# STOPOVER DECISIONS OF MIGRATORY SHOREBIRDS: AN ASSESSMENT OF HABITAT USE, FOOD AVAILABILITY, BEHAVIOR AND PHENOLOGY

by

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**STOPOVER DECISIONS OF MIGRATORY SHOREBIRDS:**

**AN ASSESSMENT OF HABITAT USE, FOOD**

**AVAILABILITY, BEHAVIOR AND PHENOLOGY**

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Habitat loss and alteration from land use change, species invasion, and more recently, climate change has reduced biodiversity and ecosystem function worldwide. Habitat decisions have important implications to individual fitness as well as population dynamics and community structure. Resource limitation, predation, competition, and unfavorable abiotic conditions all have the potential to influence survival and future reproductive potential. Understanding how changes to ecosystem structure and function impact species and populations of conservation concern is essential for conservation delivery to be effective. Similar to many migratory species, shorebird populations are declining worldwide and declines may be related to the loss of important stopover habitat in the form of mid-continental wetlands.

During 2010-2011, I examined how long-distance migratory shorebirds have responded to extensive, agriculturally-driven, alterations to wetland habitats. I focused on a suite of ecological conditions that are expected to influence migrant fitness including habitat preference, resource availability and behavior. Additionally, because land use change is expected to act in conjunction with climate change to alter wetland habitats, I examined a number of phenologic variables and made predictions on how migrants might be affected in the future.

Migrant shorebirds were more likely to use highly-altered, agricultural wetlands than wetlands embedded in native grasslands and did so in greater numbers. Preference for altered habitat was unexpected because these habitats had lower food availability, but preference may be explained by the role of mud flat as an influential cue, which would increase the attractiveness of agricultural wetlands. Such a scenario can be indicative of an ecological trap, where individuals prefer lower quality habitat. However, behavioral analysis indicates that migrants have adapted to using novel habitats through increased foraging efficiency. Despite their apparent adaptability to changing conditions, migrant shorebirds may be susceptible to further population decline as a result of changes in phenology brought about by climate change. Results show that peak migration is correlated with the availability of food resources. Given that shorebirds already prefer habitat with lower resource availability, any changes to invertebrate or migration phenology that is not congruent in magnitude and direction to the other could affect migrant populations.

# DEDICATION

To my father, who exposed me to the excitement of the natural world and showed me that exploring it was a viable option as a career.

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# Chapter 1: STOPOVER DECISIONS OF MIGRATORY *CALIDRINE* SHOREBIRDS: AN ASSESSMENT OF HABITAT USE, FOOD AVAILABILITY, AND BEHAVIOR

*Abstract:*

Habitat decisions have important fitness implications, and individual habitat decisions can affect population and community structure. Because habitat loss and alteration represent a significant threat to biodiversity, continued understanding of how individuals make habitat decisions in altered landscapes and the subsequent consequences of these decisions is important. Migratory species are declining worldwide and may be more suseptible to habitat alteration because they are required to make habitat decisions quickly and in novel environments. We surveyed *Calidrine* shorebird use of habitats in different land us types at 155 and 163 wetlands in 2010 and 2011 respectively. To determine habitat preference, we compared the proportion at which wetlands in each land use type were used with the proportion at which they were available. Migrants preferred wetlands in high intensity agricultural fields as they were significantly more likely (P = 0.016) to use wetlands in soybean fields than availability would predict. Wetlands in grassland habitats were used less than predicted (P = 0.0384). We examined micro- and macro-habitat characteristics of the preferred habitats including benthic invertebrate abundance as a measure of habitat quality. Preferred habitats had a greater proportion of mud flat, shorter vegetation and reduced invertebrate abundance. To determine whether shorebird habitat decisions were adaptive, we used behavioral observations gained from video recordings to compare foraging and anti-predator behaviors. Shorebirds foraged more actively at preferred habitats without incurring a cost to predator vigilance. Results

indicate that preference for altered habitats that have lower resource availability may be adaptive because migrants are able to buffer against the consequences of their decision through behavioral modification. Food availability is thought to be the limiting resource for avian migrants; however, our data indicate that avian species make habitat decisions based on complex tradeoffs that, in the presence of altered habitat, may not hold to historic, well-documented relationships.

# INTRODUCTION

Habitat decisions have important fitness implications which help determine population dynamics and community structure (Martin 1992, 1998; Pulliam 2000; Johnson 2007). Resource limitation, predation, competition, and unfavorable abiotic conditions all have the potential to constrain fitness, and as such successful habitat decisions should minimize these costs (Fretwell and Lucas 1970; Bernstein et al. 1991; Cody 1985; Morris 2003).However at large spatial scales or when faced with temporal constraints, individuals are under selection pressure to minimize the search effort necessary to make 'ideal' habitat decisions (Alerstam and Lindstr□m 1990; Moore et al. 1990; Moore and Aborn 2000; Petit 2000). The use of habitat cues as an indicator of habitat quality has ostensibly evolved as a means to hasten habitat decisions, but is reliant upon a predictable relationship between the habitat, the evolved cue, and the resources that individuals are ultimately interested in acquiring. Although selection favors individuals that use habitat-cues to select higher quality habitats (Hildén 1965; Martin 1992, 1998), the indirect nature of the relationship between the resource, the cue, and the individual make such habitat decisions susceptible to the vagaries of anthropogenic change (Battin 2004; Robertson and Hutto 2006). Migratory species may be particularly vulnerable to anthropogenic disruptions in the relationship between habitat-cues and habitat resources as the nature of migration requires individuals 'stop over' at habitats to replenish energy reserves en route (Meyers et al. 1987), and thus repeatedly make habitat decisions in novel environments under temporal constraints (Hutto 1985; Loria and Moore 1990; Moore and Aborn 2000; Petit 2000). Moreover, because each subsequent habitat decision has important and interrelated fitness consequences, the costs of making

poor habitat decisions can have cascading implications throughout the annual cycle of an individual (Hutto 1985; Loria and Moore 1990; Marra et al. 1998; Moore et al. 2005).

Migrants face a variety of constraints when selecting stopover sites including predation and competition (Petit 2000), but food is presumed the limiting factor affecting habitat decisions (Hutto 1985; Moore et al. 1995; but see Ydenberg et al. 2002). Evidence has emerged that migratory birds may prefer stopover habitats with higher food availability (Hutto 1985, Moore et al. 1995; McGrath et al. 2009), as variation in food availability affects both survival and future reproduction (Lima and Dill 1990; Piersma 1990; Moore et al. 1995). For migratory birds that exhibit long distance migratory strategies, such as shorebirds, choosing stopover habitats with adequate food resources may be particularly critical to survival and future reproduction. Given the importance of energy acquisition in concert with evidence that shorebirds spend the majority of their time foraging during stopover (Davis and Smith 1998; DeLeon and Smith 1999), it is reasonable to assume that food availability is the ultimate driver of stopover decisions. The fact that shorebirds tend to use wetlands with higher food availability (Andrei et al. 2008) and exhibit dietary plasticity across invertebrates (Skagen and Oman 1996), allowing individuals to feed opportunistically as they move across latitudes and encounter different communities, further suggests the importance of food resources in shaping shorebird stopover decisions.

Favorable shorebird habitat is typified by shallow water and sparse vegetation (Colwell and Oring 1988; Skagen and Knopf 1994a; Davis and Smith 1998). For populations that migrate along the coast, 'ideal' habitat is predictable and readily available in the form of intertidal flats and coastal beaches. For inland populations that

migrate through the mid-continental United States, there is less certainty in habitat availability and suitability en route (Skagen and Knopf 1994a). Suitable habitat is located at ephemeral wetlands and riverine sandbars that are largely influenced by the effects of winter and spring precipitation (Kantrud et al. 1989). So although the conditions that produce shorebird habitat are common, resulting in extraordinarily high densities of wetlands (Kantrud et al 1989), the location and overall availability of suitable habitat is subject to the vagaries of climatic conditions and therefore seemingly unpredictable (Diaz 1983, 1986). Moreover, intensifying land-use practices throughout the prairies of North America have further complicated the predictability of appropriate stopover habitats by altering both the availability and functionality of wetland and riverine habitats (Dahl 2000). Although the loss of stopover habitat is predicted to reduce mid-continental shorebird populations (Skagen 1997; Harrington et al. 2002), the extent to which anthropogenic modification to the functionality of the remaining wetland habitats affects migrating shorebirds remains largely unknown (Skagen 2006). Indeed, shorebirds continue to stop and refuel at inland wetlands, but stopover decisions are now made in highly altered, agriculturally dominated landscapes. The result is that habitat decisions are increasingly leading to the selection of agrarian habitats (Elphick and Oring 1998; Taft and Haig 2005; Niemuth et al. 2006). The use of agrarian habitats by migrating shorebirds is surprising as agriculture practices clearly alter wetland ecosystem services, including reducing the diversity and abundance of invertebrates (e.g. Euliss and Mushet 1999; Davis and Bidwell 2008). Thus that shorebirds use agrarian habitats during stopover appears paradoxical and even indicative of an ecological trap as reductions in prey availability are known to affect shorebird populations and may

ultimately help explain why mid-continental shorebird populations are in decline (Skagen and Oman 1996; Davis and Smith 2001, Thomas et al. 2006).

To assess the extent to which land-use change across the prairies ofNorth America has led to an ecological trap for migrating shorebirds we examined the habitat decisions of arctic-nesting sandpipers (*Calidris spp.*) during stopover in the Prairie Pothole Region. Although shorebird use of agrarian fields is widely documented (Elphick and Oring 1998; Taft and Haig 2005; Niemuth et al. 2006) , the extent to which this choice represents a habitat preference and a maladaptive decision, both key components of an ecological trap (Robertson and Hutto 2006), remains unknown. Systematically addressing questions of habitat use and behavior as well as examining the potential costs and benefits can provide insight into how migratory species select habitat, how cues can potentially lead to poor decisions, and ultimately what may be driving migratory shorebird population declines. To this end, we **1)** assessed shorebird habitat preference based on land use practice; **2)** identified cues associated with habitat decisions; and **3)** determined whether habitat decisions are adaptive based on multiple sources of selection (i.e., food abundance, food accessibility, predation risk).

## METHODS

### STUDY AREA

Data were collected in the Prairie Pothole region of north-central North America, specifically McPherson, Edmunds and Brown counties in northeast South Dakota (Fig. 1). The Prairie Pothole Region of central North America is characterized by millions of small depressional wetlands left by receding ice sheets in the late Pleistocene and by a

seasonal and relatively dry climate punctuated by severe droughts and deluges (Johnson et al. 2005). The area experiences daily average high temperatures between 14.1° C and 21.2° C and receives about 11.48 cm. of precipitation during the study period. The region has high wetland density and diverse land use practices, including row crops, range lands, hay fields, conservation reserve grassland as well as many native prairie remnants. Because shorebirds use shallow water for foraging (Skagen and Knopf 1994a; Davis and Smith 1998), sampling included seasonal and temporary wetlands as well as flooded fields (Stewart and Kantrud 1971). All sampling was done from early April through mid-June of 2010 and 2011 in order to encompass the entire migration period of all northbound migratory shorebirds in the region (Skagen et al. 2008).

## TARGET SPECIES

Surveys were conducted on arctic-nesting sandpipers (*Calidris spp.).* Due to small sample sizes for individual species', *Calidris spp.* were analyzed together. Although there are subtle differences in micro-habitat use and foraging technique between species, these differences are negligible in the scope of this study because *Calidris* shorebirds that migrate through the study area essentially occupy the same ecological niche whereby they forage in shallow water/mudflat habitats for benthic invertebrates (Skagen and Oman 1996; Davis and Smith 2001; Skagen 2006). Stopover periods of *Calidrine* species overlap, but do not completely coincide (Skagen et al. 2008) By including all *Calidrine* species' in subsequent analysis, we improved the scope of inference of the study.

# MACRO-HABITAT PREFERENCE

## *Transects*

We established sample wetlands along nine road transects within the study area and surveyed shorebird habitat use at 155 and 163 wetlands in 2010 and 2011 respectively, with 85% of the wetlands visited in both years. Transects were selected following a systematic random sampling protocol, constrained by logistics like road passability and safety, and were between 15 and 30 km long. We selected transects that were separated by at least three km. to ensure independence in habitat availability. We surveyed transects every 7-10 days, as this time exceeds average stopover duration for shorebirds in the region (Skagen and Knopf 1994b) and reduces the likelihood of resampling individuals. All wetlands were classified according to the primary (>50%) land use type in which they were imbedded, including: corn, soybean, tilled, or grassland.

To maximize detection of shorebirds, we only sampled wetlands that were located within 150 m. of the transect. Wetlands along transects were separated by a minimum of 0.8 km, creating a sample of wetlands randomly distributed in different land-use types. Using binoculars and a spotting scope, all shorebirds using each wetland were identified and enumerated within a 10 minute sampling window. A standardized sampling window was used to control for sampling effort and detection probability.

## *Land Use Types*

Because the majority of migrants pass through the study region in the early spring and prior to when the sampling year's agricultural practices might affect stopover habitat, land-use type for wetlands were classified according to the most recent active land

practice Four primary land use types were included in our analysis (Fig. 2). Wetlands in **grasslands** included those imbedded in Conservation Reserve Program (CRP), native prairie or rangeland, and hay fields. Wetlands classified as **corn** or **soybean** included those that were imbedded in both harvested and unharvested fields, as well as fields that had been mulched or flattened in preparation for planting. Finally, wetlands were classified as **tilled** when the field they were in had been disked or otherwise prepared for planting through the removal of stubble. Tilled fields may have included fields that had been planted to winter wheat the previous fall if wheat growth was not apparent.

*Habitat Covariates*

We collected habitat variables from each wetland to describe shorebird preference as it pertains to local wetland characteristics in an attempt to explain drivers of macro-habitat preference. Percent full was estimated from the amount of water currently in the wetland relative to the basin's edge which we estimated based on changes in topography and vegetation (Cowardin et al. 1979). We hypothesized that shorebirds may use wetland plant phenology as a cue for making habitat decisions because timing of spring green up is an indicator of invertebrate phenology and migrating species use vegetative characteristics as a visual cue to select sites with favorable foraging conditions (e.g. McGrath et al. 2009). To quantify wetland plant phenology and vegetative characteristics, we visually estimated the proportion of mudflat and green vegetation of all non-submerged vegetation and shore within a 10 m. buffer of the water's edge for each wetland. In 2011, we used the same protocol to estimate the proportion of open water, litter, and brown vegetation. Vegetation height at wetlands was also estimated

visually. Finally in both years, we classified each wetland's emergent vegetation cover type (adopted from Niemuth et al. 2006), land use type, and estimated wetland size using a range finder.

*Statistical analysis*

We compared the probability of use and flock size between land use types using generalized linear models (hereafter GLM) that were identified using backwards selection from a global model containing biologically relevant covariates and two-way interactions. Correlated variables were not included in the model. Here we only report the final model. We considered probability of use as the likelihood that a wetland was used by at least one individual. Probability of use was calculated after converting shorebird observations to presence/absence. Our approach was to eliminate potential bias caused by differing detection probabilities resulting from differences in vegetation structure at the various land use types. Because we assumed that our sampling design allows observers to detect at least one individual if any are present, any bias in abundance estimates are minimized by using presence/absence data.

Because we had a large number of wetland observations with no shorebird detections, we restricted our analysis of flock size to used wetlands (≥ 1 *Calidris* individual). By limiting our analysis of flock size to 'used' wetlands, we only compared habitats that were considered suitable by at least one individual, making them more likely to contain attractive habitat cues. We performed an ANCOVA on the GLM for both use and flock size, using a binomial and Poisson distribution, respectively. We then used a

LSD post-hoc test with a Bonferroni correction to test for differences in use and flock size between land use types.

We also compared the proportion at which wetlands in corn, soybean, and grassland were used with their estimated available proportion using a paired *t*-test. We estimated wetland availability for each land use type by averaging the proportion of each land use type from the USDA Agricultural Statistics data from the study region (USDA 2012). Grassland availability estimates include Conservation Reserve Program, pasture, and hayed acres from the counties in study area. However, wetlands in tilled fields were not included in this analysis because tilled acres are not available from the USDA Agricultural statistics.

## FOOD AVAILABILITY

### *Wetland Sampling*

In 2011, we measured benthic invertebrate availability at 26 wetlands (19 agricultural, 7 grassland) and compared relative abundance across land use type. Each wetland was resampled up to three times every 10-14 days or until dry, resulting in 70 wetland sampling visits. Three soil cores were taken to a depth of 5 cm. using a 5 cm. diameter corer (Sherfy et al. 2000) at 3m x 3m sample plots. Three to five plot locations were selected for a total of 9-15 soil cores/wetland. When possible, plots were placed at known foraging locations based on previous observations. This non-random design was used to ensure that a portion of our sampling was done in areas that were used by shorebirds, and to correspond with behavioral observations (see below). In all cases, plots were separated by > 10 m. Core samples were washed through a 0.5 mm soil sieve

and invertebrates enumerated at the wetland to establish relative abundance. Benthic invertebrates were not classified because *Calidris* shorebirds exhibit high dietary plasticity across invertebrates (Skagen and Oman 1996), allowing individuals to feed opportunistically as they move across latitudes and encounter different communities.

### *Wetland Covariates*

We measured a number of covariates expected to influence benthic invertebrate abundance and phenology at both the plot and wetland level. Soil pH, moisture content, temperature and compactness were measured once at a 5cm depth in the center of each plot using a Kelway soil meter, standard soil thermometer, and a soil penetrometer. We measured land use and water temperature at the wetland level because they were not expected to vary within a wetland. However, due to lack of sample size of specific land use types and high variability in farming practices within a given land use type, we classified wetlands only as “agricultural” or “grassland”.

### *Statistical Analysis*

To test for the influence of land use type and other covariates on food availability, we used a GLM that was identified through backwards selection from a global model that contained relevant covariates and had a normal distribution. We performed an ANCOVA to test for the significant differences between land use types.

## SHOREBIRD BEHAVIOR

### *Behavior Recordings*

We recorded *Calidris spp.* behavior using digital video cameras to test for differences in foraging behavior and time allocation between individuals using wetlands in different land use types. Three to five camouflaged cameras, each separated by >10m, were placed at up to three occasions at 26 wetlands (19 agricultural, 7 grassland) focused on known foraging habitats (3-5 n of shoreline at the water's edge). Recordings of shorebird behaviors were made in high resolution and at a magnification level so that individual birds are distinguishable and in focus.

*Behavioral Observations*

We used program *JWatcher* (Blumstein et al. 2006) to record specific behavioral data of every *Calidris* individual in all video recordings; however, we did not make observations until 15 minutes into the recording to reduce the effects of disturbance from camera set-up. *JWatcher* allows observers to simultaneously record the number of behavioral events and the duration of each event through the use of a computer keyboard where keys are associated with specific behaviors. Behaviors were measured by watching every individual at ¼ normal speed for the duration of time that the individual was in the frame. Species and the maximum number of *Calidris* individuals that were visible during the duration of the observation were recorded as covariates.

We recorded every occurrence of the following behaviors: foraging attempts (pecks/probes), steps (walking or running), scanning, flight, aggression, submission, and body maintenance (modified from DeLeon and Smith 1999). These behavioral categories were used to calculate pecking rate (forage attempts/second), which has been shown to correlate with food availability and feeding rate (Kuwae 2007); search effort

(steps/foraging attempt), as movement is a measure of foraging efficiency (Dias et al. 2009); and visual scanning, an anti-predator behavior in shorebirds (Fitzpatrick and Bouchez 1998).

*Micro-habitat Covariates*

To examine the influence of micro-habitat conditions on shorebird behavior the following day we revisited the locations of the behavioral observations and measured a number of covariates. Data were collected in 3m x 3m plots placed in the center of the camera's frame,with one side placed along the wetland's edge. We visually estimated the proportion of litter, water, dry soil, wet soil, and vegetation within a 0.10 $m^2$ quadrat (modified from Daubenmire 1959) at three random locations in each plot. We measured the maximum height of vegetation or litter within each quadrat as an index of visual obstruction. Finally we measured benthic invertebrate abundance at specific recording locations (see above). Due to a large number of zeroes, invertebrate data were log transformed after adding a constant. We also estimated the slope of the wetland's primary shorebird foraging zone by measuring water depth at multiple locations.

*Statistical Analysis*

We tested for the influence of land use type and micro-habitat covariates on shorebird pecking rate, search effort and anti-predator scanning. Both pecking rate and search effort were analyzed using a normal distribution after being *log* transformed. We used a GLM for each behavioral response variable, and using backward selection we removed correlated covariates and non-significant variables ($p > 0.05$) from all models.

Individuals spent an extremely small proportion of their time scanning which led to extremely skewed data. Thus, we converted scanning data into a binomial distribution, and tested for the influence of covariates on the probability of an individual scanning at least one time. We also compared proportion of time spent scanning between land use type for observations with at least one scanning event. Here, we used a GLM that included visible flock size as a covariate and tested for differences using a LSD post-hoc test with a Bonferroni correction.

## RESULTS

### MACRO-HABITAT PREFERENCE

Shorebirds showed a clear preference for wetlands in altered habitats as wetland in soybean fields were used more than expected based on availability (Fig. 3c; $t_1$ =38.90, P =0.016) while wetlands in grasslands were ostensibly avoided ($t_1$ = -16.54, P =0.0384). Moreover, occupancy (Fig. 3a; land use type: $F_{3, 1464}$ =48.41, P < 0.001; year: $F_{1, 1464}$ =14.48, P < 0.001; date: $F_{1, 1464}$ =6.66, P = 0.009; mud flat: $F_{1, 1464}$ = 5.36, P = 0.02; green vegetation: $F_{1, 1464}$ =11.58, P < 0.001) and abundance (Fig. 3b; land use: $F_{3,80}$ = 135.00, P>0.001; year: $F_{3, 30}$ =33.08, P < 0.001; cover type: $F_{2, 80}$ = 74.59, P < 0.001; mud flat: $F_{1, 80}$ =16.52, P < 0.001; green vegetation: $F_{1, 1464}$ =325.60, P < 0.001; wetland size: $F_{1, 80}$ =6.00, P = 0.01; land use x mud flat: $F_{3, 80}$ =9.08, P < 0.001) were greatest for wetlands in soybean and tilled fields.

### FOOD AVAILABILITY

Land use significantly influenced invertebrate abundance at wetlands (Fig. 4c; land use: $F_{1, 68} = 350.11$, $P = 0.006$; soil compactness: $F_{1, 68} = 303.71$, $P = 0.002$) as grassland wetlands had greater invertebrate abundance than agricultural wetlands.

## SHOREBIRD BEHAVIOR

As predicted, pecking rate within land use types increased with increased food availability (invertebrate abundance: $F_{1, 2732} = 32.26$, $P < 0.001$;) while scanning rate increased with vegetative structure (vegetation height: $F_{1, 2732} = 3.96$, $P = 0.047$;). However, after accounting for food availability, shorebirds occupying agricultural wetlands tended to forage faster (Fig. 5a; land use: $F_{3, 2732} = 83.28$, $P < 0.001$; invertebrate abundance: $F_{1, 2732} = 32.26$, $P < 0.001$; vegetation height: $F_{1, 2732} = 19.62$, $P < 0.001$; vegetative cover: $F_{1, 2732} = 15.23$ , $P < 0.001$; slope: $F_{1,2732} = 23.20$, $P < 0.001$); search more actively (Fig. 5b; land use: $F_{3, 2732} = 70.14$, $P < 0.001$; invertebrate abundance: $F_{1, 2732} = 32.17$, $P < 0.001$; vegetation height: $F_{1, 2732} = 4.15$, $P = 0.042$; visible flock size: $F_{1, 2732} = 12.98$, $P < 0.001$; vegetative cover: $F_{1, 2732} = 4.31$, $P = 0.038$; slope: $F_{1, 2732} = 12.76$, $P < 0.001$); and were more likely to scan for predators (Fig. 5c; land use: $F_{3, 2732} = 41.02$, $P < 0.001$; vegetation height: $F_{1, 2732} = 3.96$, $P = 0.047$; visible flock size: $F_{1, 2732} = 56.29$, $P < 0.001$; litter cover: $F_{1, 2732} = 10.27$, $P = 0.001$). Land use also influenced proportion of time spent scanning when individuals scanned at least once (land use: $F_{3, 422}=3.75$, $P = 0.011$; visible flock size: $F_{1, 422}=3.75$, $P = 0.053$), and although migrants using wetlands in soybean fields also spent the greatest proportion of time scanning, the differences were not significant (Fig. 5d).

# DISCUSSION

Habitat loss and alteration is an important driver of global species declines (Fahrig 2003; Botkin et al. 2005; Hooper et al. 2005; Fischer and Lindenmayer 2007). Restoring altered habitats, while often the goal of conservation, is generally economically and socially unfeasible, thus it is imperative that we understand how species make habitat decisions in altered environments and what the consequences of these decisions are if conservation efforts are to be effective. Species that use habitat on a hemispheric or global scale may be particularly vulnerable to large scale habitat change because they depend on widely distributed and unfamiliar habitats. Migration for mid-continental shorebirds has very likely always been a major constraint, due in part to the immense scale and the highly variable and unpredictable nature of wetland stopover habitat throughout the region (Diaz 1983, 1986; Skagen and Knopf 1994a). But with U.S. corn and soybean production having increased by >3 million and >8 million hectares respectively since 1960 (FAO 2011), presumably at the cost of wetlands and native habitat, the constraint of migration has likely become more severe. Conversion to agricultural is the primary driver of wetland loss in North America and many of the wetlands that remain are vastly altered in function, and thus the ecosystem services they provide (Euliss and Mushet 1999; Dahl 2000; Davis and Bidwell 2008). It is clear then, that changing land use practices have the potential to exacerbate the unpredictability of wetland resources and the corresponding costs of migration.

Still, it is widely known that shorebirds use highly-altered, agricultural habitats (Elphick and Oring 1998; Twedt et al. 1998; Taft and Haig 2005; Niemuth et al. 2006) and our results support that conclusion. Not only did we find that shorebirds were more

likely to use wetlands in agricultural fields (Fig. 3a), they did so in greater numbers (Fig. 3b). In part, this is likely due to micro-habitat differences among land-use types. The availability of mud flat was positively correlated with shorebird use and flock size, and differed significantly among land-use types with agricultural wetlands having more mud flat and shorter vegetation (Fig. 4a, b).

That shorebirds use mud flats is not surprising (Colwell and Oring 1988; Skagen and Knopf 1994a; Davis and Smith 1998), as a mud flat cue likely evolved as an adaptive indicator of foraging conditions, similar to the habitat cues that indicate food availability for other migratory taxa (e.g., McGrath et al. 2009). Furthermore, local vegetation has been shown to influence shorebird habitat decisions (DeLeon 1996), and our data show used wetlands had a higher proportion of mudflat across land use type than did unused wetlands (Fig. 4d). That agricultural practices reproduce this cue may increase the attractiveness of agrarian wetlands independent of the actual habitat value. A scenario that may be indicative of an ecological trap given that agricultural practices can reduce the invertebrate food resources on which shorebirds depend (e.g. Euliss and Mushet 1999; Gleason et al. 2003). Still, verifying an ecological trap requires demonstrating that shorebirds not only use, but prefer lower quality habitats. The difference between an ecological trap and a habitat sink (Pulliam 1988) is illustrated by the difference between habitat use and habitat preference (Jones 2001; Robertson and Hutto 2006). Although sinks are important, traps are of greater conservation concern because they are more difficult to mitigate (Robertson and Hutto 2006). Unfortunately, despite the importance of doing so, it is extremely difficult to distinguish between use and preference, and as

such, studies that document habitat preference and the subsequent consequences are rare (Jones 2001).

Here we show for the first time a significant preference by mid-continental, migrant shorebirds for highly altered wetland habitats (Fig. 3c). Similar to the use pattern, the preferred land use type was soybean fields, as migrants were >2.5 times more likely to use wetlands in soybean fields than their availability would predict. Although significant, our estimates of preference for wetlands in soybean fields are likely conservative because our estimates of wetland availability were gleaned from USDA land-use statistics, and assume that wetlands are equally available across all land use types. This is unlikely however, as tilling and ditching of wetlands is common in agricultural fields making the presence of a wetlands less likely.Suggesting that the true preference for wetlands in soybean fields may be higher than our estimates indicate.

Migrant shorebirds clearly avoided grassland wetlands, the land use type that ostensibly most resembles the historic conditions under which their migratory ecology evolved. Avoidance of grassland wetlands is difficult to explain, and begs the question of what did shorebirds use as stopover habitat prior to agricultural expansion? Change in ecosystem function resulting from the removal of habitat modifiers such American bison (*Bison bison*), prairie dogs (*Cynomys ludovicianus*) and fire (Fuhlendorf and Engle 2004; Samson et al. 2004) may hold the answer. Pre-settlement North America experienced frequent late summer fires, after which new vegetative growth would have been limited, potentially creating ideal shorebird habitat when these areas flooded the following spring. In concert with intensive grazing, these conditions may have created a perfect storm for shorebird habitat formation as the combination of limited cover within a large mudflat

and local ponding from hoof traffic may have created ideal habitat for migrating shorebirds. Indeed, anecdotal evidence from the few heavily grazed grassland wetlands we surveyed indicates that they are more likely to be used by migrants, although sample sizes were too small for analysis. However, modern grazing practices may not be a sufficient substitute for historical disturbances (Augustine and Derner 2012).

Although shorebirds clearly preferred agrarian wetlands, documenting an ecological trap also requires demonstrating that individuals incur a cost. Here we show that the agrarian wetlands preferred by migrating shorebirds had lower invertebrate abundance (food availability) than the grassland wetlands they avoided (Fig. 4c). Although logistically we were unable to measure invertebrate biomass, which may be a better index of total caloric availability, invertebrate abundance is generally correlated with biomass and responds similarly to changing conditions (e.g., Whiles and Goldowitz 2001; Hamer et al. 2006). Additionally, we predict that shorebirds are more likely to forage on larger prey items which would create a scenario where a lower abundance of individual prey items would result in disproportionately lower biomass available for foraging.

As food availability during migration is generally assumed to have fitness implications (Hutto 1985; Moore et al.1995; Newton 2006), we may assume that the preference by shorebirds for agrarian wetlands would have population implications. At a minimum, reduced food availability might force individuals to extend stopover duration or the number of stops, which in turn delays breeding and reduces productivity (Piersma 1987; van Eerden et al. 1991; Kuenzi et al. 1991; Russell et al. 1992; Yong and Moore 1997). Alternatively, lower food availability may cause individuals to shorten duration

and undertake their next flight with inadequate energy reserves (Farmer and Wiens 1999). However, more severe implications may include starvation and depredation as individuals are unable to buffer against uncertainty (Lima & Dill 1990; Piersma 1990), and more likely to display risky behaviors in unfavorable environments (Ydenberg et al. 2002).

Still, it is important to note that less food may not necessarily mean *insufficient* food, and resource abundance alone may not be a sufficient measure of habitat quality (reviewed by Johnson 2007). It is reasonable that even the lower abundance of food at agrarian wetlands may still exceed the threshold necessary to support populations of migratory shorebirds, especially if agricultural expansion has led to an overall increase in available foraging habitat. Although this is counterintuitive considering that agriculture is the primary contributor to the loss and alteration of North America's freshwater wetlands (Dahl 2000), it is possible if suitable shorebird habitat was historically limited by a specific suite of conditions predicated on fire and grazing regimes. If the remaining highly-altered agricultural wetlands occur in greater abundance than suitable shorebird habitat did historically, it would reduce the overall intensity of use at each wetland and may allow individual habitats to be less productive while regionally still providing sufficient food resources. Moreover, while food availability is assumed to be the major limiting factor affecting migratory success (Hutto 1985; Moore et al. 1995; Newton 2006), it remains possible that the habitat decisions of migrating shorebirds are driven by a different limiting resource (i.e. predation, foraging rate, habitat itself), or more likely, a suite of selection pressures acting in concert.

To address whether food was truly limiting, we examined pecking rate (forage attempts/s) as a measure of foraging efficiency and found that it was highest in agrarian habitat types (Fig. 5a), despite the fact that agricultural habitats had a lower overall food availability (Fig. 4c). Our results were surprising because pecking rate is thought to be positively correlated with food availability (Shepherd and Boates 1999; Yasué 2005; Kuwae 2007) and more importantly, prey intake rate (Kuwae 2007). Given there was less food in agrarian wetlands (Fig. 4c), higher foraging rates indicate that individuals using agrarian wetlands were foraging more efficiently, possibly because they were more likely to have access to food resources despite the limited availability of food. Indeed it has been postulated that changes in foraging behavior would allow migrant species to buffer against the effects of habitat loss (Weber et al. 1999). Alternatively, because we were not able to differentiate between successful and unsuccessful foraging attempts, it is possible that the higher foraging rates we documented at agrarian wetlands are indicative of increased search effort and not increased efficiency. Indeed other shorebird species have been shown to increase their foraging activity in the absence of food (Vezina et al. 2009). However, this alternative seems unlikely as pecking rate predicted food availability *within* each land use type, as others have shown (Yasué 2005; Kuwae 2007). Moreover, search effort (steps/peck) was highest in preferred habitat types (Fig. 5b) which is what we would predict if individuals are more efficient at detecting and acquiring prey or less constrained by the potential risk of predation (Yasué 2005; Dias et al. 2009).

Although the behavioral modification we see expressed in agrarian wetlands likely has inherent costs, such as increased energy expenditure with greater foraging

effort, it is important to note that individuals increased foraging rates without decreasing predator vigilance (Fig. 5c, d). Rather vigilance was highest in birds using soybean fields, followed by those using grassland wetlands (3c). It is not clear why individuals using two habitat types that differ so greatly in structure would be the most likely to scan. One explanation may be that individuals are scanning for shorter periods of time in soybean fields, although we did not find a difference in proportion of time spent scanning for predators (Fig. 5d). Predation risk clearly constrains behavioral expression (Lima and Dill 1990; Lindstr□m 1990; Cresswell 1994; Ydenberg et al. 2002; Lank et al. 2003; Thomas et al. 2003; Fontaine and Martin 2006), and measuring behavior during migration can be ambiguous (Lind and Cresswell 2006). However, the rate that shorebirds scanned for predators was highly correlated with factors that influence the likelihood of detecting a predator, including flock size (Lima 1995) and vegetation height (Whittingham and Evans 2004). That we failed to find a consistent difference in vigilance between grassland and agricultural habitat types is interesting because it is generally thought that predation risk constrains foraging activity through direct tradeoffs between foraging behaviors and predator detection behaviors (Lima and Dill 1990; Lindstr□m 1990; Lima 1998; Ydenberg et al. 2002). However, while early detection of predators (i.e., greater vigilance) has benefits for facilitating escape behaviors; in environments where predator detectability is limited regardless of vigilance (i.e., highly vegetated grassland wetlands), behavioral strategies that reduce vulnerability to predators are likely more beneficial. Prey activity alters predation risk by influencing detection of and by predators, and there is increasing evidence that prey express less activity in high risk environments even when subsequent behavioral expression comes at significant costs

to other important sources of selection such as energy acquisition (Lima 1998). Thus, foraging less actively in grassland wetlands may be an adaptive response to reduce predation risk when predators are difficult to detect because of vegetative screening (Whittingham and Evans 2004).

Given the greater availability of food resources at grassland wetlands it is possible that peck rate (Fig. 5a), and thus food acquisition, is not constrained by food availability per se, but rather the ability to detect and move between prey items while minimizing predation risk: both by detecting predators earlier and avoiding being detected by predators. Although subtle, this distinction has important implications for what is driving habitat decisions as it is possible that habitat alteration has created a novel suite of selection pressures in which access to one resource (i.e., food availability) is increased by the increased availability of others (i.e., safety). That shorebirds settling in agrarian wetlands are free to actively forage indicates that habitat alteration may have changed the nature (slope) of the relationship between foraging and vigilance to the point where individuals can acquire food in agrarian habitats faster without the associated cost of decreased vigilance. If this is the case, it suggests that choosing altered habitats is adaptive in regard to both foraging and predation and thusly, much more sophisticated than initially thought. This finding indicates that avian species' make habitat decisions based on complex tradeoffs, that in the presence of altered habitat, may not hold to historic, well-documented relationships. Furthermore, it supports the need for careful examination of multiple selection pressures when exploring the complexities of habitat selection and what makes a choice adaptive or not.

Successfully managing shorebird populations as they migrate through mid-continental North America requires understanding the extent to which habitat decisions are maladaptive and thus impacting individuals and subsequently populations. It remains unclear how agricultural expansion is affecting mid-continental *Calidrine* shorebird populations. Preference for apparent lower quality habitat in terms of food resources suggests an ecological trap. However, we were able to use behavioral observations to illustrate some of the tradeoffs that migrants experience, and how behavioral plasticity has allowed for adaptation to changing conditions. Our data indicate that individuals may be able to avoid, or at the very least buffer against the potentially negative effects of using habitat with lower resources through behavioral modification. However, the potential that land use changes are independently driving shorebird declines still exists. Further investigation into the bio-energetic requirements of shorebirds and the overall caloric availability through the region is required before such determinations can be made.

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# TABLES AND FIGURES

Table 1: Important terminology and associated definitions.

| Term | Definition | Source |
|---|---|---|
| *Habitat* | "the resources and conditions present in an area that produce occupancy-including survival and reproduction-by a given organism" | Hall et al. 1997 |
| *Habitat Use* | "habitat currently occupied by the focal individual or species" | Jones 2001 |
| *Habitat Availability* | "refers to all habitat types in a prescribed area and includes habitats currently in use" | Jones 2001 |
| *Habitat Selection* | "a hierarchical process involving a series of innate and learned behavioral decisions made by an animal about what habitat it would use at different scales of the environment" | Hutto 1985 |
| *Habitat Quality* | "the per capita contribution to population growth expected from a given habitat" | Johnson 2007 |
| *Habitat Preference* | "the consequence of the process (of habitat selection), resulting in the disproportional use of some resources over others" | Hall et al. 1997 |

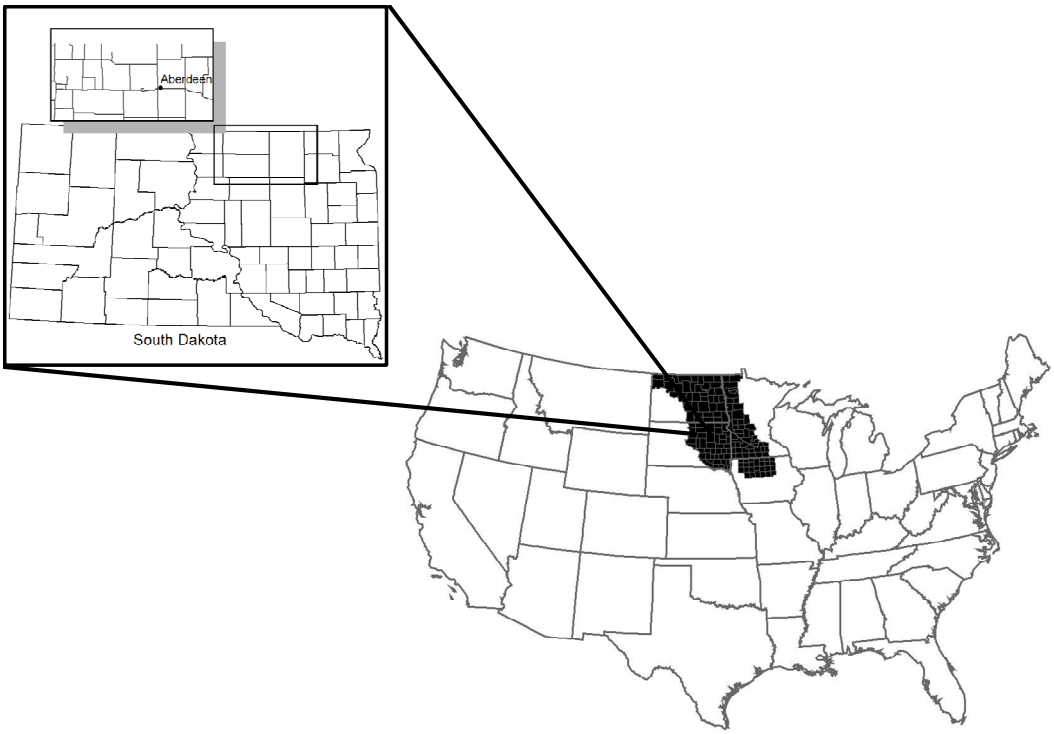


**Figure 1:** Prairie Pothole Region of North America with inset of study area.

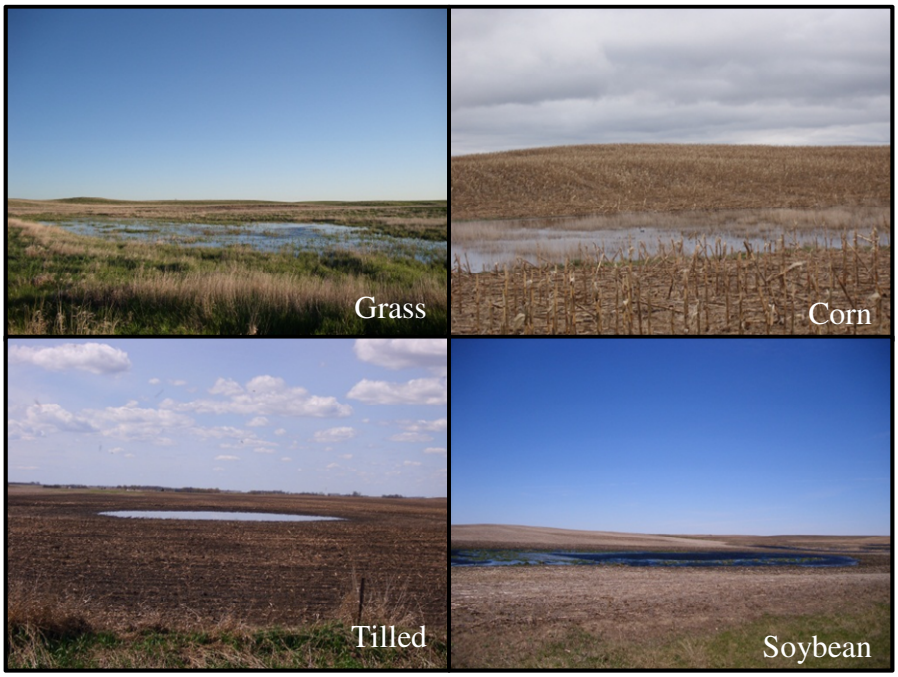


**Figure 2:** Examples of wetlands in the primary land use types.

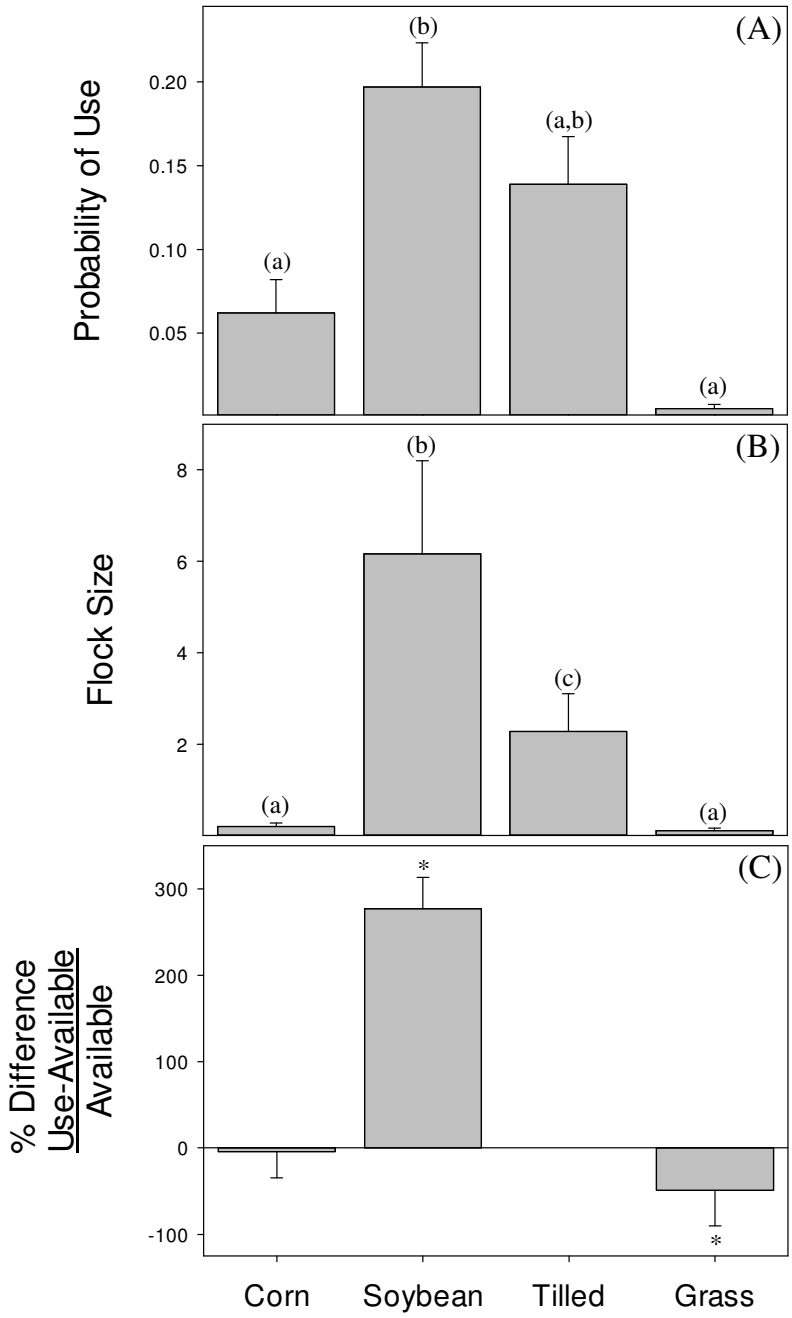


**Figure 3:** (A) Migrants use agricultural wetlands more and (B) occur in greater numbers on agricultural wetlands, (C) moreover they are more likely to use soybean wetlands than availability would predict while avoiding grassland wetlands. Columns denoted by different letters are significantly different at the 0.05 level according to an LSD-post hoc test and columns denoted by an asterisk represent significant differences between use and availability.

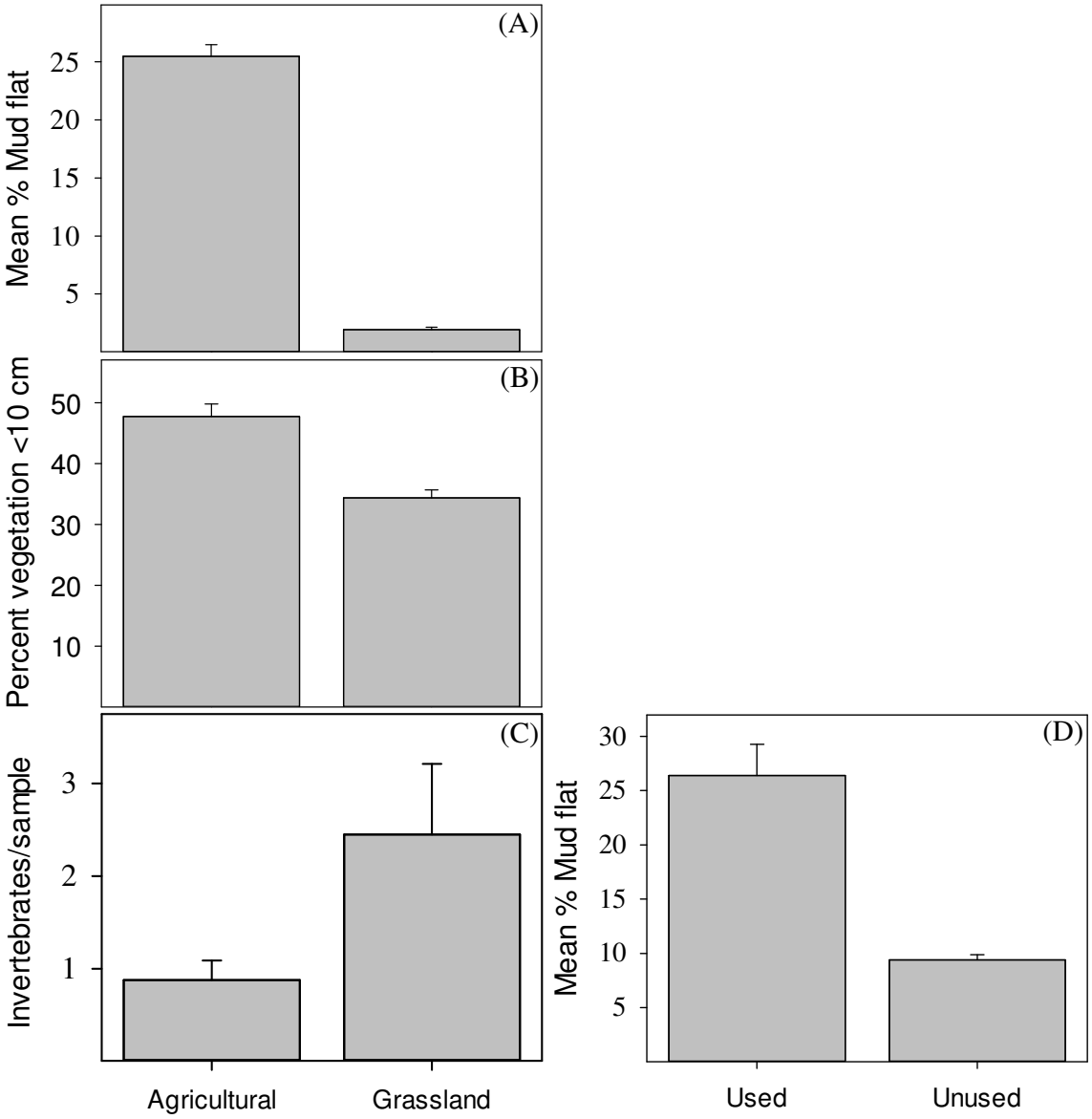


**Figure 4:** (A) Agrarian wetlands have significantly more mudflat available and (B) shorter vegetation, but lower (C) invertebrate (food) abundance. Preference for habitats with lower resource abundance may be driven by cues (D).

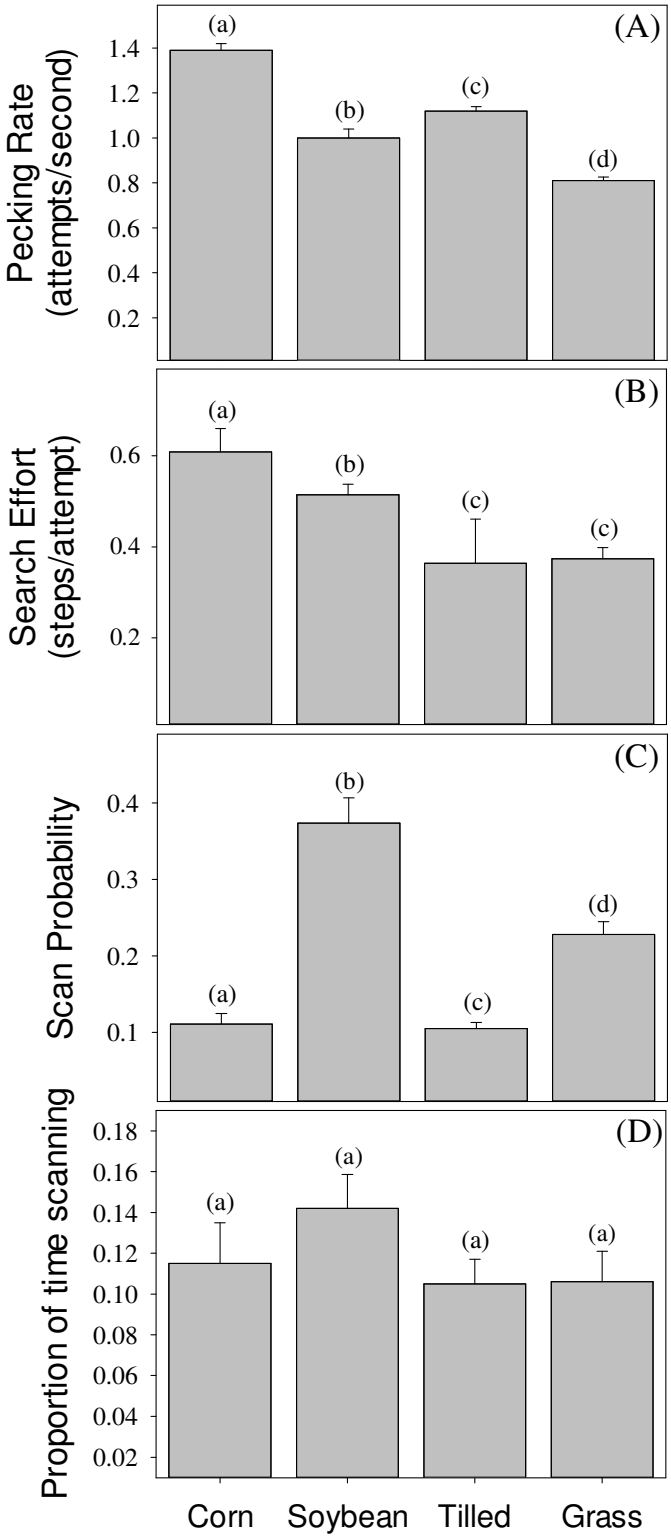


**Figure 5:** Figure 5: (A) Migrants forage faster at agricultural wetlands and (B) search more actively. (C) Migrants are more likely to scan at least once at preferred wetland types but (D) although proportion of time spent scanning was greatest at soybean fields, the differences were not significant. Columns represent estimated marginal means after controlling for significant variables. Columns with different letters signify significantly different according to an LSD-post hoc test.

# Chapter 2: SHOREBIRD MIGRATION IN THE FACE OF CLIMATE CHANGE: PHENOLOGY, RESOURCE AVAILABILITY AND SCENARIO PLANNING

*Abstract:*

Changes in temperature and seasonality resulting from climate change are heterogeneous, potentially altering important sources of natural selection acting on species phenology. Although some species have apparently adapted to climate change, the ability of most species to adapt remains unknown. Because their life history is dictated by seasonal factors, migratory species may be particularly vulnerable to heterogeneous changes in climate and phenology. Here, we examine the phenology of migratory shorebirds, their habitat, and their primary food resources and make predictions as to how climate change may affect migrants through predicted changes in phenology. Daily abundance of shorebirds was correlated with local phenology as migrant abundance peaks immediately prior to peaks in invertebrate food resources. A close relationship between migrant and invertebrate phenology indicates that shorebirds may be vulnerable to changes in seasonality driven by climate change. Although it is possible that shifts in migrant and invertebrate phenology will be congruent in magnitude and direction, because migration phenology is dependent on a suite of ecological factors, any response is likely to occur at a larger temporal scale and may lag behind the response of invertebrate food resources. The resulting lack of sufficient access to food at stopover habitats may cause migrants to extend migration and have cascading effects throughout their life-cycle. If the heterogeneous nature of climate change results in uneven changes

in phenology between migrants and their prey, it may threaten the long-term viability of migratory populations.

# INTRODUCTION

Global climate change is proceeding at an unprecedented rate (IPCC 2007), creating both known and unknown challenges for conservation and research professionals alike. That climate change is spatially and temporally heterogeneous (IPCC 2007) makes predicting ecological consequences difficult and designing effective mitigation strategies challenging. Spatial and temporal disparity in changes to seasonality, resource availability, and phenology are predicted to have far reaching implications for biodiversity (Sala et al. 2000; Thomas et al. 2004; Botkin et al. 2007), particularly for species that occupy large geographic areas and have complex life history strategies such as long-distance migrants (Both and Visser 2001; Robinson et al. 2009; Both et al. 2010). Understanding the degree to which life history events are dependent on intertwined phenological events is essential for wildlife professionals to mitigate the effects of climate change. Unfortunately, despite the importance of seasonality in shaping life history evolution (e.g., McGrath et al. 2009) and the apparent ability of some species to adapt to changes in phenology (e.g. Walther et al. 2002; Root et al. 2003; Jonzén et al. 2006), general information concerning the phenological sensitivity and progression for most species is lacking. Moreover, while there is increasing interest in addressing the implications of climate change to species phenological relationships, few studies have considered these relationships in the context of additional sources of anthropogenic change (but see Opdam and Wascher 2004).

Avian migration is among the most studied of phenological events, but our understanding of the sources of selection driving migratory phenology and the potential for climate change and other sources of anthropogenic change to influence migration

behaviors remains limited (Ahola et al. 2004; Gordo 2007; Petersen 2009). Avian species often show preference for stopover habitats with greater food availability (Hutto 1985; Moore et al. 1995) and variation in food availability at stopover sites affects both survival and reproduction (Moore et al. 1995). However, anthropogenic change, be it from climate change or other forces such as land-use changes, can change the cues that predict food resources, the food resources themselves, or both (Battin 2004; Robertson and Hutto 2006; Stutzman and Fontaine 2012), potentially leading to an ecological trap. Moreover, heterogeneity in the rate of climate change across the range of many migratory bird species (Fontaine et al. 2009), has the potential to affect habitats and resources differently at various locations throughout the migration cycle (Visser et al. 2004; Jones and Cresswell 2010). Strong selection pressure and a reliance on predictable spatial and temporal relationships has resulted in stopover events that often occur during optimal resource availability at an single location en route (Chapter 1, McGrath et al. 2009), despite the fact that migrants make habitat decisions far in advance and without prior knowledge of habitat conditions (Hutto 1985; Loria and Moore 1990; Moore et al. 1990; Moore and Aborn 2000; Petit 2000).

Although some migratory species are flexible in their ability to respond to changes in seasonality (e.g. Crick et al. 1997; Hüppop and Hüppop 2003; Jenni and Kéry 2003; Lehikoinen et al. 2004; Stervander et al. 2005; Jonzén et al. 2006; Tøttrup et al. 2006; Swanson and Palmer 2009), leading to variability in arrival dates among years, results are inconsistent across species (Inouye et al. 2000; Both and Visser 2001; Gordo et al. 2005; Weidinger and Král 2007; Wilson 2007; Møller et al. 2008; Both 2010). It is reasonable that changes in food availability or phenology driven by climate change, land-

use change, or the interactions among them could lead to long term population declines for species or populations of migrants that are not able to effectively adapt migratory patterns to changing conditions. Food availability prior to and during migration clearly has the potential to impact the timing and duration of migration (e.g. Piersma 1987; Russell et al. 1992; Yong and Moore 1997; Newton 2006); furthermore, populations that have responded to changes in resource phenology through advanced migration phenology are seemingly less prone to decline than populations that have been unable to advance the timing of their migration (Strode 2003; Møller et al. 2008). These effects may be manifesting in the form of higher rates of population decline in long-distance migrants relative to non-migrants (Sherry and Holmes 1996; Sanderson et al. 2006; Both et al. 2010). Migratory populations are likely to be negatively affected when migration events and periods of peak resources that were once synchronized become decoupled due to independent changes in phenology (Jones and Cresswell 2010; Both 2010).

Two factors, degree of phenologic mismatch and migratory distance, influence the effect that changes in phenology will have on migratory populations (Jones and Cresswell 2010). Decoupling between migrant arrival and availability of resources can occur one of four ways; changes in migration phenology, changes in resource phenology, changes in cue phenology, or a combination of these (Jones and Cresswell 2010). For example, it is possible that changes in resource phenology and/or cue phenology are occurring in the Prairie Pothole region as the region is experiencing warmer winters (Swanson and Palmer 2009), which may cause earlier peaks in invertebrates abundance and/or phenological cues such as vegetation green up. While the resource and cues are dependent on local climatic conditions, migrant arrival at stopover sites is dependent on endogenous and

external factors at over-wintering locations, previous stopover sites and predicted phenological conditions at breeding grounds (Gwinner 1996; Yong and Moore 1997; Marra et al. 1998; Ottick and Dierschke 2003; Studds and Marra 2011). Given the heterogeneous nature of climate and climate change, it is possible that migrants will not respond in the same manner as local phenological conditions at one or more stopover locations. If there is not a corresponding shift in avian migration, it would likely lead to a mismatch in timing of migration and resource availability that would ultimately lead to a corresponding decrease in stopover success.

There is considerable uncertainty as to how flexible migratory birds are to seasonality, especially during stopover (Marra et al. 2005; Gordo 2007; Lehikoinen and Sparks 2010; but see Kaňuščák et al. 2004; Both 2010). Here, we examine the influence of local phenologic factors on shorebird migration and invertebrate abundance to compare the potential sensitivity of each to climate change and other phenologic factors. We then use our findings to make predictions for how shorebird populations may respond to a number of climate change induced phenological shifts.

## METHODS

### STUDY AREA

Data were collected in the Prairie Pothole region of north-central North America, specifically McPherson, Edmunds and Brown counties in northeast South Dakota. The Prairie Pothole Region of central North America is characterized by millions of small depressional wetlands left by receding ice sheets in the late Pleistocene and by a seasonal, relatively dry climate punctuated by severe droughts and deluges (Johnson et al. 2005).

The area experiences daily average high temperatures between 14.1° C and 21.2° C and receives about 11.48 cm. of precipitation during the study period. The region has high wetland density and diverse land use practices, including row crops, range lands, hay fields, conservation reserve grassland as well as many native prairie remnants. Because shorebirds use shallow water for foraging (Skagen and Knopf 1994a; Davis and Smith 1998), sampling was restricted to seasonal and temporary wetlands (Stewart and Kantrud 1971) to avoid sampling non-habitat. All sampling was done from early April through mid-June of 2010 and 2011 in order to encompass the entire migration period of all northbound migratory shorebirds in the region (Skagen et al. 2008).

## TARGET SPECIES

Surveys were conducted on arctic-nesting sandpipers (*Calidris spp.)*. We established sample wetlands along nine road transects within the study area and surveyed shorebirds at 155 and 163 wetlands in 2010 and 2011 respectively, with 85% of the wetlands visited in both years. Transects were selected following a systematic random sampling protocol, constrained by logistics like road passability and safety, and were between 15 and 30 km long. We surveyed transects every 7-10 days, as this time exceeds average stopover duration for shorebirds in the region (Skagen and Knopf 1994b) and reduces the likelihood of resampling individuals. To maximize detection of shorebirds, we only sampled wetlands that were located within 150 m. of the transect. Wetlands along transects were separated by a minimum of 0.8 km, creating a sample of wetlands randomly distributed in different land-use types. Using binoculars and a spotting scope, all *Calidris* using each wetland were identified and enumerated within a 10 minute

sampling window. A standardized sampling window was used to control for sampling effort and detection probability.

Due to small sample sizes for individual species', *Calidris spp.* were analyzed together. Although there are subtle differences in micro-habitat use and foraging technique between species, these differences are negligible in the scope of this study because *Calidris* shorebirds that migrate through the study area essentially occupy the same ecological niche whereby they forage in shallow water/mudflat habitats for benthic invertebrates (Skagen and Oman 1996; Davis and Smith 2001; Skagen 2006). Stopover periods overlap, but do not coincide between species (Skagen et al. 2008) and by including all *Calidrine* species' in subsequent analysis, we improved the scope of inference of the study.

## MIGRATION PHENOLOGY

We compared migration phenology with wetland phenology as indicated by local characteristics. Daily bird abundance was used as an index of migration phenology. We used Generalized Linear Models (hereafter GLM) with a 'poisson' distribution and included date as a covariate to examine the relationship between migration phenology (total daily abundance), mean daily values for green vegetation, invertebrate abundance and daily minimum water temperature. Independent analysis was done for each year due to high variability in local conditions between years. However, we did test for the influence of green vegetation and water temperature on daily migrant abundance across 2010-2011, using year as a factor. We estimated the proportion of green vegetation of all non-submerged vegetation and shore within 10m of the water's edge for each wetland.

Timing of spring green up is an indicator of wetland phenology and migrating species use vegetative characteristics as a cue to select sites with favorable foraging conditions (McGrath et al. 2009). We measured green vegetation as a potential cue because it changes predictably through the season and may indicate food availability.

Food availability is a primary concern for migratory species (Hutto 1985) and is often cited as the limiting resource during stopover (Moore et al. 1995; Newton 2006). Benthic invertebrate phenology was measured at multiple wetlands and daily migrant abundance was predicted to peak immediately prior to the peak in invertebrates. The relationship between migration phenology and invertebrate abundance is important because the two are influenced by climatological variables at different scales that are not expected to change uniformly with climate (Cresswell and McCleery 2003; Fontaine et al. 2009; Visser et al. 2004; Jones and Cresswell 2010). We included water temperature in the migration phenology model as a predicitor and potential driver of local phenology. Temperature is known to influence the overall bio-phenological progression of invertebrates (Corbet 1965; Wiggins et al. 1980; Hogg and Williams 1996) and therefore may act as a reliable indicator of food potential. Furthermore, invertebrates are expected to be sensitive to changes in temperature associated with climate change (Bale et al. 2002). Both vegetation and temperature have the potential to change in response to climate and create a mismatch in the cue-resource relationship. A key distinction however, is that migrants may be responding to vegetation as a cue whereas it is the invertebrate community that might respond to water temperature as a product of optimal emergence conditions.

We deployed digital temperature loggers (HOBO pendant loggers; Onset instruments; 2010: n=21; 2011: n=51) at wetlands before migration began (late April). Temperature loggers were deployed in the water column using a weight and buoy system that ensured they remain at a consistent depth. Data-loggers recorded water temperature every hour and were deployed before migration began and retrieved after northward migration through the region was completed. All analyses were performed using the minimum mean daily temperature as an indicator of biophenological progression.

## INVERTEBRATE PHENOLOGY

In 2011, we measured benthic invertebrate availability at 26 wetlands. Each wetland was resampled up to three times every 10-14 days or until dry, resulting in 70 wetland sampling visits. Three soil cores were taken to a depth of 5 cm. using a 5 cm. diameter corer (Sherfy et al. 2000) at 3m x 3m sample plots. Three to five plot locations were selected for a total of 9-15 soil cores/wetland. In all cases, plots were separated by > 10 m. Core samples were washed through a 0.5 mm soil sieve and invertebrates enumerated at the wetland to establish relative abundance. Benthic invertebrates were not classified because *Calidris* shorebirds exhibit high dietary plasticity across invertebrates (Skagen and Oman 1996), allowing individuals to feed opportunistically as they move across latitudes and encounter different communities. Although invertebrate biomass may be a better index of total caloric availability, invertebrate abundance is generally correlated with biomass and responds similarly to changing conditions (e.g. Whiles and Goldowitz 2001; Hamer et al. 2006). Additionally, we predict that shorebirds are more likely to forage on larger prey items which would create a scenario where a

lower abundance of individual prey items would result in disproportionately lower biomass available for foraging.

Using data collected in 2011, we compared local conditions with invertebrate abundance using a GLM that included date as a covariate. The importance of food availability to migrants is well documented and invertebrate populations are sensitive to changes in temperature (Wiggins et al. 1980; Bale et al. 2002), creating the potential for the primary resource of migrant shorebirds to undergo relatively rapid changes in phenology which may result in a disparity of the cue-resource relationship. Estimates of invertebrate abundance were compared to water temperature values from the wetland data loggers and with estimates of dissolved chlorophyll *a* from wetlands where invertebrates were sampled. These parameters are predicted to influence invertebrate abundance and may be even more sensitive as indicators of changing phenology. Before sampling invertebrates at each wetland, we measured the dissolved chlorophyll *a* fluorescence using an *in vivo* probe (Aqua*flor* handheld flourometer; Turner designs). Water samples were placed in the probe whereby a relative chlorophyll *a* reading is returned. Chlorophyll *a* is an indicator of phytoplankton growth (Desortova 1981; Canfield et al. 1984) and thus a sensitive index of overall wetland productivity.

## SCENARIO DEVELOPMENT

Using our data, we examined how the existing relationship between shorebird migration and invertebrate food resources might change given hypothetical changes in phenology. We used our models to predict new relationships between migrant phenology

and invertebrate abundance by applying our existing data to predicted changes in phenology driven by climate change.

Furthermore, because we have data from different land use types, all of our scenarios contain an invertebrate phenology comparison between agricultural and grassland wetlands. Migratory shorebirds prefer agricultural wetlands during stopover (Chapter 1; Elphick and Oring 1998; Taft and Haig 2005; Niemuth et al. 2006) and these habitats have lower food availability than do grassland wetlands (Chapter 1; Euliss and Mushet 1999). Although, migrants may be able to buffer against the effects of using novel habitats through behavioral modification (Chapter 1), it is worth exploring how climate change might affect resource and migration phenology at the preferred habitat because the degree of behavioral modification and subsequently, the ability of migrants to adapt to change, may be limited. There is no reason to suspect that land use preference among migrants will change with changing climate, so all scenarios were developed with the assumption that agricultural wetlands are the preferred habitat type. Because the region's spring temperatures are expected to increase, resulting in advancing phenology, all scenarios involve either no change or advances in phenology.

## RESULTS

### PHENOLOGY

Daily abundance of shorebirds was correlated with local conditions in both years. In 2010, migration phenology was significantly correlated with both green vegetation and water temperature (green vegetation: $F_{1, 36} = 378.35$, $P < 0.001$; water temperature: $F_{1, 36} = 13.28$, $P < 0.001$; date: $F_{1, 36} = 104.41$, $P < 0.001$). Data from 2011 produced a similar

pattern as all three phenologic variables were significant (green vegetation: $F_{1, 26}$ = 523.40, P < 0.001; water temperature: $F_{1, 26}$ = 62.69, P < 0.001; invertebrate abundance: $F_{1, 26}$ = 99.37, P < 0.001; date: $F_{1, 26}$ = 4.46, P = 0.035). Across years, green vegetation and date were significantly correlated with daily migrant abundance (green vegetation: $F_{1, 69}$ = 1743.41, P < 0.001; water temperature: $F_{1, 69}$ = 14.09, P =0.294; date: $F_{1, 69}$ = 51.66, P < 0.001; Year: $F_{1, 69}$ = 0.69, P = 0.41). Invertebrate abundance was not significantly correlated with either green vegetation or dissolved chlorophyll *a* but was significantly correlated with date (water temperature: $F_{1, 30}$ = 0.143, P = 0.708; chlorophyll *a*: $F_{1, 30}$ = 0.218, P = 0.644; date: $F_{1, 30}$ = 5.24, P = 0.028).

In both years, migrant daily abundance was positively correlated with water temperature early in the season before peaking and eventually becoming negatively correlated (Fig. 1a). The relationship between green vegetation and daily migrant abundance showed an initial positive correlation in both years, before the peak of migration fell off (Fig. 1b). Finally, the relationship between bird migration and food availability showed that peak shorebird migration occurs immediately prior to peak resource availability (Fig. 1c).

## SCENARIO 1: CURRENT CONDITIONS; FOOD AVAILABILITY REDUCED FROM USING AGRICULTURAL FIELDS

Here, we show the current relationship between migration and invertebrate phenology with the added effect of migrants using habitats with reduced food availability (Fig. 2a). Mid-continental migratory shorebirds prefer using agricultural wetlands for

stopover (Chapter 1), despite the likelihood that they have a lower abundance of benthic invertebrates.

## SCENARIO 2: MIGRATION AND INVERTEBRATE FOOD RESOURCES EACH PEAK EARLIER

Scenario 2 assumes that migration and invertebrate food resources respond to changing climatic conditions by both peaking earlier than under current conditions (Fig. 2b). Here, invertebrates respond quickly to local wetland conditions and migrants are able to respond at an equal rate. In this scenario, the relationship between migration and invertebrate phenology is unchanged, although migrants still face reduced food availability through preference of agricultural fields. An additional potentially negative effect of advancing migration phenology is increased exposure to extreme weather events (Moore et al. 1995, 2005; Decker and Conway 2009).

## SCENARIO 3: MIGRATION PEAKS EARLIER; NO CHANGE IN INVERTEBRATE FOOD RESOURCES

Scenario 3 represents the relationship between migrant and invertebrate phenology if only peak migration advances (Fig. 2c). This set of circumstances is likely to occur if southern stopover or overwintering locations warm at a faster rate than does our study area. Although the timing of migration is dependent on many complex factors including endogenous factors, photoperiod and conditions at over-wintering grounds (Gwinner 1996; Marra et al. 1998; Studds and Marra 2011), extreme late-winter warming

in the southern latitudes may drive migrants to depart earlier than they have historically. In this case, migrants may arrive prior to the peak in food resources.

## SCENARIO 4: INVERTEBRATE FOOD RESOURCES PEAK EARLIER; NO CHANGE IN MIGRATION

Scenario 4 (Fig. 2d) represents the phenologic relationship if only invertebrate phenology changes. Given that our study area is expected to experience warmer temperatures, such a response would likely manifest as an earlier peak in food resources as found by others (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). Conversely, because previous stopover sites occur nearer the equator, they are not expected to experience congruent changes in climate (but see Fontaine et al. 2009). Furthermore, because migration arrival dates are dependent on a suite of ecological conditions (Gwinner 1996; Yong and Moore 1997; Marra et al. 1998; Ottick and Dierschke 2003; Studds and Marra 2011), any response is likely to occur at a larger temporal scale and may lag behind the response of invertebrate food resources (Jones and Cresswell 2010). Here, migration abundance peaks after the predicted peak in food resources, which may preclude migrants from effectively extending their stopover duration. In this case, migrants face depressed food availability in concert with the potentially negative effects of foraging in agricultural habitats.

## SCENARIO 5: INVERTEBRATE FOOD RESOURCES PEAK EARLIER; MIGRATION IS EXTENDED

Here (Fig. 2e) we show the same change to invertebrate phenology as in scenario 4, with the peak in food resources occurring earlier. However, because migrants are likely to experience the effects of climate change at each stop during migration, the response to this suite of changing conditions would be cumulative. As a consequence of continuously missing periods of peak resources at stopover sites, migrants would likely have to extend their stopover duration at each site, leading to a prolonged period of migration for individuals and the population.

## DISCUSSION

We provide a cursory examination of the relationship between migratory shorebird phenology and local phenologic factors and examine a number of scenarios and how they may affect shorebird populations. The potential consequences of climate change and the resulting changes in phenology to migratory shorebirds remain unclear. Migratory shorebirds use widely distributed habitats and the nature of migration requires individuals to repeatedly make habitat decisions in novel environments under temporal constraints (Moore et al. 1990; Moore and Aborn 2000; Petit 2000). Given the nature of their migration strategy and their reliance on specialized habitat in the mid-continental region, shorebirds may be particularly vulnerable to the effects of climate change. Alternatively, because migrants encounter a wide range of habitats and climatic conditions, they may be well suited to adapt to changing conditions. For example, it is well known that shorebirds prefer agricultural fields that have lower resource availability (Chapter 1; Elphick and Oring 1998; Taft and Haig 2005; Niemuth et al. 2006); thus even in the no-change scenario (Fig. 2a), migrants still face the potentially negative effects of

using a habitat type with lower food availability. However, migrants have seemingly adapted to a new suite of conditions by compensating for the limited food resources available in these habitats through behavioral modifications that optimize trade-offs with predation risk (Chapter 1).

It is possible that shorebirds and other migrants may similarly be able to adapt to changing conditions brought about by climate change through further behavioral modification, dietary flexibility or by making adjustments to migration routes. However, climate change, and the corresponding changes in phenology, may compound the impacts of land use changes on shorebird stopover success in the mid-continent region and eventually result in population level effects. For example, if resource phenology shifts to earlier in the migration season and migrants do not adapt (Fig. 2d) it would likely prolong migration through increases in stopover duration and number (Fig. 2e) and delay arrival to the breeding grounds which can reduce recruitment and may lead to population declines (Piersma 1987; Van eerden et al. 1991; Kuenzi et al. 1991; Russell et al. 1992; Moore et al. 1995; Yong and Moore 1997).

To examine the potential impacts of changing phenology, we examined the relationship between migration phenology and local phenologic factors. Predictably, bird abundance increased throughout the early migration period before falling off by the end of May. All three local phenologic variables we examined were significantly correlated with shorebird abundance, but the relationship between abundance and green vegetation was inconsistent (Fig. 1a). Bird migration apparently coincides with increasing water temperature through the migration period and was significantly correlated with invertebrate phenology. In both cases the pattern is just as theory would predict, with the

peak in migration occurring immediately prior to the peak in food resources (Fig. 1c). By arriving slightly before the peak in resources (macroinvertebrates), or the abiotic factors driving resource phenology (temperature), migrating shorebirds ensure themselves adequate food resources if stopover duration is extended. This is the most important phenologic pattern because it indicates that bird migration is closely linked to timing of limiting resources such as food, as others have found (e.g., McGrath et al. 2009). We did not find any significant correlation between invertebrate abundance and the local phenological conditions that we measured. The relationship was slightly positive for chlorophyll *a* and slightly negative for temperature, which is inconsistent with what theory would predict, but may be an artifact of small sample sizes. Given that shorebird migrants already prefer habitat with lower resource availability, any changes to either invertebrate or migration phenology that is not congruent in both magnitude and direction to the other could have severe impacts on migrant populations. Further negative impacts are possible because climate change is heterogeneous and migrants respond at different phenological scales than the resources on which they depend (Both and Visser 2001; Both et al. 2006; but see Marra et al. 2005).

Climate change is expected to be spatially and temporally heterogeneous (IPCC 2007) and has been shown as such in the context of North American migratory bird species (Fontaine et al. 2009). Although some species have shifted their phenology as the climate changes, patterns across taxa are inconsistent (Root et al. 2003). We explored a number of conceptual models that represent possible scenarios of how invertebrates and migrants might respond to changing climatic conditions. While certainly these are simplified scenarios in the scope of global climate change, they explore a wide range of

circumstances under which shorebird migration is likely to occur in the future. Warming is known to lead to earlier migrant arrival in some species, suggesting that migratory species are flexible in their phenology (Crick et al. 1997; Hüppop and Hüppop 2003; Jenni and Kéry 2003; Lehikoinen et al. 2004; Stervander et al. 2005; Jonzén et al. 2006); however, it is unclear if migrants will be able to adapt to changes in resource phenology at various locations along their migratory route, especially when that phenology does not change at the same amplitude in all locations.

Successful stopover depends on many environmental and behavioral factors (Newton 2006) and is driven by many selection pressures (Petit 2000), but given that the primary reason for stopover is assumed to be the acquisition of energy, adequate access to food resources is critical for migratory species survival (Hutto 1985; Moore et al.1995). Due to a collection of human impacts, migratory bird species are often required to migrate through highly altered landscapes that may have reduced resource availability (Chapter 1; Niemuth et al. 2006), and certainly loss of stopover habitat is predicted to result in migratory species declines (Skagen et al. 1997; Weber et al. 1999; Harrington et al. 2002). However, some migrants, including arctic-nesting shorebirds, have shown the ability to adapt to alterations to stopover habitats (Chapter 1; Krapu et al. 1984; Taft and Haig 2005). One possible reason for the persistence of migratory species despite altered habitat is a strong phenologic link between resources and migration. However, migrants may be less able to buffer against the consequences of using novel habitats if migration and resource phenology are no longer congruent due to climate change (Visser et al. 2004; Both et al. 2006; Both 2010; Jones and Cresswell 2010). Changes in resource or migrant phenology will cause habitats to have further reduced food availability relative to

historical conditions. Given that spring temperature changes may be more extreme at stopover locations than at breeding sites at the times birds are using them (Fontaine et al. 2009), migrants may encounter novel trade-offs in resource availability en-route. For example, migrants may advance their peak migration date in order to track similarly-advancing invertebrate food resources at stopover sites (Fig. 2b) however, they may then be more likely to encounter adverse weather events en-route, or reach the breeding grounds before adequate food resources are available (Alerstam 1991; Decker and Conway 2009). Given that invertebrates are more sensitive to local conditions, in concert with the heterogeneous nature of climate change, this scenario might be considered unlikely. However, it is the best-case scenario for conservation planners, and in that sense is worth documenting.

Earlier peaks in migration may also allow individuals to extend their stopover duration beyond the historical norm in order to take advantage of invertebrate peaks, given no change to food resource phenology (Fig. 2c).Although the peaks in migration and food availability become decoupled under this scenario, the fact that migrants still arrive prior to the peak in food resources may allow them to counteract the negative effects by extending stopover. Migratory species are highly adaptable in regards to stopover duration, with duration dependent on both local conditions and individual body condition (review by Newton 2006). Stopover may be extended when food resources are lower (Piersma 1987; Ydenberg et al. 2002) or when individuals have inadequate fat reserves (e.g. Moore and Kerlinger 1987; Kuenzi et al. 1991). However, lean birds are unlikely to stay at stopovers with inadequate food reserves, prompting potentially risky flights that may result in mortality (Newton 2006). Extending stopover duration comes

with increased costs such as predation risk (Ydenberg et al. 2004), but given that stopover initiation is earlier in this scenario, individuals may not face the traditionally cited costs of late arrival to the breeding grounds (e.g. Potti 1998; Currie et al. 2000; Weggler 2006). However, if resource phenology shifts to earlier in the year independent of migration phenology, as shown by others (e.g. Both et al. 2006), and represented in Fig. 2d, then migrants may not be able to obtain adequate energy during stopover and population viability will be threatened. Such a conclusion is supported by the fact that migratory species that advance their arrival date are less likely to decline than those that do not (Møller et al. 2008).

While climate change is expected to negatively affect the integration of migration phenology and resource availability resulting in population declines, the extent of such effects is unknown relative to more longstanding stressors such as habitat loss (Opdam and Wascher 2004). The likely scenario is that the effects of multiple stressors will interact and compound the effects of one another (Robinson et al. 2009). For example, climate change is predicted to alter precipitation and evapotranspiration rates (IPCC 2007) which is expected to alter wetland habitat in the mid-continental region (Johnson et al. 2005). However, such a change will also have implications on which crops are planted in the region and how they are cultivated, potentially leading to further land-use changes. Furthermore, the push for alternative energy sources, such as corn based ethanol, may motivate land owners to alter farming practices. The effects of continued land-use change, along with the potential of climate change to alter wetland habitat (e.g. Euliss and Mushet 1999; Gleason et al. 2003; Johnson et al. 2005), will certainly act in conjunction to further effect shorebird migration in the region. Although migrants in

general (Krapu et al. 1984; Stervander et al. 2005, Jonzén et al. 2006) and shorebirds in particular (Chapter 1; Taft and Haig 2005) may be particularly adaptable to changing ecological conditions, it is unknown if they'll be afforded the evolutionary time needed to adapt to such a suite of negative impacts. Further research is needed to examine the potential for land use changes and changing global climate to act in concert to drive migrant species declines.

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# FIGURES

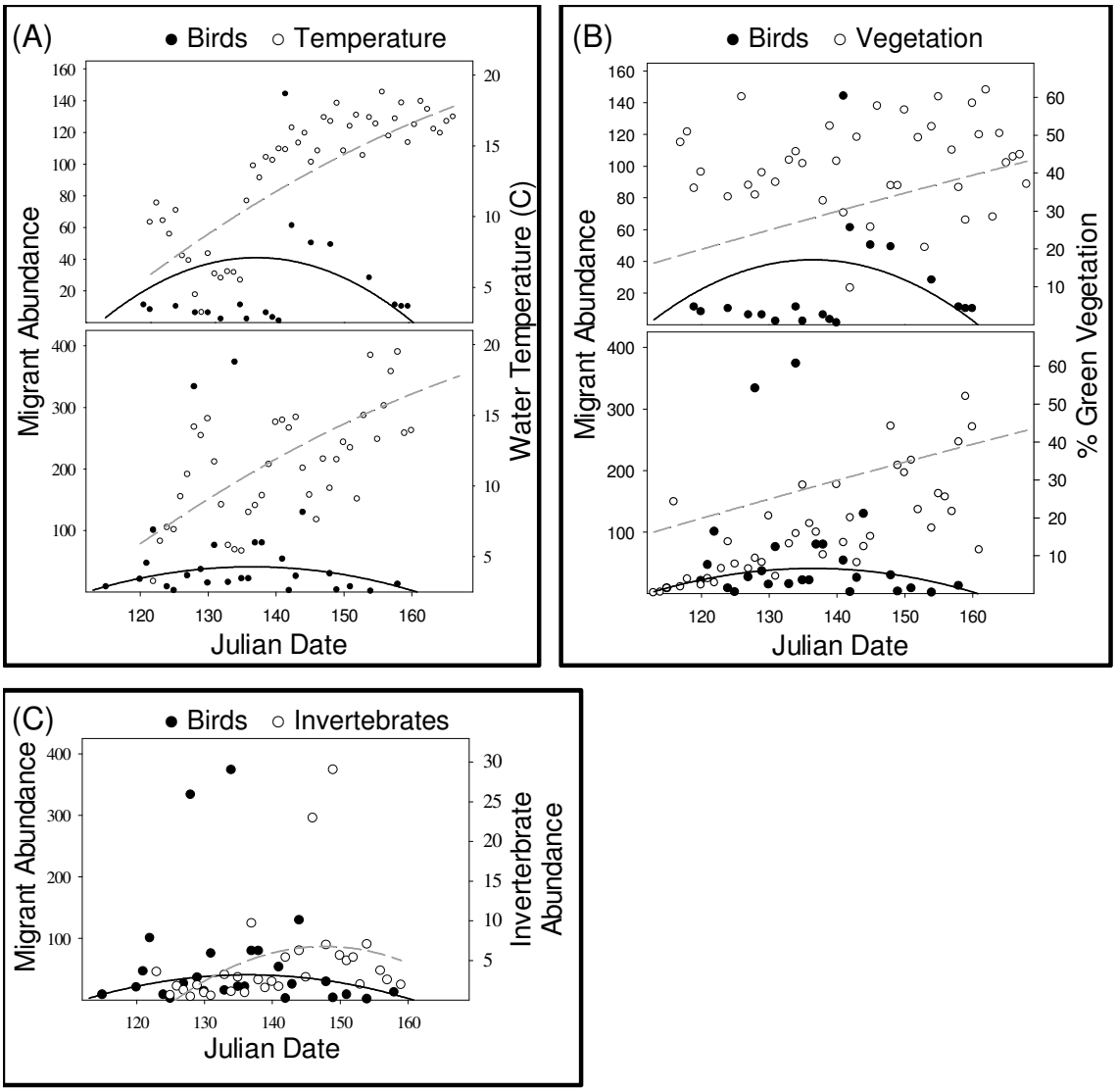


**Figure 1:** (A) In 2010 (top panel) and 2011 (bottom panel), total daily bird abundance increased with water temperature early in the season, before falling off. (B) Total daily abundance was slightly negatively correlated with green vegetation in 2010 (top panel) and slightly positively correlated in 2011 (bottom panel). (C) Total daily migrant abundance is correlated with invertebrate abundance and peaked just prior to invertebrate peak, just as theory would predict and indicative of an important relationship between migration and invertebrate phenology.

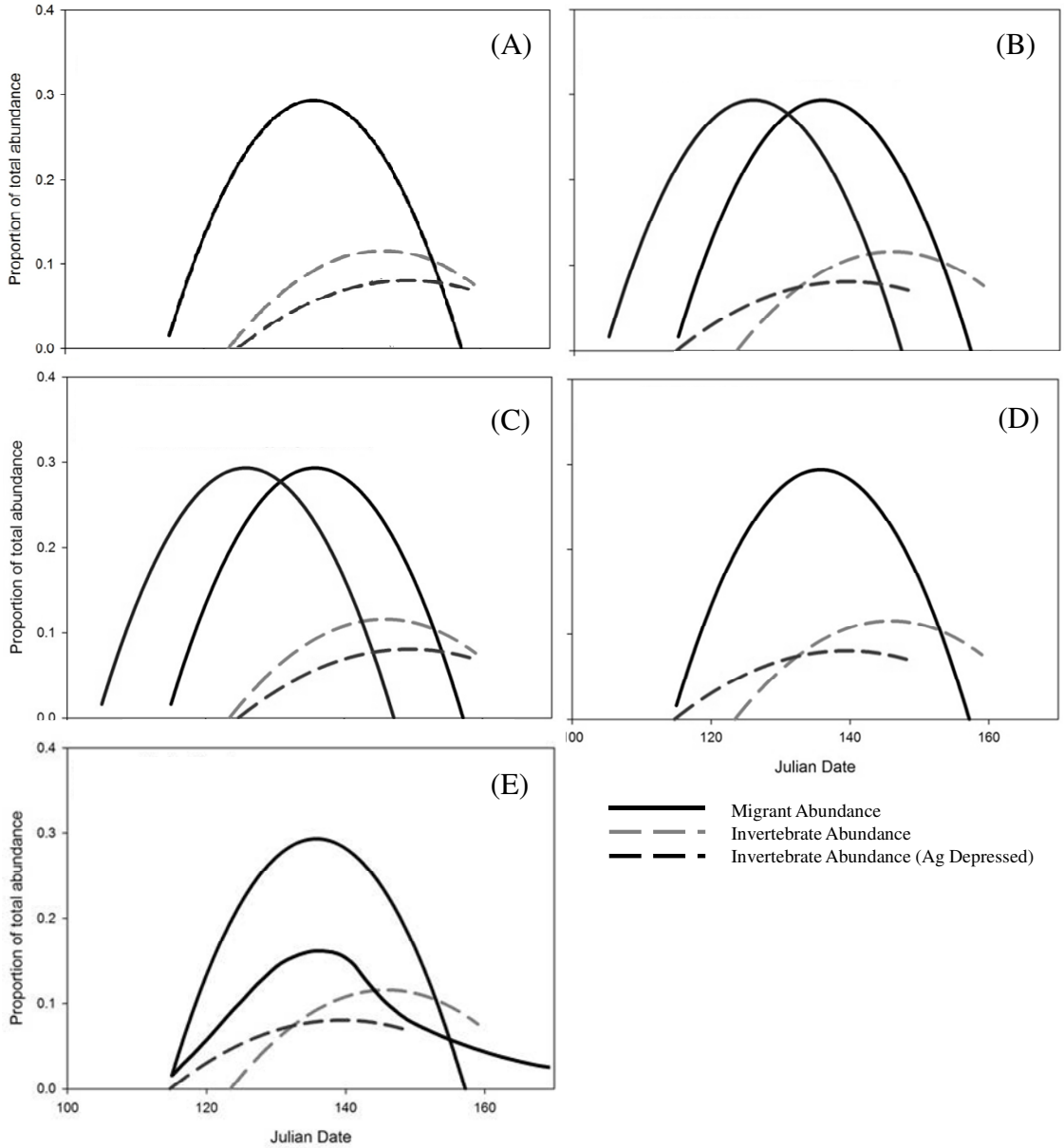


**Figure 2:** (A) Scenario 1: Current conditions; available food resources in agricultural fields represented by lower dotted line. (B) Scenario 2: Peaks in migration and food resources both occur earlier, but the relationship remains unchanged. (C) Scenario 3: Peak in migration occurs earlier, but invertebrate phenology is unchanged. (D) Scenario 4: Peak in migration remains unchanged, but invertebrate food resources peak earlier. (E) Scenario 5: Peak in migration remains the same, but duration is extended.