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Caitlyn Gillespie

University of Nebraska-Lincoln, caitlyn.gillespie@gmail.com

Joseph J. Fontaine

University of Nebraska-Lincoln, jfontaine2@unl.edu

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Research Article

Shorebird Stopover Habitat Decisions in a Changing Landscape

CAITLYN R. GILLESPIE,¹ *Nebraska Cooperative Fish and Wildlife Research Unit, University of Nebraska–Lincoln, Lincoln, NE, USA*

JOSEPH J. FONTAINE, *U.S. Geological Survey Nebraska Cooperative Fish and Wildlife Research Unit, University of Nebraska–Lincoln, Lincoln, NE, USA*

ABSTRACT To examine how habitat use by sandpipers (*Calidris* spp.; Baird's sandpipers, dunlin, least sandpipers, pectoral sandpipers, semipalmated sandpipers, stilt sandpipers, and white-rumped sandpipers) varies across a broad suite of environmental conditions, we conducted surveys at wetlands throughout the spring migratory period in 2013 and 2014 in 2 important stopover regions: the Rainwater Basin (RWB) in Nebraska, USA, and the Prairie Pothole Region (PPR) in South Dakota, USA. Because providing adequate energetic resources for migratory birds is a high priority for wetland management, we also measured invertebrate abundance at managed wetlands in the RWB to determine how food abundance influences the occupancy and abundance of sandpipers on wetlands throughout the migratory period. To quantify habitat use, we surveyed wetlands every 7–10 days in both regions and visually estimated wetland attributes. Our results indicate that invertebrate abundance predicted occupancy, but not abundance, of sandpipers at wetlands in the RWB. The wetland vegetation characteristics that predict sandpiper occupancy are similar in both regions, but wetlands in the PPR support a higher abundance of sandpipers than wetlands in the RWB. Our results suggest that sandpipers make stopover decisions that balance local and regional wetland conditions. Managers should maintain the cues (i.e., mudflat) and ecological conditions beyond invertebrate abundance that predict sandpiper habitat use to successfully provide resources for sandpipers during migratory stopover if that is a goal of wetland management. © 2017 The Wildlife Society.

KEY WORDS benthic invertebrate sampling, *Calidris*, food availability, habitat selection, landscape, migration, wetland management.

Finding and taking advantage of stopover habitat to rest and refuel during migration is essential for many long-distance migrants, but individuals must select habitat in unfamiliar environments under severe time and energetic constraints (Hutto 1985, Moore and Aborn 2000). For example, dunlin (*Calidris alpina*), Baird's (*C. bairdii*), least (*C. minutilla*), pectoral (*C. melanotos*), semipalmated (*C. pusilla*), stilt (*C. himantopus*), and white-rumped (*C. fuscicollis*) sandpipers migrating northward through mid-continental North America rely on ephemeral wetlands during stopover (Skagen et al. 2008), but wetland distribution and availability changes rapidly (Kantrud et al. 1989). Even when water is available, foraging conditions necessary for *Calidris* (i.e., sandpipers), such as shallow-water, abundant invertebrates, and sparse vegetation change rapidly in response to temperature, precipitation, and the ensuing onset of spring (Kantrud et al. 1989, Albanese et al. 2012). Sandpipers have evolved flexible migratory strategies to cope with a dynamic landscape (Skagen and Knopf 1994a,b; Skagen and Omen 1996; Davis and Smith 1998), but

land-use change continues to alter the availability, distribution, and predictability of wetlands in the Great Plains, USA (Johnson et al. 2005, Johnston 2013, Dahl 2014). Row-crop agriculture disrupts local hydrological regimes, eliminating or reducing the phenology of available shallow-water in temporary and seasonal wetlands (Euliss and Mushet 1996). Climate change increases the frequency of dry winters and unpredictable severe spring storms, narrowing the phenology of water availability and invertebrate abundance (Johnson et al. 2005, Dahl 2014). Although loss of stopover opportunities in wetland landscapes have unknown consequences for inland sandpiper populations, in other systems stopover conditions affect migratory phenology, individual fitness, and ultimately population dynamics (Baker et al. 2004).

Wetland management presumably offsets wetland loss and alteration by creating or maintaining water levels and food resources that ensure the energetic needs of migratory waterbirds are met (Rainwater Basin Joint Venture 2013), but it remains unclear to what extent management actions may mitigate the consequences of escalating change. Although managers can alter wetlands to provide the necessary resources for migratory shorebirds (Taft et al. 2002, Davis and Bidwell 2008, O'Neal et al. 2008), individuals may not use managed wetlands if they fail to provide the

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¹E-mail: caitlyn.gillespie@gmail.com

appropriate cues. Bioenergetic models in regional and national shorebird management plans assume that resource availability for shorebirds may be predicted by estimating invertebrate biomass within wetlands (Nugent et al. 2015). Although vegetation conditions often predict sandpiper habitat use (Colwell and Oring 1988, Skagen and Knopf 1994*b*, Davis and Smith 1998), how local food availability shapes stopover habitat use is less clear and remains largely unknown despite the importance to migratory theory and species management (Newton 2006, Colwell 2010, Moore et al. 2005). Indeed, sandpipers often use sparsely vegetated mudflats on flooded agricultural fields adjacent to intact wetlands despite reduced food availability (Niemuth et al. 2006, Stutzman and Fontaine 2015, Murphy and Dinsmore 2017). Addressing uncertainties in how migratory shorebirds respond to local management actions, and thus the value of wetland management, requires reassessing how habitat use differs across a broad suite of environmental conditions.

We evaluated the effects of local, regional, and annual variation in wetland availability and management on spring stopover decisions of a suite of migratory sandpipers to test the hypothesis that transitory populations respond to habitat availability opportunistically and at scales that reflect resource conditions (Hutto 1985, Skagen and Knopf 1994*b*). Our objective was to assess the relationships between sandpiper habitat use (presence and abundance) and wetland attributes and resource conditions in 2 important stopover regions that contrast in wetland availability and scale of land-use change, to understand what predicts the presence and abundance of sandpipers on managed wetlands.

STUDY AREA

We conducted the study in 2013–2014 in 2 ecoregions: the Rainwater Basin (RWB) in south-central Nebraska, USA (Hall, Adams, Clay, Seward, Franklin, Kearney, Hamilton, Saline, York, Fillmore, Phelps, and Gosper counties) and a portion of the Prairie Pothole Region (PPR), South Dakota, USA (Charles Mix, Brule, Aurora, and Douglas counties). Lying on the transition between mixed- and short-grass prairies, both regions consisted of flat to gently rolling topography. Elevations ranged from 450 m to 600 m in our study areas in the RWB and PPR. Over the previous 100 years, the mean temperature and total precipitation over the 3-month migratory period from April to June varied from 13.83°C to 20.11°C and 10.05 cm to 46.71 cm in the RWB and from 11.11°C to 17.39°C and 9.64 cm to 39.14 cm in the PPR (National Oceanic and Atmospheric Administration [NOAA] 2017). The mix soils and semiarid climate supported large expanses of native rangelands and a diversity of irrigated and dryland crops including corn, soy, winter wheat, and sorghum. The playa and pothole wetlands in each region contain a diverse array of wetland vegetation communities and hydrological regimes that host a diversity of waterbirds during spring migration (Kantrud et al. 1989, Bishop and Vrtiska 2008). Historically, the RWB consisted of a network of >80,000 ha of temporary playa wetlands stretching across much of south-central Nebraska (Bishop and Vrtiska 2008). Large-scale conversion to agriculture has left fewer than 10%

of the wetland basins intact, most of which have compromised hydrological regimes, and as such wetlands in the RWB are fragmented and concentrated in a few highly managed public areas (Bishop and Vrtiska 2008). The southern PPR, located 300 km north of the RWB, is another ephemeral wetland system that acts as an important stopover area for migratory sandpipers. Although land-use change has also diminished and altered the function of wetlands in the PPR (Dahl 2014), wetland function more closely resembles historical conditions because anthropogenic change is considerably less advanced when compared to the RWB (Bishop and Vrtiska 2008). The proportion of the landscape dedicated to row-crop agriculture (i.e., planted corn and soy beans) in the southern PPR during the study years was about 37 ha/km², compared to >75 ha/km² in the RWB (U.S. Department of Agriculture 2016). We confined our survey area in the PPR to a select 4-county region for 2 reasons. First, the relative proximity to the RWB allowed for sampling in 2 regions with almost simultaneous expected migratory phenology and weather patterns, which reduced the likelihood that confounding extrinsic factors influencing migratory progression and stopover patterns would affect relative bird abundance. Second, although only approximately 16,000 ha of wetland basins remain in the nearly 1,600,000 ha of the RWB (Bishop and Vrtiska 2008), nearly 45,000 ha of wetland basins remain in the much smaller area (810,000 ha) covering 4 counties in the PPR, making the wetland density about 5 times greater than in the RWB (U.S. Fish and Wildlife Service [USFWS] 2014). This region of the PPR is only the southern tip of a 300,000-km² region with nearly 3 million shallow wetlands, where shorebird habitat occurs in high densities (Skagen et al. 2008). Thus, we expected our surveys of sandpiper habitat use to reflect a contrast in availability of potential stopover habitat, especially considering the larger regional context of the PPR extending beyond our survey area. Although annual and within-season dynamics often vary the actual availability of shallow water conditions within each region, in dry years, most of the large wetlands in the RWB are dry and only a few actively managed wetlands remain on the landscape (Bishop et al. 2016). In the PPR, where land-use change is less advanced, many large wetlands (both managed and unmanaged) remain and hold water, even during dry periods. Thus, the relative disparity in existing wetland basins between the regions, combined with unusually dry conditions during our study period provided a useful contrast for assessing how habitat use varies between 2 distinct wetland landscapes within a single migratory season. In the RWB, the Palmer Drought Severity Index (PDSI; scaled from -4 [extreme drought] to 4 [extreme wet]) was -3.37 in 2013 and -1.93 in 2014, whereas in the PPR the PDSI was -3.86 in 2013 and 1.96 in 2014 (NOAA 2014).

METHODS

Field Methods

We visually surveyed wetlands in spring 2013 and 2014 for a suite of sandpipers that migrate through our study region (dunlin, Baird's, least, pectoral, semipalmated, stilt, and white-rumped sandpipers). We conducted surveys from the

last week in March through the second week in June, encompassing the entire spring migratory period for sandpipers in the region (Skagen et al. 2008, Webb et al. 2010). To minimize our chances of recounting the same bird, survey sites were ≥ 0.8 km apart and visited every 7–10 days, a sampling period that exceeds the typical stopover duration of sandpipers (Skagen and Knopf 1994a). We did not survey dry wetlands, but monitored sites and conducted surveys if conditions changed in subsequent sampling periods (e.g., following rainfall or reflooding by management). We used binoculars and a spotting scope to count and identify all sandpipers at each wetland within a 10-minute sampling window, which allowed us to control for sampling effort. In the PPR, the relative abundance of wetlands allowed us to conduct road-side surveys of wetlands along transects 25 km long that we selected based on a systematic random sampling protocol following Stutzman and Fontaine (2015). Although road-side sampling may result in biased survey estimates, such biases more often result in underestimates of habitat and bird populations due to increased likelihood of land-use change near roads (Keller and Scallan 1999). In the RWB, road placement required us to approach wetlands on foot to conduct surveys; however, we mimicked the PPR survey protocol (and thus relative biases) by conducting surveys from a single survey point and from a distance and elevation that maximized visibility of the entire wetland. As such, we conducted 95% of all surveys within 200 m of the wetland.

In the RWB, we focused our sampling on public management areas. Although public management areas are not representative of all wetlands in the RWB every year, wetland availability was limited because of intense drought at the beginning of our survey period. In March of 2013, about 631 ha of water was available in the RWB, of which 54% was on or directly adjacent to public management areas. Similarly, in March 2014, about 836 ha of water was available, of which 64% was on or adjacent to public management areas (Bishop et al. 2016). In 2013, dry conditions at the beginning of the study period so severely limited water availability in the RWB that we surveyed every inundated wetland that was available on public management areas. We used the same approach to select sampling locations in 2014, and selected survey sites on the basis of water availability on all public management areas in the RWB as of March 2014. In the RWB, we sampled 47 wetlands in 2013 and 43 wetlands in 2014, but we sampled only 28 in both years because of annual variation in wetland inundation. Study sites in the PPR were also drier than normal. Because of local weather events the number of wetlands along each transect varied by sampling period with

a maximum of 43 wetlands per sampling period in 2013 and a maximum of 27 in 2014. Again, because of annual variation in wetland inundation, we sampled 19 of 43 wetlands in both years.

Although wetlands can be larger in the PPR ($>1,300$ ha) 98% of wetlands are <10 ha and the mean wetland size is similar in both regions (PPR = 0.79 ha, RWB = 0.89 ha; USFWS 2014). Because of the dry conditions that persisted during our study, many of the smallest temporary and seasonal wetland basins were dry. Thus, we sampled a similar diversity of wetland sizes in both regions (RWB: 6.97 ± 11.14 [SD] ha, PPR: 6.06 ± 10.90 ha). We sampled wetlands throughout the migratory period, even when wetlands were nearly dry or expanded by rainfall, resulting in a wide range of wetland size throughout our study period in both regions (RWB: 32 m²–100 ha, PPR: 5 m²–77 ha).

We recorded wetland attributes by visual assessment of the wetland from the survey point, and estimated the proportion of each of 4 cover types at the wetland (water, mud, green vegetation, and brown vegetation or litter) and the percentage of vegetation in each of 3 height classes (<15 cm, between 15 and 60 cm, and >60 cm). In the RWB, we estimated wetland size using a handheld global positioning system (Garmin GPSMAP 62 s, Garmin International, Olathe, KS, USA) to record the edge of the ponded area of the wetland basin (i.e., mudflat) at 4 points around the wetland perimeter. Because of logistical constraints associated with access to private lands in the PPR, we instead used a rangefinder (ProStaff 550, Nikon, New York, NY, USA) to visually estimate the total ponded area of the wetland basin (wetland area). Although less precise, visual estimates of wetland area are widely adopted and correlate with habitat use of a range of waterbirds, including sandpipers (Murphy and Dinsmore 2017).

In the RWB, we assessed food availability by sampling invertebrate abundance immediately following most bird surveys, thus, following the same 7–10 day repeat sampling protocol (Table 1). Because of logistical constraints, we did not measure food availability in the PPR. To measure invertebrate abundance, we randomly placed up to 5, 3-m \times 3-m sample plots within the inundated wetland area surrounding the water (i.e., on the mudflat), the primary foraging area for sandpipers, and when possible used known bird locations as a guide. We separated plots by ≥ 20 m. If the wetland was too small, we used fewer plots, but 78% of assessments included 5 plots. Using a 5-cm diameter soil core we took 3, 5-cm deep samples from each plot, washed each through a 0.5-mm soil sieve, and counted and weighed the

Table 1. Summary of the sampling effort in the Rainwater Basin (RWB), Nebraska, USA, and Prairie Pothole Region (PPR), South Dakota, USA for shorebird surveys and invertebrate assessments, 2013 and 2014.

| Region | Yr | Sampling dates | Wetlands surveyed | Bird surveys | Wetlands sampled | Invertebrate samples |
|--------|------|----------------|-------------------|--------------|------------------|----------------------|
| RWB | 2013 | 31 Mar–28 May | 47 | 202 | 41 | 141 |
| RWB | 2014 | 24 Mar–7 Jun | 42 | 235 | 39 | 180 |
| PPR | 2013 | 25 Apr–11 Jun | 43 | 174 | NA | NA |
| PPR | 2014 | 11 Apr–16 Jun | 27 | 195 | NA | NA |

wet invertebrate mass from each sample on a digital scale accurate to 0.001 g (GemPro 250, MyWeigh, Phoenix, AZ, USA). Sandpipers express high dietary plasticity (Skagen and Oman 1996), so we deemed classification to species unnecessary. In each plot we visually estimated the percent vegetative cover in each of 5 classes (litter, water, dry soil, wet soil, and vegetation) and measured vegetation height at 3 random locations (Daubenmire 1959). In the center of each plot we also assessed soil conditions at a 5-cm depth (pH, moisture content, temperature, compactness) using a Kelway soil tester (Kelway Soil pH and Moisture Meter, Kel Instruments, Tokyo, Japan), standard soil thermometer (Rapitest Digital Soil Thermometer, Luster Leaf products, Woodstock, IL, USA), and a soil penetrometer (E-280 Pocket Penetrometer, AMS, American Falls, ID, USA). We calculated the slope of the sandpiper foraging area by measuring water depth 1 m and 5 m toward the water from the edge of each sample plot.

Analysis

We used generalized linear mixed models (GLMMs) developed using program R (R Core Team 2014), package lme4 (Bates et al. 2015). Because sandpiper species tend to cluster in large groups at relatively few wetlands, resulting in a high number of unoccupied wetlands, it is often more ecologically relevant to examine abundance at wetlands with ≥ 1 bird present (Elphick and Oring 1998). Moreover, we expected detection errors to more likely influence our estimates of abundance than presence because we assumed our survey protocols were sufficient to determine wetland occupancy. Thus, we evaluated sandpiper occupancy and abundance separately. We examined the probability of occupancy using a GLMM with a binomial distribution after converting all observations to simple presence-absence. We considered wetlands with ≥ 1 bird present to be occupied. Although not as rigorous as an occupancy model, which accounts for detection, our sampling protocols minimized the probability that observers would miss a group of birds on a wetland because we maintained a sampling window of 10 minutes and sandpipers tend to cluster in large groups on wetlands during migration. Because of a high number of unoccupied wetlands, we analyzed abundance only at wetlands with ≥ 1 bird present. We analyzed abundance (the count of all individuals on a wetland) using a GLMM with a Poisson distribution. Unless otherwise stated below, we selected models using backward selection from a global model, which included all relevant ecological variables after removing highly correlated terms and interactions with a variance inflation factor (VIF) > 2 (Zuur et al. 2007). To improve model convergence, we grand-mean centered all continuous variables and scaled each to 1 standard deviation (Gelman 2008). We removed the least important variables one at a time, using a likelihood ratio test to ensure variable removal did not reduce model fit (Zuur et al. 2007). We used a Wald χ^2 test for significance of the fixed effects in each final model (Bolker et al. 2009).

Habitat use.—To assess habitat use, we used the modeling procedure described above to identify wetland vegetation characteristics associated with sandpiper occupancy and

abundance. We analyzed each region separately to explore for differences in habitat use between regions.

In general, sandpiper species have similar habitat requirements, occupy the same functional niche, and rely on the same food resources during migration (Skagen et al. 2008). Given their small size, rapid movements, and relatively nondescript plumage, it can be challenging to identify individuals to species. Thus, to widen our scope of inference, increase our power, and lessen concern about errors in species identification, we analyzed habitat use in 2 sets of analyses. First, to establish a broad reference for how sandpipers respond to wetland attributes, we analyzed individuals of all species as one group with the expressed purpose of identifying overarching relationships. We used a global model that originally included sampling period and site as random effects, year as a fixed effect, and all biologically relevant variables and interactions. Because vegetation characteristics are inherently correlated with local phenology and each other, we included the percentage of vegetation (i.e., green plus brown) in our global models to explore for local habitat use in each region. After removing highly correlated terms, our global model to test for occupancy and abundance within each region included percent mud, percent total vegetation, wetland size, a wetland size by percent mud interaction, percent of vegetation 15–60 cm tall, and year, with the survey site and sampling period included as random effects.

Second, to acknowledge slight differences in migratory phenology and microhabitat use among species (Skagen et al. 2008), we independently assessed habitat use of the 3 most common species (white-rumped, stilt, and semipalmated sandpipers). Rather than performing a series of independent tests, which raises concerns over Type I error associated with multiple testing, we ran the top model from our clade analysis on each species. This approach is not meant to identify species-specific habitat use, because the small sample sizes significantly limited our power. Instead, this approach focuses on the generality of the relationships. By comparing β values among all models we can better understand which patterns are strongly supported, and which relationships may need further examination.

To test for differences in overall sandpiper occupancy and abundance between the RWB and the PPR, we used a GLMM with either a binomial or a Poisson distribution, respectively. Both models included percent mudflat, size, and year as fixed effects, with site and sampling period specified as random effects. Finally, to verify that there was comparable availability of mudflat on occupied wetlands of similar size between regions, we used a GLM to test for the relationship of percent mudflat to wetland size, region, and a size by region interaction.

Food availability.—Benthic invertebrates have a patchy distribution and a rapid phenology; thus, sampling produces a highly zero-inflated distribution and estimates of invertebrate abundance that tend to be conservative with high sampling error. Although this can be a problem, our aim was to evaluate the relative availability of food resources among wetlands, and not total invertebrate abundance within a wetland (Davis and Smith 1998). Thus, we followed standard protocols that reliably predict relative invertebrate

abundance among wetlands. First we evaluated wetland invertebrate abundance by averaging the sum of invertebrates per plot. Second, we calculated wetland invertebrate occupancy from the proportion of cores in a sampling day with ≥ 1 invertebrate present. Using both metrics allowed us to have 2 perspectives on relative food availability among wetlands and through comparison helped verify the robustness of our sampling technique.

To assess sandpiper occupancy and abundance in relation to food availability, we used GLMMs with a binomial or a Poisson distribution. We developed models that assessed sandpiper response to either abundance or occupancy of invertebrates, adding the percent mud and year as fixed effects and sampling period and site as random effects to all models.

We also examined the soil and vegetation characteristics that were associated with invertebrate abundance in our plots, using a GLMM with a Poisson distribution. We determined models using the same approach described above, removing highly correlated variables and performing

backward 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 identification and the sampling period included as random effects.

RESULTS

In 2013 and 2014 we conducted 437 shorebird surveys in the RWB and 369 shorebird surveys in the PPR. Over the 2 years we counted 9,300 shorebirds (Appendix A). In the RWB, we conducted 321 food availability assessments at 41 wetlands in 2013 and 39 in 2014 (Table 1).

Habitat Use

There was significant inter-annual variation in sandpiper abundance in both regions, and 2014 had higher wetland occupancy rates in the PPR (Table 2). The increase in

Table 2. Results from habitat use models assessing occupancy and abundance at wetlands in the Rainwater Basin (RWB), Nebraska, USA, and the Prairie Pothole Region (PPR), South Dakota, USA, 2013–2014, based on wetland characteristics. We modeled each of 3 common *Calidris* shorebirds (white-rumped, stilt, and semipalmated sandpipers) and for all *Calidris* species analyzed together (dunlin, Baird's, least, pectoral, semipalmated, stilt, and white-rumped sandpipers). All models were generalized linear mixed models that included sample period and site as random effects. We do not show terms that we removed during backward selection. We assessed abundance only at wetlands with ≥ 1 bird present. In single-species models, to correct for phenology we excluded surveys that were >1 sample period earlier than arrival of the species in that region. We present the number of wetland surveys that we included in each model (n).

| | White-rumped sandpiper | | | | Stilt sandpiper | | | | Semipalmated sandpiper | | | | All | | | |
|---------------------------|------------------------|------|----------|--------------|-----------------|------|----------|--------------|------------------------|------|----------|--------------|-----------|------|----------|--------------|
| | β | SE | χ^2 | P | β | SE | χ^2 | P | β | SE | χ^2 | P | β | SE | χ^2 | P |
| RWB occupancy | $n = 233$ | | | | $n = 369^a$ | | | | $n = 369$ | | | | $n = 436$ | | | |
| Mud (%) | 0.23 | 0.19 | 1.38 | 0.24 | -0.11 | 0.30 | 0.13 | 0.72 | 0.08 | 0.21 | 0.13 | 0.72 | 0.25 | 0.13 | 3.99 | 0.04 |
| Total vegetation (%) | -0.58 | 0.27 | 4.56 | 0.03 | -0.42 | 0.35 | 1.48 | 0.22 | 0.25 | 0.23 | 1.34 | 0.25 | -0.39 | 0.14 | 7.83 | 0.01 |
| Year 2014 | 1.63 | 0.50 | 10.41 | 0.001 | 0.83 | 0.61 | 1.76 | 0.18 | 0.90 | 0.45 | 4.02 | 0.05 | 0.53 | 0.28 | 3.71 | 0.05 |
| PPR occupancy | $n = 260$ | | | | $n = 321$ | | | | $n = 369$ | | | | $n = 369$ | | | |
| Mud (%) | 0.33 | 0.16 | 2.69 | 0.10 | 0.10 | 0.17 | 0.32 | 0.57 | 0.49 | 0.15 | 10.99 | ≤ 0.001 | 1.09 | 0.22 | 9.53 | 0.002 |
| Wetland size (ha) | 0.27 | 0.17 | 1.07 | 0.30 | 0.17 | 0.19 | 0.80 | 0.37 | 0.32 | 0.16 | 4.82 | 0.03 | 1.04 | 0.23 | 5.16 | 0.02 |
| Mud \times wetland size | 0.28 | 0.20 | 2.01 | 0.16 | -0.01 | 0.17 | 0.00 | 0.97 | 0.14 | 0.12 | 1.33 | 0.25 | 1.55 | 0.4 | 15.25 | ≤ 0.001 |
| Total vegetation (%) | -0.45 | 0.18 | 6.03 | 0.01 | -0.09 | 0.18 | 0.27 | 0.61 | -0.17 | 0.19 | 0.76 | 0.38 | -0.35 | 0.15 | 5.56 | 0.02 |
| Year 2014 | 0.78 | 0.33 | 5.45 | 0.02 | 0.65 | 0.38 | 2.82 | 0.09 | 1.52 | 0.37 | 16.99 | ≤ 0.001 | 1.2 | 0.28 | 18.18 | ≤ 0.001 |
| RWB abundance | $n = 39$ | | | | $n = 13^a$ | | | | $n = 28$ | | | | $n = 150$ | | | |
| Mud (%) | -2.05 | 0.57 | 79.15 | ≤ 0.001 | -1.86 | 0.87 | 3.36 | 0.07 | 0.35 | 0.23 | 5.15 | 0.02 | -0.16 | 0.03 | 50.98 | ≤ 0.001 |
| Wetland size (ha) | -2.78 | 0.98 | 33.08 | ≤ 0.001 | -0.43 | 0.55 | 0.00 | 1.0 | 0.29 | 0.26 | 1.89 | 0.17 | -0.46 | 0.04 | 150.22 | ≤ 0.001 |
| Mud \times wetland size | -0.69 | 1.01 | 0.47 | 0.49 | -0.72 | 0.62 | 1.35 | 0.24 | -0.05 | 0.14 | 0.12 | 0.73 | 0.13 | 0.02 | 28.53 | ≤ 0.001 |
| Vegetation 15–60 cm (%) | 0.38 | 0.20 | 3.57 | 0.06 | -1.25 | 0.66 | 3.53 | 0.06 | 0.47 | 0.54 | 5.28 | 0.02 | 0.15 | 0.03 | 28.12 | ≤ 0.001 |
| Year 2014 | -0.16 | 0.49 | 0.11 | 0.74 | 0.34 | 0.86 | 0.15 | 0.70 | 0.15 | 0.54 | 0.07 | 0.78 | 1 | 0.06 | 284.12 | ≤ 0.001 |
| PPR abundance | $n = 67$ | | | | $n = 46$ | | | | $n = 56$ | | | | $n = 132$ | | | |
| Mud (%) | 1.30 | 0.05 | 679.45 | ≤ 0.001 | 0.97 | 0.06 | 128.44 | ≤ 0.001 | 0.36 | 0.06 | 41.54 | ≤ 0.001 | 0.65 | 0.02 | 1557.92 | ≤ 0.001 |
| Wetland size (ha) | 0.57 | 0.04 | 75.36 | ≤ 0.001 | 0.39 | 0.05 | 22.91 | ≤ 0.001 | 0.08 | 0.08 | 1.30 | 0.25 | 0.07 | 0.02 | 1.93 | 0.17 |
| Mud \times wetland size | 0.45 | 0.04 | 116.72 | ≤ 0.001 | 0.79 | 0.06 | 178.45 | ≤ 0.001 | -0.01 | 0.06 | 0.06 | 0.81 | -0.12 | 0.02 | 56.31 | ≤ 0.001 |
| Total vegetation (%) | 0.26 | 0.02 | 114.16 | ≤ 0.001 | 0.26 | 0.04 | 34.79 | ≤ 0.001 | -0.15 | 0.06 | 6.52 | 0.01 | 0.19 | 0.01 | 178.71 | ≤ 0.001 |
| Vegetation 15–60 cm (%) | -0.01 | 0.04 | 0.14 | 0.71 | -0.37 | 0.07 | 34.79 | ≤ 0.001 | 0.51 | 0.15 | 6.84 | 0.01 | -0.11 | 0.02 | 24.7 | ≤ 0.001 |
| Year 2014 | 1.14 | 0.09 | 160.27 | ≤ 0.001 | 0.83 | 0.14 | 33.88 | ≤ 0.001 | 0.51 | 0.15 | 11.94 | ≤ 0.001 | 0.95 | 0.04 | 496.48 | ≤ 0.001 |

^a Sample period random effect was not included in this model because of insufficient data.

sandpiper occupancy and abundance coincided with an increase in wetland availability in the RWB, which was 32% higher in March 2014 than in March 2013 (Bishop et al. 2016), and inundated wetland area was 54% higher on our study sites in March 2014 than in March 2013. In the PPR, local conditions were drier in 2014 than in 2013; 54% of the wetlands we sampled in April of 2013 were dry in 2014.

In general, sandpipers occupied wetlands with abundant mudflat (Fig. 1A) and little vegetation (Fig. 1B), but there were subtle differences between regions; occupancy rates increased with wetland size in the PPR (Fig. 1C). Sandpiper abundance estimates in the PPR were consistent with occupancy rates (with higher abundance on larger wetlands with more mudflat, Fig. 2C), but in the RWB although higher mudflat percentages increased abundance estimates, larger wetlands had fewer birds (Fig. 2A). Abundance estimates increased in association with taller vegetation in the RWB (Fig. 2B), but declined in the PPR (Fig. 2E). In the PPR there was also a slight increase in abundance estimates with more vegetation (Fig. 2D). Separate analyses of white-rumped, semipalmated, and stilt sandpipers revealed similar trends. With few exceptions, the predictors of wetland occupancy for sandpipers as a whole remained consistent at the species level; 87% of the β values remained consistent in direction, with many remaining significant despite reductions in sample sizes (Table 2).

Predictors of abundance, however, were less robust at the species-specific level; a third of the β values changed direction, and some remained significant even after the change in direction.

After controlling for year, sampling period, size, and percent mudflat of wetlands, we found occupancy did not differ between regions (PPR: $\bar{x}=0.30 \pm 0.08$ [SE], RWB: $\bar{x}=0.30 \pm 0.08$), but there were significantly more birds per occupied wetland in the PPR ($\bar{x}=21.94 \pm 11.88$) than in the RWB ($\bar{x}=8.40 \pm 4.54$; Table 3). Mudflat percentages were lower on larger wetlands ($\beta = -0.02 \pm 0.11$, $\chi^2 = 3.97$, $P = 0.046$), but did not differ between regions ($\beta = 4.486 \pm 2.07$, $\chi^2 = 1.96$, $P = 0.16$), and were not significantly related to any interaction between wetland size and region ($\beta = -0.29 \pm 0.16$, $\chi^2 = 3.33$, $P = 0.07$), suggesting that occupied wetlands in each region had comparable availability of mudflat.

Food Availability

Invertebrate abundance was correlated with invertebrate sample mass ($R^2 = 0.77$, $F_{1,145} = 498.8$, $P < 0.001$), suggesting that abundance is a meaningful proxy of macroinvertebrate biomass. Invertebrate abundance was higher in 2014 (\bar{x} invertebrates/plot 2013 = 0.23 ± 0.80 , 2014 = 1.72 ± 5.02 ; Table 4), and positively associated with soil temperature, vegetation, and dry soil, and negatively with litter (Table 4). Invertebrate abundance in

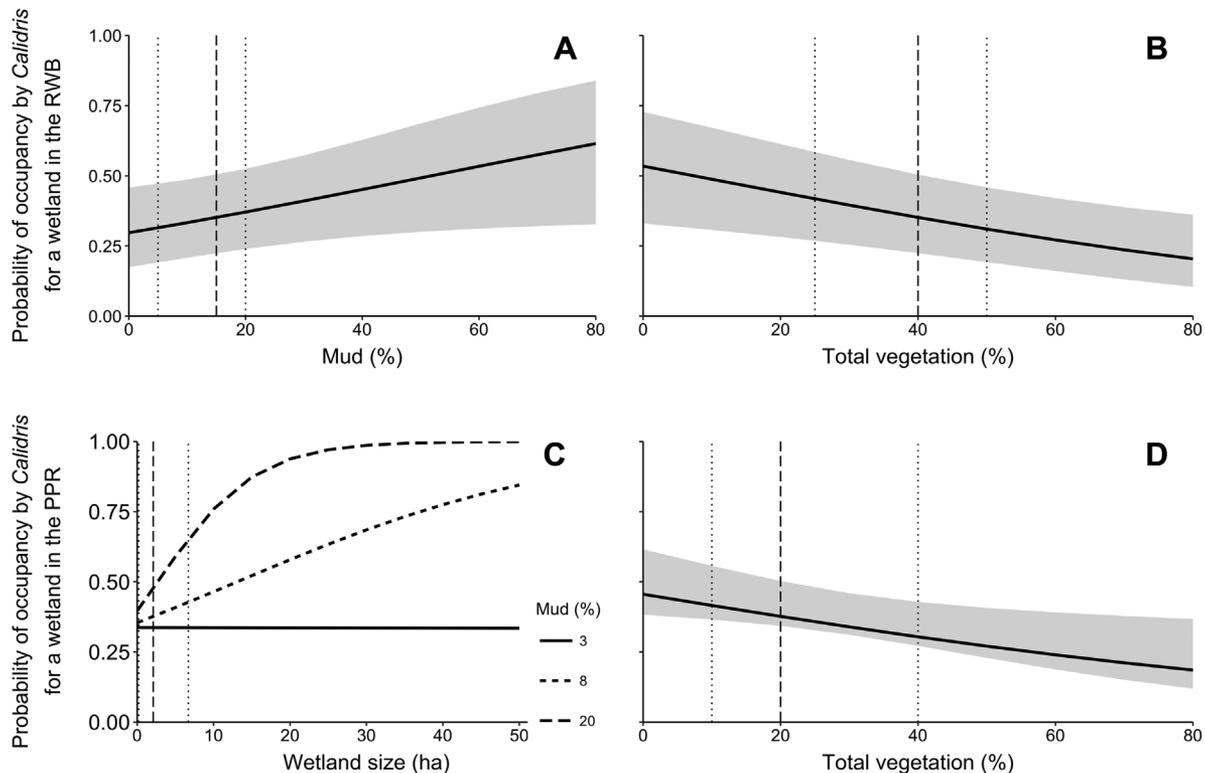


Figure 1. *Calidris* (dunlin, Baird's, least, pectoral, semipalmated, stilt, and white-rumped sandpipers) occupancy at wetlands in the Rainwater Basin (RWB), Nebraska, USA, 2013–2014 was predicted by percent mud (A), and percent total vegetation (B), whereas occupancy at wetlands in the Prairie Pothole Region (PPR), South Dakota, USA, was predicted by an interaction of percent mudflat and wetland size (C), and percent total vegetation (D). Lines and shaded areas represent predicted probability of occupancy with 95% confidence intervals; for ease of comparison, confidence intervals are not included on (C). Vertical lines represent the median and first and third quartile for the parameter across sampled wetlands.

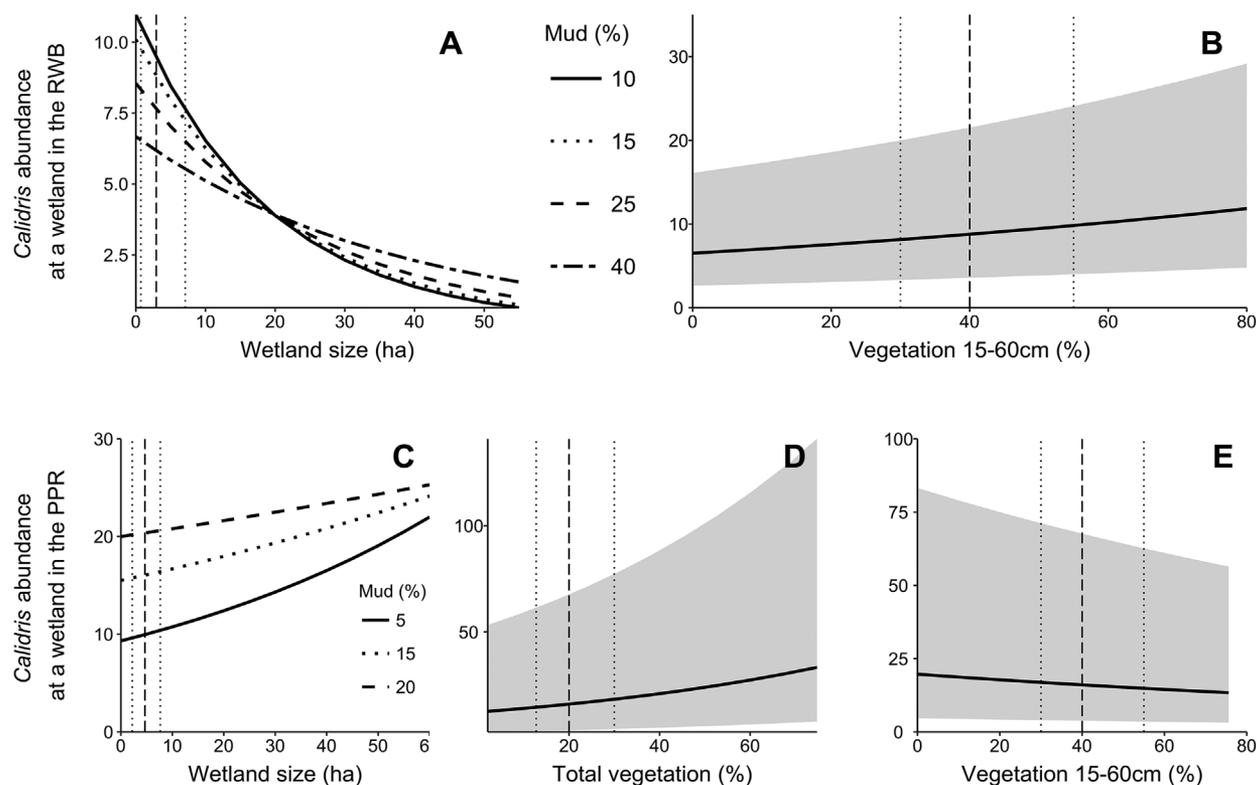


Figure 2. *Calidris* (dunlin, Baird's, least, pectoral, semipalmated, stilt, and white-rumped sandpipers) abundance at wetlands in the Rainwater Basin (RWB), Nebraska, USA, 2013–2014 was predicted by an interaction of percent mud and wetland size (A) and vegetation height (B). Abundance at wetlands in the Prairie Pothole Region (PPR), South Dakota, USA, was predicted by an interaction of percent mud and wetland size (C), percent vegetation (D), and vegetation height (E). Lines and shaded areas represent predicted probability of occupancy with 95% confidence intervals; for ease of comparison, confidence intervals are not included on (A) or (C). Vertical lines represent the median and first and third quartile for the parameter across sampled wetlands.

both years was positively correlated with sandpiper occupancy, but negatively correlated with sandpiper abundance at occupied wetlands (Table 4; Fig. 3A, C). Analysis of invertebrate presence or absence in our sampling cores exhibited the same positive relationship with sandpiper occupancy and negative relationship with sandpiper abundance (Table 4; Fig. 3B, D).

DISCUSSION

Local wetland characteristics are important in shaping sandpiper habitat use, and our results are generally consistent with our existing understanding. As a group, sandpiper occupancy rates were higher at wetlands with greater percent mudflat and less vegetation, a pattern that is consistent in the literature (Colwell and Oring 1988, Skagen and Knopf 1994b, Davis and Smith 1998) and substantiated at the species level (Table 2). Patterns of bird abundance were less clear; in many cases predictors of sandpiper abundance differed between regions. For example in the PPR, sandpiper abundance increased with less vegetation taller than 15 cm and more mudflat; however, in the RWB we found the opposite relationship. The number of sandpipers using vegetated wetlands in the RWB may suggest that the presence of shallow-water alone is the primary predictor of habitat use (Webb et al. 2010). The cycle of wetland inundation and drawdown naturally leads to a correlation between shallow-water and mudflat. In the RWB, however, water levels are

actively managed to maintain moist soil vegetation for migrating waterfowl (USFWS 2007). Still, where mudflat was available in the RWB we saw higher occupancy rates, indicating that mudflat is important for sandpipers. It may be that in a system where wetland availability is increasingly constrained by anthropogenic change, the added constraints imposed by drought make sandpipers more likely to use

Table 3. Results from generalized linear mixed models assessing *Calidris* occupancy and abundance (dunlin, Baird's, least, pectoral, semipalmated, stilt, and white-rumped sandpipers) of all individuals among all wetlands sampled based on percent mudflat, year, and region (Rainwater Basin [RWB] Nebraska, USA, or Prairie Pothole Region [PPR], South Dakota, USA), 2013–2014. We included site and sample period in all models as random effects. Because of a high proportion of unoccupied wetlands, we analyzed presence-absence (occupancy) and abundance separately, and included only wetlands with ≥ 1 bird present in abundance models.

| | β | SE | Wald χ^2 | P |
|---------------------------|---------|------|---------------|--------------|
| Occupancy | | | | |
| Region RWB | -0.03 | 0.26 | 0.01 | 0.92 |
| Mud (%) | 0.36 | 0.10 | 14.36 | ≤ 0.001 |
| Year 2014 | 0.67 | 0.21 | 10.32 | 0.001 |
| Abundance | | | | |
| Region RWB | -0.96 | 0.27 | 12.54 | ≤ 0.001 |
| Mud (%) | 0.06 | 0.02 | 5.78 | 0.02 |
| Wetland size (ha) | -0.11 | 0.03 | 10.62 | 0.001 |
| Mud \times wetland size | 0.08 | 0.02 | 19.24 | ≤ 0.001 |
| Year 2014 | 0.96 | 0.06 | 293.80 | ≤ 0.001 |

Table 4. Results from generalized linear mixed models from analyses of food availability in the Rainwater Basin, Nebraska, USA, 2013–2014, in relation to *Calidris* occupancy and abundance (dunlin, Baird's, least, pectoral, semipalmated, stilt, and white-rumped sandpipers), and in relation to vegetation and soil characteristics within plots. We used average total invertebrate abundance per 3-m × 3-m plot as a measure of invertebrate abundance. We used a proportional occupancy of invertebrates among all sample cores taken at the wetland (calculated after converting all core values to 1 or 0 indicating presence-absence). All models included site and sample period as random effects.

| | Invertebrate abundance | | | | Invertebrate proportional occupancy | | | |
|-------------------------------------|------------------------|-------|----------|----------|-------------------------------------|------|----------|----------|
| | β | SE | χ^2 | <i>P</i> | β | SE | χ^2 | <i>P</i> |
| <i>Calidris</i> occupancy | | | | | | | | |
| Mud (%) | 0.29 | 0.13 | 5.03 | 0.02 | 0.02 | 0.01 | 4.58 | 0.03 |
| Invertebrates | 0.40 | 0.18 | 5.02 | 0.02 | 2.68 | 0.88 | 9.22 | 0.002 |
| Year 2014 | 0.24 | 0.26 | 0.86 | 0.35 | 0.15 | 0.26 | 0.32 | 0.57 |
| <i>Calidris</i> abundance | | | | | | | | |
| Mud (%) | -0.19 | 0.03 | 51.73 | ≤0.001 | -0.15 | 0.03 | 38.09 | ≤0.001 |
| Wetland size (ha) | -0.53 | 0.04 | 168.95 | ≤0.001 | -0.47 | 0.05 | 142.48 | ≤0.001 |
| Mud × wetland size | | | | | 0.09 | 0.03 | 11.46 | ≤0.001 |
| Invertebrates | -0.15 | 0.04 | 16.50 | ≤0.001 | -0.30 | 0.03 | 108.97 | ≤0.001 |
| Year 2014 | 1.09 | 0.06 | 325.17 | ≤0.001 | 1.32 | 0.06 | 420.43 | ≤0.001 |
| Invertebrate abundance within plots | | | | | | | | |
| Vegetation (%) | 0.005 | 0.002 | 4.64 | 0.03 | | | | |
| Dry soil (%) | 0.017 | 0.005 | 9.48 | 0.002 | | | | |
| Litter (%) | -0.006 | 0.003 | 5.13 | 0.02 | | | | |
| Soil temperature (C) | 0.045 | 0.012 | 15.40 | ≤0.001 | | | | |
| Soil pH | -0.056 | 0.042 | 1.78 | 0.18 | | | | |
| Year 2014 | 1.310 | 0.324 | 18.56 | ≤0.001 | | | | |

wetlands with more vegetation, but with unknown consequences for stopover duration or foraging efficiency. It is also worth noting that the difference in habitat use between regions presents sampling challenges that affect our ability to understand patterns of sandpiper abundance. When sandpipers use wetlands with more vegetation there is likely a corresponding reduction in detection probability (Webb et al. 2010). Although detection issues cannot explain the differences between regions in what predicts sandpiper abundance, we cannot rule out detection bias as a potential explanation for why there appear to be more birds using wetlands in the PPR. Indeed, the extent to which abundance estimates in different vegetation conditions differ because of actual habitat use versus sampling error is an unresolved issue in studies of shorebird migratory ecology.

Food availability during stopover is often identified as the primary determinant of migratory success (Rodewald et al. 2007, McGrath et al. 2009, Strode 2009, Fontaine et al. 2015, Stutzman and Fontaine 2015), and is increasingly prioritized in management plans for migratory species (Bishop and Vrtiska 2008, Rainwater Basin Joint Venture 2013). Thus, it is surprising that although we found a positive relationship between invertebrate abundance and sandpiper occupancy, we failed to find a positive relationship with sandpiper abundance. One likely possibility for our observation is that in our system, macroinvertebrate abundance is positively correlated with vegetation, but vegetation also increases predation risk for ground-foraging birds such as sandpipers (Whittingham and Evans 2004). That food availability does not predict sandpiper abundance may simply reflect an ecological trade-off between food and predation risk (Lima and Dill 1990). Alternatively, although we used standard protocols in assessments of avian food availability (Davis and Smith 1998), the systematic random approach we employed may have limitations in estimating

resources that are patchy in distribution. Still, given that we find the same relationships when we reduce sampling error by looking for invertebrate presence rather than abundance, we are confident that our results reflect important ecological relationships.

We observed differences in sandpiper abundance between years in both regions, which may reflect annual changes in population size; yet differentiating among sources of ecological variation driving differences in abundance between years and study regions is challenging. Spring temperatures were colder than normal in 2013 (NOAA 2013), potentially causing migratory populations to adjust stopover duration, frequency, and migratory progression in response to climatic conditions (Marra et al. 2005, Tøttrup et al. 2008), which could have reduced our abundance estimates. The dry conditions in 2013 may have also caused shorebird populations to adjust migratory routes to take advantage of wetlands outside of our study area; annual shifts in wetland availability in the Great Plains can result in large inter-annual fluctuations in bird numbers at individual survey locations (Skagen et al. 2008). Abundance differences between the RWB and the PPR may simply reflect intrinsic historical differences between the regions. Still, it is worth considering that the differences we find between the RWB and the PPR may also reflect the influence of regional land-cover driving habitat selection at local stopover sites (Hutto 1985, Buler et al. 2007), and local species abundance in agricultural landscapes (Jorgensen et al. 2014). Many studies have specifically noted the importance of dense networks of wetlands for sandpiper species (Skagen and Knopf 1994b; Farmer and Parent 1997; Niemuth and Solberg 2003; Albanese and Davis 2013, 2015). As land-use change continues to develop and row-crop agriculture more frequently dominates area surrounding managed wetlands, managers may need to increasingly consider how the

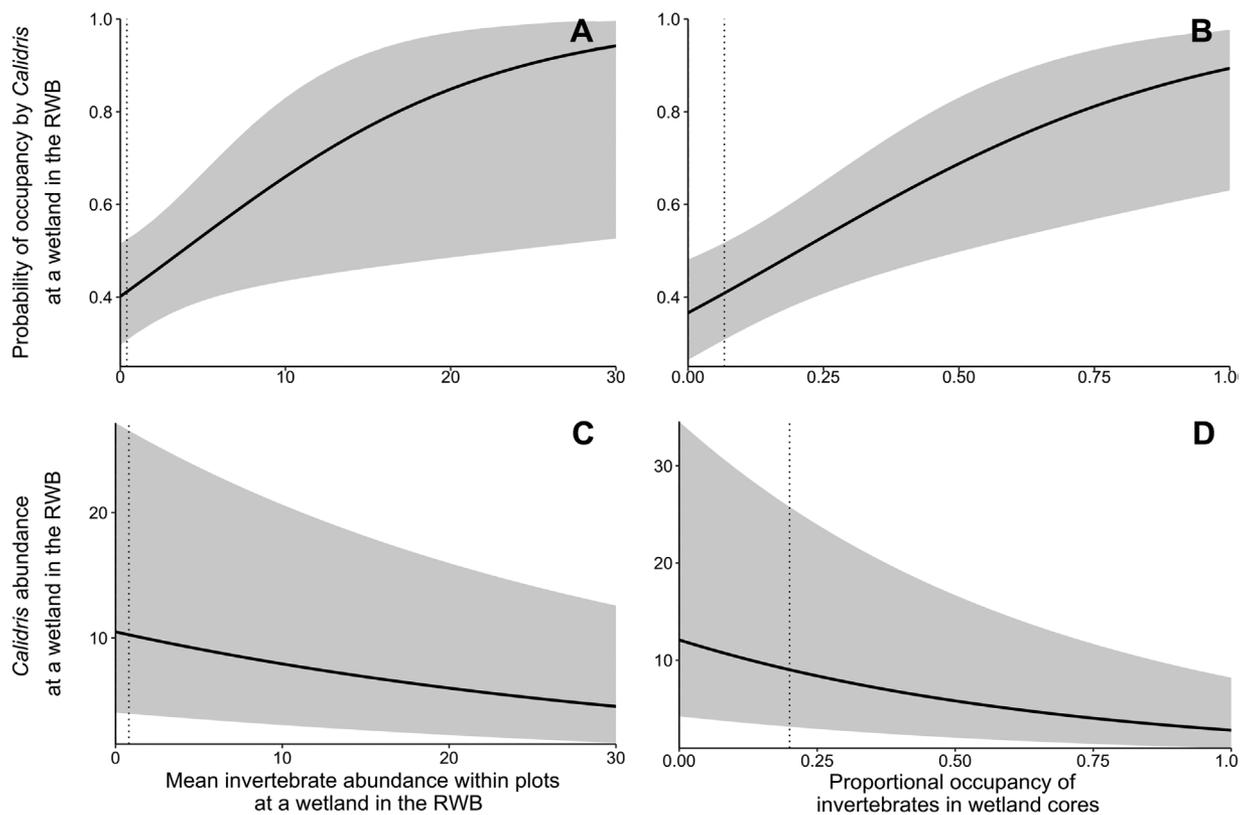


Figure 3. Invertebrate abundance (average sum of invertebrates counted in 3 5-cm depth sample cores in 3-m × 3-m plots in a wetland) predicts higher occupancy (A), but not higher abundance (C), of *Calidris* shorebirds (dunlin, Baird's, least, pectoral, semipalmated, stilt, and white-rumped sandpipers) at wetlands in the Rainwater Basin (RWB), Nebraska, USA, 2013–2014. The proportional occupancy of invertebrates detected in sample cores (calculated as a proportion of up to 15 cores taken at a wetland after converting all values to 1 or 0 based on presence-absence of invertebrates in the core) also predicted a positive relationship with sandpiper occupancy (B) but not abundance (D). Lines and shaded areas represent predicted probability of occupancy with 95% confidence intervals. Vertical lines represent the median and first and third quartile for the parameter across all sampled wetlands.

distribution and abundance of wetlands may constrain or facilitate shorebird use of managed resources.

MANAGEMENT IMPLICATIONS

Unfortunately for wetland managers, actions favoring moist soil vegetation for other migratory waterbirds may often be at odds with sandpiper habitat use, and thus, may require alternative management strategies (USFWS 2007). When dry conditions make pumping water necessary, managers should consider fluctuating pumping rates across a network of wetlands to create dense mosaics of mudflat and shallow water, rather than prioritizing actions aimed only at increasing food availability (macroinvertebrates or seeds) at individual wetlands. To successfully provide adequate resources for shorebirds during migratory stopover, managers should be cognizant that energy acquisition, not availability, is what determines migratory success, even though regional management plans tend to focus on biomass estimates of food availability (Nugent et al. 2015). Even when food is abundant, birds may not acquire the necessary resources if managers do not maintain the cues and ecological conditions that predict habitat use (e.g., dense mosaics of abundant wetlands; Albanese and Davis 2015). At individual wetlands, our occupancy results would

suggest that sparsely vegetated mudflat is the best predictor of sandpipers habitat use. Although our findings indicate that sandpipers will use vegetated wetlands in a highly altered landscape coupled with extreme drought, it is unclear whether vegetated wetlands meet the energetic needs of migratory sandpipers.

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Appendix A

Number of individuals of all *Calidris* sandpipers observed in the Rainwater Basin Nebraska, USA, and Prairie Pothole Region, South Dakota, USA, 2013–2014.

| Species | Rainwater Basin | | Prairie Pothole Region | |
|------------------------|-----------------|-------|------------------------|-------|
| | 2013 | 2014 | 2013 | 2014 |
| Baird's sandpiper | 161 | 295 | 15 | 614 |
| Dunlin | 0 | 67 | 4 | 1 |
| Least sandpiper | 5 | 116 | 86 | 22 |
| Pectoral sandpiper | 19 | 56 | 6 | 33 |
| Semipalmated sandpiper | 46 | 240 | 87 | 497 |
| Stilt sandpiper | 45 | 147 | 291 | 1,109 |
| White-rumped sandpiper | 179 | 700 | 297 | 2,435 |
| Unidentified sandpiper | 237 | 817 | 571 | 102 |
| Total | 692 | 2,438 | 1,357 | 4,813 |