that the same habitat attributes which interfere with detection co-varied with key habitat attributes predicting bird abundance. For example, variance in estimates increases with green vegetation and short vegetation on the wetland, both of which show parallel phenological patterns with flock size in this system (Chapter 1) and likely many other migratory stopover locations.

While we cannot draw conclusions concerning the relative efficacy of alternative survey techniques for accurately estimating bird abundance, we can point to habitat structure within wetlands which seems to be particularly problematic. Our examination of the patterns predicting variance among surveys at the same wetland on the same day

reveal that while estimates tend to be fairly consistent among wetlands with varying percentages of water and mudflat, variance in abundance estimates tends to be higher in wetlands with less brown vegetation, more green vegetation, more vegetation shorter than 15cm, and a larger total area. Although green vegetation was consistently negatively associated with shorebird abundance, the fact that there was a significant positive relationship between the percent of green vegetation present at a surveyed wetland and the total variance among all four shorebird estimates suggests that shorebirds may actually use heavily vegetated wetlands more frequently than typically indicated. Thus, it is possible that the error rate associated with our detection probability in vegetated habitats may play a larger role than actual habitat use in dictating predications concerning shorebird use of vegetated wetlands.

Short green vegetation proliferates across playa wetlands seasonally as water recedes (Chapter 1), and thus is likely to cover shallow-water and mudflat habitats usually favored by *Calidris* species. Given that it is difficult to accurately count large flocks of birds in heavily vegetated wetlands unless they are in flight, and birds in heavily vegetated wetlands tend to minimize activity to avoid predation (Stutzman 2012), observers may be more likely to miscount flocks especially when using traditional visual point survey methods. The tremendous amount of variation in our survey estimates within accessible, but less-open, habitat is of particular concern because it limits our ability to assess the value of these habitats for shorebirds. Wetland area also increases variance in survey estimates, likely because detection of birds on very large wetlands is more difficult for a single observer due to increased distance to the opposite shore and the

heightened possibility of visual obstruction. While we may alleviate some error by sampling in multiple locations (e.g., Brown and Dinsmore 1986), it remains unclear to what extent increased sampling of larger habitats is necessary, especially as larger wetland habitats are often structurally heterogeneous and thus even more vulnerable to the inconsistent biases in survey estimates we see demonstrated across wetland types.

Still, the relative contribution of variation in shorebird habitat use versus variation in detection probability remains equivocal, and thus we find it an imperative avenue for further research and discussion. While our analyses here focuses on the variance in surveys associated with habitat, and not necessarily the efficacy of sampling approaches, our results draw attention to potential weaknesses of traditional sampling methods for shorebirds in highly heterogeneous wetland habitats. In highly altered landscapes like the RWB, as accessible habitat becomes increasingly sparse shorebirds may be forced to utilize less-open habitat (Webb *et al* 2010, Chapter 1); however, the dynamics dictating shifts in habitat use have not been precisely quantified across seasons or among wetland classes, leaving uncertainty in our ability to estimate trends in waterbird populations in the face of forecasted land-use and climate change. Indeed, due to severe logistical constraints associated with monitoring long-distance migrants, shorebird population estimates are already difficult to ascertain (Morrison *et al* 2007), and without adequate understanding of biases associated with habitat heterogeneity our ability to assess long-term trends in populations will certainly diminish if we are unable to determine to what extent loss and alteration of habitat drives population dynamics versus variance in habitat use and detection probability. Due to the ecological processes associated with highly

ephemeral wetland systems, the vegetative structure and thus the proportion of open habitat within ponded wetlands is highly variable annually and seasonally. Moreover, as climate change may alter not only the abundance and phenology of water across landscapes, but also the relative abundance of more highly vegetated wetland habitat (e.g., Johnson *et al* 2010), inherent biases in our survey estimates may become especially problematic as escalating habitat loss and alteration require birds to more frequently occupy marginal or less preferred habitat (Stutzman 2012). If we cannot distinguish between errors in detection versus variation in habitat use, we run the risk of misidentifying sources of variation in stopover behavior in response to annual and seasonal habitat dynamics, and thus we may fail to detect important long-term phenological trends relevant to migratory stopover ecology. More importantly, without adequate understanding of the efficacy of our survey approaches, it may be difficult to establish patterns in habitat use relevant for management of wetland complexes, at a time when effective management is becoming especially critical for the support of waterbird populations.

Tables and Figures

Table 1. Results of models predicting *Calidris* abundance in association with each wetland covariate according to point surveys and perimeter surveys. Model set 1 included site as a random effect, while model set 2 did not.

Model Set 1	β	SE	Wald χ^2	p	β	SE	Wald χ^2	p
	Point Surveys				Perimeter Surveys			
%Mud	-0.004	0.390	3.010	0.083	-0.012	0.002	47.042	<0.001
Year	1.191	0.109	118.517	<0.001	0.807	0.085	90.170	<0.001
%Water	-0.002	0.001	1.810	0.179	0.010	0.001	81.36	<0.001
Year	1.221	0.107	129.763	<0.001	0.999	0.084	140.37	<0.001
%Brown Vegetation	0.017	0.002	61.825	<0.001	-0.000	0.002	0.056	0.813
Year	1.102	0.110	99.475	<0.001	0.924	0.085	118.463	<0.001
%Green Vegetation	-0.010	0.002	18.074	<0.001	-0.010	0.002	44.255	<0.001
Year	1.310	0.109	144.835	<0.001	0.989	0.084	138.301	<0.001
%Total Vegetation	0.005	0.002	1.7920	<0.01	-0.008	0.001	36.54	<0.001
Year	1.149	0.111	107.338	<0.001	1.058	0.087	149.33	<0.001
% Veg <15cm	-0.008	0.001	41.004	<0.001	-0.009	0.001	64.811	<0.001
Year	1.001	0.112	79.606	<0.001	0.652	0.089	53.336	<0.001
Area (ha)	-0.079	0.008	93.305	<0.001	-0.056	0.006	77.134	<0.001
Year	1.242	0.116	113.826	<0.001	0.987	0.870	128.660	<0.001
Model Set 2								
%Mud	0.026	0.002	250.81	<0.001	0.012	0.001	82.38	<0.001
Year	1.200	0.055	397.96	<0.001	1.104	0.047	556.89	<0.001
%Water	0.009	0.001	73.131	<0.001	0.009	0.001	107.51	<0.001
Year	0.906	0.053	294.812	<0.001	1.065	0.046	541.99	<0.001
%Brown Vegetation	-0.006	0.001	19.967	<0.001	-0.016	0.001	182.59	<0.001
Year	0.943	0.053	316.725	<0.001	1.080	0.045	564.33	<0.001
%Green Vegetation	-0.017	0.001	207.81	<0.001	-0.006	0.001	45.53	<0.001
Year	0.930	0.053	305.36	<0.001	1.043	0.453	530.80	<0.001
%Total Vegetation	-0.018	0.001	274.43	<0.001	-0.014	0.001	247.10	<0.001
Year	1.008	0.054	344.66	<0.001	1.192	0.047	631.15	<0.001
% Veg <15cm	0.009	0.001	105.41	<0.001	-0.001	0.001	2.297	0.130
Year	0.943	0.054	299.77	<0.001	0.950	0.046	434.943	<0.001
Area (ha)	-0.023	0.002	150.74	<0.001	0.010	0.001	116.19	<0.001
Year	0.912	0.532	293.39	<0.001	0.920	0.046	407.88	<0.001

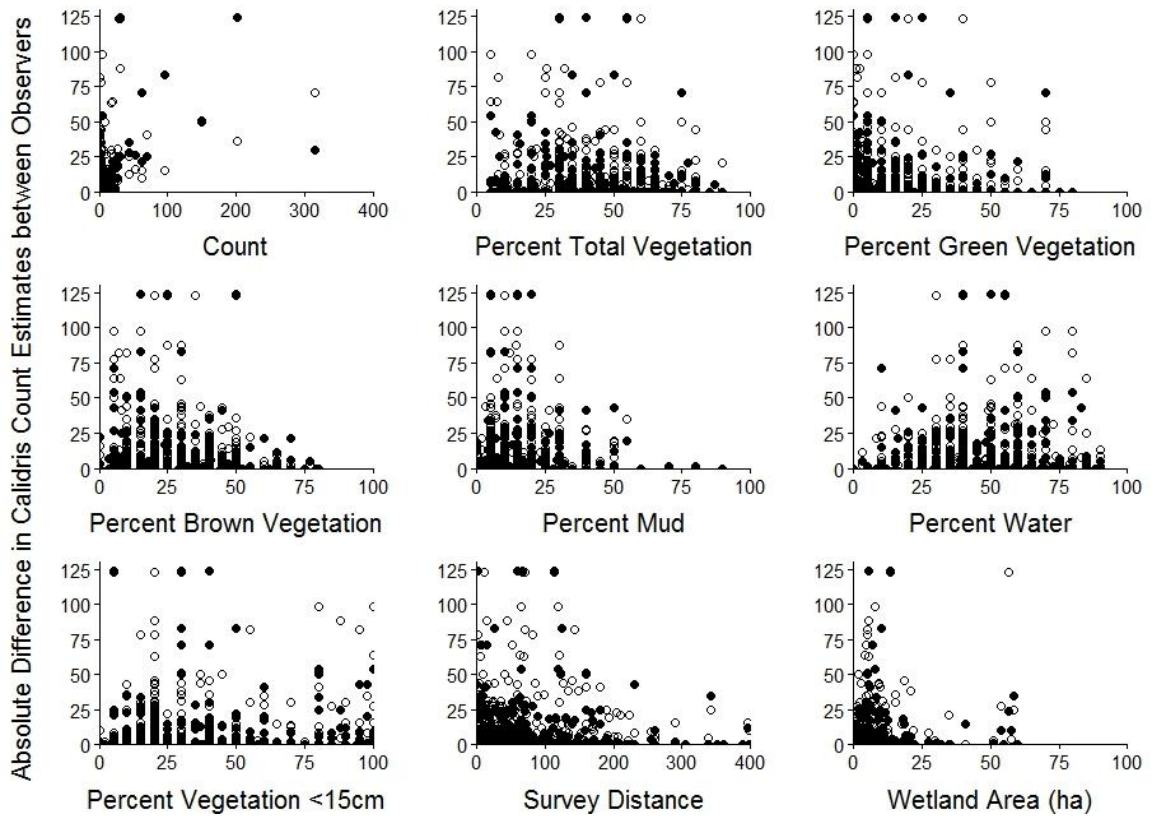


Figure 1. Shorebird count estimates differed between observers independent of survey method, and the difference in count estimates was not predicted by any of the habitat attributes we measured. White circles represent point surveys, while black circles represent perimeter surveys.

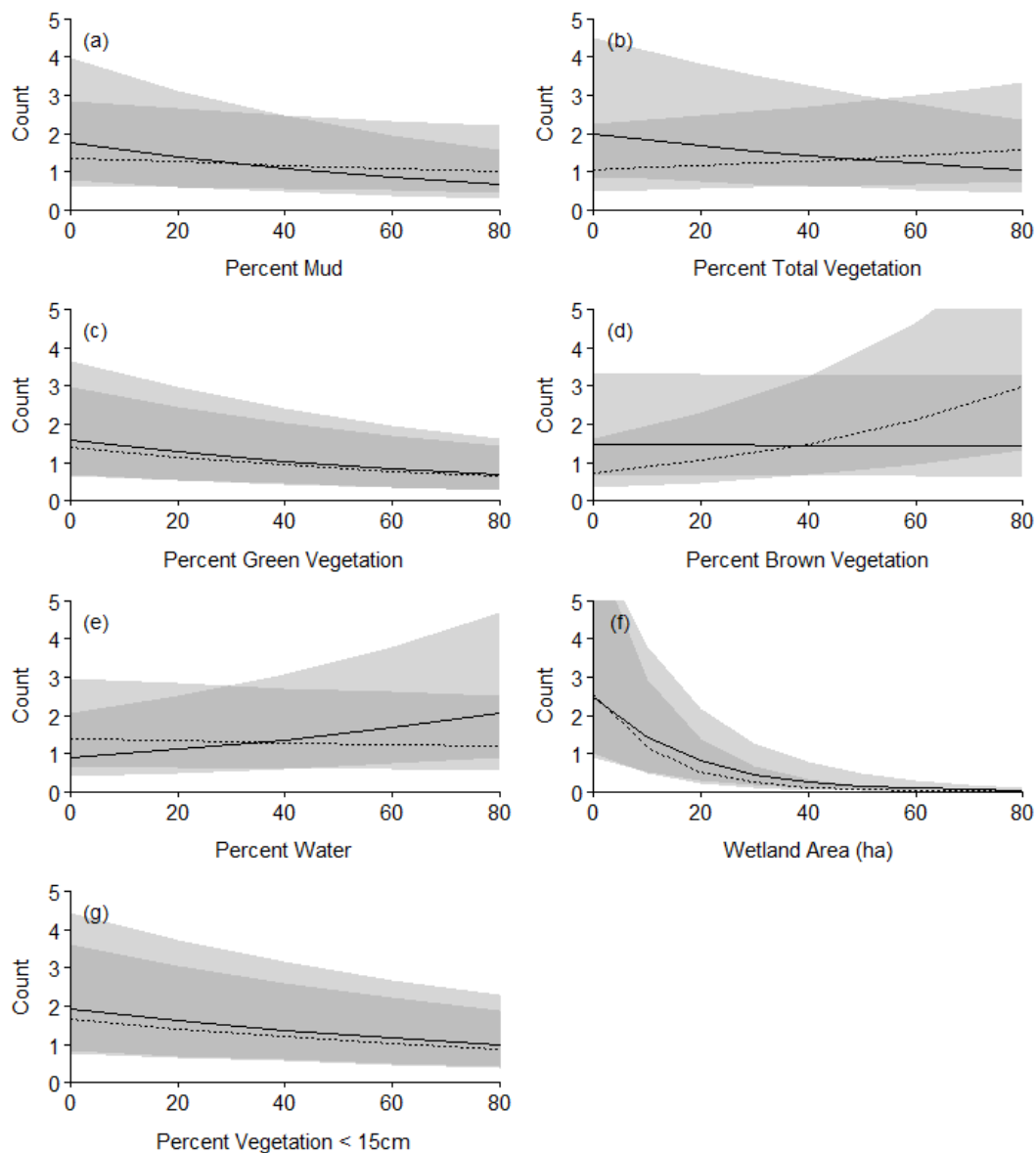


Figure 2. Predicted relationships between habitat characteristics and *Calidris* abundance according to point surveys (dotted line) versus perimeter surveys (solid line) based on our original models with site ID included as a random effect. Point surveys demonstrated a positive correlation with brown vegetation, while perimeter surveys showed significant negative relationships with mud and water. Short vegetation, green vegetation and area demonstrated significant negative relationships in both survey types. Details of results are presented in Table 1. Shaded areas represent 95% confidence intervals for each prediction.

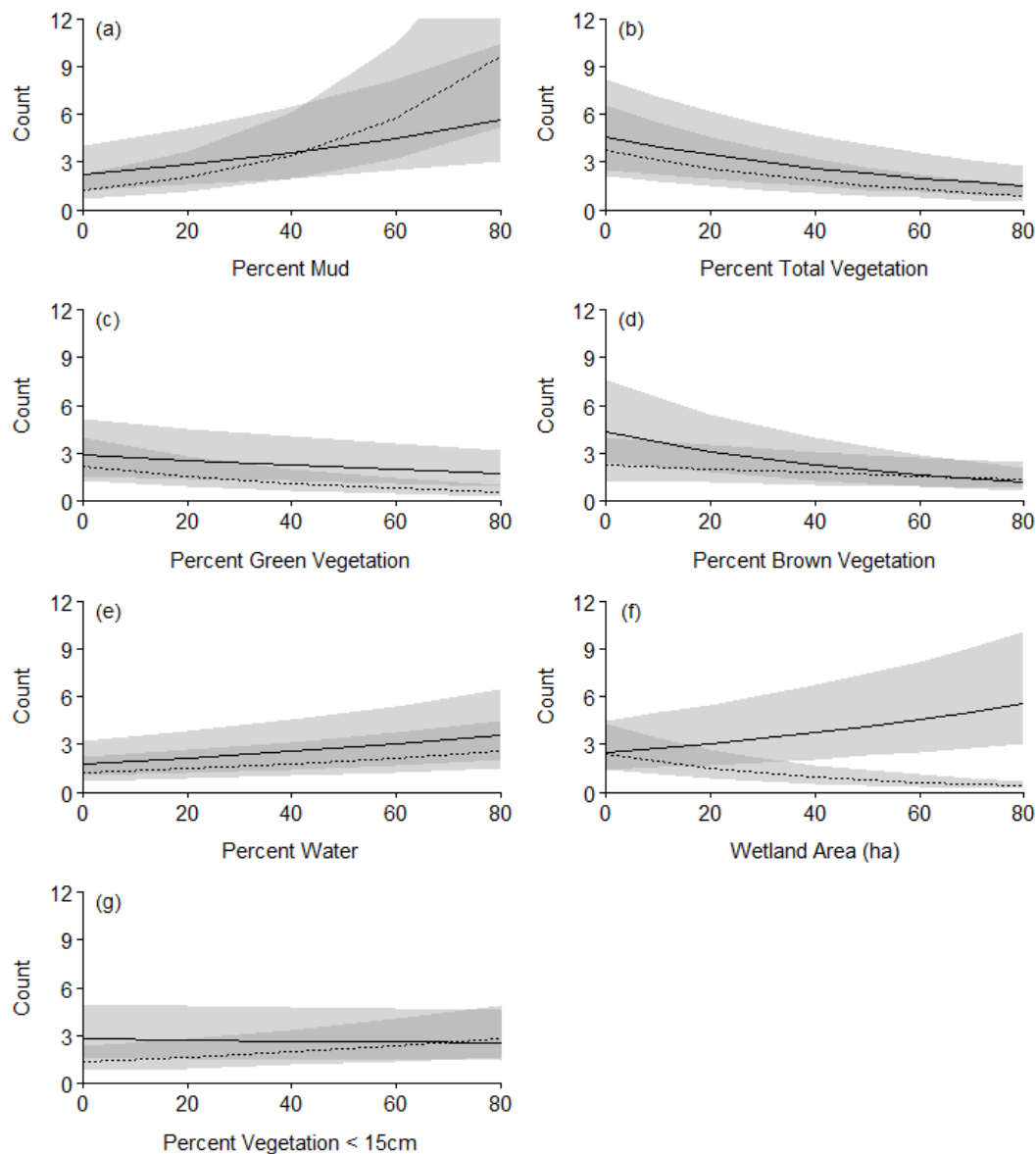


Figure 3. Predicted relationships between habitat characteristics and *Calidris* abundance according to point surveys (dotted line) versus perimeter surveys (solid line) based on our second set of models which did not include site ID as a random effect. Point surveys and perimeter surveys both demonstrated positive relationships with mud and water, and negative relationships with total, green and brown vegetation. Short vegetation and wetland area were negatively associated with abundance in point surveys, but wetland area was positively associated with bird abundance in perimeter surveys. Details of results are presented in Table 1. Shaded areas represent 95% confidence intervals for each prediction.

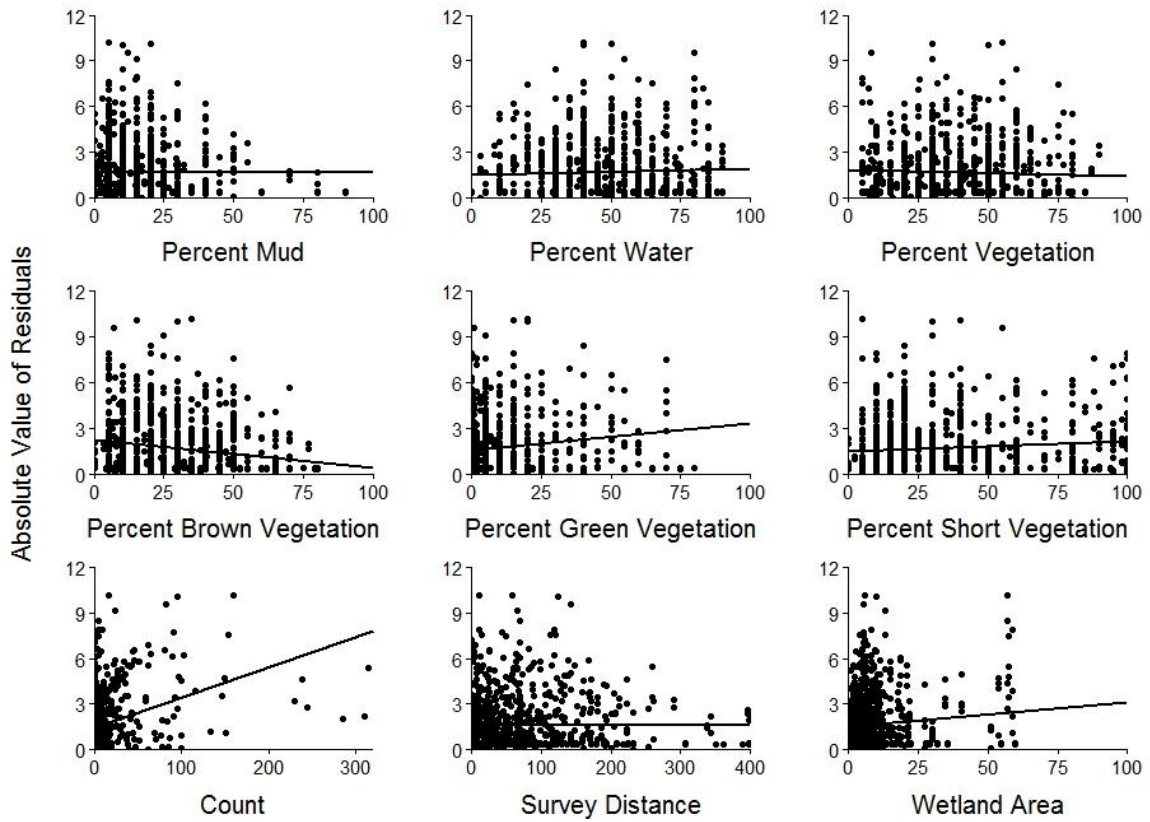


Figure 4. Variance in the residuals of the model comparing estimates of *Calidris* abundance among the four surveys at each wetland. Variance was positively correlated with green vegetation, vegetation less than 15cm, count, and wetland area, and was negatively correlated with brown vegetation. Percent mud, water, total vegetation, and survey distance did not demonstrate any pattern predicting variance in the model.

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