The Effects of Landscape, Movement, and Spillover on Avian Occupancy in the Sierra Nevada Foothills of California

By

Sean M. Peterson

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Committee in charge:

Professor Steven R. Beissinger, Chair

Professor Iryna Dronova

Professor Justin S. Brashares

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Abstract

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One of the most fundamental questions facing ecologists is: why do animals live where they do? Patch occupancy depends on a myriad of biotic and abiotic factors, any of which may encourage or discourage the presence of a species. Understanding the relationship between occupancy and environmental characteristics is integral to managing and conserving species in a dynamic environment. This dissertation studies avian occupancy in widely dispersed emergent wetlands in the Sierra Nevada foothills of California and relates occupancy to the characteristics of wetland patches, behaviors of the birds using those wetlands, and landscape composition.

The first chapter of this dissertation focuses on violations of the assumption of closure in occupancy models for two secretive marsh birds, Black Rails (*Laterallus jamaicensis*) and Virginia Rails (*Rallus limicola*). For occupancy models, a key assumption is that there is no immigration and emigration between survey periods. Violating this assumption could overestimate occupancy and lead to an improper understanding of the characteristics that influence site occupancy. I found that there were significant closure violations for both Black and Virginia Rails, although the characteristics of those violations differed. Black Rails were more likely to colonize wetlands between surveys, and the wetlands colonized were those that were occupied in the previous year. Virginia Rails were more sensitive to environmental changes and would abandon drying wetlands more readily than Black Rails.

The second chapter of this dissertation uses a multispecies occupancy model to understand the importance of spillover effects on occupancy across the entire avian assemblage using wetlands in the Sierra Nevada Foothills. The presence of animals in a patch of habitat is dependent not only on the characteristics of that patch, but also the landscape surrounding it. I investigated whether there was a spillover effect from matrix habitats such as grassland and forest on wetland bird species or the reverse, a spillover effect from the wetlands on species inhabiting the matrix habitat surrounding each wetland. I observed spillover effects in both directions, with matrix species assemblages depending on wetland water source and wetland species assemblages depending on the landscape composition around the wetland.

The final chapter of this dissertation uses aerial remote sensing to assess Black and Virginia Rail habitat, compares the predictive power of remote sensing to ground-truthed data,

and assess the ability of occupancy models to predict rail occupancy at novel sites using only aerial imagery. For this chapter, I differentiated occupied habitat from unoccupied habitat using known locations and occupancy status at wetlands. I classified sites using a maximum likelihood classifier and high resolution imagery from the National Agriculture Imagery Program. I found that raw spectral reflectance accurately predicted wetland occupancy for both Black and Virginia Rails, although the effectiveness of characterizing a wetland varied between years. For Black Rails, spectral reflectance was most similar to the wetland structure, whereas for Virginia rails, spectral reflectance was most similar to wetland wetness. However, in both cases, spectral reflectance was informative when included alongside ground-collected data.

Although the data collected in this dissertation are focused on a very specific habitat type and location, my results clearly demonstrate the importance of biological context on understanding animal occupancy. My results are broadly applicable in other study systems and help inform conservation strategies for multiple species. By understanding landscape composition, the drivers of animal movement, and the biotic and abiotic factors correlated with occupancy, I can better predict changes in animal populations in an increasingly changing environment.

For Lynn and Vireo

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Introduction

This dissertation focuses on the avifauna of the Sierra Nevada foothills of California, a biologically complex landscape comprised of emergent wetlands, agriculture, natural oak savannah, forest, and grazing land. My research builds on previous work in the region that specifically studied Black Rails (*Laterallus jamaicensis*) and Virginia Rails (*Rallus limicola*). The long-term study of rails in the Sierra Nevada foothills began after the discovery of a breeding population of Black Rails in 1994 (Richmond et al. 2008). Prior to the discovery of the foothills population, Black Rails were only known in the western United States of America in three small populations in the San Francisco Bay Area, San Diego, and the Imperial Valley. Although Black Rails are a highly secretive species, the fact that their presence was unknown in the foothills until 1994 speaks to the relative lack of avian research that had been performed in the region. My interest in this dissertation was to build on previous studies of Black and Virginia Rails in the Sierra Nevada foothills and to better understand the greater avian assemblage using wetlands in the region.

The research presented in this dissertation depends greatly on the work of previous work in this study system. Here, I will briefly outline past work in the Sierra Nevada foothills and identify the knowledge gaps that I studied. Some of the first research performed on Black Rails in the foothills was a description of their distribution and habitat associations (Richmond et al. 2008, 2010a), followed by an investigation between rail occupancy and cattle grazing, as many of the wetlands in our study system are dependent on ranchland irrigation (Richmond et al. 2012). Richmond et al. also developed novel parameterizations of occupancy models that could accommodate two species, focusing on the relationship between Black Rail and Virginia Rail (Richmond et al. 2010b). Subsequent work in this study system focused on Black Rail genetic markers, population connectivity, and dispersal (Girard et al. 2010, Hall and Beissinger 2017, Hall et al. 2018). Using genetic markers and banding data, it was determined that although the majority of dispersal within a population was short-distance, there was occasional gene flow between the Sierra Nevada foothills population and the San Francisco Bay population of Black Rails. As occupancy surveys continued, work focused on the relationship between the natural system of wetlands and its relationship to the humans living on and using the same landscape. Much of the wetland habitat in the Sierra Nevada foothills is dependent on irrigation water, which is threatened by drought, urbanization, and changes in water management (Van Schmidt et al. 2019, 2021). Van Schmidt et al. also investigated between-season movement within the metapopulation and the importance of the rescue effect on maintaining site occupancy (Van Schmidt and Beissinger 2020). Below, I summarize the key research gaps that directed my dissertation.

Animal Movement and Site Closure

Our understanding of rail habitat use in this study system follows the foundational metapopulation work of Hanski (1998) and uses occupancy models to understand patch occupancy when detection probability is < 1 (MacKenzie et al. 2002, 2003). Both Black and Virginia Rails are highly secretive and detecting them can be largely dependent on inducing responses from call-playback surveys. Based on previous research, the foothills metapopulation behaves very similarly to others, with individual wetlands changing in suitability and occupancy status over time. In dry years, spring-fed wetlands may disappear and be abandoned by rails, or wetlands caused by irrigation leaks may dry if a leak is fixed. The Sierra Foothills are a dynamic environment and our research has demonstrated that there is substantial movement between habitat patches (Hall et al. 2018, Van Schmidt and Beissinger 2020). However, we lack an understanding of the frequency of movement within a breeding season, when the occupancy status of wetlands is assumed to remain unchanged. The closure assumption of occupancy models is a key assumption that is required to estimate the probability of detecting individuals and, if invalid, may bias estimates of occupancy (Rota et al. 2009). When performing surveys in my first summer of data collection, it struck me how frequently we observed individuals in the exact same location in each visit. The frequency in which I observed birds in the same location with aggressive territorial made me question whether birds that were not detected in some visits were even occupying wetlands during those surveys. My first chapter investigates the extent rails in the Sierra Nevada foothills violated the closure assumption by moving between wetland patches within the metapopulation, the potential biological drivers of closure violations and movement, and the effect of movement on occupancy estimates. Understanding the impact of closure violations on occupancy and the potential environmental causes of closure violations may inform conservation decisions and allow for a more accurate understanding of how animals use the space they live in.

Occupancy of Avian Assemblages and the Spillover Effect

Black and Virginia Rails are two of many species that use the wetlands of the Sierra Nevada foothills. However, our understanding of the relationship between the avian assemblage and the habitat composition in the Sierra Nevada foothills is limited. Wetlands in the foothills are a unique resource that provide a near-constant water source on a semi-arid landscape. On many landscapes with complex structures of differing habitat types, the presence of a species or groups of species can be at least partially driven by spillover effects from one habitat to another (Tscharntke et al. 2012, Schneider et al. 2016, Barros et al. 2019). My second chapter seeks to understand the relationship between avian occupancy of wetlands and the surrounding matrix habitats and how spillover effects might affect occupancy. However, the avian assemblage of the Sierra Nevada foothills is not monolithic. Each species has differing habitat requirements and relationships with wetland characteristics. To better understand how the avian assemblage responded to wetlands, I broadly divided the avifauna into three categories: wetland obligates, facultative species that used wetlands, but not exclusively, and matrix species that primarily used matrix habitat. By analyzing spillover effects in the context of these three groups, I hoped to identify what habitat characteristics are important for all birds on a complex landscape and what habitat characteristics are only important for a subset of species.

Remote Sensing and Rail Occupancy

One of the most important results yielded from occupancy models of species is associating occupancy with habitat characteristics. For Black and Virginia Rails, we know that three important habitat characteristics are: area, isolation, and wetland structure (Richmond et al.

2010a, b; Van Schmidt et al. 2019). However, some of the habitat characteristics that were *a priori* assumed would be important, such as wetland vegetation and wetland wetness were not as informative in occupancy models as was initially expected. This ran counter to the experience of many on-the-ground surveyors, who could often predict the location of a rail in a wetland with high accuracy simply through visual clues. The human brain is exceptionally effective at recognizing patterns, often using minute details that are difficult to quantify. My goal with the third chapter of this thesis was to determine if we could mathematically mimic some of the human brain's natural analytical and predictive capabilities and effectively identify quality habitat just by looking at it. In some ways, this chapter is asking the question: can we quantify a picture of a species' realized niche? Although using remote imagery to classify habitat and quantify characteristics is widely used, directly assessing occupancy is still uncommon (Nagendra 2001). To integrate remote sensing into occupancy models, I used occupancy status to classify wetlands as either "occupied" or "unoccupied" based on spectral reflectance from aerial imagery. This method of quantifying habitat allows for naïve classification that is driven by animal presence and absence, rather than *a priori* assumptions of what habitat characteristics an animal prefers.

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I owe a particular debt of gratitude to my academic mentors, most importantly, my guiding professor, Steve Beissinger. Steve pushed my research into awesome new directions and taught me more than I thought I was capable of learning about being a scientist. The data in this thesis is a continuation of an 18-year dataset that has been diligently cared for by many before me. In particular, I would like to thank Jerry Tecklin, Orien Richmond, Laurie Hall, and Nathan Van Schmidt for creating an amazing foundation that I was able to build off of. The data collected for this work was a monumental effort by many technicians who performed thousands of wetland surveys. I would like to thank Erica Iacona, Connor Bernard, Cedric Duhalde, Laine Yandell, Jonathon Lueck, Garrett Duncan, Ellie Resendiz, and William Wiskes. I can't thank you all enough for all of your hard work.

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Finally, this research took place at hundreds of small wetlands on both public and private property in the Sierra Nevada foothills. None of this would have been possible without the landowners that graciously allowed us onto their land. The Sierra foothills are full of kind, welcoming people who care deeply about their land, including the animals that call it home. This research is unique in that it depended extensively on the participation of private landowners. It was a privilege to work with these stewards and study the wildlife that lived on their land.

Chapter 1: Closure violations reveal insights into occupancy and movement within rail metapopulations

1.1 Abstract

Occupancy modeling is an analytical framework that accounts for imperfect detection but assumes sites remain continually occupied or unoccupied between survey visits. This assumption of closure is rarely tested and can lead to biased occupancy estimates if rates of movement into and out of sampling units differ. I quantified the occurrence and effects of closure violations on occupancy estimates and identify the factors associated with movement (patch colonization and extinction) during the breeding season in metapopulations of secretive Black Rails (*Laterallus jamaicensis*) and Virginia Rails (*Rallus limicola*) in wetland patches in California, USA. I used a robust sampling design with three primary periods composed of four secondary periods at 48 sites, and maximized detection probability using automated recording units accompanied by audio playback of rail vocalizations. Both metapopulations exhibited significant violation of closure, with 21% of sites surveyed for Black Rails and 23% of sites surveyed for Virginia Rails changing occupancy status within a breeding season. Species appeared to move for different reasons. Black Rail colonization and extinction was strongly related to site occupancy in the previous year, with survey period and site isolation having weak effects. Virginia Rail turnover was related to wetland size, with site occupancy in the previous year, site isolation and geomorphology exhibiting weak effects. Wetlands with Virginia Rail turnover were smaller than wetlands that were continually occupied, suggesting sites may be used for different purposes within the breeding season. In contrast with previous studies that assessed closure violations for point-count surveys, site-level occupancy estimates were not significantly biased for either species. While closure violations are often ignored or treated as a nuisance in occupancy modeling, they provide evidence of important biological processes that can lead to a better understanding of habitat requirements, space use, and metapopulation dynamics.

1.2 Introduction

Occupancy modeling is a common tool used to assess the occurrence and dynamics of wildlife populations (MacKenzie et al. 2002, Royle and Kéry 2007). By surveying sites on multiple visits, it is possible to reduce bias due to imperfect detection by estimating both a detection and an occupancy probability for a target species (MacKenzie et al. 2002, 2018). A key assumption of occupancy models is that a site remains continually unoccupied or unoccupied between survey visits (MacKenzie et al. 2002, Rota et al. 2009). Violations of the closure assumption reduce estimates of detection probability, which can lead to a corresponding increase in estimates of occupancy (Kendall 1999, Rota et al. 2009) or an improper definition of site occupancy (Latif et al. 2016, MacKenzie et al. 2018). Occupancy estimates are most susceptible to this bias when closure violations are frequent (Rota et al. 2009), and when the rate of movement into and out of survey sites differs (MacKenzie et al. 2018).

Closure violations are more than a statistical nuisance caused by animal movements, because discerning the causes of closure violations can produce a more complete understanding of a species' habitat and conservation needs, its response to changing environments, and the drivers of movement across landscapes (Klemp 2003, Walk et al. 2004, Betts et al. 2008). Movement is inherently dangerous (Lima 1985, Brown 1988, Nathan et al. 2008), so closure violations may be evidence of behaviors with potential evolutionary consequences. Closure violations do not have a single unifying cause; nonrandom movement can result from local changes in habitat or food availability (e.g., Klemp 2003), or may be the result of territorial prospecting, territory shifts, competitive exclusion, or extra-territorial movement (Walk et al. 2004, Fletcher Jr. 2006, Berigan et al. 2019). Many species shift their habitat use over time to meet changing biological needs, such as caring for juveniles (e.g., Streby et al. 2014) or molting (Robert and Laporte 1999). Whether movements into and out of survey sites occur frequently may also depend on their magnitude compared to the size of a survey site. Point counts often sample a small area relative to the size of bird home ranges and are more likely to experience temporary immigration-emigration than patch-level surveys composed of multiple points sampling a larger area (Valente et al. 2017).

Statistical tests to assess site closure exist (Rota et al. 2009), but potential closure violations are rarely evaluated. Of 89 peer-reviewed publications that cited the foundational paper by Rota et al. (2009) and implemented occupancy models with field data, five explicitly tested closure and only one used the recommended likelihood-ratio test (Appendix S1.1: Table S1.1). Most studies simply assumed some degree of closure or accounted for the effects of closure violations without testing for them (Fig. 1.1).

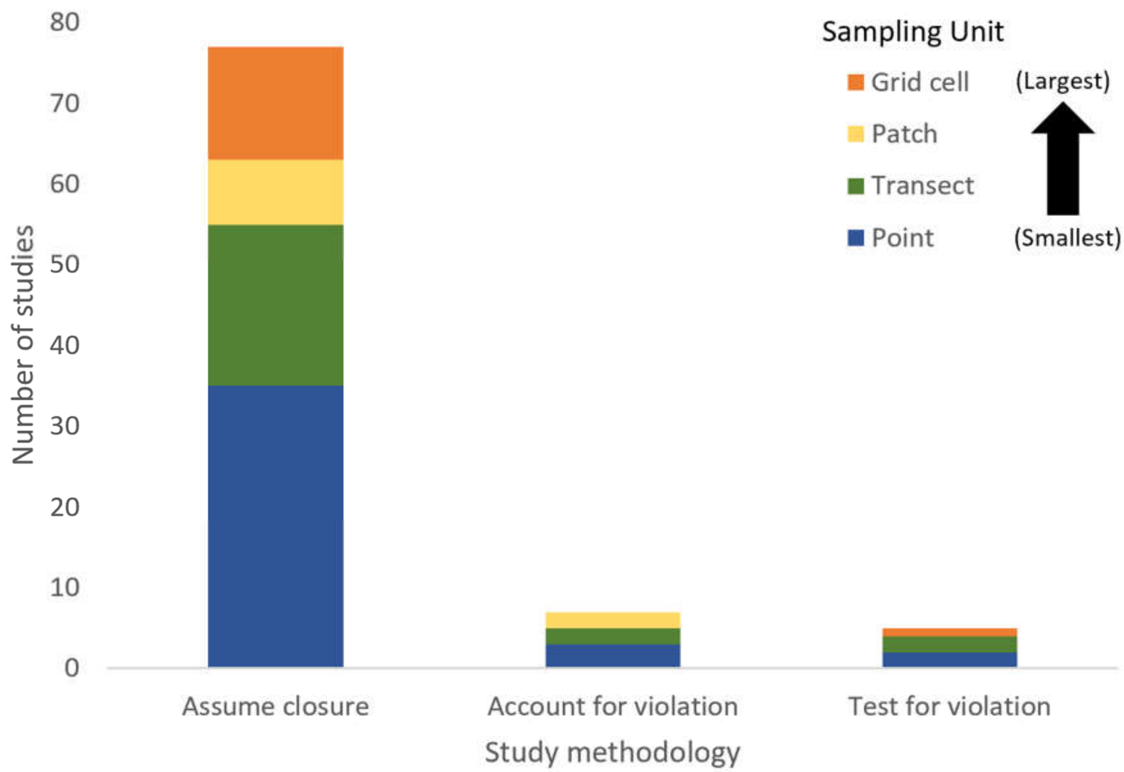


Figure 1.1 Summary of peer reviewed publications citing Rota et al. (2009) between 2009 and November 2020. For each publication, I determined scale (sampling unit) and whether the publication assumed closure, accounted for potential closure violations, or explicitly tested for closure violations.

The effects of closure violations at large spatial scales have received even less consideration. Of the same set of 89 publications, only one study tested for closure violations at the patch or grid area scale (Appendix S1.1: Table S1.1). A staggered-entry occupancy model was developed to account for closure violations (Kendall et al., 2013), but it has rarely been implemented (n = 10 publications; Appendix S1.1: Table S1.2) and assumes closure occurs once a species has arrived at a site. Thus, most studies simply acknowledge the closure issue and attempt to mitigate the effects of violations by minimizing the duration of the sampling period, rather than directly testing for closure violations or accounting for biases through modeling.

There are several ways to directly test the assumption of closure in occupancy models (Rota et al. 2009, Otto et al. 2013, Valente et al. 2017). A general method described by Rota et al. (2009) tests for closure violations by coupling a robust sampling design (Fig. 1.2), which employs surveys conducted during secondary sampling periods that occur within each primary sampling period (Pollock, 1982), with single season and multi-season occupancy models (MacKenzie et al. 2002, 2003). The robust sampling design assumes closure over the short time intervals that comprise primary sampling periods, but allows for turnover to occur during the longer time intervals between primary sampling periods (Fig. 1.2). Closure violation is tested by comparing the fit of a single-season occupancy model generated from the entire set of surveys to the fit of a multi-season occupancy model that uses each primary sampling period as a season.

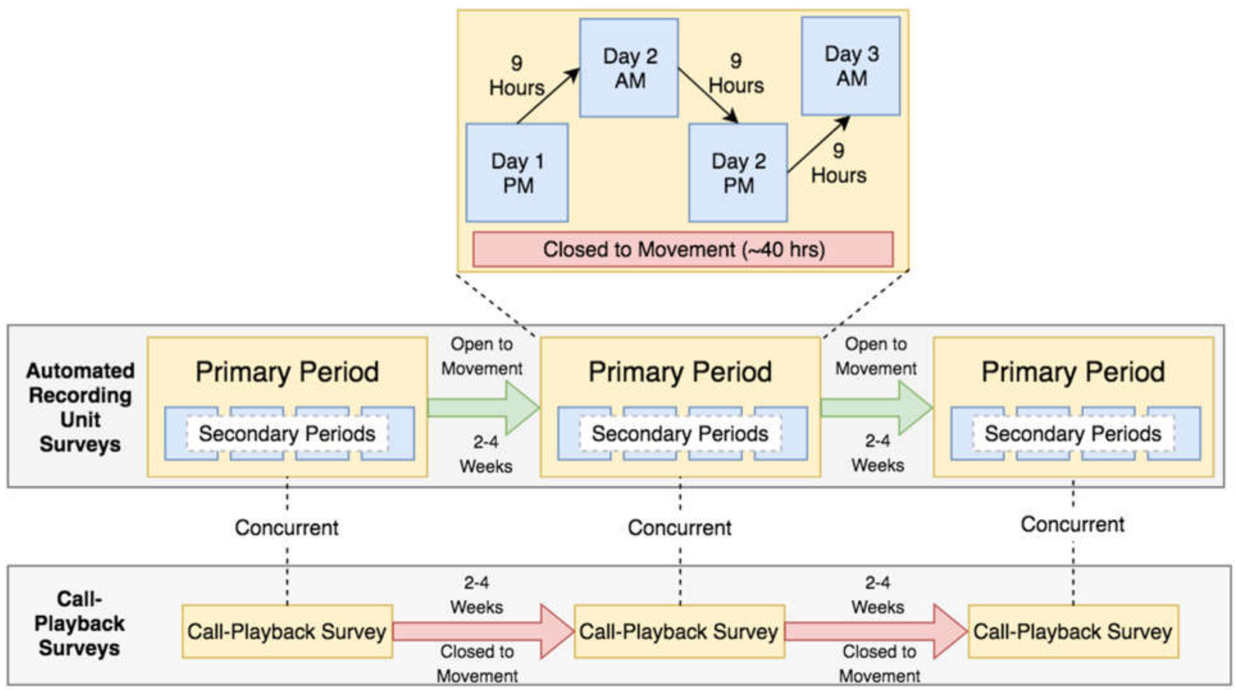


Figure 1.2. Sampling protocol and timing for automated recording unit (ARU) and concurrent call-playback surveys. ARU surveys were composed of three primary periods each made up of four secondary periods spread out over two days. Concurrent call-playback surveys occurred within one week of ARU surveys. Closure was assumed between ARU secondary periods and between call-playback visits.

Implementing the robust design model, however, requires the execution of additional surveys, which often requires repeated visits to sites and has associated expenses. This cost may be partly overcome by using autonomous sampling devices, such as automated recording units (ARUs), to sample intensively during primary sampling periods.

I tested for closure violations and its effect on occupancy estimates in metapopulations of secretive marsh birds, Black Rails (*Laterallus jamaicensis*) and Virginia Rails (*Rallus limicola*), that occupy I tlands in the Sierra Nevada Foothills of California (Fig. 1.3). My study populations of rails are territorial and year-round residents in shallow marshes (<3 cm water depth) with dense vegetation, where they feed on aquatic invertebrates and seeds (Eddleman et al. 1994, Conway 1995, Richmond et al. 2008). My study area is comprised of hundreds of small, often irrigated wetlands within a matrix of oak savannah and ranchland (Richmond et al. 2010a, Van Schmidt et al. 2019). Colonization of unoccupied sites and extinction of occupied sites occur between breeding seasons, and wetland habitat quality can change substantially within weeks as irrigation water is turned off and on (Risk et al. 2011, Van Schmidt et al. 2019). However, wetlands are thought to be continuously occupied by rails throughout the breeding season (Hall and Beissinger 2017, Hall et al. 2018), despite ample evidence of rescue effects occurring between breeding seasons (Van Schmidt and Beissinger 2020).

I used ARUs to sample sites for rail occupancy in a robust design scheme to estimate occupancy and test for closure during the breeding season (Fig. 1.2). My objectives were to: (1) determine whether rails violated closure by colonizing unoccupied sites and abandoning occupied sites within the breeding season; (2) evaluate the environmental factors governing movement within the breeding season; and (3) assess the effect of closure violations on occupancy estimates (Appendix S1.1: Table S1.3). I hypothesized that both Black and Virginia Rails would rarely exhibit violations of closure because of their sedentary nature and because surveys occurred at the patch-level rather than as point-counts. When closure violations occurred, I predicted they should be related to individuals moving from wetlands with deteriorating conditions (i.e. drying) to better (i.e. wetter) sites. Finally, I predicted the effect of closure violations on occupancy estimates should be small because wetland patches would typically be continuously occupied.

1.3 Methods

1.3.1 Study Sites

I surveyed 48 wetlands for rails in Yuba and Nevada counties in California, USA (Fig. 1.3). Individual wetlands were generally small ($\bar{x} = 0.79 \pm 0.12$ ha) and dominated by *Typha* spp. and *Juncus* spp. Wetland typology varied from sloping hillsides with shallow flowing water to ponds and impoundments with still water surrounded by a fringe of wetland vegetation (Richmond et al. 2010a, Van Schmidt et al. 2019). Wetlands included both natural (i.e. fed by a spring, creek, or other natural water source) and irrigated water sources. Irrigated wetlands in the study area were either unintentional habitat created by runoff from agricultural activities such as ranching, or intentional habitat created for wetland species (Richmond et al. 2010a, Van Schmidt et al. 2019). Natural wetlands and irrigated wetlands intended to create rail habitat often had continuous or nearly continuous water flow, whereas irrigated wetlands created as a byproduct of ranching or other activities had more varied flow depending on the desires of landowners (Huntsinger et al. 2017, Van Schmidt et al. 2019). Wetlands were located within an oak savannah and ranchland matrix and were sparsely spread across the landscape. For the purpose of estimating site occupancy and to account for discontinuities in wetland habitat, I defined a "site" to include all patches of wetland vegetation within 50 m of each other that were fed by the same water source(s) (Van Schmidt et al. 2019).

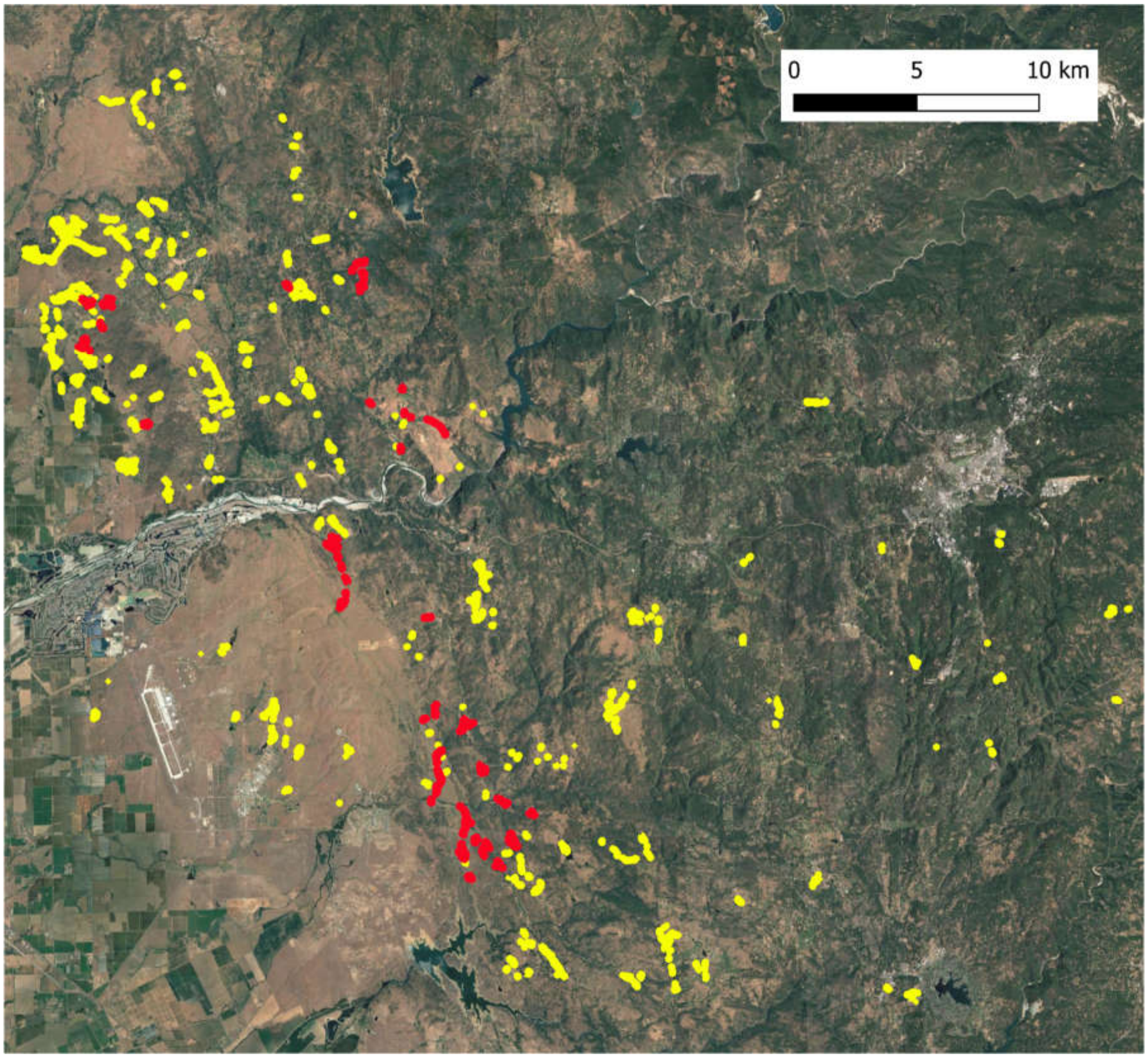


Figure 1.3. Wetlands used by metapopulations of Black and Virginia rails in the Sierra Nevada foothills. Sites where ARUs were placed for this study are marked in red. Sites in yellow were used only to calculate measures of isolation.

1.3.2 Study Design and Data Collection

I estimated rail occupancy by recording vocalizations at each wetland with Wildlife Acoustics SM4 ARUs (Maynard, MA). I sampled each site 12 times during the summer following the robust design (Fig. 1.2) as described by Pollock (1982) and Rota et al. (2009). Primary visits for ARU recordings occurred 2-4 weeks apart from May 15 – Aug. 15. Each ARU primary visit was composed of four 3.5-hour secondary recording sessions spread over approximately 48 hours. I assumed closure to emigration and immigration within each ARU primary period.

I determined effective recording radius of the ARUs by using playbacks to induce Black Rails to vocalize at a known location with three ARUs spaced 25m apart from 25m to 100m. All vocalizations were detectable at a 50m radius and ~75% of vocalizations were detectable at a 75m radius. As a result, I deployed ARUs approximately 100m apart at each wetland to provide coverage of the entire area. To increase detection probability, I placed a Haoponer

B010DHKLAS MP3 speaker by each ARU that was timed to play conspecific recordings twice during each secondary recording session, approximately 0.5 and 1.5 hours after sunrise or 1.5 and 0.5 hours before sunset. Vocalizations were played at ~75-80 decibels measured at a 2m distance.

I identified recorded rail vocalizations to species using Kaleidoscope 4.3.2 (Wildlife Acoustics, Maynard, MA). First, I created a clustering template that focused on rail vocalizations from recordings at three sites with copious rail activity. I then manually identified all clusters with rail vocalizations to train a Kaleidoscope's Hidden Markov Model. Next, I applied the trained model to all 48 sites. I used a maximum distance of one from cluster centers to categorize likely rail vocalizations. I then manually verified each likely rail vocalization to confirm its validity. Common false-positives identified by Kaleidoscope included Northern Mockingbirds (*Mimus polyglottos*) and audio playback from my speaker units in the wetland. I used these recordings to construct a detection/non-detection history for input into occupancy models.

Within one week of each ARU primary period, I performed call-playback surveys using conspecific recordings following the standard protocol used over the past 15 years to survey these metapopulations for occupancy. Briefly, call-playback surveys were conducted every 50m within each wetland until the entire area was covered or a rail was detected. For detailed call-playback methodology, see Richmond et al. (2008, 2010) and Risk et al. (2011). I visited each site three times, or until both species were detected at a site, following the removal method (MacKenzie et al. 2018).

I collected site-level covariates after completing a call-playback survey or deploying ARUs to assess the effect of habitat on detection probability, occupancy estimates, and movement within the breeding season (i.e. colonization and extinction). I calculated wetland area (ha) from aerial imagery as described by Van Schmidt et al. (2019). For each visit, I visually estimated percent wet cover (flowing or standing water or saturated mud; Richmond et al. 2010) and calculated wet area (wetland area * percent wet cover). Due to a high correlation between total wetland area and wet area, I modeled occupancy using only wet area, as it was a more informative parameter. To characterize wetlands, we: (1) categorized wetland geomorphology as being slope, fluvial, or fringe (Brinson and Malvárez 2002, Van Schmidt et al. 2019); (2) identified wetlands with plant cover > 25% of *Juncus* spp. or *Typha* spp., which are preferred by Black and Virginia Rails, respectively; (3) calculated wetland isolation (i.e. the geometric mean distance to the three nearest occupied wetlands; Richmond et al. 2012); (4) recorded whether a site had been grazed within the last year; and (5) determined if a wetland was occupied by rails during call-playback surveys in the previous year. Site-level detection probability (p*) was > 0.95 for all wetlands in the previous year. I also recorded Julian date of surveys, number of ARUs present in each wetland, and whether a survey took place in the morning or evening.

ARU surveys were designed to maximize detection probability and minimize the likelihood of obtaining a false absence at a site during a primary period. At four sites rails were detected during call-playback surveys but not by ARUs. There were four likely sources of this error: false positives during call-playback surveys, incomplete ARU coverage of a wetland, failure to detect recorded vocalizations in Kaleidoscope, and violation of closure in the period between call-playback surveys and ARU surveys. To ensure that detection failures were not due to an error in Kaleidoscope's clustering algorithm, I created naïve clusters using Kaleidscope for each site and listened to each 10-minute segment that corresponded with conspecific recordings being played. For all four sites, I were unable to detect any rail vocalizations in additional analysis of ARU data. After reviewing the data, I censored the playback encounter histories for two sites, but did not have enough evidence to make a conclusion about the other two sites (Appendix S1.1: Table S1.4).

1.3.3 Testing for Closure

I tested for violations of the closure assumption using the likelihood ratio test described in Rota et al. (2009). For each species, I used the encounter history from ARU recordings to implement both a multi-season occupancy model (hereafter: "open model"; MacKenzie et al. 2003) and a single-season occupancy model (hereafter: "closed model"; MacKenzie et al. 2002). Models were implemented using the *colext* (open) and *occu* (closed) functions in the R package *unmarked* (Fiske and Chandler 2011, R Foundation for Statistical Computing 2019). The open model contained three primary periods each composed of four secondary sessions, and the closed model consisted of one season comprising all twelve recording sessions from my three primary visits. To reduce the potential effect of biases introduced in parameter estimates from closure violations, I did not use covariates when estimating detection probability (p) and initial occupancy (ψ). For open models, I estimated colonization (γ) and extinction (ε) between primary surveys, but did not introduce covariates into the model to describe turnover.

1.3.4 Testing Factors Governing Rail Movement

I hypothesized that rail movement between wetlands within the breeding season would reflect (1) prospecting unoccupied sites by adults and juveniles, and (2) abandoning occupied sites where conditions became unfavorable. To quantify these movements, I formulated a set of candidate multi-season occupancy models (MacKenzie et al. 2003) for use with the ARU data set. To assess hypotheses relevant to closure violations, I first modeled initial occupancy and detection probabilities, and then modeled colonization and extinction using stepwise selection. Although stepwise selection has been criticized as a form of data dredging (Whittingham et al. 2006), my model sets were constructed from a limited number of biologically-meaningful covariates and none of the stepwise models progressed beyond two covariates, leading to evaluation of a set composed of simple and biologically-informed models. When modeling initial occupancy and detection probability following MacKenzie et al. (2018, page 209), I parameterized colonization and extinction with slope, wet area, and isolation for both for both rail species based on *a priori* knowledge from past studies (Hall et al. 2018, Van Schmidt et al. 2019). I then performed forward stepwise selection to determine the top-ranked model for both detection and initial occupancy using AIC (Burnham and Anderson 2004). I modeled ψ using wet area and slope following *a priori* knowledge (Van Schmidt et al. 2019), and modeled p using the number of ARUs, Julian date, secondary session, and AM/PM as covariates.

I then evaluate the effect of covariates on γ and ε using the top model for ψ and p, and a forward stepwise selection on turnover parameters. When modeling colonization and extinction, I generally added the same covariates to both parameters because a covariate was expected to act similarly but in opposite directions on the two processes. For example, grazed sites should be less likely to be colonized and more likely to go extinct. There were only two extinction events for Black Rails, which prevented us from building models with more than one extinction covariate to avoid overfitting. For both species, I tested the hypotheses that colonization increased with Julian date or primary period, decreased with isolation, and increased if a site was occupied in the previous year, with opposing effects expected for extinction. Candidate models for the hypothesis that movement was the result of habitat conditions predicted that extinction would decrease with wetland size and that colonization would increase with preferred vegetative cover (*Juncus* for Black Rails and *Typha* for Virginia Rails). For Virginia Rails, I expected colonization would increase with non-slope geomorphologies (Van Schmidt et al. 2019, Van Schmidt and Beissinger 2020).

1.3.5 Effect of Closure Violations on Occupancy Estimates

To determine the effect of closure violations on occupancy estimates for both rails, I compared three model-dataset combinations: closed and open models using ARU data, and a closed model using call-playback surveys. For both closed models, I used forward stepwise selection to identify the effect of covariates on occupancy estimates and detection probability for the top-ranked single-season model using AIC. For the closed ARU model set I used the same covariates described in the open model set above. For the call-playback model, I used log area and Julian date as potential covariates for p, and the same covariates described above for occupancy. I calculated site-level detection probability (p*) for the breeding season as:

$$p^* = 1 - \prod_{i=1}^{k} 1 - p_i$$

where k is the total number of surveys (MacKenzie et al. 2018). I compared 95% confidence intervals of breeding season occupancy estimated using both closed models with derived occupancy estimated using ψ, γ, and ε in the open model (MacKenzie et al. 2003). I then compared the effect of environmental covariates on estimated occupancy across all three models using 95% confidence intervals. To assess the effect of closure violations on detection probability estimates for call-playback surveys, I compared two single-season occupancy models using call-playback data. For one model, I used all detections and non-detections. For the other model, I censored visits to occupied wetlands in which both ARU surveys and call-playback surveys recorded no detection concurrently (i.e. probable absences). Models were parameterized as described for previous call-playback model sets following MacKenzie et al. (2018). I then compared detection probability estimates between the full data set and the data set with probable absences removed using 95% confidence intervals.

1.4 Results

1.4.1 Testing for Closure

The likelihood ratio test found significant violations of the closure assumption for Black Rails (χ^2 = 65.64, df = 2, P < 0.001) and Virginia Rails (χ^2 = 42.07, df = 2, P < 0.001). Ten sites exhibited turnover of Black Rails during the breeding season (21%), with eight sites colonized and two sites abandoned, while 19 sites were occupied in all primary periods (40%) and 18 sites remained unoccupied all summer (39%). I observed turnover by Virginia Rails at 11 sites (23%), with 7 sites colonized and 5 sites abandoned. One site occupied by Virginia Rails was both colonized and abandoned during the breeding season. Twelve sites (25%) remained occupied by Virginia Rails over the entire summer and 25 sites were never occupied (53%).

The top-ranked model for Black Rails included the number of ARUs and Julian date as covariates for detection probability, and wet area of wetland and slope as covariates for initial ψ

(Appendix S1.1: Table S1.5). Detection increased as number of ARUs increased and detection decreased over the breeding season (Appendix S1.1: Fig. S1.1a). Initial occupancy was greater at sites with slope geomorphologies and increased with area (Appendix S1.1: Fig. S1.1b). The top-ranked model for Virginia Rails included secondary session and Julian date as covariates for detection probability and wet area of wetland as a covariate for initial occupancy (Appendix S1.1: Table S1.6). Detection decreased through the primary period and as the breeding season progressed, suggesting Virginia Rails may have acclimated to conspecific vocalizations within each primary survey period (Appendix S1.1: Fig. S1.1c). Initial occupancy of Virginia Rails increased with wet area (Appendix S1.1: Fig. S1.1d). For both species, site-level detection for each primary period was high, with $p^* > 0.999$.

1.4.2 Factors Governing Rail Movement

Both rail species exhibited frequent movement during the breeding season, but they differed in the timing and pattern of movement as well as the factors that influenced turnover. In the top-ranked model for Black Rails, colonization was greater and extinction was lower at sites occupied in previous years (Table 1.1; Figs. 1.4a & 1.4b). Black Rails were more likely to colonize wetlands than abandon them and, as a result, occupancy increased during the breeding season (Fig. 1.5a). In the top-ranked model for Virginia Rails, colonization was greatest at large sites, whereas extinction was highest at small sites (Table 1.1; Figs. 1.4c & 1.4d). Given the habitat characteristics of this metapopulation, Virginia Rail colonization and extinction were nearly identical, leading to stable occupancy estimates throughout the breeding season (Fig. 1.5b). The relative frequency of different encounter histories differed between rail species. Whereas detections of Black Rails at sites most frequently occurred in all three primary periods and occurred infrequently in only one primary period, Virginia Rails were most commonly detected in one or three primary periods and were least detected in two periods (Fig. 1.6).

Table 1.1. AIC results of occupancy models explaining variation in colonization (γ) and extinction (ε) for Black and Virginia rails. AIC: Akaike's information criterion; ΔAIC: change in AIC; *k*: number of modeled parameters; AIC Wt: Akaike weight.

Species	γ	ε	*k*	AIC	Δ AIC	AIC Wt
Black Rail	Previous BLRA	Previous BLRA	10	277.16	0	0.37
	Previous BLRA + Primary Period	Previous BLRA	11	277.89	0.73	0.26
	Previous BLRA + Isolation	Previous BLRA	11	278.15	0.99	0.23
	Isolation	Isolation	10	281.56	4.4	0.04
	Primary Period	Primary Period	10	281.7	4.54	0.04
	Null	Null	8	282.62	5.46	0.02
	Slope	Slope	10	284.5	7.34	0.01

	Isolation	Wet Area	10	284.62	7.45	0.01
	Julian Date	Julian Date	10	284.62	7.45	0.01
	Wet Area	Wet Area	10	284.92	7.76	0.01
	Juncus	Juncus	10	285.43	8.27	0.01
	Grazing	Grazing	10	285.67	8.51	0.01
Virginia Rail	Wet Area	Wet Area	11	250.13	0	0.27
	Wet Area + Previous VIRA	Wet Area + Previous VIRA	13	250.29	0.16	0.25
	Wet Area + Slope	Wet Area + Slope	13	251.34	1.21	0.15
	Wet Area + Isolation	Wet Area + Isolation	13	251.44	1.31	0.14
	Isolation	Wet Area	11	251.58	1.45	0.13
	Wet Area + Typha	Wet Area + Typha	13	252.97	2.84	0.06
	Typha	Typha	11	259.51	9.38	0
	Previous VIRA	Previous VIRA	11	266.37	16.24	0
	Slope	Slope	11	266.65	16.51	0
	Isolation	Isolation	11	266.8	16.67	0
	Null	Null	9	268.45	18.32	0
	Primary Period	Primary Period	11	270.91	20.77	0
	Grazing	Grazing	11	271.48	21.35	0
	Julian Date	Julian Date	11	271.75	21.62	0

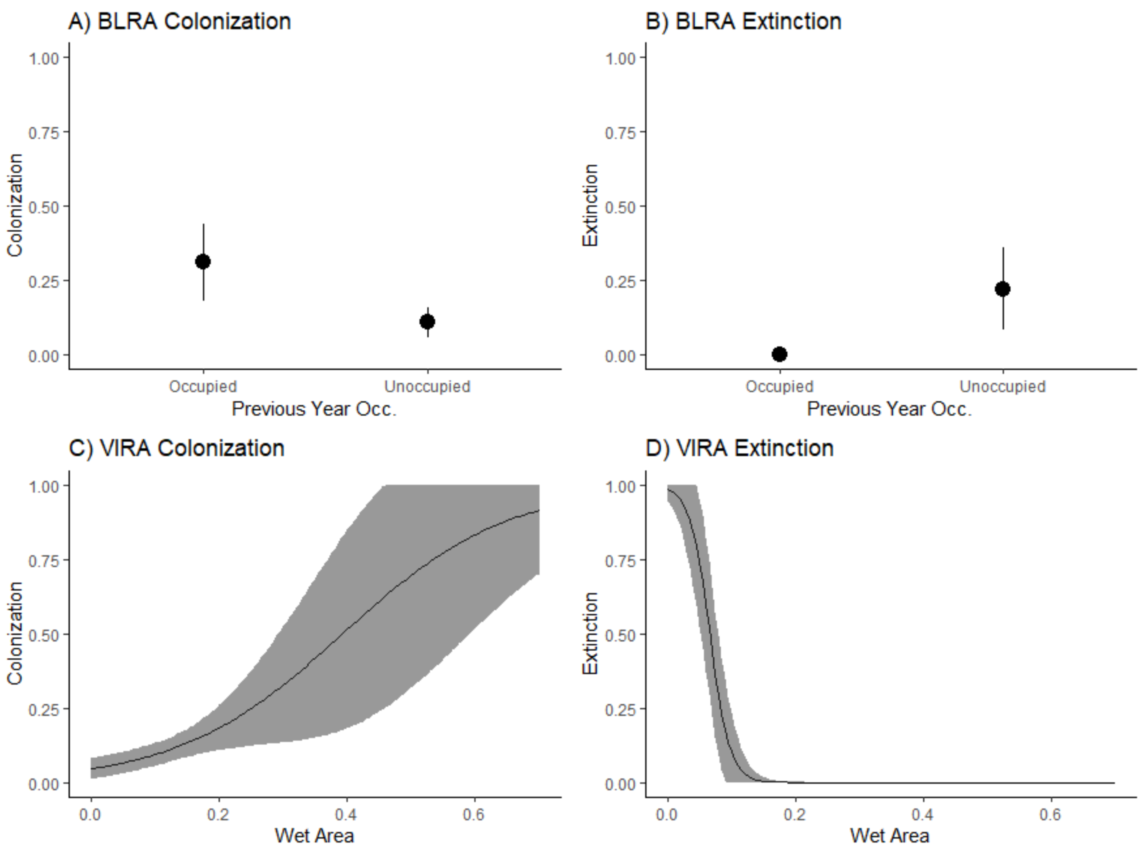


Figure 1.4. Black Rail (**A**) colonization and (**B**) extinction probabilities as a function of occupancy in the previous year, and Virginia Rail (**C**) colonization and (**D**) extinction probabilities as a function of wet area (± 1 SE, truncated at 0 and 1).

1.4.3 Effects of Closure Violations on Rail Occupancy Estimates

Black Rail occupancy estimates were similar for both closed and open ARU datasets (Fig. 1.5a). Although Black Rails colonized more sites than they abandoned, I did not observe a significant increase in occupancy estimates between the first visit and the last visit during the full survey period (Fig. 1.5a). Occupancy estimates were also similar between call-playback surveys and both the open and closed ARU models for Black Rails (Fig. 1.5a). Call-playback surveys detected Black Rails at every site where they were detected by ARUs. In contrast, ARUs did not detect Black Rails at one site where they were detected by call-playback surveys (S Appendix S1.1: Table S1.4). Call-playback surveys recorded 16 non-detections during visits to occupied wetlands, which are considered to be false absences in occupancy modeling. Of those 16 non-detections, 10 coincided with ARU non-detections, indicating these wetlands were likely unoccupied. Censoring probable absences from the call-playback dataset increased modeled detection probability per visit by 0.13 (Censored $\bar{x} = 0.86 \pm 0.05$, Uncensored $\bar{x} = 0.73 \pm 0.06$). Nevertheless, p^* was > 0.95 for both censored and uncensored datasets.

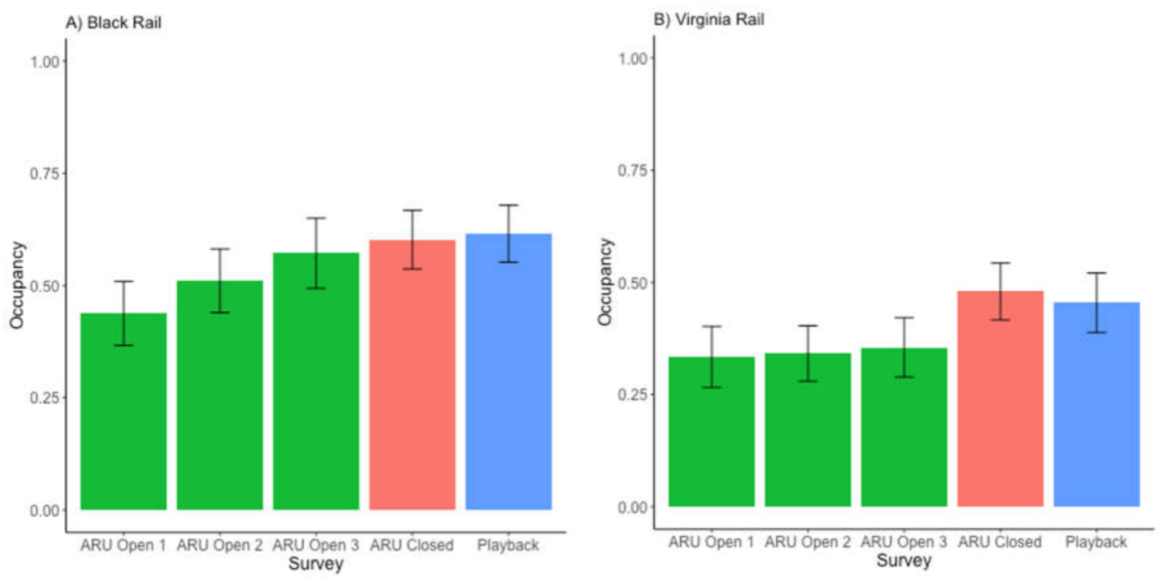


Figure 1.5. Occupancy (± SE) of **A**) Black Rails and **B**) Virginia Rails using ARU detections with an open model (green) or closed model (red) or call-playback detections with a single season model (blue).

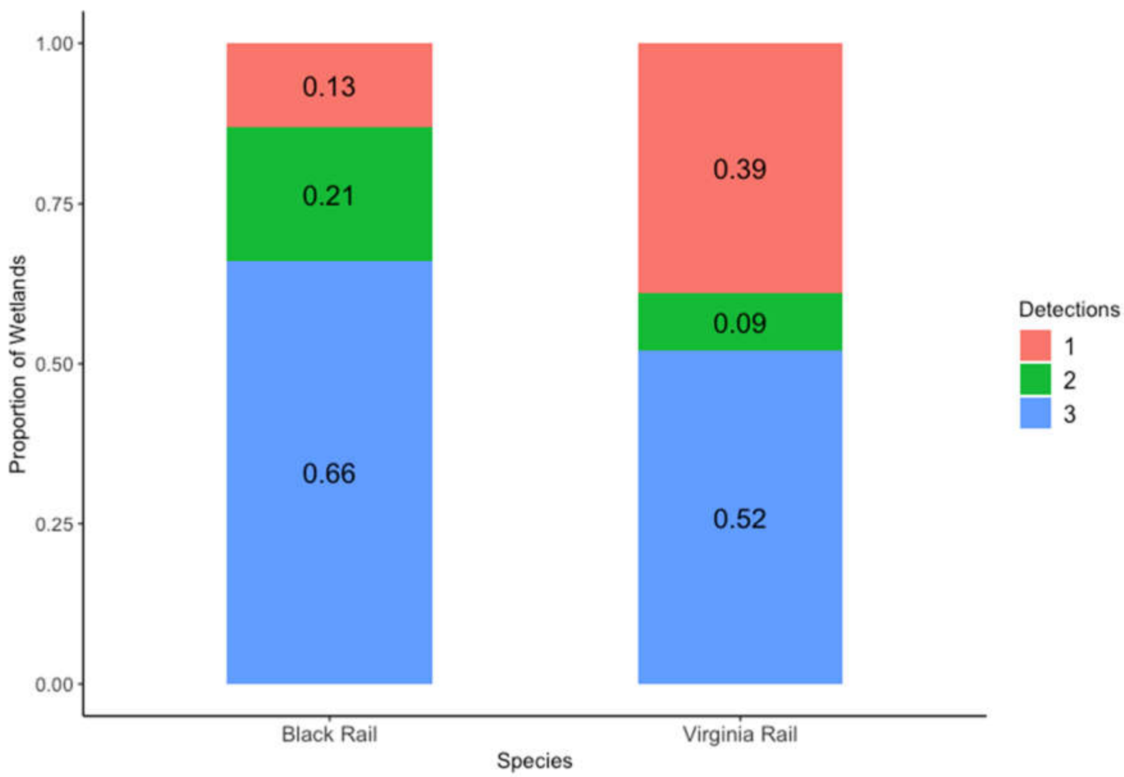


Figure 1.6. Proportion of occupied wetlands with detections in 1, 2, or 3 primary periods for Black and Virginia rails.

Virginia Rail occupancy estimates were similar between call-playback data and ARU datasets as well as between secondary periods using ARU data (Fig. 1.5b). Call-playback surveys failed to detect Virginia Rails at two sites where they were detected by ARUs. ARUs failed to detect Virginia Rails at one site where they were detected during call-playback surveys (Appendix S1.1: Table S1.4). Call-playback surveys recorded 18 non-detections at occupied wetlands based on ARU detections. Of those 18 non-detections, 14 coincided with ARU non-detections. Censoring probable absences from the dataset increased detection probability by 0.16 at mean wetland area (Censored $\bar{x} = 0.91 \pm 0.05$, Uncensored $\bar{x} = 0.75 \pm 0.09$). Although detection probability varied by wetland area, p^* was > 0.95 for all wetlands in the censored dataset and at wetlands > 0.55 ha in the uncensored dataset.

1.5 Discussion

1.5.1 Closure Violations and Effects on Occupancy

Occupancy models are a commonly used tool for monitoring wildlife, but their utility can be reduced by violations of the closure assumption (Rota et al. 2009). I assessed closure violations for patches in metapopulations of two species of secretive rails. Not only was there substantial turnover at sites during a period of the breeding season when they were assumed to be closed, but those closure violations were indications of biological processes that could have implications for how wetlands are evaluated and conserved. Nevertheless, the violations of closure had little effect on overall estimates of estimates for Black and Virginia rails. My results provide the first assessment of the effect of closure violations on metapopulation occupancy estimates, and offer a contrast to previous studies of closure that noted the potent for larger effects on point-level measures of occupancy (Rota et al. 2009, Otto et al. 2013, Valente et al. 2017). Closure violations reduce estimates of the probability of detection (p), which correspondingly inflate estimates of ψ (Rota et al. 2009). In my study the probability of detection was high for both species, which reduced the effect of closure violations.

There are several methods for addressing closure violations, and no method is applicable for all study systems (MacKenzie et al. 2018). The magnitude of bias caused by closure violations can be reduced through modeling approaches (Kendall et al. 2013, Otto et al. 2013), or by designing a study to account for the potential of closure violations (Rota et al. 2009). For example, after obtaining an initial estimate of detection probability, studies can be designed to attain a $p^* >$ 0.95, which will greatly reduce the effect of closure on occupancy estimates. However, if a study organism exhibits extensive and permanent emigration during a survey period, it may difficult to attain a $p^* > 0.95$. Another common method is to adjust the duration of sampling period to minimize closure violations (Rota et al. 2009, Valente et al. 2017, MacKenzie et al. 2018). However, designing a study with a short temporal duration reduces the inferences that can be made from a study (MacKenzie et al. 2018). Although closure violations are often the result of temporal processes, they can also be caused when the survey unit is smaller than the ecological scale of interest (Valente et al. 2017). Metapopulation studies that make inference at a patch scale are less likely to suffer from the effects of temporary immigration and emigration than small-scale studies, such as unaggregated point counts. In that case, survey data from several points could be consolidated to produce a scale where closure violations are less impactful. Nevertheless, the biology of the study species and the nature of the research questions should be primary considerations when designing a sampling protocol (MacKenzie et al. 2018).

1.5.2 Closure, Movement, and the Meaning of Occupancy

Closure violations are often considered to be a nuisance when estimating occupancy, yet they can yield novel insights into animal movements that have implications for population dynamics, complex habitat requirements across multiple life stages, and conservation strategies. Generally, closure violations indicate something about animal movement in relation to a survey location. The movement can either be temporary (Valente et al. 2017), or reflect colonization or local extinction events between surveys (Rota et al. 2009). Temporary immigration and emigration may be evidence of habitat use and territory size larger than expected for a species (e.g., Streby et al. 2012), or indicative of certain behaviors, such as extra-pair copulations (Petrie and Kempenaers 1998) or foraging outside of a territory (Evens et al. 2018). Colonization or local extinction can indicate a long-term change in habitat use, as individuals transition to different phases of the annual cycle (e.g., Peterson et al. 2016) or respond to changing habitat conditions. Closure violations may also be evidence of demographic changes, such as when independent juveniles move to new habitat (Anders et al. 1998, Streby et al. 2015).

There was no unifying characteristic responsible for closure violations in Black and Virginia rails despite their ecological similarities. Black Rails were more likely to colonize wetlands during the breeding season than to abandon them, and neither colonization nor extinction was related to measured environmental factors. Rather, Black Rail colonization was associated with wetlands that had been occupied during the previous survey year, and extinction was associated with wetlands that had not been occupied in the previous year. This may indicate that conditions at some sites typically improve during the breeding season and attract dispersing individuals, individuals may return to sites they had previously occupied, or birds assess habitat based on characteristics I did not quantify. Black Rails returning to previously occupied wetlands could be evidence of several different behaviors, including assessing territories for future breeding seasons (Hanski 1998, Bonte et al. 2012), establishing winter occupancy (Van Schmidt and Beissinger 2020), molting (Robert and Laporte 1999), or foraging in nearby patches. In contrast to Black Rails, Virginia Rails were much more sensitive to habitat quality, and exhibited nearly identical colonization and extinction rates. Nearly 40% of surveyed wetlands occupied by Virginia Rails during the breeding season in the Sierra Nevada Foothills were occupied during only one primary survey period. Wetlands experiencing extinction were smaller than wetlands that were continuously occupied. It is likely that only the continually occupied wetlands were used for breeding by Virginia Rails and that wetlands exhibiting turnover were used for a different purpose, such as non-breeding territories or temporary refugia.

Occupancy models can address many ecological questions, including species abundance, habitat relationships and metapopulation dynamics (MacKenzie et al. 2018), and the meaning of site occupancy can differ for each of those applications (Latif et al. 2016). Many studies define occupancy as the proportion of habitat used during a time period of interest (e.g., the breeding season; MacKenzie et al. 2017; McFarland et al. 2012; Wiest and Shriver, 2016), giving equal weight to all occupied sites when estimating the effect of covariates on parameters (MacKenzie et al. 2018). In an open system, however, sites may be occupied for different lengths of time and used for different purposes (Betts et al. 2008, Rota et al. 2009, Latif et al. 2016, Arbeiter et al. 2018). For Black and Virginia rails, closure violations were apparently the result of wetlands being used for different purposes during the breeding season, and provide a more complete understanding of the variation through time of habitat needs of these species.

1.5.3 Conservation and Management Implications

Occupancy models are commonly used to inform management plans and monitor populations (MacKenzie and Reardon 2013, MacKenzie et al. 2018), but failure to account for closure violations can cast doubt on the efficacy of conservation strategies (Ganey et al. 2017, Berigan et al. 2019, Jones et al. 2020). Without confidence in the effectiveness of monitoring programs, it could be difficult to detect population changes or differences in occupancy patterns. For example, Berigan et al. (2019) found that there may have been a 20% error in occupancy estimation due to animal movements, which would substantially change management plans. Movement is a dangerous for most animals because it is elevates mortality risk (Belichon et al. 1996), highlighting the importance of recognizing closure violations and their associated behaviors for conservation and management. Rota et al. (2009) wrote that occupancy models used for conservation and management should be designed specifically to account for closure violations, especially for rare or declining species (Stauffer et al. 2004). To ensure confidence in measures of occupancy, it may be worth performing an exploratory study of managed populations to identify the potential effects of closure violations, even if they are not monitored long-term. These closure estimates could be performed using acoustic monitoring (Darras et al. 2019), camera traps (Burton et al. 2015) or other methods of supplemental data collection that do not infringe on long-term data collection protocols.

Our study suggests that Black Rails appear to use different patches during the breeding season in the Sierra foothills and further study is needed to fully understand the management implications of these movements. If Black Rails use memory to inform their choice of wetlands to colonize, managing and monitoring previously occupied sites may be more beneficial than creating new ones (Fagan et al. 2013, Doherty and Driscoll 2017). However, if previously used sites correlated with a previously unmeasured habitat characteristic, creating new habitat with that unknown habitat characteristic in mind would be productive as well. Monitoring activities should be performed across the entire breeding season to characterize the spectrum of wetlands used. Recently Black Rails were listed under the Endangered Species Act as “threatened” in the eastern, southern and midwestern United States. There is substantial variation in habitat requirements of Black Rails across its range (Eddleman et al. 1994). Nevertheless, biologically important movements that violate the closure assumption and indicate complex habitat requirements are likely to occur in other populations.

Virginia Rails are more common than Black Rails and less likely to require management, but relatively little is known about their biology. Conservation of this species would benefit from a greater understanding of its movements within breeding-seasons. In my study area, wetlands used continuously by Virginia Rails were larger than sites that were used transiently. Management of mobile species can be difficult, as multiple habitat requirements need to be considered. By analyzing occupancy in a framework that accounts for closure violations and describes its causes, managers can better understand the movements that drive turnover and how habitat requirements change over time.

Chapter 2: Spillover of species from matrix to wetland habitats diversifies avian assemblages on a semi-arid landscape

2.1 Abstract

On complex landscapes with distinct habitat patches, spillover effects occur when material, energy, or organisms move between habitats. Habitat patches can have spillover of generalist species that may interact with species specializing in the focal habitat. I studied spillover effects on avian assemblages associated with wetlands in the Sierra Nevada foothills, California, USA, which was broadly comprised of wetland obligates that nested and foraged almost entirely within wetlands, and two groups of spillover species: (1) facultative species that used wetlands for nesting and foraging, but not exclusively; and (2) matrix species that specialized in non-wetland habitat, but used wetlands on an *ad hoc* basis. I employed automated recording units at 98 wetlands to survey birds and detected 74 species, 19 of which were wetland obligates (26%). I used a multispecies occupancy model to assess the importance of intrinsic wetland patch characteristics and extrinsic landscape characteristics surrounding the patch on the assemblage, each group and individual species. I found a strong effect of water source on wetland obligate and facultative species, as well as a spillover effect on matrix species. I also observed an effect on wetland obligates from landscape composition, suggesting that not only is the habitat matrix important for the species using it, but also for wetland obligates isolated by it. I observed significant turnover between wetlands based on site characteristics, with turnover being highest for wetland obligates. Assemblages differed the most between impoundments and other wetland geomorphologies and turnover increased as differences between wetlands in landscape composition and geophysical characteristics increased. I identified two diversity hotspots in my study area: one on private property managed for hunting that was important habitat for all species and another on public land that was primarily important for wetland obligates. My results demonstrate the importance not only of wetland characteristics on spillover species and biodiversity but also the effect of landscape composition on habitat specialists isolated by matrix cover types.

2.2 Introduction

Habitat spillover effects are defined as the movement of material, energy, and organisms between habitat patches (Blitzer et al. 2012, Tscharntke et al. 2012, Boesing et al. 2018a). Ecological spillover can affect plant and animal abundance, ecosystem functions, and trophic dynamics (McCoy et al. 2009, Blitzer et al. 2012, Tscharntke et al. 2012). On complex landscapes, species may use multiple habitat types, and the characteristics of one habitat patch can affect species' occupancy and use of different, nearby habitats (Boesing et al. 2018b, Barros et al. 2019). Spillover effects are frequently bi-directional, with matrix habitats affecting occupancy within habitat patches and vice versa (Lucey and Hill 2012, Frost et al. 2015, Schneider et al. 2016). Due to the importance of ecosystem services for humans provided by natural landscape patches, research on habitat spillover effects has frequently quantified the relationship between natural and human-modified and -used habitats (Bianchi et al. 2006, Ricketts et al. 2008, Blitzer et al. 2012, Tscharntke et al. 2012). Relatively little research has investigated spillover occurring between natural habitat patches (Soykan and Sabo 2009, Tscharntke et al. 2012, Schneider et al. 2016). Understanding spillover effects on a landscape with multiple habitat types can provide insights into biodiversity patterns, including how occupancy of habitat patches is affected by landscape characteristics across an assemblage of species.

The mechanisms that determine how different habitats effect one another are not well understood (Tscharntke et al. 2012). Energy and nutrients can move between habitat types through both physical and biological processes, including flow of nutrients across the landscape as well as organismal movement (Cadenasso et al. 2003). Spillover can affect animal assemblages even between habitats with relatively low permeability, such as marine and terrestrial ecosystems (Polis et al. 1997). The movement of animals between habitats can also significantly affect trophic relationships within assemblages, even between spatially distinct ecosystems (McCoy et al. 2009, Blitzer et al. 2012). It has been hypothesized that the strength of the spillover of species is related to differences in primary productivity between habitat types, with more spillover from higher productivity habitats to lower productivity habitats than vice-versa (Frost et al. 2015). Spillover might be an especially important aspect of assemblages in rare habitats in complex landscapes with substantial variation between habitat patches and matrix habitat, where even small habitat patches can be important for maintaining biodiversity (Tscharntke et al. 2012, Wintle et al. 2019).

I studied spillover effects in the composition of avian assemblages of wetlands in the seasonally-arid foothills of the Sierra Nevada of California, USA. Wetlands worldwide are primarily unprotected (Reis et al. 2017) and sensitive to environmental change, including changes in water supply, pollution, and precipitation (Poiani et al. 1995, Sha et al. 2010). Wetlands are one of the highest-productivity habitat types in the world, contrasting with the lower-productivity matrix habitats of the Sierra Nevada foothills (Leith and Whittaker 2012). The wetlands in my study system host bird species that I delineated into three broad categories based on their habitat affinities: wetland obligates that nest and forage almost exclusively within wetlands; and two spillover groups, (1) facultative species that nest and forage opportunistically within wetlands but also in the nearby matrix habitats; and (2) matrix species that use matrix habitats for most of their needs, may be associated with transitional habitat between wetlands and uplands, and use wetlands on an *ad hoc* basis primarily for foraging. The majority of wetland obligate species forage in water or wet mud, whereas facultative and matrix species are more likely to forage in the vegetation or air above the water.

I used automated recording units (ARUs) to assess avian occurrence in wetlands. I related measures of occupancy and species richness to intrinsic wetland characteristics (vegetation, geomorphology, water source, and geophysical conditions) as well as matrix characteristics of the surrounding landscape (forest, open, wetland, and developed cover) at two scales. I predicted that the occurrence of wetland obligates would be primarily dependent on intrinsic characteristics of wetlands (vegetation, geomorphology, area, and elevation). In contrast, I predicted that spillover species would be primarily affected by landscape composition. I predicted that if I observed any effect of wetland characteristics on spillover species, it would likely be present in facultative species, rather than matrix species. I predicted that spillover of non-obligate species would be greater in irrigated wetlands that remain wet all summer and are more productive than natural wetlands that may dry out (Van Schmidt et al. 2021). I also assessed assemblage turnover (β-diversity) across wetland sites with Jaccard similarity and predicted turnover would be greater: (1) in wetland obligates than other groups because they would be more sensitive to key wetland characteristics; (2) between sites with dissimilar landscape characteristics, (3) between sites with substantially different geomorphologies and water flows; and (4) between sites that were exclusively irrigated and those that were exclusively natural. In addition, I produced estimates of species richness for wetland obligate, facultative and matrix species within a spatial context to better understand what areas are most important for conservation.

2.3 Methods

2.3.1 Study Area

I sampled the bird assemblages of 98 small ($\bar{x}$ = 0.83 ha) wetlands in the Sierra Nevada foothills of California that ranged from 36 m to 576 m in elevation (Fig. 2.1). Wetlands in the Sierra Nevada foothills are relatively widely dispersed in a matrix of natural oak savannah and grazed pastureland with sparse human development (Richmond et al. 2010a, Van Schmidt et al. 2019). Human activity around wetlands varies from minimal on state-managed wildlife areas, to high on ranches or suburban areas. The region is seasonally-arid, receiving only trace amounts of rainfall in summer between May and October (Richmond et al. 2010a, Van Schmidt et al. 2019), when small wetlands become susceptible to drying and land conversion in other Mediterranean climates (Gallego-Fernández et al. 1999, Brinson and Malvárez 2002). Wetlands were fed by natural water sources only, by irrigation water only, or by both water sources (Van Schmidt et al. 2019). Natural wetlands are most commonly sourced by springs, creeks, or groundwater, while irrigated wetlands are created by irrigation ditches or are the result of runoff from ranching or farming activities.

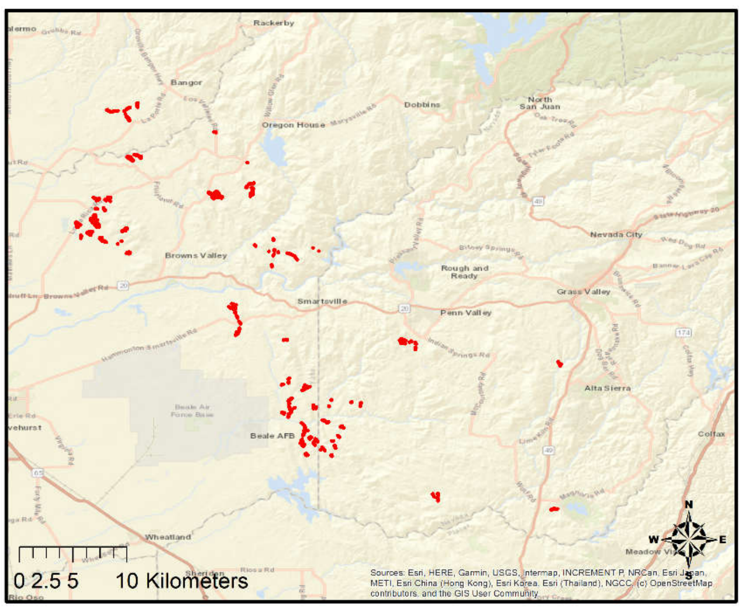


Figure 2.1. Distribution of surveyed wetlands in the Sierra Nevada foothills, California, USA.

Wetlands fed solely by irrigation water can change condition dramatically through the summer as water is turned off and on (Risk et al. 2011, Van Schmidt et al. 2021). Wetlands are often shallow (< 3cm) and are dominated primarily by *Juncus* spp. and *Typha* spp. Secondary vegetation in and immediately surrounding the wetland include *Schoenoplectus* spp., *Salix* spp., sedges, grasses, and invasive Himalayan blackberry (*Rubus armeniacus*). For a detailed description of study area and the plant composition of these wetlands, see Richmond et al. (2010).

2.3.2 Data Collection

I deployed SM4 Song Meters (Wildlife Acoustics, Maynard, Massachusetts, USA) between May 15 and July 15 at 39 wetlands in 2017 and 59 wetlands in 2018. Each ARU recorded three 5-minute sessions per day, 30 minutes prior to sunrise, at sunrise, and 30 minutes after sunrise. This sampling regime simulated a protocol of a 50-m fixed-radius point count at each site, which is commonly used by the California Department of Fish and Wildlife for monitoring avian diversity across California (Furnas and Callas 2015, Furnas and McGrann 2018). Recording sessions lasted for two consecutive days (six total recordings) in 2017 and three consecutive days (nine total recordings) in 2018. At all wetlands, I randomly placed ARUs > 25m from the edge of the wetland (if possible), or near the center of the wetland if wetland diameter was < 50m. I manually identified vocalizations using audio and spectrograms viewed using Audacity (version 2.3.2, Audacity Team).

I characterized wetland habitat at each site using the criteria described in Richmond et al. (2010) and Van Schmidt et al. (2019). Briefly, I determined if a site had a natural water source, man-made source, or both water sources by following water flow on the ground and identifying springs using aerial imagery collected prior to the 1950s. Structurally, I categorized wetlands as slopes (gently sloping and flowing, non-channelized), fringes (still water on edge of pond), fluvial (wetlands in flowing water on the edge of a creek or stream), and impoundments (man-made wetlands of still water surrounded by a berm; Brinson and Malvárez 2002). I assessed other habitat characteristics by identifying wetlands with > 25% cover of *Juncus* spp. or *Typha* spp., estimated percent wet ground cover within each wetland, and calculated wetland area from digital imagery (Van Schmidt et al. 2019). To estimate landscape composition, I used two datasets, the 30-m resolution 2011 National Land Cover Dataset (NLCD; Homer et al. 2011) and the 1-m resolution Sierra Foothills Emergent Wetland dataset (Van Schmidt et al. 2019), which had ground-truthed locations of rice fields, open water, and emergent wetlands. Where the datasets overlapped, I censored the NLCD data in favor of the ground-truthed wetland dataset. I categorized 30m^2 pixels as wetland (NVS wetland dataset, NLCD open water, woody wetlands, emergent herbaceous wetlands classes), forest (NLCD deciduous, evergreen, and mixed forest classes), developed (NLCD developed open space and low, medium, and high intensity classes), and open (NLCD barren land, shrub/scrub, grassland/herbaceous, and pasture/hay classes). For each wetland, I characterized the surrounding landscape at two scales that could be biologically relevant to species with differing space use patterns by calculating the percentage of each of these categories present within 100m and 500m buffers around each wetland.

2.3.3 Data Analysis

I pooled ARU detections across all samples and species to fit a Bayesian multispecies occupancy model (MSOM) to examine patterns of occupancy and species richness while accounting for imperfect detection (Dorazio and Royle 2005, Zipkin et al. 2009, Iknayan et al. 2014). MSOMs increase the power of inference for the data collected for an assemblage by fitting a hyperparameter that increases the precision of coefficient estimates for each covariate, which facilitates modeling species that are rarely encountered (Dewan and Zipkin 2010, Iknayan et al. 2014). For each habitat characteristic assessed, I fit a hyperparameter that estimated the impact of that characteristic across the entire bird metacommunity.

I modeled occupancy for each species (i) at each site (j) as:

$$\text{logit}(\psi_i) = \beta_{0,i} + \beta_{1,i} * \text{juncus}_j + ... + \beta_{20,i} * \text{wetland500}_j$$

where $\beta_{0,i}$ ... $\beta_{20,i}$ are model coefficients for occupancy. I included Julian date as an explanatory covariate for detection probability (p), because the frequency of singing by birds – which was the only way they were detected in this study – often changes during the breeding season (Wilson and Bart 1985). I modeled detection probability for each species (i) and visit (j) as:

$$\text{logit}(p_i) = \alpha_{0,i} + \alpha_{1,i} * \text{julian}_j$$

I centered and scaled all continuous variables by 2*SD to improve comparability with binary variables (Gelman 2008).

To fit the MSOM, I used a Markov chain Monte Carlo algorithm (Link et al. 2002) implemented in JAGS (version 4.3.0) using the package 'jagsUI' for R (Kellner 2019, R Development Core Team 2020). I used uninformative priors for all models and ran three independent chains. I iterated 500,000 samples, with a burn-in period of 10,000 and a thinning rate of three. I considered the model to be converged if the R-hat value was < 1.1 (Gelman et al. 2013). I present 95% credible intervals for all parameters to assess significance. The MSOM estimated parameter coefficients for 1,875 parameters, of which 1,843 had an effective sample size > 10,000. I calculated estimates of species richness and assemblage similarity using 10,000 draws from the posterior distribution of detections for each site. I calculated species richness (N) at each site (j) as:

$$N_j = \sum_{i=1}^{n} z_{i,j}$$

where $z_{i,j}$ is the model-estimated matrix of true occurrence for each species at a site (Dorazio and Royle 2005) and n is the number of potential species (74). I calculated similarity in assemblage composition (J) between two sites (a and b) using the Jaccard index (Real and Vargas 1996) as:

$$J_{a,b} = \frac{N_{a,b}}{A+B-N_{a,b}}$$

where $N_{a,b}$ is the number of species occupying both sites, A is the number of species occupying site a, and B is the number of species occupying site b. I performed this calculation for each pair of sites, yielding 4,753 unique site pairs. I then related Jaccard similarity to differences in habitat characteristics between sites. For continuous habitat characteristics (area, elevation, % wet, and landscape characteristics), I estimated a mean linear model with 95% credible intervals using 10,000 linear models estimated from draws from the posterior. For each draw, I created a linear model using the function "lm" in R (R Development Core Team 2020). I then calculated 95% credible intervals of modeled similarity using the "percentile" function at 200 points between the minimum and maximum observed values for each continuous variable. I considered linear models with 95% credible intervals not overlapping a slope of 0 to be significant. I related Jaccard similarity to categorical variables by estimating 95% credible intervals for mean Jaccard similarity for all sites within that category. I considered any overlapping credible intervals for categorical sites to be not significantly different. To determine the effect of parameters on occupancy and species richness within each group (wetland obligates and facultative and matrix species), I estimated mean parameter effects, 95% credible intervals, and mean occupancy using 10,000 draws from the model parameter estimates for each species within each group.

To illustrate the effect of landscape composition on species richness, I simulated occupancy at hypothetical landscapes comprised of varying amounts of the two primary landscape matrix parameters: forest and open. I simulated all possible combinations of these two landscape parameters ranging from all forest to all open, with all other model parameters held at their mean value, or zero in the case of binomial parameters. For each combination of % forest and % open, I estimated species richness using 10,000 simulations. I assessed the spatial distribution of species richness across the landscape using 130 additional wetlands within the study area that did not have ARUs deployed at them, but for which I collected all habitat covariates (228 total wetlands). I estimated mean species richness using estimated occupancy from 10,000 simulations for each species at each wetland. For each wetland, I also calculated the proportion that wetland obligate species comprised of the entire avian assemblage. I delineated species richness and obligate proportion contours using the 'kriging' and 'contour' tools in ArcGIS 10.7.1. I created a surface for each measure using the 12 wetlands closest to each square meter pixel using ordinary kriging and a spherical semivariogram.

2.4 Results

2.4.1 Detection Probability and MSOM Results

I detected 74 bird species at 98 sites in the Sierra Nevada foothills (Appendix S2.1: Table S2.1). Nineteen species (26%) were wetland obligates, 25 were facultative species (34%), and the remaining 30 were matrix species (41%; Appendix S2.1: Table S2.1). Five species had a listing status in California, of which four were wetland obligates (Appendix S2.1: Table S2.1). MSOM coefficient estimates for all parameters and all species are located in Table S2.2. The mean detection probability across all species was 0.17 per 5-min recording (95% CI: 0.04 – 0.28; Table S3). Detection probability decreased with Julian date for 12 species and increased for 7 species (Appendix S2.1: Table S2.2). Detection did not significantly differ among groups, although wetland obligates were, on average, slightly more detectable ($\bar{x}$ = 0.21, 95% CI: 0.05 – 0.33) than facultative ($\bar{x}$ = 0.17, 95% CI: 0.04 – 0.26) or matrix species ($\bar{x}$ = 0.15, 95% CI: 0.05 – 0.26; Appendix S2.1: Table S2.3). The site-level detection rate (P*) > 0.9 for nine visits (Appendix S2.1: Table S2.3) in 22 of 74 species (30%).

2.4.2 Occupancy

Assemblage composition was most influenced by water source and matrix composition around each wetland. Hyperparameter estimates were significant for all water source parameters (natural, irrigated, and natural + irrigated) but did not differ among avian species groups (Fig. 2.2). Occupancy of 18 species was significant negatively related to one or more water sources (Appendix S2.1: Table S2.2; Fig. 2.2). Occupancy was positively related to forest and open habitats surrounding wetlands at the 500m scales and was negatively related at the 100m scale (Fig. 2.2). Occupancy of 34 species was significantly affected by forest or open habitats surrounding wetlands at either scale (Appendix S2.1: Table S2.1; Fig. 2.2). Assemblage effects were significant or nearly significant for all bird groups, which did not differ from one another (Fig. 2.2). However, wetland obligates responded to several other patch attributes that did not affect occupancy of non-obligates. Occupancy was significantly lower for wetland obligates at sites that had flowing water (fluvial or slope geomorphologies), were smaller, and were located at higher elevations (Fig. 2.2). Occupancy of all groups was unaffected by dominant wetland vegetation in patches and by the proportion of matrix habitats surrounding patches that were developed or wetlands at both scales (Fig. 2.2).

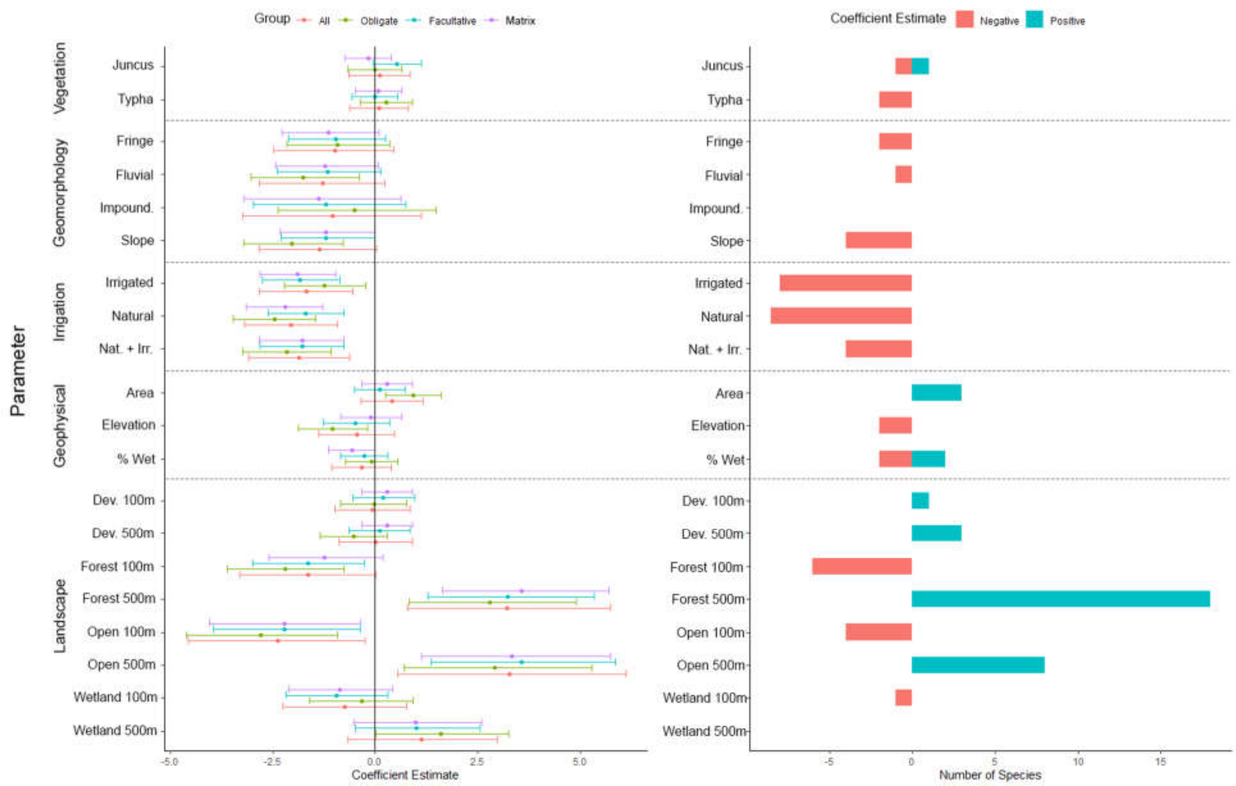


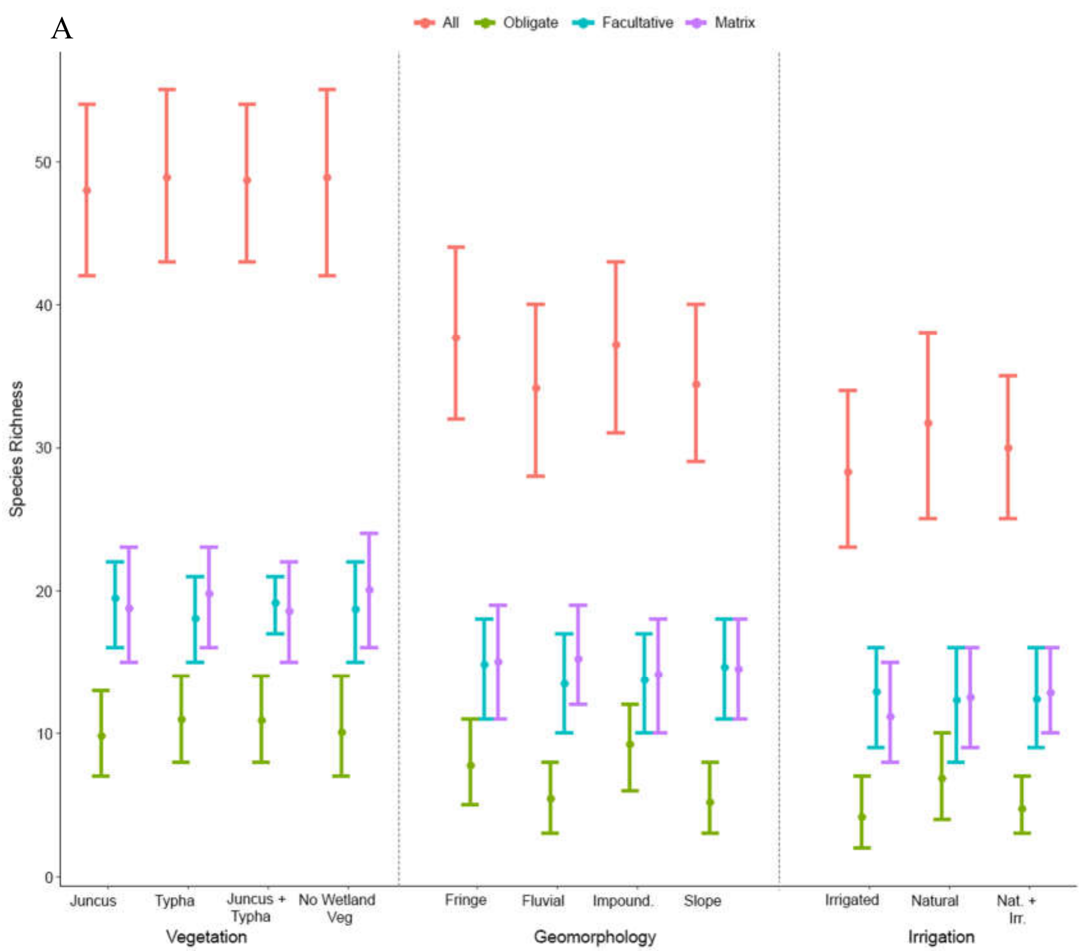
Figure 2.2. Coefficient estimates for multispecies occupancy model hyperparameters for each species group and number of significant species-level coefficient estimates for each parameter with negative effects in red and positive effects in teal.

2.4.3 Species Richness

Species richness for both wetland obligates and non-obligate species was influenced by landscape composition, whereas intrinsic site characteristics only influenced species richness for wetland obligates and facultative species. Species richness did not differ significantly among sites due to wetland vegetation, geomorphology, water source, or the percent wetness – a pattern that held for wetland obligate and non-obligate species (Figs. 2.3a,b). However, species richness was positively related to wetland size for wetland obligates but not for spillover species, and was significantly lower at higher elevations, a pattern driven by wetland obligate and facultative species (Fig. 2.3b). Landscape composition had varying effects, but they were similar for wetland obligate and spillover species (Fig. 2.3c). Development had no significant effect on species richness at either scale (Fig. 2.3c). Forest, open, and to a lesser extent, wetland landscape coverage exerted opposing effects on species richness at different scales; there was a negative relationship between species richness and percent coverage at the 100m scale, and a positive relationship at the 500m scale (Fig. 2.3c). The effects of the two most common matrix habitats (forest and open) were stronger at the 500m scale than at the 100m scale.

For a hypothetical landscape with equal proportions of landscape composition at 100m and 500m scales, species richness at wetlands increased as the percent of forest or open matrix habitat increased (Fig. 2.4). The effect occurred across obligate and spillover species, although it was weaker for wetland obligates (Fig. 2.4). For the entire avian community as well as for matrix species, landscapes with dominant forest, open, or mixed habitats exhibited similar species richness (Figs. 2.4a & 2.4d). However, species richness was highest for wetland obligates in a landscape with more forest (Fig. 2.4b), and it was highest for facultative species on a landscape with more open habitat (Fig. 2.4c).

A



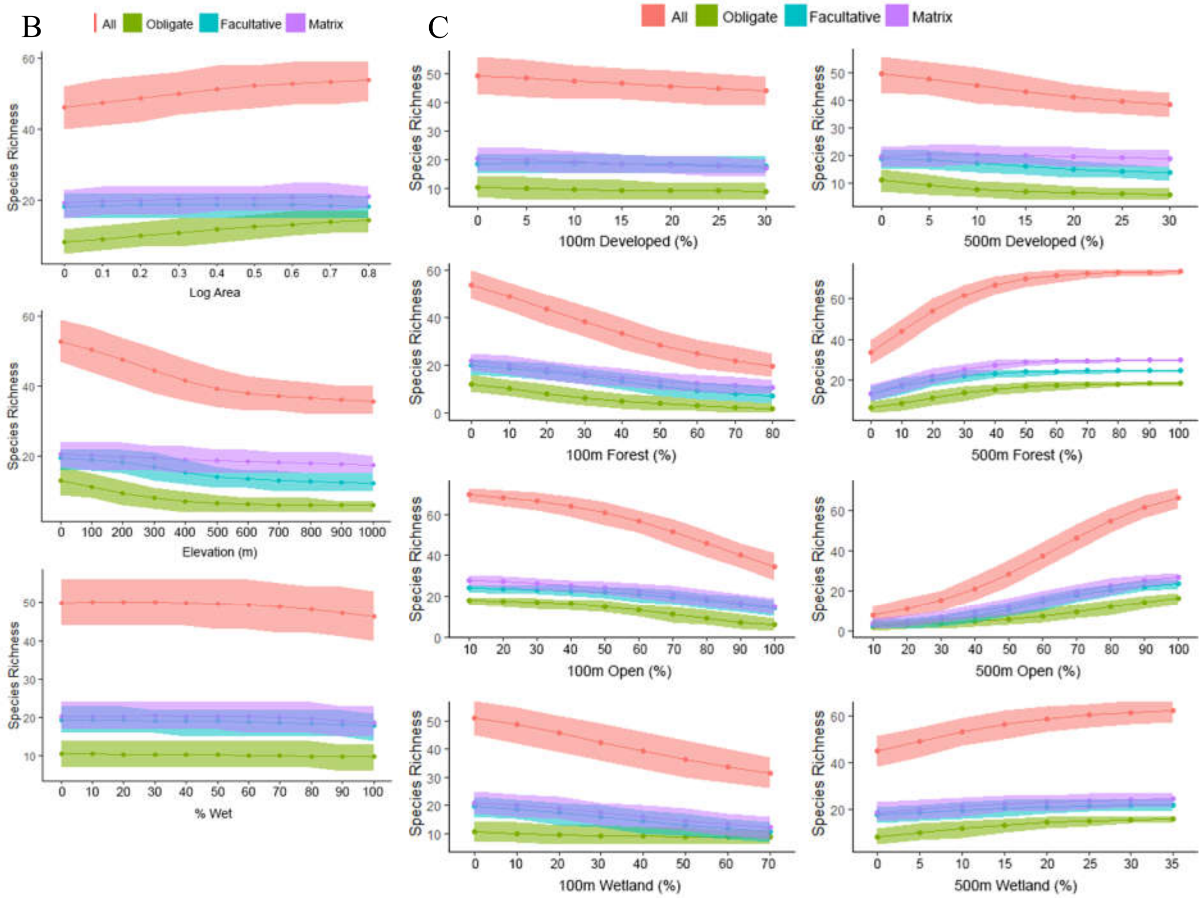
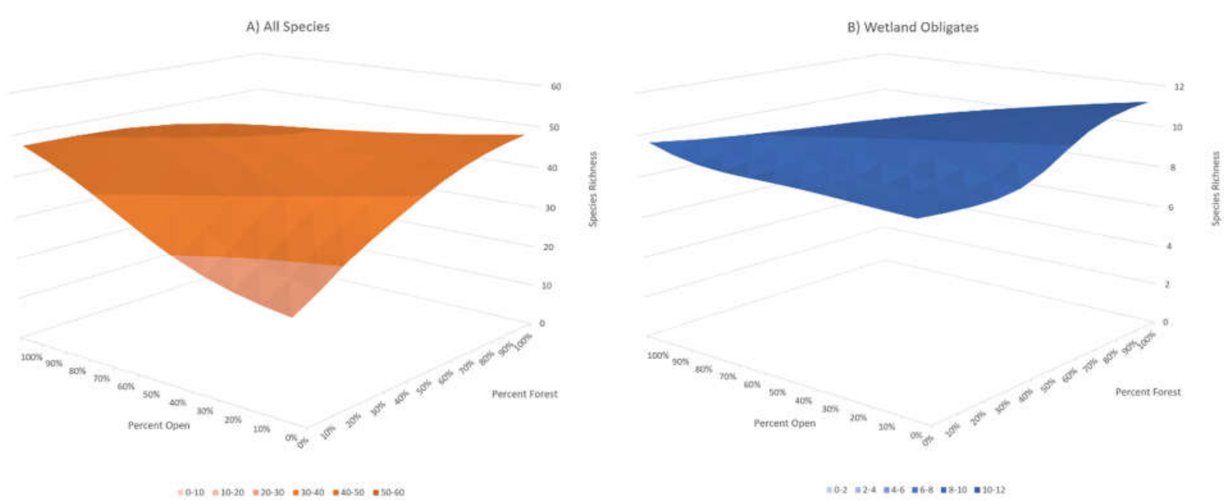


Figure 2.3. Effect of a) vegetation, geomorphology, or irrigation; b) area, elevation, or % wet; and c) landscape composition on species richness estimates for different assemblages of birds if all other parameters are held constant.



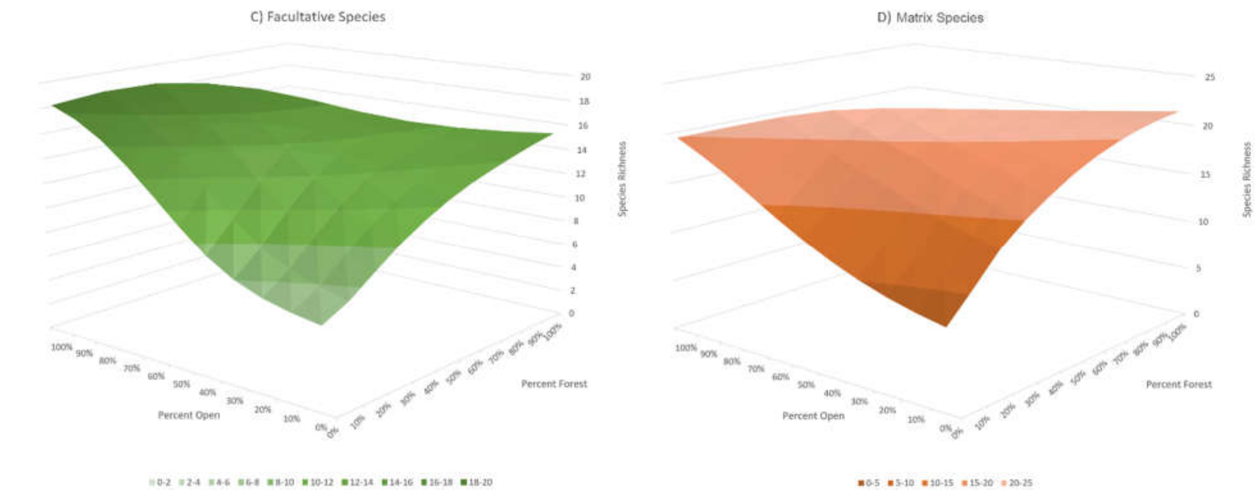
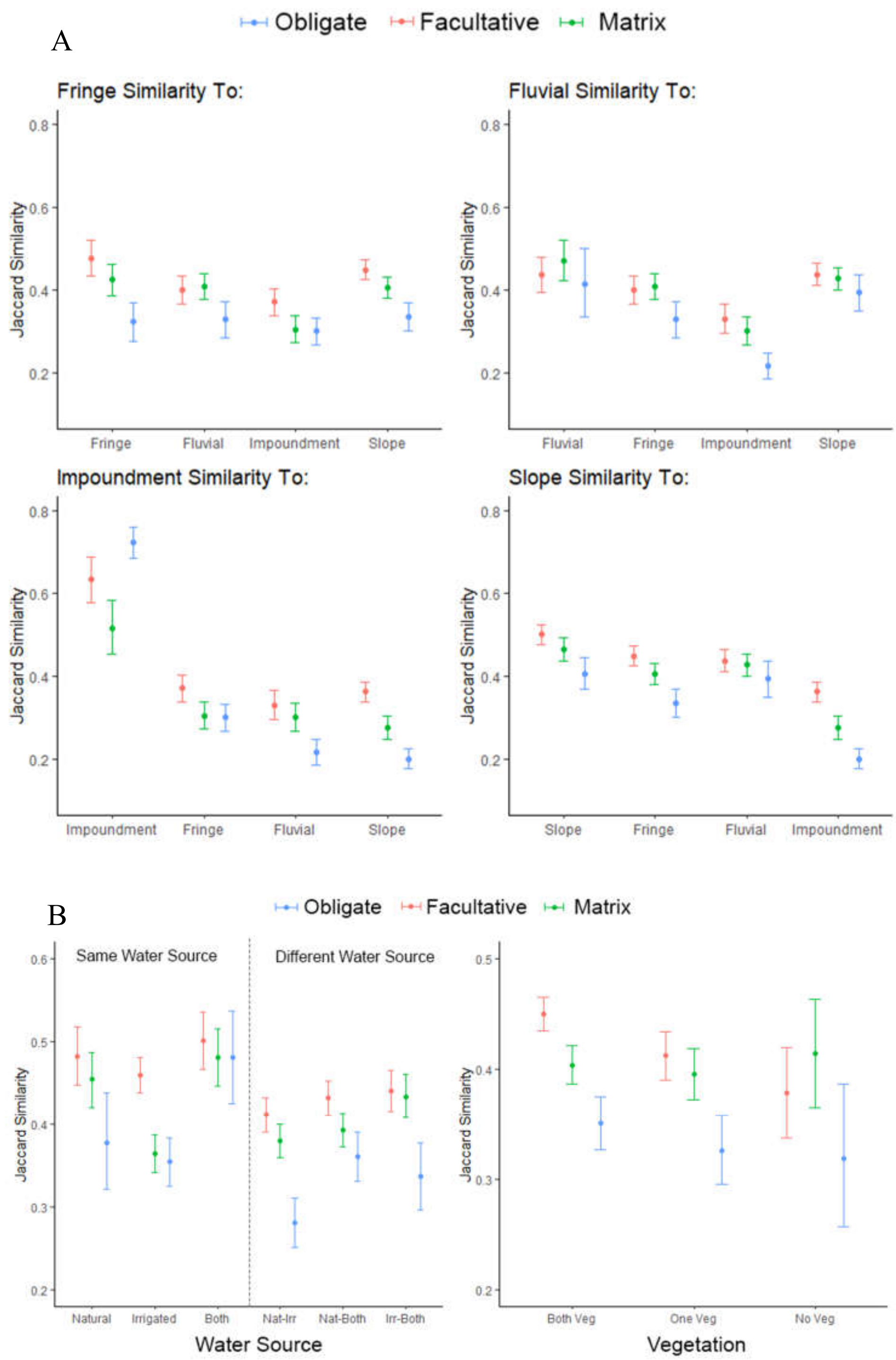


Figure 2.4. Estimated species richness for hypothetical landscapes comprised of varying proportions of forest and open cover types for a) all species, b)wetland obligates, c) facultative species, and d) matrix species. 95% Credible intervals omitted for clarity.

2.4.4 Assemblage Similarity

In general, wetland obligates exhibited the greatest turnover between sites and facultative species exhibited the least (Fig. 2.5). Turnover was similar for most wetland geomorphologies across all three groups, with the exception of impoundments. Turnover between impoundments was low, especially for obligate and facultative species, whereas turnover for other wetland geomorphologies was significantly higher, suggesting that avian assemblages differed less among impoundments compared with other wetland types (Fig. 2.5a). All three groups also exhibited lower similarity between impoundments and other wetland geomorphologies. Specifically, composition of wetland obligates and facultative assemblages differed more between impoundments and sites with moving water (slopes and fluvial wetlands), while matrix species demonstrated high assemblage turnover between impoundments and all other geomorphologies (Fig. 2.5a). With two exceptions, there was no significant difference in turnover between sites-pairs that shared a water source (Fig. 2.5b). Wetland obligate assemblages were less similar between irrigated sites compared with sites with both irrigated and natural water, and matrix species assemblages were less similar at irrigated sites than sites with other water sources (Fig. 2.5b). When compared with exclusively natural wetland-pairs, species assemblage differences were greater between natural sites and sites with other water sources for all groups with the exception of wetland obligate turnover between natural sites and sites with both natural and irrigation water sources (Fig. 2.5b). Species assemblages also exhibited higher turnover between wetlands with both water sources and wetlands with one water source when compared with site-pairs with shared natural and irrigated water sources, although this effect was most pronounced in wetland obligates (Fig. 2.5b). Jaccard similarity was unrelated to wetland vegetation, except that the composition of facultative species in vegetated wetlands and wetlands with no wetland vegetation differed significantly (Fig. 2.5b). I detected no relationship between landscape development and assemblage similarity for any group. All wetland geophysical variables (area, elevation, % wet) and surrounding landscape cover type at both scales (except developed) exhibited a negative relationship between Jaccard similarity for all three groups (Fig. 2.5c). The strongest effects occurred for wetland obligates in relation to a site area and wetland cover at both 100m and 500m scales (Fig. 2.5c).



C

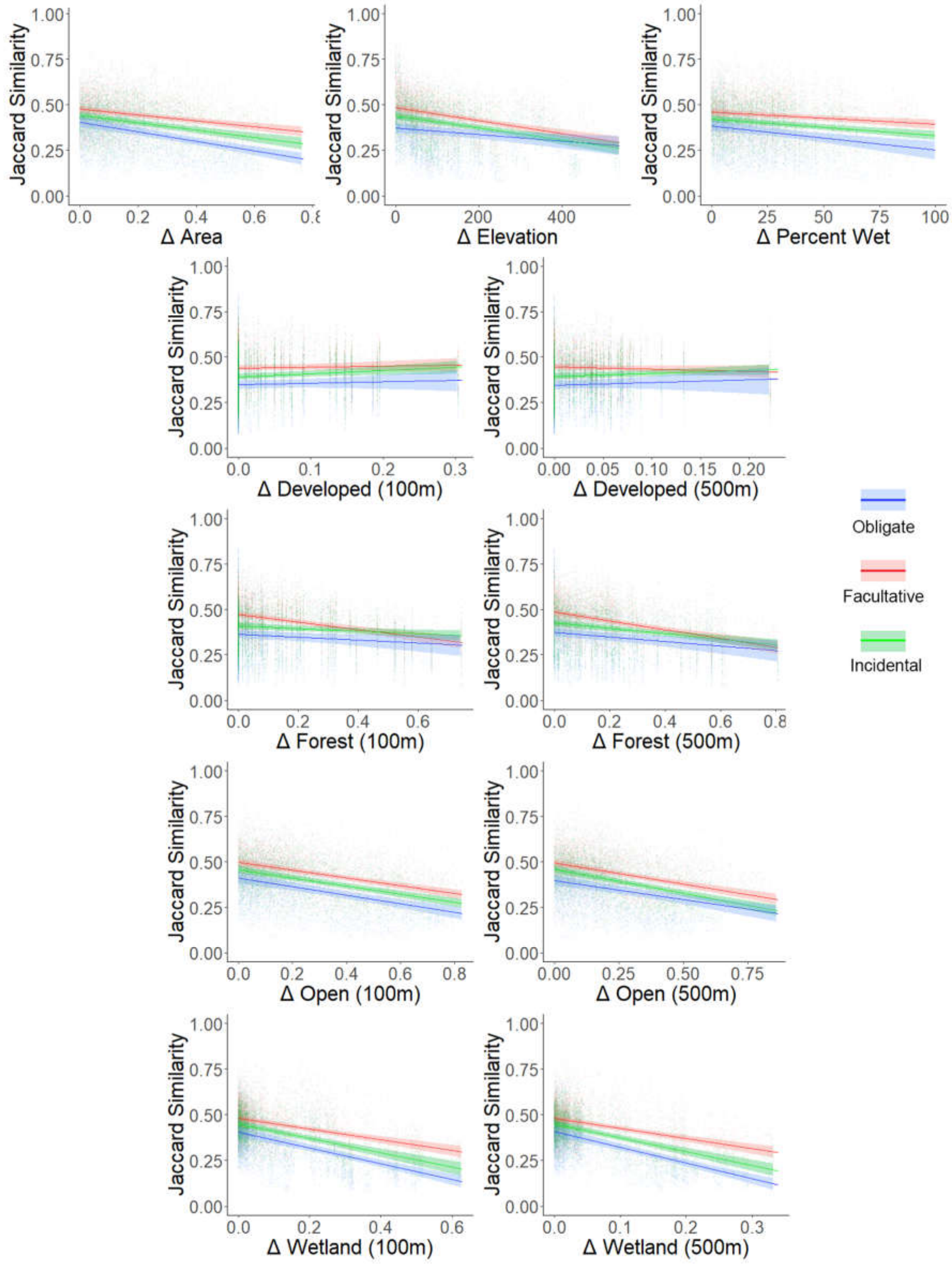


Figure 2.5. Jaccard similarity in relation to A) wetland geomorphology, B) water source and vegetation, and C) area, elevation, % wet, and percent cover for four cover types measured at 100m and 500m scales. Model estimated mean Jaccard similarity for three bird groups and 95% credible intervals are shown.

2.4.5 Spatial Distribution of Species Richness

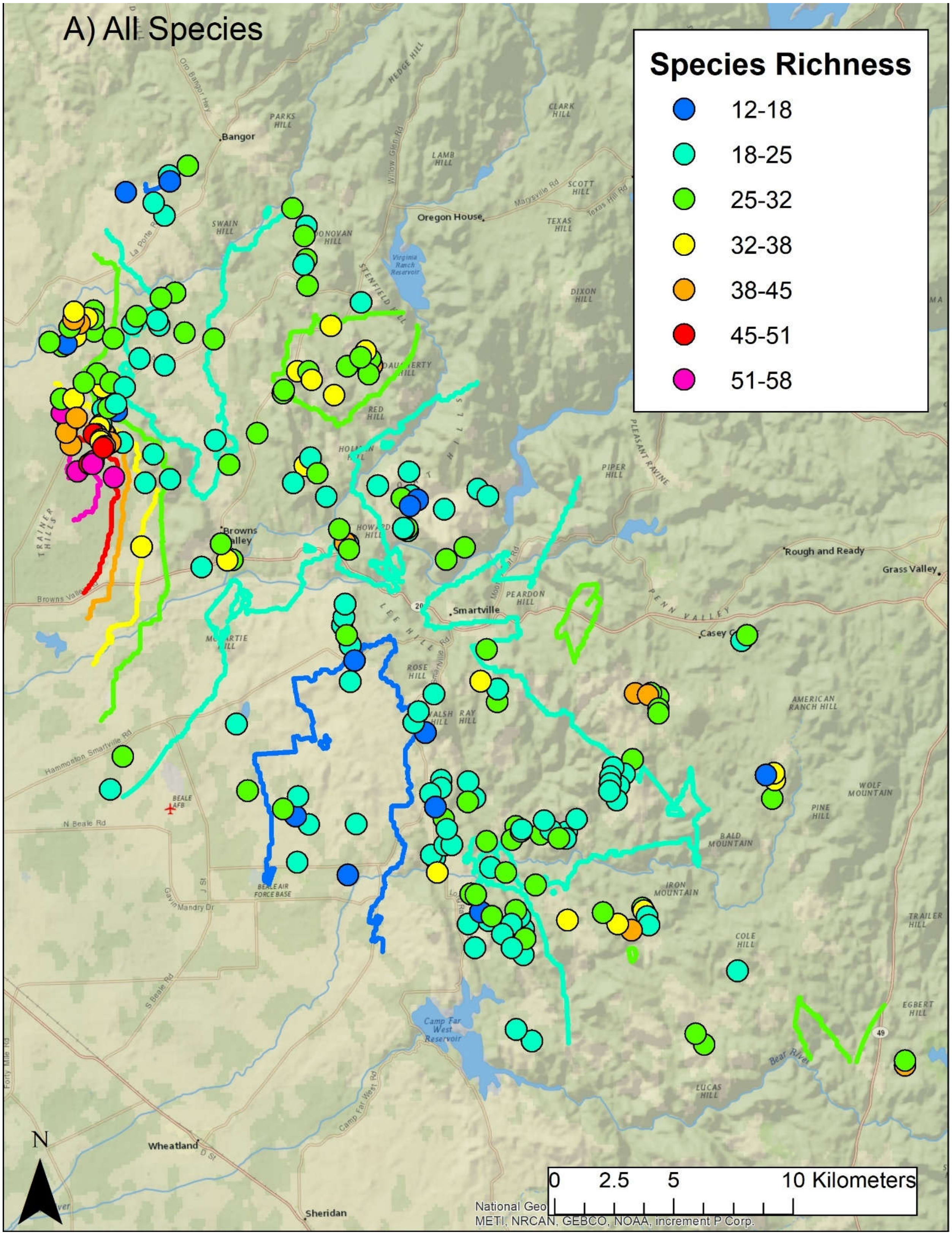
Species richness appeared to be relatively evenly distributed across the study area, with the exception of a hotspot at wetlands on the valley floor on the northwest edge of the study area (Fig. 2.6a). These sites are located within a private ranch set aside for waterfowl hunting. The distribution of wetland obligates on the landscape was similar to total species richness (Fig. 2.6b). However, wetland obligates composed a much greater proportion of the entire avian assemblage at sites in lower elevations at the western and southwestern portions of the study area (Fig. 2.6e). Facultative species generally avoided wetlands in the southwest that were largely surrounded solely by open habitat (Fig. 2.6c). Matrix species avoided wetlands in the lower elevation portions of the foothills except for sites in the northwest, which was highly occupied (Fig. 2.6d).

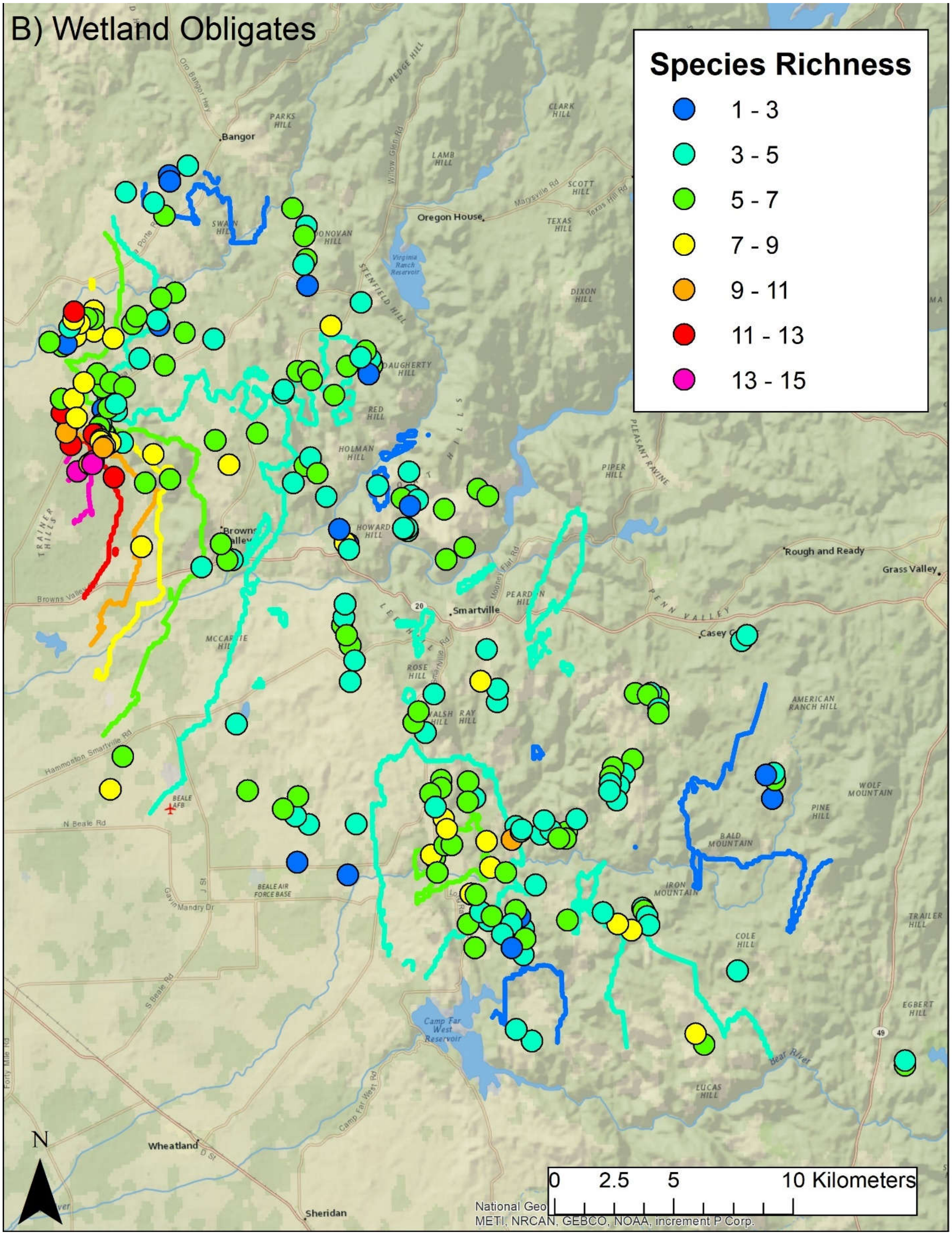
2.5 Discussion

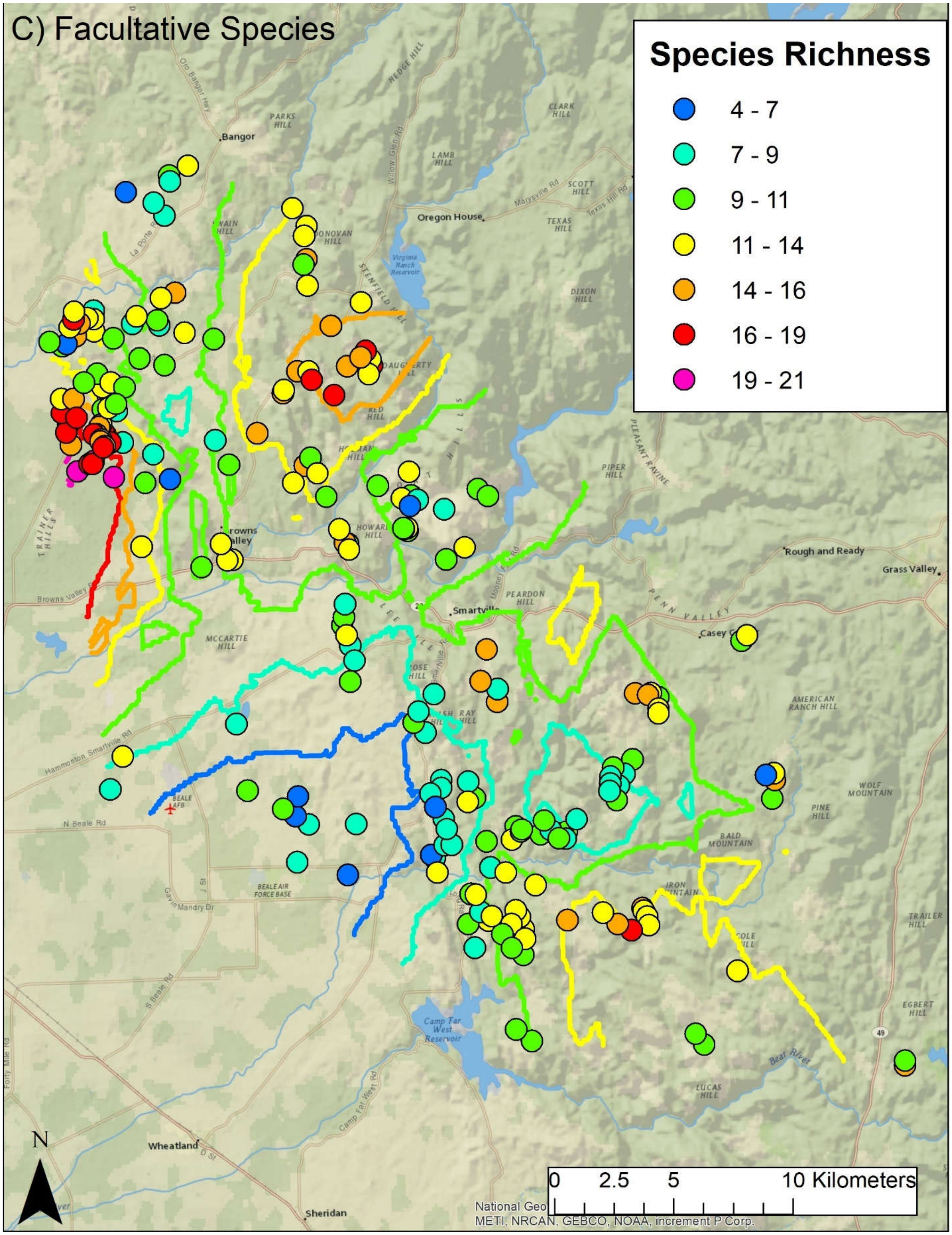
The wetlands of the Sierra Nevada foothills are unique habitats that are threatened by drought, changing hydrology regimes, and encroaching urbanization (Van Schmidt et al. 2019). They comprise some of the last low-elevation inland wetlands remaining in the state (Dahl and Johnson 1991) and provide habitat to numerous wetland obligates as well as species that spillover from other matrix habitats. As hypothesized, the assemblage of wetland obligate species using wetlands of the Sierra Nevada foothills was related to intrinsic wetland characteristics and the assemblage of spillover species was related to landscape composition around each wetland. I observed spillover effects of irrigation type on both facultative and matrix species and spillover effects from surrounding habitats on wetland obligates, a relationship which has rarely been studied in fully natural systems (Tscharntke et al. 2012). Contrary to expectations (Frost et al. 2015), I observed bi-directional spillover despite wetland habitats exhibiting higher productivity than the surrounding matrix habitats. My results support previous studies that have demonstrated the importance of studying species assemblages in the context of the landscape they are using (Rodewald and Yahner 2001, Radford and Bennett 2007, Matthews 2021). My observations may be indicative of the importance of assemblage structure around a habitat patch (e.g., predator presence) or nutrient flow from low-productivity areas to high-productivity patches.

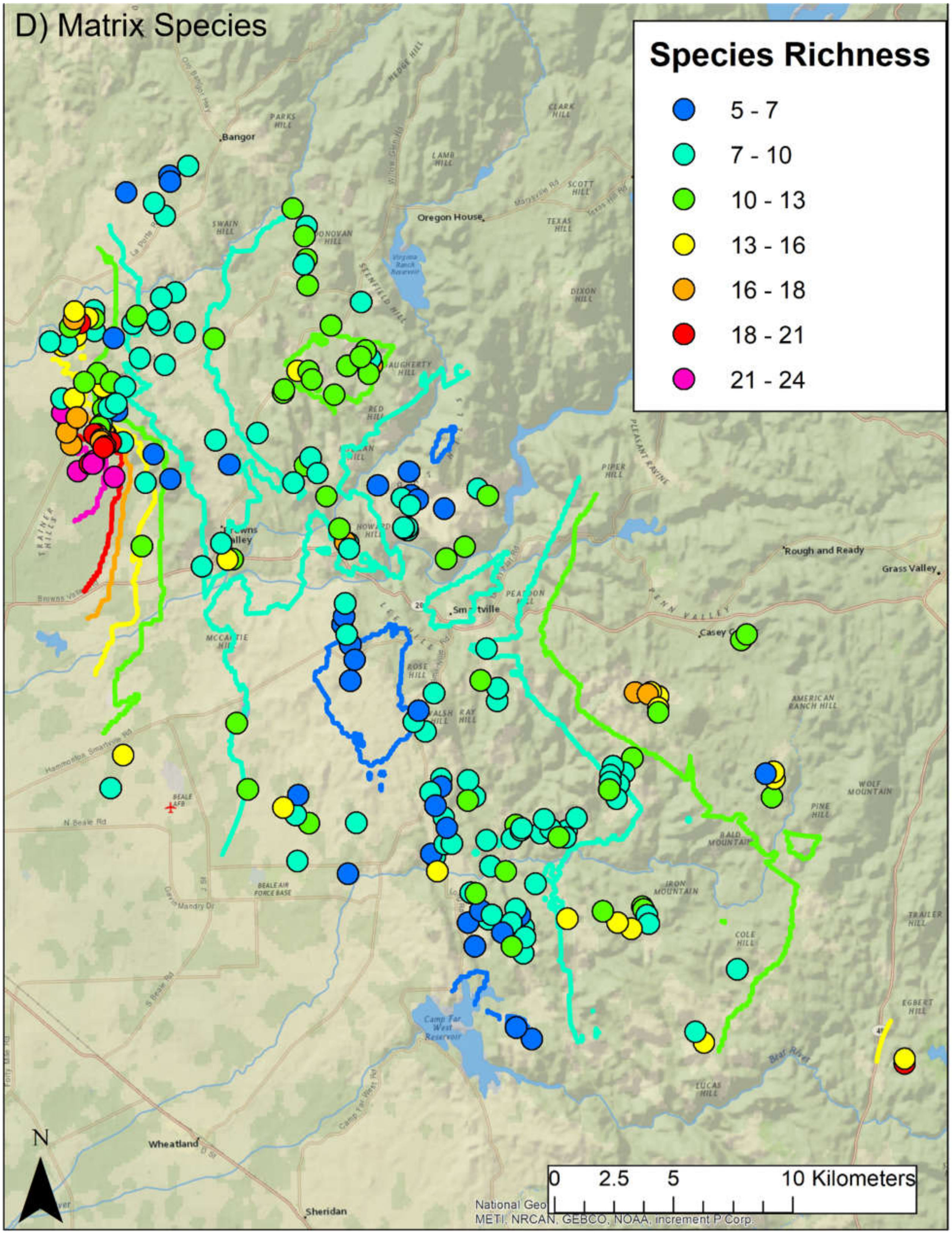
2.5.1 Wetland Characteristics and Site Occupancy

Amongst intrinsic wetland characteristics, water source was the largest contributor to variation in occupancy for all groups, with 18 species exhibiting negative associations with one or more water sources. Water source has a direct effect on how often a wetland receives water and how resistant a wetland is to drying. Natural wetlands are more vulnerable to drought and changing water supply (Van Schmidt et al. 2021), whereas irrigated wetlands in the Sierra Nevada foothills remain wet to provide pastureland for grazing (Richmond et al. 2010a). Three of four non-native bird species detected in this study (House Sparrow, Ring-necked Pheasant, and Eurasian Collard-dove) had significantly lower occupancy at natural wetlands, suggesting that they prefer landscapes augmented by human water sources. Only one wetland obligate (Black Rail) had significantly lower occupancy at irrigation-only wetlands. However, previous studies of Black Rails in the Sierra Nevada foothills have not found this relationship (Richmond et al. 2010a, Van Schmidt et al. 2019).




B) Wetland Obligates
Species Richness
1 - 3
3 - 5
5 - 7
7 - 9
9 - 11
11 - 13
13 - 15
N
0 2.5 5 10 Kilometers
Bangor
Oregon House
Smartville
Rough and Ready
Grass Valley
Wheatland
Sheridan
Camp Far West Reservoir
Bear River
Beale AFB


C) Facultative Species
Species Richness
4 - 7
7 - 9
9 - 11
11 - 14
14 - 16
16 - 19
19 - 21
N
0 2.5 5 10 Kilometers


D) Matrix Species
Species Richness
5 - 7
7 - 10
10 - 13
13 - 16
16 - 18
18 - 21
21 - 24
N
0 2.5 5 10 Kilometers
Bangor
Oregon House
Rough and Ready
Grass Valley
Smartville
Casey
Wheatland
Sheridan
Camp Far West Reservoir
National Geo
METI, NRCAN, GEBCO, NOAA, increment P Corp.

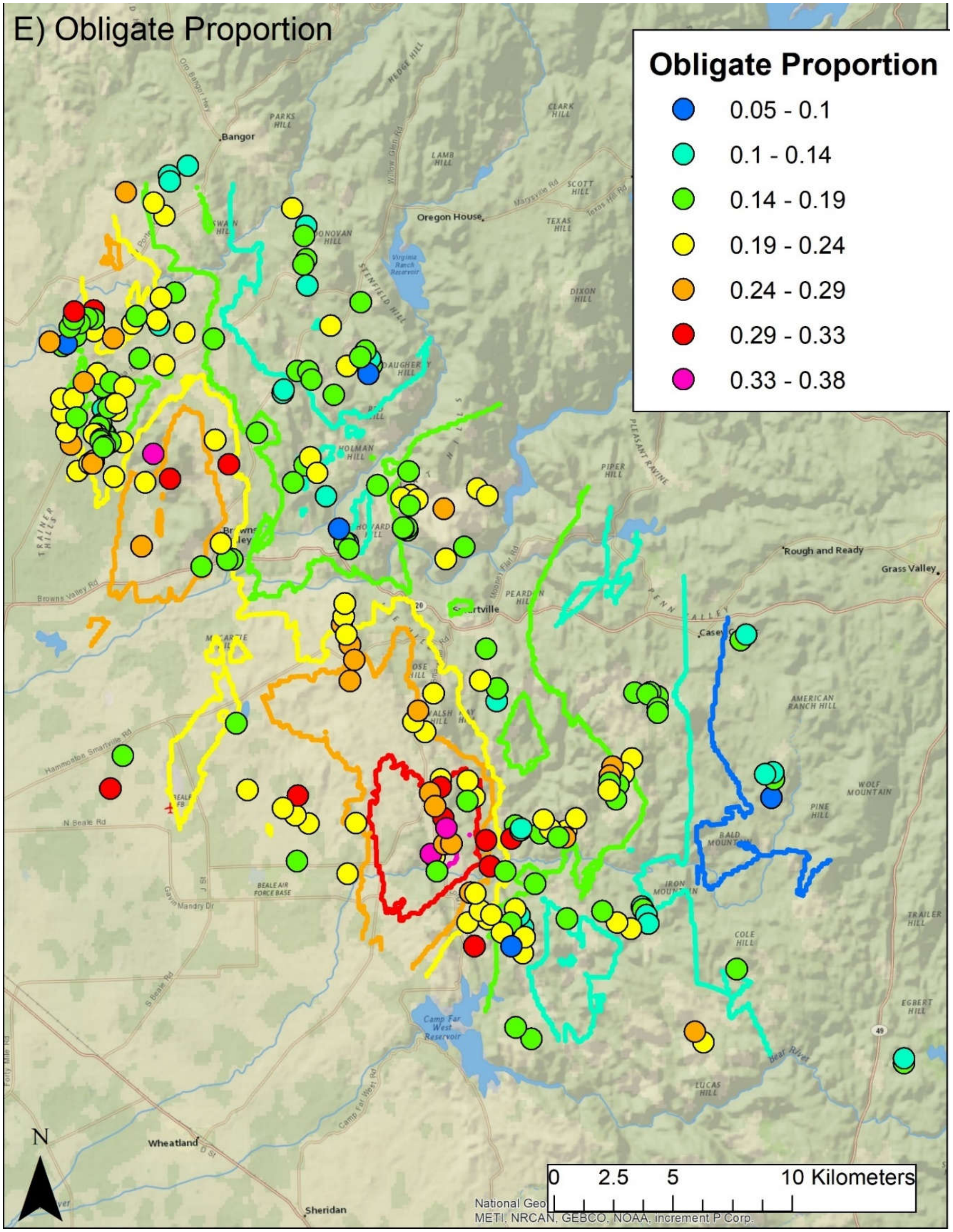


Figure 2.6. Estimated species richness for a) all species, b) wetland obligates, c) facultative species, and d) matrix species, and e) the proportion of wetland obligates making up the avian assemblage at wetlands in the Sierra Nevada foothills. Contours indicate regional species richness.

No intrinsic wetland characteristic, aside from water source, had a significant effect on spillover species but intrinsic site characteristics did influence occupancy of wetland obligates. Obligate occupancy increased with wetland size and decreased at higher elevations and in wetlands that had flowing water (slope and fluvial wetlands). The wetlands of California are generally more common and larger at low elevations in the central valley, so it was not surprising to observe an elevational gradient in obligate occupancy. I did not detect a relationship between non-obligate species and wetland size, suggesting that spillover species did not abandon the landscape in the presence of a habitat they would not normally use. However, mean wetland size in the foothills is relatively small (mean ~0.5 ha) and the matrix surrounding wetland sites was never less than 65% forest or open habitats within 500m. Larger wetland complexes may alter the landscape enough to significantly reduce the occupancy of non-wetland species, or increase the occupancy of wetland species (e.g., Tozer 2016). I observed no effect of the presence of wetland vegetation on occupancy of obligate or non-obligate species, and an only minor effect on species assemblages. However, the presence of invasive vegetation can have a significant effect on occupancy in other studies (Glisson et al. 2015, Tozer 2016), and I did not assess the impact of invasive species common in the Sierra Nevada foothills, such as *Rubus armeniacus*, *Centaurea solstitialis*, and *Bromus tectorum*, which can invade wetland patches.

2.5.2 Landscape Effects

Spillover effects and landscape composition are important factors explaining avian distribution in many different habitats (Rodewald and Yahner 2001, Radford and Bennett 2007, Boesing et al. 2018a, Barros et al. 2019). Landscape factors in my study area contributed significantly to species richness at two different scales. In the most common matrix habitat types (open and forest), there was a significant negative relationship between occupancy and habitat cover at a 100m scale and a positive relationship at a 500m scale, with a stronger effect at a 500m scale (Fig. 2.4). Although species composition changed with landscape composition, species richness was similarly diverse for wetlands surrounded by both open and forest habitats. I did not expect matrix composition to have a significant effect on wetland obligates. However, I saw similar patterns of occupancy in all three groups in relation to landscape composition measures, providing evidence that the same factors can positively influence the occurrence of wetland obligates and spillover from non-wetland habitats. My observations support other research that has shown the importance of managing the matrix for maximizing biodiversity on fragmented or small-patch landscapes (Boesing et al. 2018b, Acuña et al. 2019), including wetlands (Houlahan et al. 2006, Pillsbury and Miller 2008).

On complex landscapes, increased landscape diversity can lead to increased biodiversity (Lawton 1999, Bengtsson 2010, Tscharntke et al. 2012). My results indicate that regional biodiversity in the wetlands of the Sierra Nevada foothills follows a similar pattern. Jaccard similarity between sites differed for most measured habitat characteristics, indicating that wetland assemblages are highly variable and sensitive to many different characteristics. In particular, the avian assemblage at impoundments was significantly different from other wetland geomorphologies (Fig. 2.5a). Impoundments are structurally different from other wetland types and were less complex, had hard ecotones, and were typically surrounded by more human-influenced habitat. More research is needed to fully understand habitats heavily influenced by humans in the context of species assemblages and their relationship with surrounding natural habitats. I also observed consistently lower similarities for wetland obligates than facultative and matrix species, suggesting that wetland obligate biodiversity benefits substantially from high landscape diversity.

2.5.3 Future Research

Although most research on organism presence and species assemblages focuses on specific habitat characteristics utilized by an organism, there is an increasing understanding of the importance of the landscape context of a habitat patch (Boron et al. 2019, Morante-Filho et al. 2021). My results clearly demonstrate that the avian assemblage in the Sierra Nevada foothills depends on landscape context. However, I did not investigate the extent of the spillover effect of wetland habitat into the surrounding matrix. Understanding the how far the spillover effect extends into matrix habitat could improve my understanding of the conservation needs of species on complex landscapes. It also may be valuable to explore the relationship between species traits as and occupancy (Dray and Legendre 2008, Sarker et al. 2021) to better understand how spillover effects vary within a morphological context.

2.5.4 Management Implications

Wetland habitats and wetland communities are among the most vulnerable natural systems in the world (Keddy et al. 2009, Junk et al. 2013, Reis et al. 2017), but they are highly valuable habitat for many species (Gallego-Fernández et al. 1999, Gibbs 2000, McKinney et al. 2011). Conservation of wetlands is a high priority for many institutions across the world (Maltby and Dugan 1994, Votteler and Muir 1996, Wang et al. 2012). The Sierra Nevada foothills are a complex landscape with a myriad of interacting and overlapping species with differing habitat requirements. My results clearly demonstrate that there is no unifying factor that drives species richness in my study area and that species richness likely benefits from the complexity of the landscape. My observations indicate that managing the Sierra Nevada foothills to maximize species richness, even just for wetland obligates will require maintaining wetlands with a complex and varied suite of characteristics. In particular, to maximize avian species richness, it will be important to conserve wetlands with varying water sources and differing geomorphologies.

Our research demonstrates that both private and public property in the Sierra Nevada foothills provide important habitat for avian assemblages. In a highly heterogenous world with mixed land use, it is important to manage working landscapes to the benefit of both humans and wildlife (Tscharntke et al. 2012, Huntsinger et al. 2017, Kremen and Merenlender 2018). The majority of wetland habitat in the Sierra Nevada foothills is found on private property. My research indicated that there are two important hotspots for wetland obligate conservation: Spenceville Wildlife Area owned by the California Department of Fish and Wildlife, and private hunting ranches. Spenceville Wildlife Area, which is located in the southwestern portion of the study area, does not have the highest species richness among wetland obligates, but does have a substantial proportion of its species richness derived from wetland obligates. The wildlife area does not support some wetland species which are highly associated with impoundments or other large wetland types (e.g., Marsh Wren and American Bittern), but its wetlands contribute substantially to the local assemblage. The large private ranches in the northwestern portion of the study area represent a biodiversity hotspot for not only wetland obligates, but also for the overall avian assemblage. These ranches are primarily managed for hunting, but provide ample habitat to non-game species as well. Managing ecosystems on a working landscape require balancing human and ecological needs (Endter-Wada et al. 1998, Keough and Blahna 2006, Huntsinger et al. 2017). Conservation of the Sierra Nevada foothills will require cooperation between many different stakeholders with differing priorities (Huntsinger et al. 2017, Van Schmidt et al. 2019), but could lead to a healthy and robust avian metacommunity supported by both public and private institutions.

Chapter 3: Association between aerial spectral reflectance and occupancy of secretive wetland birds

3.1 Abstract

Remote imagery classification generally divides spectral reflectance into discrete information classes that represent the habitat types on a landscape, but rarely captures characteristics important to a species. I classified imagery of wetlands in the Sierra Nevada Foothills of California using occupancy status for two species of secretive marsh birds, the California Black Rail and the Virginia Rail, as the information classes to create models designed specifically to differentiate wetlands occupied by rails from those not used by the birds. I hypothesized that spectral characteristics of occupied wetlands would be differentiable from unoccupied wetlands, likely due to differences in wetland condition and the vegetation community composition. I refer to this method of remote sensing biodiversity assessment as spectral habitat association. I used high-resolution NAIP imagery collected in tandem with ground surveys to determine occupancy status of rails at wetlands over 6 years to classify four-band spectral reflectance using a maximum likelihood classifier. Spectral habitat association alone was an effective method of predicting occupancy for both Black and Virginia Rails, although the effectiveness varied among years. Spectral habitat association accurately predicted occupancy status at novel wetlands not previously visited within this study system. Depending on the study year, spectral habitat association was an informative covariate compared with standard ground-based habitat covariates. The information classes obtained with spectral habitat association was most similar to wetland geomorphology for Black Rails and wetland wetness for Virginia Rails, although it remained informative even in models that included both of those covariates. Spectral habitat association can be used to accurately predict occupancy with only raw spectral reflectance, making it a valuable tool for monitoring biodiversity and habitat suitability across a wide area. It may also be valuable for predicting species occupancy outside of a known range and identifying priority targets for study and conservation.

3.2 Introduction

Ecologists can use both ground-based data collection and aerial remote sensing to characterize the habitat used by a species (Kerr and Ostrovsky 2003, Turner et al. 2003). Ground-based data is highly accurate and can have high spatial resolution, but the data collecting is often time intensive, difficult, and costly, especially across large spatial scales (Estes et al. 2018). Remotely-sensed data can provide habitat information at large spatial scales, but is limited by resolution, return rates, cost of acquisition, and the interpretation of spectral reflectance data (Kerr and Ostrovsky 2003, Turner et al. 2003, Wang et al. 2010). Habitat classification is the most commonly used method of assessing animal habitat with remote sensing and entails the classification of habitat characteristics that are identifiable using remote sensing imagery, such as cover type, vegetation type, and soil type (Austin et al. 1996, Nagendra 2001, Turner et al. 2003, Newton et al. 2009). Habitat classification relies on *a priori* assumptions about the habitat requirements of the species of interest, and often uses automated land cover classifications that utilize broad categories (Jensen 2005, Schowengerdt 2012). An alternative approach associates known occurrence or absence of a species at a location with spectral reflectance values obtained from remote imagery using either derived indices or raw reflectance (Nagendra 2001, St-Louis et al. 2006). Derived indices produce an informative layer based on raw reflectance values. Commonly used indices include those that are associated with primary productivity such as NDVI or tasseled cap (Verlinden and Masogo 1997, Laurent et al. 2005, Pettorelli et al. 2011, Sheeren et al. 2014, Cáceres et al. 2017, Aubry et al. 2018, Dittrich et al. 2020), or those that create an estimate of landscape heterogeneity using image texture (St-Louis et al. 2006, 2009; Sugai et al. 2019). Although raw reflectance is frequently used to classify habitat and analyze landscape changes, it has rarely been used to assess biodiversity and animal presence directly, and its ability to characterize the occurrence of species is poorly understood (Lewis 1994, Lavers and Haines-Young 2010, Skowronek et al. 2016, Remelgado et al. 2018). The use of raw reflectance could be useful for ecological analyses, as it does not rely on assumptions of relationships between species presence and common derived indices such as NDVI.

In this chapter I focus on the subset of remote sensing applications that associates presence with raw spectral reflectance (hereafter referred to as "spectral association"). Prior use of raw reflectance has employed either clustering algorithms or linear models to understand the relationship between species presence and reflectance (Lewis 1994, Lavers and Haines-Young 2010, Skowronek et al. 2016, Remelgado et al. 2018). Here I use a spectral habitat association method that treats occupancy status as an information class when classifying habitat from remote sensing data. In remote sensing classification, information classes are divisions of spectral space that differentiate spatial divisions of interest (Schowengerdt 2012). Information classes typically used in ecology include habitat types as well as land cover types, such as open water, bare soil, and human development (Nagendra 2001, Schowengerdt 2012). Classification using remote sensing data is effective at characterizing habitat, vegetation, and landscape composition at a study site from broad to fine scales (Nagendra 2001, Kerr and Ostrovsky 2003). However, an inherent limitation of supervised classification is that cover-type classes are determined by the researcher, and any associations with animal presence are dependent on assumptions about a species' habitat associations.

In this study I examine whether occupancy of wetlands by two secretive water birds, the California Black Rail (*Laterallus jamaicensis coturniculus*) and the Virginia Rail (*Rallus limicola*) is related to spectral reflectance in the Sierra Nevada Foothills of California, USA. My primary questions were: 1) does spectral habitat association predict occupancy of two species of secretive marsh birds as a sole predictor, 2) what is the relationship between spectral habitat association and other habitat descriptors, including both on-the-ground metrics and satellite derived indices, and 3) can you use spectral habitat association to predict occupancy at novel sites with no *a priori* knowledge of occupancy status? To assess spectral habitat association as a sole predictor, I investigated its efficacy in predicting occupancy as well as the best methods to characterize occupied and unoccupied habitat and summarize patch quality based on classified habitat. For the second primary question, I sought to understand the biology underlying observed patterns of occupancy. I predicted that spectral habitat association would improve upon a base occupancy model using *a priori* knowledge of the effects of biogeographical characteristics on site occupancy. I also compared fit between models using ground-truthed habitat characteristics as well as a common remote-sensing index, NDVI, with models using spectral habitat association data to assess whether spectral habitat association was informative in the presence of other measures of habitat suitability. I hypothesized that spectral habitat association classes contain similar information to habitat characteristics collected on the ground, specifically wetland wetness and the presence of suitable wetland vegetation, two characteristics likely to be detectable using remote sensing, but distinct from NDVI. Finally, I used the spectral habitat association classifier to predict Black Rail occupancy at novel wetlands within the Sierra Foothills metapopulation to determine if spectral habitat association could be used to identify likely occupied wetlands based solely on raw spectral data.

3.3 Methods

3.3.1 Study Area

The study took place at 277 wetlands located in Yuba, Nevada, and Butte counties in California, USA (Fig. 3.1). Wetlands in the Sierra Nevada foothills are generally small ($\bar{x}$ = 0.79 ± 0.12 ha) with typology varying from sloping hillsides to ponds and impoundments and are located within a matrix made up of oak savannah, forest, and open grassland (Richmond et al. 2010a, Van Schmidt et al. 2019). Primary wetland vegetation included *Juncus* spp., *Typha* spp., with secondary *Schoenoplectus* spp., and a shrub layer dominated by *Rubus* spp. or *Salix* spp. Wetlands in the Sierra Nevada foothills can have natural water sources, irrigated water sources, or both (Richmond et al. 2010a, Van Schmidt et al. 2019). Irrigated wetlands are either associated with runoff from agricultural activities such as ranching or the intentional creation of wetland habitat (Richmond et al. 2010a, Van Schmidt et al. 2019). The Sierra Nevada foothills are a semi-arid environment during the summer, with little rainfall, which can cause substantial fluctuations in wetland wetness and extent during the year. Some wetlands were maintained for habitat had continuous water flow even in drought years, whereas other wetlands would vary in wetness depending on the choices of landowners (Huntsinger et al. 2017, Van Schmidt et al. 2019).

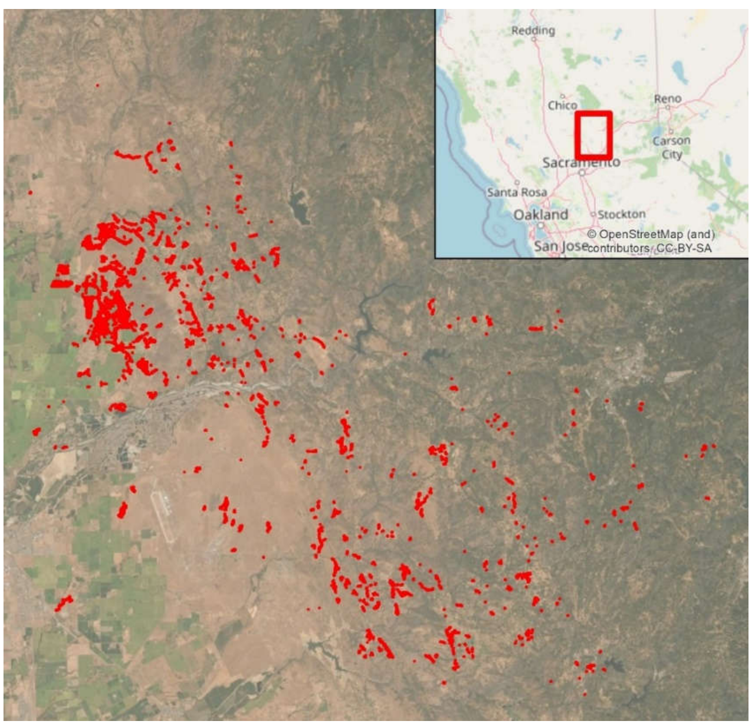


Figure 3.1. Location of wetlands used to assess spectral habitat association of Black and Virginia Rails in the Sierra Nevada Foothills of California, USA.

3.3.2 Study Species

Black Rails are wetland specialists that are broadly, but very patchily, distributed across portions of the western hemisphere (Eddleman et al. 1994). The California Black Rail subspecies is listed as threatened by the state of California and the subspecies in the eastern United States is federally listed as threatened. Black Rails are particularly threatened by wetland destruction, climate change, sea-level rise, drought and West Nile Virus (Richmond et al. 2010a, 2012; Van Schmidt et al. 2019). They inhabit both salt- and fresh-water marshes, and feed on seeds and invertebrates. Black Rails typically occupy wetlands with shallow standing water and dense, low vegetation such as *Juncus* spp. or *Salicornia pacifica* (Eddleman et al. 1994, Richmond et al. 2008, 2010a). Virginia Rails, in contrast, are much more widespread across North America and are not a species of conservation concern. Virginia Rails exploit similar food sources to Black Rails, but are three times larger than Black Rails, can forage in deeper water and generally prefer taller wetland plants such as *Typha* spp. (Conway 1995, Richmond et al. 2010b).

3.3.3 Data Collection

From May through August in 2009, 2010, 2012, 2014, 2016, and 2018, I surveyed wetlands for Black and Virginia Rails using standard call-playback surveys with conspecific recordings. Call-playback surveys were conducted every 50m within each wetland until the entire area was covered or a rail was detected. I performed playback surveys three times per summer, or until both rail species were detected at a site following the removal method (MacKenzie et al. 2018). When a rail was detected, its approximate location was estimated and digitized. Typical detections within this study system occurred within 20m of the surveyor. For detailed call-playback methodology, see Richmond et al. (2008, 2010) and Risk et al. (2011). Overall detection probability for three visits was > 0.95 for all species in all years, so I considered all sites with 3 non-detections to be unoccupied. Although closure violations occurred in both species, they did not have a significant effect on occupancy estimates (Peterson, Chapter 1).

I characterized wetland patches using three sets of covariates: habitat characteristics, geophysical characteristics, and spectral characteristics. Habitat characteristics are site characteristics that assess vegetation and habitat quality, and were collected on the ground during surveys. These characteristics include percent wet cover (flowing or standing water or saturated mud, collected starting in 2014; Richmond et al. 2010), plant cover > 25% of *Juncus* spp. or *Typha* spp, and site geomorphology (either slope, fluvial, fringe, or impoundment; (Brinson and Malvárez 2002, Van Schmidt et al. 2019). Geomorphology is a geophysical characteristic, but in this case it also affected the vegetative community present in a wetland. For example, the vegetation community in a fringe wetland is different from that in a slope wetland (Richmond et al. 2010a), and would therefore potentially be spectrally differentiable. Geophysical characteristics are site characteristics that are defined by the structure and location of the site, including elevation, area (Log_{10}), and isolation (geometric mean to nearest three occupied sites). Because wetland size changes based on water availability, I calculated area for each site for each year from aerial imagery and ground-truthed wetland outlines using the methods described by Van Schmidt et al. (2019).

I used aerial imagery from the National Agriculture Imagery Program (NAIP) for remote sensing characteristics, including raw spectral reflectance and NDVI. NAIP imagery was collected between July 1 and August 15 each study year, and was comprised of four bands in my study system: blue (400-500nm), green (500-600nm), red (600-700nm), and near infrared (800-900nm). I calculated NDVI using the near infrared and red bands (Pettorelli et al. 2011). NAIP imagery was at 1-m resolution from years 2009-2016, and at 0.6-m resolution in 2018.

3.3.4 Wetland Characterization, Summarization, and Classifier Validation

For spectral habitat association, I classified wetland pixels into occupied and unoccupied information classes using a supervised maximum likelihood classification. For each year, I used half of the wetlands of each occupancy status as training data for classification and half of the wetlands as a test data for validation. I created a classification signature file for each year and species using the “Create Signatures” tool in Arc GIS 10.7.1 and all four bands of NAIP imagery. I then used the “Class Probability” tool in Arc GIS 10.7.1 to calculate the probability that any pixel within our study area was within the occupied or unoccupied information class. Because I had no *a priori* knowledge about how best to delineate occupied habitat, I performed the maximum likelihood classification using three different measures of each wetland: all wetland pixels within 25m of a rail observation, all wetland pixels within 50m of a rail observation, and all pixels within an occupied wetland. For the unoccupied information class, I used all pixels in unoccupied wetlands for all classifiers. This method resulted in three class probability rasters for each species in each year, corresponding to the probability the pixel was similar to unoccupied habitat or occupied habitat at three different characterization scales.

After classifying individual pixels within each wetland, I summarized the class probability raster as a single value for each wetland. With no *a priori* knowledge of the best way to summarize the probability raster for these species, I tested three different methods of summarizing the class probability raster: mean occupied class probability for all pixels, number of pixels with ≥ 0.5 occupied class probability, and number of pixels with ≥ 0.6 occupied class probability (to test whether a higher confidence in pixel classification would improve occupancy estimates). Combining three methods of characterizing occupied wetlands with three methods of summarizing classified data yielded nine different validation models for each year and species.

For each year and species, I validated spectral habitat association using a sample of test wetlands that were not used to define the information classes in a single-season occupancy models (MacKenzie et al. 2002). I used single-season occupancy models rather than multi-season occupancy models, because the classification was performed for each year and what the classifier considered to be “occupied” and “unoccupied” pixels could change in any given year based on annual conditions. I used the ‘occu’ function in the package ‘Unmarked’ for all occupancy models (Fiske and Chandler 2011), with a null model for detection probability. Test datasets ranged from 105 – 160 sites, of which 18 – 36% were occupied, depending on the survey effort, year, and species. For each year and species, I developed a set of 10 occupancy models, including a null model, and one model for each combination of wetland classification method and wetland characterization method (e.g., classification using a 25 m buffer and characterization using a ≥ 0.5 occupied class probability). I assessed model fit using Akaike’s Information Criterion adjusted for small sample size (AICc; Burnham and Anderson 2004). For each species, I selected the combination of classification and characterization with the greatest mean difference from the null model across all years of the study. I considered any classifier model with ΔAICc from the null model < -2 to be an informative parameter. I calculated Matthews' Correlation Coefficient (MCC) values using the 'mcc' function within the 'mltools' package in R. I compared occupied and unoccupied sites and predicted occupancy using the *'predict'* function in the package 'Unmarked' with a 50% threshold for predicted site occupancy (Fiske and Chandler 2011).

3.3.5 Comparison with Ground-truthed Metrics

After assessing whether spectral habitat association predicted occupancy as a lone covariate, I assessed its effectiveness after accounting for known characteristics that influence occupancy as well as comparing it with other measures of habitat quality. For both Black Rails and Virginia Rails, I considered the base model to be the *a priori* model based on geophysical characteristics of wetlands. This model included elevation, area ($\log_{10}$), and isolation (geometric mean to the three nearest occupied wetlands) and was based on *a priori* models of this study system (Van Schmidt et al. 2021). I identified four covariates that could potentially covary with spectral habitat association: wetland wetness (beginning in 2014), productivity estimated through remote sensing (NDVI), vegetation, and site geomorphology (slope, impoundment, fringe, or fluvial; Richmond et al. 2010a, Van Schmidt et al. 2019). To avoid correlation with base model covariates as well as other known occupancy limiters, I made two corrections to the spectral habitat association metric for this analysis. My initial raw spectral habitat association parameter correlated with area measures (both species mean $r^2 = 0.91$), and area is already known to be a strong predictor of rail occupancy (Richmond et al. 2010a, Van Schmidt et al. 2019). To isolate the effect of reflectance, I converted my measure of spectral habitat association to the proportion of pixels classified as "occupied wetland" using the top-ranked validation model rather than total number of pixels within a wetland. I also know that there was an area threshold below which Black and Virginia Rails would not occupy a wetland. I did not observe Black and Virginia Rails occupying wetlands < 400 m^2 and < 800 m^2, respectively, so I censored wetlands below those sizes for each species in this analysis. This affected 6 – 13% of study wetlands for Black Rails, and 14 – 22% of wetlands for Virginia Rails, depending on the year, but allowed us to exclude any masking effects that wetlands that were limited by area would have on coefficient estimates.

The purpose of these model sets was to understand how effective spectral habitat association was at informing occupancy estimates when compared to other measures of habitat. I performed both direct comparisons (e.g., was a model with spectral habitat association more informative than a model with habitat parameters?) and additive comparisons (e.g., is the occupancy explained by spectral habitat association more similar to that explained by habitat parameters or greenness?). For the former comparisons, I compared AICc values between model sets to determine if spectral habitat association was more or less informative than other categories. For the latter comparisons, I compared the relative difference in log likelihood value between the spectral habitat association model, the other parameter of interest model, and the model that contained both.

3.3.6 Testing Predictions at Novel Wetlands

In 2019, I surveyed 19 wetlands within the geographical boundaries of the Black Rail metapopulation that had never been visited before. 10 wetlands were located within the geographical confines of the core study area and 9 were located within the metapopulation boundary, but up to 50km north or south of the core study area. I selected a broad range of predicted occupancy using only spectral habitat association values. Due to logistical constraints, I were only able to visit each of these wetlands twice within a few days at the end of my typical survey window (mid-August), so my estimates of occupancy status may not accurately reflect breeding-season conditions. For each site, I calculated the percentage of occupied pixels as described above using 2018 imagery and compared a null occupancy model with an occupancy model using percent spectral habitat association as a covariate.

3.4 Results

3.4.1 Wetland Characterization and Classifier Validation

Spectral habitat association was an informative parameter for occupancy models in all years for both Black and Virginia Rails compared with the null model (Appendix S3.1: Table S3.1). Black Rails exhibited substantial variation in model performance over time, with relatively weak models in 2009 and 2012 that improved AICc scores over the null model only by < 3 (Table 3.1). In contrast, the Virginia Rail spectral habitat association model was consistently better than the null model in all years (Table 3.2). Using mean AICc scores across all years, the best wetland characterization and classification model for both species was a 25-m characterization radius around rail locations with a 50% class probability threshold (Tables 3.1 & 3.2). The 25-m, 50% spectral habitat association parameter effectively discriminated between classes in the validation dataset in 4/6 years for Black Rails and all years for Virginia Rails (Figs. 3.2 & 3.3).

Table 3.1. AICc difference between validation models of differing methods of characterizing occupied habitat and summarizing wetlands for Black Rails and a null model without spectral habitat association parameters. Top model across all years is in bold.

Character.	Summariz.	2009	2010	2012	2014	2016	2018	Mean
Full	Mean	1.71	1.99	-0.91	1.74	-1.86	-12.20	-1.59
50m	Mean	2.00	1.14	-0.31	1.98	0.57	-6.05	-0.11
25m	Mean	1.99	-0.79	-0.78	1.95	0.07	-5.58	-0.52
Full	50% Thresh.	-4.64	-24.62	1.65	-16.71	-25.85	-63.46	-22.27
50m	50% Thresh.	-4.30	-27.27	0.33	-15.40	-25.00	-61.27	-22.15
25m	**50% Thresh.**	**-2.60**	**-28.19**	**-2.39**	**-16.10**	**-25.44**	**-62.48**	**-22.87**
Full	60% Thresh.	-2.74	-14.99	-0.48	-17.99	-16.62	-71.38	-20.70
50m	60% Thresh.	-3.85	-25.86	1.40	-18.97	-10.43	-65.91	-20.60
25m	60% Thresh.	-1.27	-3.67	1.20	-1.80	-30.18	-15.37	-8.51

Table 3.2. AICc difference between validation models of differing methods of characterizing occupied habitat and summarizing wetlands for Virginia Rails and a null model without spectral habitat association parameters. Top model across all years is in bold.

Character.	Summariz.	2009	2010	2012	2014	2016	2018	Mean
Full	Mean	0.04	-0.84	-8.15	-13.01	-5.14	-6.23	-5.56
50m	Mean	-4.33	1.29	-8.93	-16.16	-6.72	-3.54	-6.40
25m	Mean	-3.82	0.36	-10.37	-14.57	-8.28	-4.21	-6.82
Full	50% Thresh.	-18.95	-29.22	-37.05	-44.55	-39.37	-59.16	-38.05
50m	50% Thresh.	-23.35	-38.10	-40.95	-49.20	-40.69	-50.75	-40.51
25m	**50% Thresh.**	**-23.99**	**-35.39**	**-44.06**	**-50.77**	**-41.86**	**-52.25**	**-41.39**
Full	60% Thresh.	-17.41	-25.36	-29.45	-38.11	-39.78	-44.86	-32.50
50m	60% Thresh.	-22.19	-31.09	-30.75	-45.52	-42.69	-39.30	-35.25
25m	60% Thresh.	-22.77	-29.89	-32.39	-48.15	-44.66	-40.73	-36.43

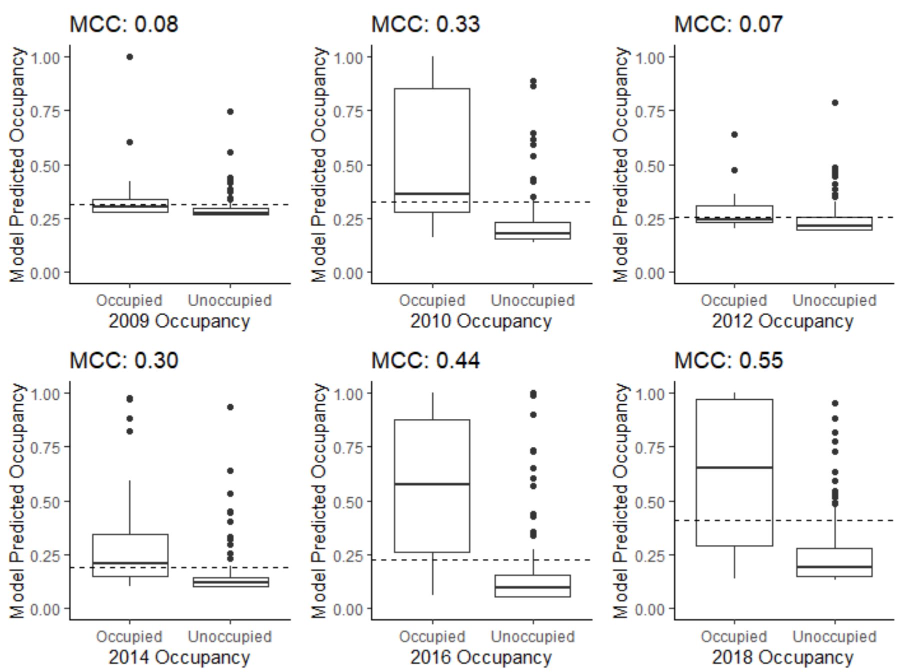


Figure 3.2. Model validation for Black Rail spectral habitat association using a 25-m characterization radius and 50% threshold for site summarization. Dashed line denotes mean occupancy during each year and MCC value denotes Matthews' Correlation Coefficient.

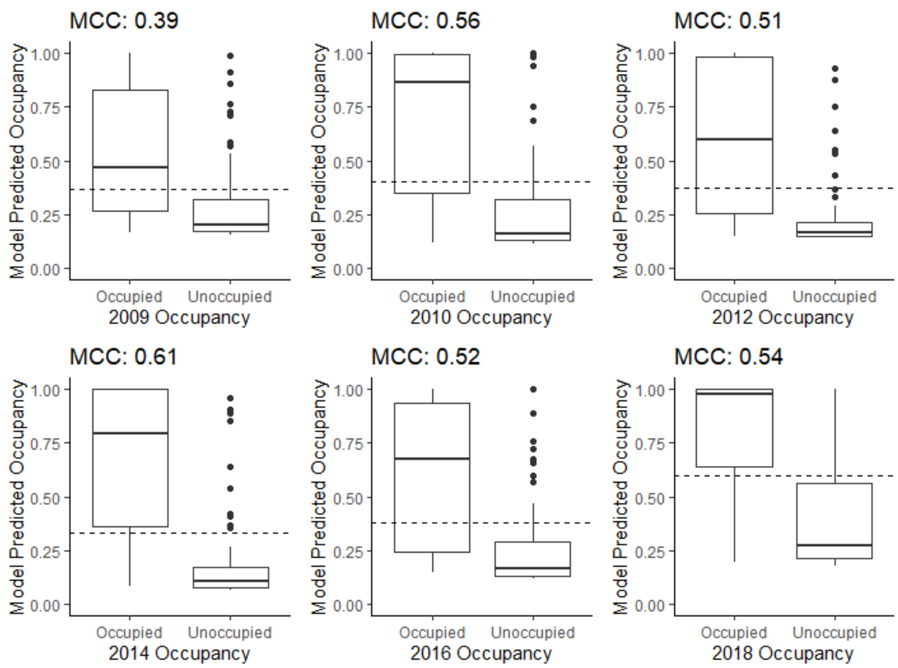


Figure 3.3. Model validation for Virginia Rail spectral habitat association using a 25-m characterization radius and 50% threshold for site summarization. Dashed line denotes mean occupancy during each year and MCC value denotes Matthews' Correlation Coefficient.

3.4.2 Comparison with Ground-truthed Metrics

Spectral habitat association was an informative parameter in four years for Black Rails and three years for Virginia Rails when compared with the *a priori* base model that included elevation, geomorphology, and isolation, (Table 3.3). The effect size and variance differed between years, with strong effects in 2010, 2016, and 2018 for Black Rails (Fig. 3.4) and 2014 and 2016 for Virginia Rails (Fig. 3.5). When compared with other measures of habitat, spectral habitat association varied by year and species in its predictive strength (Table 3.3). Spectral habitat association was a better predictor of Black Rail occupancy than wetland wetness in two years (66%), and *Juncus* and NDVI in four years (66%), but was only a better predictor than geomorphology in one year (17%; Table 3.3). In contrast, spectral habitat association outperformed geomorphology in a majority of years for Virginia Rails (4 years, 66%), but was less predictive than *Typha* or wetland wetness in four (66%) and three (100%) years, respectively (Table 3.3). The only habitat measure that was outperformed by spectral habitat association for both species in a majority of years was NDVI (4 years for Black Rails [66%] and 5 years for Virginia Rails [83%]; Table 3.3). As measured by log likelihood differences, there was little similarity between spectral habitat association and either NDVI or vegetation measures in either species (Fig. 3.6). However, when accounting for geomorphology, spectral habitat association was less informative than in the base model for Black Rails (Fig. 3.6a). For Virginia Rails, spectral habitat association was less informative than in the base model when paired with wetland wetness (Fig. 3.6b).

Table 3.3. AIC results of occupancy models explaining wetland occupancy as a function of site geomorphology (Geom), *Juncus* or *Typha* presence, mean NDVI, and spectral habitat association (S.A.) for Black and Virginia Rails between 2009-2018.

Species	Year	Model	N. Params	AIC	ΔAIC	AIC Weight	Log Like.
Black Rail	2009	Base + Geom	9	263.24	0.00	0.59	-122.62
		Base + Geom + S.A.	10	264.05	0.81	0.39	-122.03
		Base + Juncus	6	272.71	9.47	0.01	-130.36
		Base + NDVI	6	272.94	9.70	0.00	-130.47
		Base	5	272.94	9.71	0.00	-131.47
		Base + Juncus + S.A.	7	273.14	9.90	0.00	-129.57
		Base + S.A.	6	273.53	10.29	0.00	-130.77
		Base + NDVI + S.A.	7	273.80	10.56	0.00	-129.90
	2010	Base + Geom + S.A.	10	263.38	0.00	0.85	-121.69
		Base + Geom	9	267.15	3.76	0.13	-124.57
		Base + S.A.	6	273.08	9.69	0.01	-130.54
		Base + Juncus + S.A.	7	273.45	10.07	0.01	-129.72
		Base + NDVI + S.A.	7	273.96	10.57	0.00	-129.98
		Base + Juncus	6	279.58	16.20	0.00	-133.79
		Base	5	280.64	17.25	0.00	-135.32
		Base + NDVI	6	282.22	18.84	0.00	-135.11
	2012	Base + Geom + S.A.	10	338.01	0.00	0.65	-159.01
		Base + Geom	9	339.21	1.20	0.35	-160.61
		Base + Juncus	8	354.30	16.29	0.00	-169.15
		Base + NDVI	6	354.61	16.60	0.00	-171.31
		Base + Juncus + S.A.	9	355.16	17.15	0.00	-168.58
		Base + NDVI + S.A.	7	355.29	17.28	0.00	-170.64
		Base	5	355.42	17.41	0.00	-172.71
		Base + S.A.	6	355.88	17.87	0.00	-171.94
	2014	Base + Geom	9	247.74	0.00	0.62	-114.87
		Base + Geom + S.A.	10	248.82	1.08	0.36	-114.41
		Base + Wet + S.A.	7	255.41	7.67	0.01	-120.70
		Base + Juncus + S.A.	9	261.86	14.12	0.00	-121.93
		Base + Wet	6	262.40	14.66	0.00	-125.20
		Base + S.A.	6	265.06	17.32	0.00	-126.53
		Base + NDVI + S.A.	7	265.45	17.71	0.00	-125.73
		Base + Juncus	8	267.99	20.25	0.00	-125.99
		Base	5	272.43	24.69	0.00	-131.22
		Base + NDVI	6	273.31	25.56	0.00	-130.65
	2016	Base + Juncus + S.A.	7	313.06	0.00	0.77	-149.53
		Base + Geom + S.A.	10	315.91	2.85	0.19	-147.96
		Base + S.A.	6	320.18	7.11	0.02	-154.09
		Base + Wet + S.A.	7	321.56	8.50	0.01	-153.78
		Base + NDVI + S.A.	7	321.60	8.54	0.01	-153.80

		Base + Geom	9	326.54	13.48	0.00	-154.27
		Base + Juncus	6	330.64	17.58	0.00	-159.32
		Base + Wet	6	336.25	23.19	0.00	-162.13
		Base	5	340.00	26.94	0.00	-165.00
		Base + NDVI	6	341.31	28.24	0.00	-164.65
		Base + Juncus + S.A.	7	313.06	0.00	0.77	-149.53
	2018	Base + Geom + S.A.	10	324.20	0.00	1.00	-152.10
		Base + Geom	9	336.64	12.44	0.00	-159.32
		Base + S.A.	6	342.40	18.20	0.00	-165.20
		Base + Wet + S.A.	7	342.59	18.39	0.00	-164.29
		Base + Juncus + S.A.	7	342.99	18.79	0.00	-164.49
		Base + NDVI + S.A.	7	344.33	20.13	0.00	-165.16
		Base + Wet	6	359.76	35.56	0.00	-173.88
		Base + Juncus	6	366.48	42.28	0.00	-177.24
		Base	5	367.11	42.91	0.00	-178.55
		Base + NDVI	6	369.06	44.86	0.00	-178.53
		Base + Geom + S.A.	10	324.20	0.00	1.00	-152.10
Virginia Rail	2009	Base + Geom	9	338.55	0.00	0.31	-160.27
		Base + NDVI	6	339.06	0.51	0.24	-163.53
		Base + Geom + S.A.	10	340.13	1.58	0.14	-160.06
		Base + NDVI + S.A.	7	340.33	1.78	0.13	-163.16
		Base	5	341.26	2.71	0.08	-165.63
		Base + Typha	6	342.18	3.63	0.05	-165.09
		Base + S.A.	6	342.73	4.19	0.04	-165.37
		Base + Typha + S.A.	7	343.73	5.19	0.02	-164.87
	2010	Base + Typha	6	319.52	0.00	0.54	-153.76
		Base + Typha + S.A.	7	319.88	0.36	0.45	-152.94
		Base	5	328.69	9.17	0.01	-159.34
		Base + S.A.	6	329.56	10.04	0.00	-158.78
		Base + NDVI	6	330.40	10.88	0.00	-159.20
		Base + NDVI + S.A.	7	331.20	11.68	0.00	-158.60
		Base + Geom	9	335.91	16.39	0.00	-158.95
		Base + Geom + S.A.	10	336.36	16.84	0.00	-158.18
	2012	Base + Typha + S.A.	7	437.94	0.00	0.37	-211.97
		Base + Geom + S.A.	10	438.35	0.41	0.30	-209.17
		Base + Typha	6	439.85	1.92	0.14	-213.93
		Base + Geom	9	441.38	3.44	0.07	-211.69
		Base + S.A.	6	441.80	3.86	0.05	-214.90
		Base	5	443.01	5.07	0.03	-216.50
		Base + NDVI + S.A.	7	443.67	5.73	0.02	-214.83
		Base + NDVI	6	444.91	6.97	0.01	-216.45
	2014	Base + Wet + S.A.	7	385.68	0.00	0.77	-185.84
		Base + Typha + S.A.	7	388.83	3.14	0.16	-187.41
		Base + Wet	6	390.57	4.89	0.07	-189.29

	Base + S.A.	6	396.02	10.34	0.00	-192.01
	Base + NDVI + S.A.	7	397.84	12.15	0.00	-191.92
	Base + Geom + S.A.	10	400.59	14.91	0.00	-190.29
	Base + Typha	6	402.36	16.68	0.00	-195.18
	Base	5	410.64	24.95	0.00	-200.32
	Base + NDVI	6	412.56	26.88	0.00	-200.28
	Base + Geom	9	414.29	28.60	0.00	-198.14
	Base + Wet + S.A.	7	385.68	0.00	0.77	-185.84
	Base + Wet + S.A.	7	438.55	0.00	1.00	-212.28
	Base + Wet	6	454.23	15.67	0.00	-221.11
	Base + Typha + S.A.	7	457.04	18.48	0.00	-221.52
	Base + NDVI + S.A.	7	460.04	21.49	0.00	-223.02
	Base + Geom + S.A.	10	460.59	22.04	0.00	-220.30
2016	Base + S.A.	6	460.60	22.05	0.00	-224.30
	Base + Geom	9	486.21	47.66	0.00	-234.11
	Base + Typha	6	487.01	48.46	0.00	-237.51
	Base	5	489.82	51.26	0.00	-239.91
	Base + NDVI	6	489.83	51.27	0.00	-238.91
	Base + Wet + S.A.	7	438.55	0.00	1.00	-212.28
	Base + Wet	6	460.59	0.00	0.67	-224.30
	Base + Wet + S.A.	7	462.05	1.46	0.33	-224.03
	Base	5	492.09	31.50	0.00	-241.05
	Base + Typha	6	492.11	31.52	0.00	-240.06
	Base + S.A.	6	492.55	31.96	0.00	-240.27
2018	Base + Typha + S.A.	7	493.21	32.61	0.00	-239.60
	Base + NDVI	6	493.74	33.15	0.00	-240.87
	Base + NDVI + S.A.	7	494.17	33.58	0.00	-240.09
	Base + Geom	9	497.01	36.42	0.00	-239.50
	Base + Geom + S.A.	10	498.03	37.44	0.00	-239.02
	Base + Wet	6	460.59	0.00	0.67	-224.30

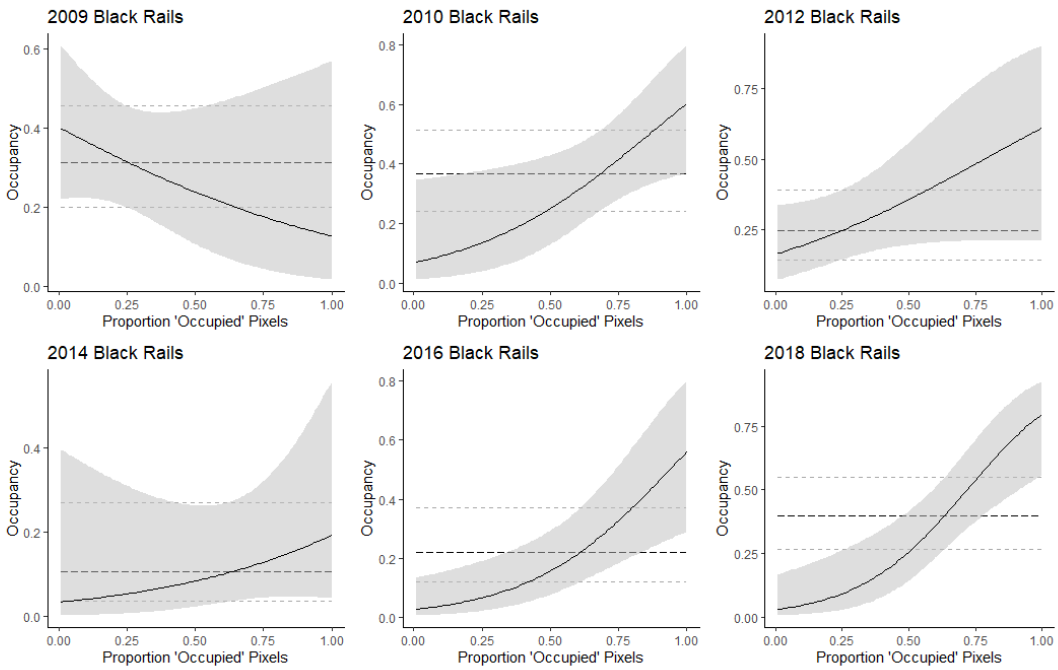


Figure 3.4. The effects of the proportion of pixels classified as "occupied" using a spectral habitat association classifier for Black Rails on a slope wetland with > 25% Juncus cover and all other characteristics held to their mean value.

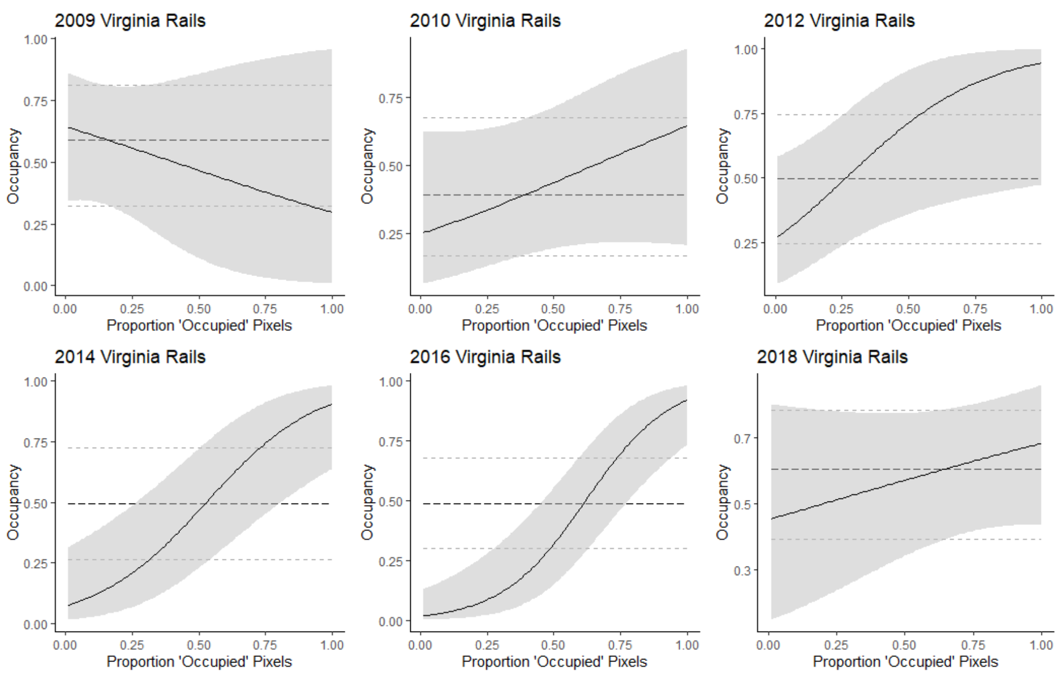


Figure 3.5. The effects of the proportion of pixels classified as "occupied" using a spectral habitat association classifier for Virginia Rails on a fringe wetland with > 25% Typha cover and all other characteristics held to their mean value.

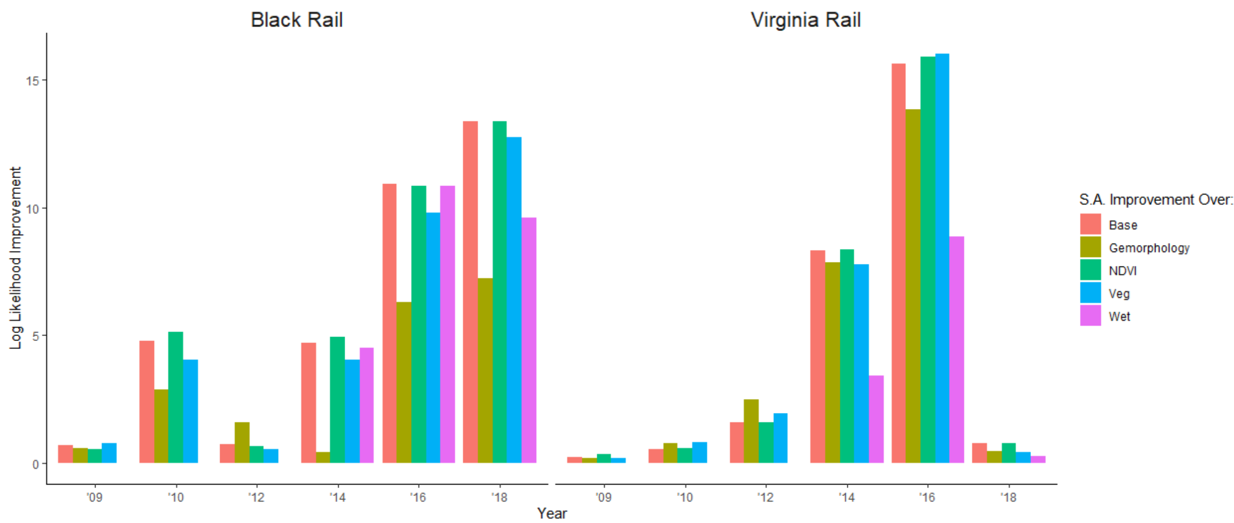


Figure 3.6. Change in Log Likelihood when adding spectral habitat association to the base model (red), geomorphology model (gold), NDVI model (green), vegetation model (blue), and wetland wetness model (purple) for occupancy models between 2009-2018.

3.4.3 Occupancy Prediction at Novel Wetlands

I detected Black Rails at 3/19 (16%) of novel wetlands. One occupied novel wetland was located within the core study area, but the other two occupied wetlands occurred ~45km from the core study area. The occupancy model including spectral habitat association percentage from 2018 (AICc = 19.55) was slightly better than the null model (AICc = 20.57), although both models were competitive. However, model MCC indicated that spectral habitat association was an good predictor (MCC = 0.57). Wetlands with Black Rails had a higher proportion of pixels classified as similar to occupied habitat (Fig. 3.7). Only one unoccupied wetland had a higher proportion of pixels classified as occupied than the three occupied wetlands.

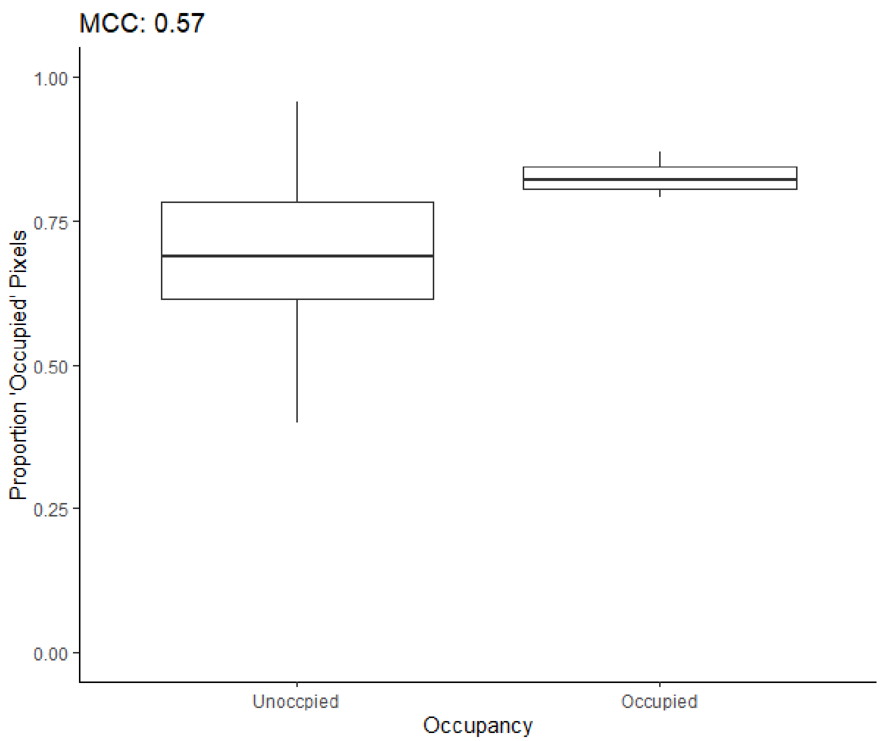


Figure 3.7. Observed Black Rail occupancy at 19 previously un-surveyed wetlands in 2019 in the Sierra Nevada Foothills of California. Spectral habitat association classification was based on known wetlands classified in 2018. MCC value denotes Matthews' Correlation Coefficient.

3.5 Discussion

Spectral habitat association was an effective and informative method of characterizing wetland occupancy for both Black and Virginia Rails. It accurately identified occupied wetlands using raw spectral reflectance and was frequently informative even when accounting for previously known geophysical predictors of occupancy (Richmond et al. 2010a, b; Van Schmidt et al. 2019, Van Schmidt and Beissinger 2020). Using spectral habitat association, in the absence of habitat data collected on the ground, I were able to accurately discriminate between occupied and unoccupied wetlands at novel sites never surveyed previously.

3.5.1 Comparison with Ground-truthed Metrics

Spectral habitat association contained similar information to other habitat metrics collected on the ground, but the habitat metric varied by species. For Black Rails, spectral habitat association was relatively similar to geomorphology, whereas for Virginia Rails, spectral habitat association was relatively similar to wetland wetness. However, the inclusion of those covariates in predictive models did not negate the benefit of including spectral habitat associations in the same models. It is unclear why the covariates that partially reduced the effectiveness of spectral habitat association varied by species. However, because spectral habitat association is a metric defined by animal presence, it is therefore a proxy for what is important for each rail species in each year and those factors can differ (Richmond et al. 2010b). Black and Virginia Rails, although closely related, differ in mobility, foraging strategies, and water depth preferences (Eddleman et al. 1994, Conway 1995, Richmond et al. 2010b). It is possible that some of these basic life history traits may drive what habitat characteristics are correlated with spectral habitat association. The exact habitat characteristic measured by spectral habitat association is likely an amalgam of characteristics solely dependent on the spectral reflectance of locations individuals occupy and therefore is likely to differ between species and years, depending on what habitat requirements each species is trying to meet at that particular point in time. By understanding spectral habitat association, ecological studies may be able to use remote sensing as a proxy for some key habitat metrics, which may reduce the need for field surveys.

3.5.2 Remote Monitoring

Spectral habitat association can be used to improve population monitoring by associating occupancy with reflectance data to predict habitat quality and occupancy across a broad area for relatively little cost when compared with ground surveys. I used spectral habitat association to identify wetlands that were likely to be occupied by Black Rails using only remotely sensed data. This method could prove to be valuable for predicting species occupancy across wide areas where data are difficult to gather on the ground. Spectral habitat association could be expanded and used to assess biodiversity of entire species assemblages across a large scale if enough presence/absence data is gathered (Nagendra 2001, Kerr and Ostrovsky 2003). Spectral habitat association could also be used to better inform population trends on a changing landscape. Traditional methods of assessing population trends during periods of environmental change rely on predicting population responses to changes in broad land-cover land-use categories (Nagendra 2001, Turner 2014, Geller et al. 2017). This method could be used to predict occupancy in a more nuanced manner that accounts for species habitat preferences and minimizes *a priori* assumptions about the habitat characteristics required for a species.

3.5.3 Study Considerations and Applications

Unlike data collected on the ground, spectral habitat association is limited by the availability and characteristics of remote sensing products. My study system necessitated the use of very high-resolution data to perform analyses, because study sites were highly heterogenous and study patches were small. Commonly used remote sensing products, such as 30m resolution LANDSAT data, would be inappropriate for this study design because my wetlands were small and frequently covered only one or two pixels, and the spectral signature of wetlands would at least partially be masked by the surrounding matrix habitat. Although high resolution sensors are becoming increasingly common (Finer et al. 2018), they are still typically limited to commercial companies and data is often expensive to acquire (Toth and Jóźków 2016). One limitation of using high resolution imagery is that high resolution sensors often have low return rates. NAIP datasets are collected approximately every two years, typically only during the summer months. Due to variation in the timing and quality of remote sensing data, it may not always feasible to apply classification algorithms between years and sensors. However, alternatives for data collection exist, such as drone or unmanned aerial vehicle sensor platforms (Tang and Shao 2015, Dronova et al. 2021). By using on-demand sensors, spectral habitat association data could be collected at the ideal resolution and timing. Despite these data limitations, spectral habitat association can be a powerful tool for assessing occupancy of species remotely, especially as technological advancements increase the prevalence of high-resolution spectral data (Nagendra 2001, Kerr and Ostrovsky 2003, Rose et al. 2015, Toth and Jóźków 2016).

Remote classification is a common and well-established suite of methods that vary in the amount of supervision and data assumptions (Jensen 2005, Schowengerdt 2012). Spectral habitat association requires classifying data using known information classes (in this case, occupancy status), so would not be appropriate for an unsupervised classification method. Skidmore (1989) noted that accurate classification of a landscape required the image analyst to have knowledge of the geography and spectral properties of the region. In the case of spectral habitat association, the study species acts as the image analyst in delineating exactly where the information classes of interest (i.e., occupied and unoccupied habitat) occur. Thus, implicit biases on the part of the image analyst are rendered moot, as the classification is driven by animal presence and absence. There are a number of classification methods used for supervised classification (Schowengerdt 2012) or multidimensional clustering (Chen et al. 2012), many of which could potentially improve the differentiation between occupied and unoccupied classes.

A consideration for future study is that the effectiveness of spectral habitat association is likely dependent on the focal species. Black and Virginia Rails are habitat specialists that are constrained to wetlands, allowing us to identify occupied habitat more easily. For example, I never risked detecting individuals inhabiting the surrounding matrix, a case which would be common in many other mobile species that use multiple habitat types. Similarly, Black and Virginia Rails both use habitat that is not obscured by non-habitat strata. The wetland vegetation that these species require is almost always directly observable with a remote sensors, in contrast with species using sub-canopy strata in forested landscapes. However, previous studies have used spectral habitat association to accurately characterize habitat for generalists, suggesting that there may be broader applications depending on analysis method and species (Remelgado et al. 2018).

Spectral habitat association can be an effective method of predicting occupancy across a large area (Skowronek et al. 2017, Remelgado et al. 2018). As the cost of acquiring high-resolution remote imagery decreases, it could be an important tool for assessing habitat suitability in the future. It is increasingly important to understand the global patterns of biodiversity and detect species loss across the world in real-time (Scholes et al. 2008). Spectral habitat association may assist in predicting occupancy and identifying changing conditions that could be indicative of habitat and biodiversity loss using remotely acquired data.

Conclusion

Summary of Key Results

In this dissertation, I investigated wetland bird occupancy in the Sierra Nevada foothills to better understand animal movement during the breeding season, the effect of habitat spillover on avian assemblages, and to identify quality habitat using remote sensing data. My results describe patterns in avian occupancy in a complex, working landscape that is a mix of natural and artificial wetlands, agriculture, forest, and grassland. In this section, I will summarize key findings from my dissertation chapters and discuss directions for future research.

My first chapter focused on Black and Virginia Rail movement during the breeding season and the violations of the closure assumptions that resulted from that movement. I found that both species significantly violated the closure assumption. Using the data collected here, I demonstrated that the majority of perceived absences for each species were true absences (i.e., no individuals were available to be detected) rather than the false absences assumed by the occupancy modeling framework. However, despite significant violations of the closure assumption, overall occupancy estimates were not significantly affected by closure violations. I observed differing patterns of occupancy changes between the two species of rails. Black Rails tended to colonize wetlands over time, whereas Virginia Rails had similar colonization and abandonment rates over time. Black Rails appeared to be less sensitive to environmental change than Virginia Rails, and their patterns of movement may have been driven by memory of habitat quality in the previous year.

My second chapter investigated the spillover effect on the complex landscape of the Sierra Nevada foothills and how the characteristics of wetlands affected avian occupancy across the entire avian assemblage. I found bi-directional spillover, with matrix characteristics influencing the occupancy of wetland obligates and wetland characteristics influencing not only wetland obligates, but also facultative and matrix species. My results demonstrate the importance of landscape context in the study of patch occupancy and emphasize the importance of considering surrounding matrix patches when implementing conservation efforts. I also demonstrated the importance of both public and private land management strategies and identified the characteristics that drove biodiversity across the landscape.

In my final chapter, I studied the relationship between raw spectral reflectance from aerial imagery and occupancy for Black and Virginia Rails. In this chapter, I hypothesized that some of the habitat characteristics that drive occupancy for these species would be detectable using maximum-likelihood classification of occupied and unoccupied wetlands. I found that in most years of the study, unoccupied wetlands could be differentiated from occupied wetlands using only spectral habitat association. I also demonstrated that you could use spectral habitat association to predict occupancy at entirely novel sites that had never previously been surveyed, suggesting there may be the potential to remotely assess habitat and predict occupancy across large areas. Spectral habitat association performed better than most habitat characteristics collected on the ground, as well as a more standardized remote sensing index (NDVI) at predicting wetland occupancy. However, I did find that spectral habitat association was less predictive of Black Rail occupancy when paired with wetland geomorphology and less predictive of Virginia Rail occupancy when paired with percent wetness. This suggests that some of the characteristics driving the predictive power of spectral habitat association estimate were made up of those two wetland characteristics.

Future Research Directions for Closure Studies

The effect of closure violations has recently come under a spotlight for management and conservation (Berigan et al. 2019). Species managers have been grappling with the meaning of animal presence on a landscape and how best to conserve a species when its use of a habitat varies from breeding to passing through. My research suggests that rails are likely using habitat for differing purposes during the breeding season. Understanding what those uses are and how best to detect breeding and non-breeding use of habitat may be vitally important for conservation strategies. Most researchers who use occupancy models assume closure and treat violations of that assumption as a nuisance (Chapter 1). However, movement is a dangerous behavior for most species (Bonte et al. 2012), so we must assume that there is a biologically important reason animals are choosing to move between patches. By understanding closure violations and the movements that cause them, researchers will have a more complete knowledge of the varying habitat requirements of species over time (Bonte et al. 2012, Westcott et al. 2012, Frey et al. 2016).

Closure violations of occupancy models represent not only a biological problem, but also a mathematical problem (Rota et al. 2009). Recent advances in occupancy variations include methods of relaxing or avoiding the closure assumption by allowing staggered entry and exit to the study system (Kendall et al. 2013), or calculating detection probability in single visit using time to detection (Halstead et al. 2018, 2021). However, these variations of occupancy models are used less than the traditional methods (MacKenzie et al. 2018). Currently, the only method for testing for closure violations is the robust design method described by Rota et al. (2009). However, that method requires substantially increased effort over the standard occupancy methodology, which makes it unattractive to many researchers. Given the importance of understanding closure violations, it would be valuable for future research to investigate alternative closure tests or methods allowing increased relaxation of the assumption.

Future Research Directions For Multispecies Occupancy Models and Spillover

Multispecies occupancy models are a variation of occupancy models that use Bayesian techniques to estimate hyperparameters for entire assemblages of species (Dorazio and Royle 2005, Zipkin et al. 2009, Iknayan et al. 2014). They allow researchers to improve inferences about rarely detected species by pooling detections across multiple species (Iknayan et al. 2014). My research utilizes multispecies occupancy models to assess the effect of habitat parameters on not only the entire avian assemblage, but also different groups within that assemblage. Dividing species by feeding guild, morphology, physiology, and genetic relatedness is very common in broad analyses of species and can yield inferences unique to those groups. My research demonstrated similar patterns, as I was able to draw inferences about habitat characteristics uniquely correlated with how wetlands are used by different groups of birds. Future research on multispecies occupancy may benefit from using interactions and other methods to divide hyperparameter effects across groups of animals with differing life histories.

There is no doubt that there is a strong relationship between occupancy and microhabitat characteristics for most species (Brown 1988, Rodewald and Yahner 2001, McClure et al. 2012), as microhabitat and patch-level characteristics are highly influential in defining a niche (Cornell and Lawton 1992, Holt 2009). However, recent research has also focused on the importance of broad-scale characteristics such as climate and landscape composition (Chambert et al. 2015, Frey et al. 2016, Boron et al. 2019, Carscadden et al. 2020, Morante-Filho et al. 2021). Just as creating a perfect breeding habitat and ignoring non-breeding requirements can lead to population bottlenecks, focusing too much on the individual habitat patches of a species and neglecting the landscape context may be detrimental to conservation. Spillover is a complex suite of processes that transfer energy and material between separate habitats (Blitzer et al. 2012, Lucey and Hill 2012, Tscharntke et al. 2012, Barros et al. 2019). The mechanisms that drive spillover are not well studied; it would be valuable to better understand the underlying processes driving spillover to better be able to account for and understand what causes matrix habitat to have significant effects on patch occupancy.

Future Research Directions for Spatial Habitat Association

Spectral habitat association is a method of naively classifying habitat. It is set apart from traditional habitat classification or habitat indices in that the categories used to process images are based on animal presence rather than known habitats or *a priori* assumptions about which indices are likely to be important. Using remote sensing to directly predict occupancy is a relatively understudied process (Nagendra 2001), so there is ample space for future research to explore. One of the primary research directions that could be explored is different classification methods. I selected maximum likelihood classification, as it is well understood and commonly used. However, there are a number of binary classification algorithms that should be tested to determine if efficacy and predictive power can be improved (Kotsiantis 2007, Lu and Weng 2007, Kirasich et al. 2018). Specifically, it would likely be valuable to explore emerging techniques in machine learning classification as an alternative to more traditional classification techniques.

In addition to mechanistic questions, spectral habitat association has a wide range of biological questions that could be explored with future research. For example, employing spectral habitat association to monitor and predict the distribution of animals in difficult terrain or wilderness areas could be a highly valuable technique for conservation (Rocchini et al. 2016, Duro et al. 2016). By accurately predicting species occupancy using only remote sensing, researchers will be able to quickly assess population trends without needing to invest the effort needed to monitor inaccessible populations from the ground. It also may be possible to use spectral habitat association to identify when a non-habitat population limitation is present. For example, in my dissertation, the effectiveness of spectral habitat association as a classifier varied annually. This annual variation could be due to annual fluctuations in data collection or a change in habitat that was uniform across all wetlands. However, it could also be an indication that the wetlands animals were using were being limited by a factor that was not capturable in remotely sensed imagery, such as disease or predation pressures. If a study system was able to assume that a spectral habitat association classifier was relatively stable across time and there were no sensor changes, it may be possible to identify when a population was being limited by a characteristic that was not detected by a remote sensor.

Conservation Implications in the Sierra Nevada Foothills

As demonstrated by the recent completion of the Nevada County breeding bird atlas, there is a demonstrable interest in the avifauna of the Sierra Nevada foothills (Rose and Rose 2020). The landscape of the foothills region is comprised mostly of private property, which is not regularly monitored by conservation entities. The landowners of the Sierra Nevada foothills often act as sole stewards and decision-makers in regards to conservation decisions (Van Schmidt et al. 2019, 2021). The avifauna of the Sierra Nevada foothills are under numerous threats, including fire, drought, climate change, and disease (Huntsinger et al. 2017, Van Schmidt et al. 2021). In this dissertation, I used occupancy models to better understand animal movement, assemblage-level habitat associations, and the power of remote sensing for predicting presence and absence. Here, I will briefly outline the conservation implications of my research.

My investigation of closure violations in Black and Virginia Rails demonstrated that conservation needs to account for frequent movement between wetland patches for both species and should acknowledge potential differences in use types between wetlands. An effort should be made to identify breeding habitat, especially potential source wetlands, for priority conservation. Further, it may be important to identify the proximate causes of animal movement to better understand why some wetlands may be abandoned during the breeding season and what could be done to prevent the potential failure of breeding pairs at some wetlands.

My research into assemblage occupancy in the Sierra Nevada foothills demonstrates that occupancy for many species is dependent on landscape context and habitat composition. I observed bi-directional spillover effects across the avian assemblage, with wetland obligate occupancy depending on the landscape composition around the wetland and non-obligate occupancy depending on wetland characteristics. Using these results, conservation of the avian assemblage in the Sierra Nevada foothills needs to account for landscape composition at a broad scale and should not focus solely on patch characteristics.

Remote sensing may be a valuable tool for assessing the biodiversity of the Sierra Nevada foothills. In chapter 3, I accurately predicted Black Rail occupancy at novel wetlands within our study area using only remote sensing data. Spectral habitat association could be implemented across the entire region to predict occupancy at all wetlands, regardless of accessibility. As Black Rails are currently listed as threatened by the state of California, there is an interest in understanding overall population trends. Predicting occupancy across the entire state-wide distribution using remote sensing could inform conservation and management plans and better detect changes in populations. Remote sensing may also be useful for identifying unknown or poorly delineated populations of species of conservation interest.

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Appendices

Appendix S1.1: Supplementary information for Chapter 1

Table S1.1. Peer reviewed publications citing (Rota et al. 2009) that implemented occupancy models using data collected in the field and were published between 2009 and November 2020. For each publication, I report sampling scale and whether the study assumed closure or tested closure.

Publication	Assume Closure	Sampling Scale	Closure Test Performed	Notes
(Betts et al. 2010)	No	Point	Yes	Comparison of single-season and multi-season models using AIC
(Fleishman et al. 2017)	No	Transect	Yes	Staggered entry/exit model (Kendall et al. 2013)
(Hansen et al. 2017)	No	Transect	Yes	Likelihood ratio test (Rota et al. 2009)
(Webber et al. 2013)	No	Grid Cell	Yes	Comparison of single-season and multi-season models using model weight
(Wilson et al. 2020)	No	Point	Yes	Staggered entry/exit model (Kendall et al. 2013)
(Albrecht-Mallinger and Bulluck 2016)	No	Patch	No	Temporary emigration model used, but closure was not tested
(Harju and Cambrin 2019)	No	Transect	No	Developed new model using robust design to help estimate latent occupancy of cryptic species.
(Goldingay 2019)	No	Transect	No	Relaxed definition of occupancy
(Neubauer and Sikora 2013)	No	Patch	No	Robust design, but closure was not tested
(Ober et al. 2020)	No	Paired Points	No	Used separate detection histories for each period with site as a random effect
(Otto and Roloff 2012)	No	Point	No	Used robust design + dynamic occupancy model across 9 minutes, but closure was not tested
(Sidie-Slettedahl	No	Point	No	Each species exhibited in-season

et al. 2015)				colonization using robust design, but closure was not tested
(Acevedo et al. 2015)	Yes	Patch	No	
(Acevedo et al. 2020)	Yes	Patch	No	
(Athreya et al. 2015)	Yes	Grid Cell	No	
(Aubry et al. 2018)	Yes	Point	No	
(Băncilă et al. 2017)	Yes	Patch	No	
(Banks-Leite et al. 2014)	Yes	Grid Cell	No	
(Beaudrot et al. 2018)	Yes	Point	No	Minimized survey period
(Berigan et al. 2019)	Yes	Point	No	
(Blanc et al. 2014)	Yes	Point	No	
(Bled et al. 2013)	Yes	Grid Cell	No	
(Chaves et al. 2017)	Yes	Point	No	Removal model - closure assumed over 10 minute point count
(Cove et al. 2018)	Yes	Point	No	Minimized survey period
(Crates et al. 2017)	Yes	Point	No	Minimized survey period
(Devoe et al. 2015)	Yes	Point	No	
(Dinsmore et al. 2019)	Yes	Transect	No	Minimized survey period
(Farhadinia et al. 2018)	Yes	Transect	No	Minimized survey period
(Farris et al. 2019)	Yes	Transect	No	Minimized survey period

(Fidino et al. 2020)	Yes	Point	No	
(Fisher et al. 2016)	Yes	Point	No	
(Fisher et al. 2020)	Yes	Point	No	Relaxed closure assumption
(Frey et al. 2016)	Yes	Point	No	Minimized survey period
(Gottlieb et al. 2017)	Yes	Transect	No	Paired surveys to minimize closure period to a visit
(Gray et al. 2013)	Yes	Transect	No	
(Gray 2012)	Yes	Point	No	
(Harings and Boeing 2014)	Yes	Patch	No	Minimized survey period
(Heim et al. 2017)	Yes	Point	No	
(Heim et al. 2019)	Yes	Point	No	
(Herse et al. 2017)	Yes	Transect	No	Minimized survey period
(Homyack et al. 2014)	Yes	Transect	No	
(Homyack et al. 2016)	Yes	Transect	No	
(Horn and Gervais 2018)	Yes	Patch	No	
(Hunt et al. 2012)	Yes	Grid Cell	No	
(Iknayan and Beissinger 2020)	Yes	Transect	No	Used similar methods for two different eras to maintain a consistent closure bias
(Keane et al. 2012)	Yes	Grid Cell	No	Minimized survey period
(Latif et al. 2018)	Yes	Transect	No	

(Latif et al. 2020)	Yes	Grid Cell	No	Minimized survey period and used removal design
(Lee and Carroll 2014)	Yes	Point	No	
(Leu et al. 2017)	Yes	Point	No	
(Lima et al. 2020)	Yes	Point	No	Minimized survey period
(Lituma and Buehler 2020)	Yes	Point	No	Used removal design
(Loffland et al. 2017)	Yes	Point	No	Biological explanation for closure assumption remaining valid
(Louvrier et al. 2018)	Yes	Grid Cell	No	Assumed closure for periods of stable populations
(Majgaonkar et al. 2019)	Yes	Grid Cell	No	
(Marescot et al. 2020)	Yes	Grid Cell	No	Relaxed definition of occupancy
(Martin and Fahrig 2012)	Yes	Point	No	
(McClure and Hill 2012)	Yes	Point	No	Minimized survey period
(McManamay et al. 2014)	Yes	Patch	No	Biological explanation for closure assumption remaining valid
(Mertes et al. 2020)	Yes	Grid Cell	No	Assumed high territoriality
(Metcalf et al. 2019)	Yes	Point	No	Noted locations of observations to assess closure
(Moreira-Arce et al. 2016)	Yes	Point	No	Minimized survey period
(Moreno-Opo et al. 2015)	Yes	Transect	No	
(Northrup and Gerber 2018)	Yes	Point	No	
(O'Connor et al. 2017)	Yes	Grid Cell	No	Minimized survey period
(Okes and	Yes	Transect	No	Minimized survey period

O'Riain 2017)				
(Olea and Mateo-Tomás 2011)	Yes	Point	No	Minimized survey period
(Panthi et al. 2017)	Yes	Transect	No	
(Penjor et al. 2018)	Yes	Point	No	Minimized survey period
(Pickens and King 2014)	Yes	Point	No	
(Reichert et al. 2017)	Yes	Point	No	Minimized survey period
(Rodtka et al. 2015)	Yes	Patch	No	Irregular sampling reduces directional biases
(Sadoti et al. 2013)	Yes	Grid Cell	No	Used only study areas which minimized closure violations
(Schank et al. 2019)	Yes	Point	No	Minimized survey period
(Schmidt et al. 2013)	Yes	Patch	No	Biological explanation for closure assumption remaining valid
(Si et al. 2018)	Yes	Transect	No	Relaxed definition of occupancy
(Socolar et al. 2017)	Yes	Transect	No	Explained that closure violations are unlikely to impact modeling of phenology
(Soroye et al. 2020)	Yes	Grid Cell	No	Closure violations unlikely to effect study design
(Steen et al. 2014)	Yes	Point	No	
(Tan et al. 2017)	Yes	Point	No	Minimized survey period
(Thapa et al. 2017)	Yes	Grid Cell	No	
(Tingley and Beissinger 2013)	Yes	Transect	No	Used similar methods for two different eras to maintain a consistent closure bias
(Tingley et al. 2012)	Yes	Transect	No	Post-hoc data management to reduce the impact of closure violations

(Tingley et al. 2020)	Yes	Point	No	
(van Strien et al. 2013a)	Yes	Transect	No	Minimized survey period
(van Strien et al. 2013b)	Yes	Point	No	Minimized survey period
(Walpole et al. 2012)	Yes	Transect	No	Relaxed definition of occupancy
(Wang et al. 2019)	Yes	Transect	No	Minimized survey period
(Webb et al. 2014)	Yes	Point	No	Minimized survey period

Table S1.2. Peer reviewed publications that implemented occupancy models using the model proposed by Kendall et al. (2013) using data collected in the field that were published between 2013 and November 2020. For each publication, I report whether that publication tested for closure and sampling scale.

Publication	Closure Test Performed	Sampling Scale
(Arbeiter et al. 2017)	No	Point
(Arbeiter et al. 2018)	No	Point
(Bardiani et al. 2017)	Yes	Point
(Campanaro et al. 2016)	Yes	Transect
(De Zan et al. 2017)	Yes	Transect & Point
(Fleishman et al. 2017)	Yes	Transect
(Graitson et al. 2018)	Yes	Patch
(Hardersen et al. 2017)	Yes	Point
(Pavlik et al. 2017)	No	Transect
(Wilson et al. 2020)	Yes	Point

Table S1.3. Datasets, statistical tests, models, and hypotheses tested to assess the impact of closure violations on two rail species.

Hypothesis Tested	Dataset(s) Used	Models Used	Statistical Test
Closure assumption was violated during the breeding season	Automated recording unit (ARU) recordings	Multiseason occupancy model and single season occupancy model	Likelihood ratio test comparing multiseason occupancy model with single season occupancy model
Closure violations were related to environmental characteristics	ARU recordings	Multiseason occupancy model	Evaluated colonization and extinction parameters using Akaike's information criterion
Closure violations biased estimates of detection probability and occupancy	ARU recordings, Call-playback surveys	Single season occupancy model (ARU data & Call-playback data), multiseason occupancy model (ARU data)	1) Compared occupancy estimates between datasets and model types 2) Validated absences during call-playback surveys using ARU recordings and compared parameter estimates between models with all absences and models with likely absences removed

Table S1.4. Description of the four sites where rails were detected during playback surveys but not by ARUs including description of detection, likely cause of detection failure and changes to encounter histories after data review.

Rail Detected	Distance from detection to ARU	Description	Likely cause of detection failure	Initial Encounter Histories	Revised Encounter Histories
Black rail	>100m	Between the 2nd and 3rd visits, the area of the wetland expanded substantially. Black rail was found detected in the 3rd visit in the area of wetland expansion outside of ARU coverage. Censored third visit of playback history.	Incomplete ARU coverage.	ARU – 000 PB – 001	ARU – 000 PB – 00-
Black rail	40m	Black rail detected in only playback visit, 7 days prior to ARU deployment. Estimated rail location was in deeper water than is typical for black rails. Inexperienced surveyor in first week of unsupervised surveys. Rail location could also have been further away than was estimated and outside of ARU recording range.	Unknown – possible misidentification or incomplete site coverage with ARUs.	ARU – 000 PB – 1--	No change

Virginia rail	20m	Virginia rail detected in 1st and 2nd playback surveys. During review of ARU recordings, common gallinule (*Gallinula galeata*) detected responding to Virginia rail vocalizations. Surveyors were inexperienced with rail identification. No common gallinule presence noted in playback data.	Misidentification of common gallinule as Virginia rail	ARU – 000 PB – 110	ARU – 000 PB – 000
Virginia rail	~10m	Virginia rail detected from > 100m for both detections and location was estimated as near the location of ARU deployment. Surveyor with 4 years experience.	Unknown – Unlikely to be closure violation, misidentification, or ARU coverage.	ARU – 000 PB – 110	No change

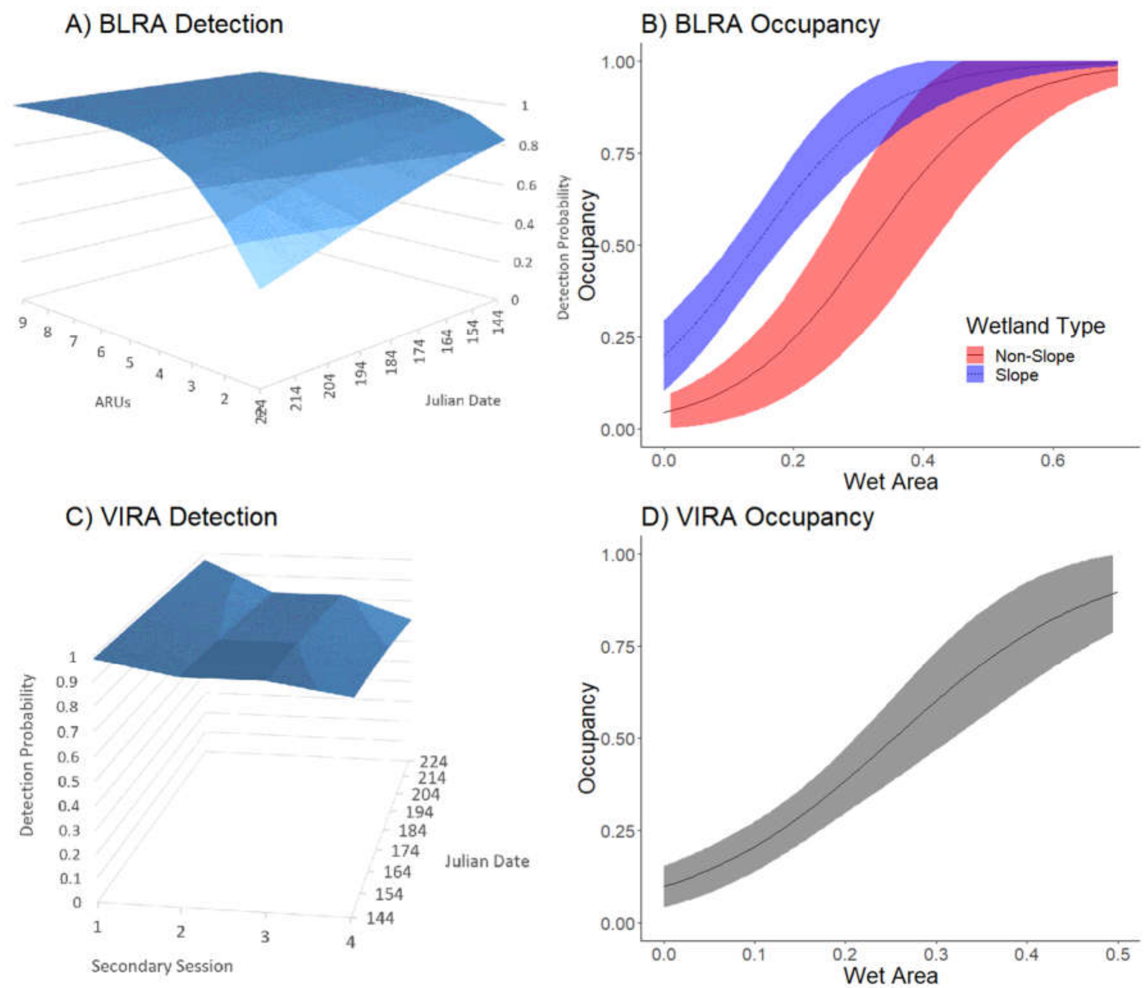
Table S1.5. AIC results of occupancy models explaining variation in initial occupancy and detection for black rails. All models included wet area, isolation, and slope as explanatory variables for both colonization and extinction. AIC: Akaike's information criterion; ΔAIC: change in AIC; *k*: number of modeled parameters; AIC wt: Akaike weight.

Occupancy	Detection	*k*	AIC	Δ AIC	AIC wt
Wet Area + Slope	ARUs + Julian Date	14	284.21	0	0.3
Wet Area + Slope	ARUs + Julian Date + AM/PM	15	284.69	0.48	0.24
Wet Area + Slope	ARUs + Julian Date + Secondary Session	17	285.85	1.64	0.13
Wet Area	ARUs + Julian Date	13	286.45	2.24	0.1
Wet Area	ARUs + Julian Date + AM/PM	14	286.92	2.71	0.08
Wet Area + Slope	ARUs	13	287.53	3.32	0.06
Wet Area	ARUs + Julian Date + Secondary Session	16	288.09	3.88	0.04
Wet Area	ARUs	12	289.76	5.55	0.02
Wet Area	ARUs + AM/PM	13	290.27	6.06	0.01
Wet Area	ARUs + Secondary Session	15	291.52	7.31	0.01
Wet Area + Slope	Null	12	317.32	33.11	0
Wet Area	Julian Date	12	318.19	33.98	0
Wet Area	Null	11	319.56	35.35	0
Wet Area	AM/PM	12	320.21	36	0
Wet Area	Secondary Session	14	321.71	37.5	0
Slope	Null	11	327.81	43.6	0
Null	Null	10	329.07	44.86	0

Table S1.6. AIC results of occupancy models explaining variation in initial occupancy and detection for Virginia rails. All models included wet area, isolation, and slope as explanatory variables for both colonization and extinction. AIC: Akaike's information criterion; ΔAIC: change in AIC; *k*: number of modeled parameters; AIC wt: Akaike weight.

Occupancy	Detection	*k*	AIC	Δ AIC	AIC wt
Wet Area	Secondary Session	14	250.25	0	0.25
Wet Area	Secondary Session + Julian Date	15	250.27	0.02	0.24
Wet Area	AM/PM	12	251.73	1.48	0.12
Wet Area + Slope	Secondary Session	15	251.92	1.67	0.11
Wet Area	Secondary Session + ARUs	15	252.17	1.92	0.09
Wet Area	Secondary Session + AM/PM	15	252.23	1.98	0.09
Wet Area	Null	11	253.82	3.58	0.04
Wet Area	Julian Date	12	254.66	4.41	0.03
Wet Area + Slope	Null	12	255.45	5.2	0.02
Wet Area	ARUs	12	255.69	5.44	0.02
Null	Null	10	264.39	14.14	0
Slope	Null	11	266.18	15.93	0

Figure S1.1. Black rail (**A**) detection probability as a function of Julian date and number of ARUs (SE omitted for clarity) and (**B**) initial occupancy as a function of log area and wetland type and Virginia rail (**C**) detection probability as a function of secondary session and Julian date (SE omitted for clarity) and (**D**) initial occupancy as a function of wet area (± SE).



Appendix S2.1: Supplementary information for Chapter 2

Table S2.1. Species detected using automated recording units placed in wetlands in the Sierra Nevada foothills, California, USA.

Species	Scientific Name	Community	Listing Status
American Bittern	*Botaurus lentiginosus*	Obligate	
Belted Kingfisher	*Megaceryle alcyon*	Obligate	
Black Phoebe	*Sayornis nigricans*	Obligate	
Black Rail	*Laterallus jamaicensis*	Obligate	State Threatened
Canada Goose	*Branta canadensis*	Obligate	
Common Gallinule	*Gallinula galeata*	Obligate	
Common Yellowthroat	*Geothlypis trichas*	Obligate	
Great Blue Heron	*Ardea herodias*	Obligate	
Great Egret	*Ardea alba*	Obligate	
Green Heron	*Butorides virescens*	Obligate	
Mallard	*Anas platyrynchos*	Obligate	
Marsh Wren	*Cistothorus palustris*	Obligate	
Red-winged Blackbird	*Agelaius phoeniceus*	Obligate	
Virginia Rail	*Rallus limicola*	Obligate	
Willow Flycatcher	*Empidonax traillii*	Obligate	State Endangered
Wilson's Snipe	*Gallinago delicata*	Obligate	
Wood Duck	*Aix sponsa*	Obligate	
Yellow Warbler	*Setophaga petechia*	Obligate	State 2nd Priority Species of Concern
Yellow-breasted Chat	*Icteria virens*	Obligate	State 3rd Priority Species of Concern
Anna's Hummingbird	*Calypte anna*	Facultative	
Ash-throated Flycatcher	*Myiarchus cinerascens*	Facultative	
Barn Swallow	*Hirundo rustica*	Facultative	
Bewick's Wren	*Thryomanes bewickii*	Facultative	
Brewer's Blackbird	*Euphagus cyanocephalus*	Facultative	
Brown-headed Cowbird	*Molothrus ater*	Facultative	
Bullock's Oriole	*Icterus bullockii*	Facultative	
Bushtit	*Psaltriparus minimus*	Facultative	
Cliff Swallow	*Petrochelidon pyrrhonota*	Facultative	
European Starling	*Sturnus vulgaris*	Facultative	
Great Horned Owl	*Bubo virginianus*	Facultative	
Great-tailed Grackle	*Quiscalus mexicanus*	Facultative	
House Wren	*Troglodytes aedon*	Facultative	
Killdeer	*Charadrius vociferus*	Facultative	
Lazuli Bunting	*Passerina amoena*	Facultative	
Mourning Dove	*Zenaida macroura*	Facultative	
Northern Mockingbird	*Mimus polyglottus*	Facultative	
Northern Rough-winged	*Stelgidopteryx serripennis*	Facultative	

Swallow			
Oak Titmouse	*Baeolophus inornatus*	Facultative	
Red-shouldered Hawk	*Buteo lineatus*	Facultative	
Red-tailed Hawk	*Buteo jamaicensis*	Facultative	
Song Sparrow	*Melospiza lincolnii*	Facultative	
Tree Swallow	*Tachycineta bicolor*	Facultative	
Western Kingbird	*Tyrannus verticalis*	Facultative	
Wrentit	*Chamaea fasciata*	Facultative	
Acorn Woodpecker	*Melanerpes formicivorus*	Matrix	
American Crow	*Corvus brachyrynchos*	Matrix	
American Goldfinch	*Spinus tristis*	Matrix	
American Kestrel	*Falco sparverius*	Matrix	
American Robin	*Turdus migratorius*	Matrix	
Black-headed Grosbeak	*Pheucticus melanocephalus*	Matrix	
California Quail	*Callipepla californica*	Matrix	
California Scrub-Jay	*Aphelocoma californica*	Matrix	
California Towhee	*Melozone crissalis*	Matrix	
Cedar Waxwing	*Bombycilla cedrorum*	Matrix	
Common Raven	*Corvus corax*	Matrix	
Dark-eyed Junco	*Junco hyemalis*	Matrix	
Downy Woodpecker	*Dryobates pubescens*	Matrix	
Eurasian Collared-Dove	*Streptopelia decaocto*	Matrix	
Grasshopper Sparrow	*Ammodramus savannarum*	Matrix	State 2nd Priority Species of Concern
House Finch	*Haemorhous mexicanus*	Matrix	
House Sparrow	*Passer domesticus*	Matrix	
Lark Sparrow	*Chondestes grammacus*	Matrix	
Lesser Goldfinch	*Spinus psaltria*	Matrix	
Northern Flicker	*Colaptes auratus*	Matrix	
Nuttall's Woodpecker	*Dryobates nuttallii*	Matrix	
Osprey	*Pandion haliaetus*	Matrix	
Ring-necked Pheasant	*Phasianus colchicus*	Matrix	
Spotted Towhee	*Pipilo maculatus*	Matrix	
Swainson's Hawk	*Buteo swainsoni*	Matrix	
Western Bluebird	*Siala mexicana*	Matrix	
Western Meadowlark	*Sturnella neglecta*	Matrix	
Western Wood-Pewee	*Contopus sordidulus*	Matrix	
White-breasted Nuthatch	*Sitta carolinensis*	Matrix	
Wild Turkey	*Meleagris gallopavo*	Matrix	

Table S2.2. All hyperparameter and individual species parameter estimates from a multispecies occupancy model.

Assemblage	Species	Parameter	Est.	SD	Lower CI	Upper CI	Sample Size
All		Intercept	1.16	0.84	-0.44	2.84	9751
All		Detection Visit 1	-2.76	0.28	-3.31	-2.20	107451
All		Detection Visit 2	-2.30	0.28	-2.84	-1.75	155464
All		Detection Visit 3	-2.42	0.28	-2.96	-1.87	299400
All		Julian Date	-0.24	0.29	-0.81	0.32	153369
All		Area	0.40	0.39	-0.35	1.16	299400
All		Elevation	-0.45	0.47	-1.38	0.47	62936
All		Juncus	0.11	0.38	-0.64	0.86	4665
All		Typha	0.08	0.37	-0.63	0.80	24877
All		Slope	-1.37	0.73	-2.83	0.04	15745
All		Impoundment	-1.05	1.11	-3.23	1.12	14777
All		Fringe	-0.98	0.75	-2.48	0.46	6310
All		Fluvial	-1.27	0.78	-2.83	0.23	9573
All		% Wet	-0.33	0.37	-1.05	0.39	79996
All		Natural	-2.05	0.58	-3.18	-0.92	55181
All		Irrigated	-1.69	0.58	-2.84	-0.55	299400
All		Natural + Irrigated	-1.85	0.62	-3.08	-0.63	149360
All		Developed [100m]	-0.07	0.46	-0.98	0.85	13215
All		Forest [100m]	-1.63	0.85	-3.31	0.01	7558
All		Open [100m]	-2.37	1.11	-4.57	-0.24	6384
All		Wetland [100m]	-0.74	0.77	-2.26	0.76	8020
All		Developed [500m]	0.00	0.46	-0.89	0.90	73861
All		Forest [500m]	3.21	1.26	0.78	5.73	8503
All		Open [500m]	3.27	1.42	0.54	6.11	8307
All		Wetland [500m]	1.12	0.93	-0.67	2.97	17451
Matrix	ACWO	Detection Visit 1	0.26	0.03	0.20	0.33	151605
Obligate	AMBI	Detection Visit 1	0.28	0.04	0.20	0.37	109244
Matrix	AMCR	Detection Visit 1	0.09	0.03	0.04	0.15	299400
Matrix	AMGO	Detection Visit 1	0.01	0.01	0.00	0.03	86894
Matrix	AMKE	Detection Visit 1	0.03	0.02	0.00	0.07	299400
Matrix	AMRO	Detection Visit 1	0.31	0.05	0.21	0.42	299400
Facultative	ANHU	Detection Visit 1	0.01	0.01	0.00	0.03	213573
Facultative	ATFL	Detection Visit 1	0.12	0.04	0.06	0.21	39890
Facultative	BASW	Detection Visit 1	0.07	0.05	0.02	0.22	56889
Obligate	BEKI	Detection Visit 1	0.01	0.01	0.00	0.03	273995
Facultative	BEWR	Detection Visit 1	0.08	0.04	0.02	0.18	16005
Facultative	BHCO	Detection Visit 1	0.08	0.02	0.05	0.12	299400
Matrix	BHGR	Detection Visit 1	0.02	0.02	0.00	0.09	121753
Obligate	BLPH	Detection Visit 1	0.30	0.03	0.23	0.36	155112
Obligate	BLRA	Detection Visit 1	0.12	0.05	0.04	0.24	299400

Facultative	BRBL	Detection Visit 1	0.05	0.07	0.00	0.26	214743
Facultative	BUOR	Detection Visit 1	0.29	0.04	0.21	0.38	277098
Facultative	BUSH	Detection Visit 1	0.05	0.02	0.02	0.10	299400
Obligate	CANG	Detection Visit 1	0.08	0.03	0.04	0.14	299400
Matrix	CAQU	Detection Visit 1	0.26	0.03	0.20	0.31	299400
Matrix	CASJ	Detection Visit 1	0.15	0.03	0.10	0.21	299400
Matrix	CATO	Detection Visit 1	0.43	0.05	0.34	0.52	84007
Matrix	CEDW	Detection Visit 1	0.07	0.10	0.00	0.38	20101
Facultative	CLSW	Detection Visit 1	0.06	0.06	0.01	0.23	153108
Obligate	COMO	Detection Visit 1	0.07	0.03	0.02	0.15	126400
Matrix	CORA	Detection Visit 1	0.01	0.02	0.00	0.06	81655
Obligate	COYE	Detection Visit 1	0.58	0.10	0.37	0.76	157977
Matrix	DEJU	Detection Visit 1	0.15	0.08	0.03	0.35	136336
Matrix	DOWO	Detection Visit 1	0.01	0.01	0.00	0.04	299400
Matrix	EUCD	Detection Visit 1	0.05	0.04	0.01	0.14	114408
Facultative	EUST	Detection Visit 1	0.10	0.03	0.06	0.16	299400
Obligate	GBHE	Detection Visit 1	0.02	0.02	0.00	0.09	36388
Facultative	GHOW	Detection Visit 1	0.07	0.06	0.02	0.22	292430
Obligate	GREG	Detection Visit 1	0.03	0.05	0.00	0.20	94849
Obligate	GRHE	Detection Visit 1	0.02	0.04	0.00	0.13	299400
Matrix	GRSP	Detection Visit 1	0.47	0.11	0.26	0.70	148712
Facultative	GTGR	Detection Visit 1	0.03	0.05	0.00	0.19	254252
Matrix	HOFI	Detection Visit 1	0.02	0.01	0.00	0.05	295696
Matrix	HOSP	Detection Visit 1	0.07	0.06	0.01	0.22	299400
Facultative	HOWR	Detection Visit 1	0.25	0.05	0.15	0.36	176148
Facultative	KILL	Detection Visit 1	0.14	0.04	0.07	0.23	156482
Matrix	LASP	Detection Visit 1	0.20	0.08	0.07	0.36	263170
Facultative	LAZB	Detection Visit 1	0.00	0.01	0.00	0.02	77336
Matrix	LEGO	Detection Visit 1	0.07	0.02	0.04	0.11	299400
Obligate	MALL	Detection Visit 1	0.27	0.07	0.16	0.42	117425
Obligate	MAWR	Detection Visit 1	0.37	0.07	0.27	0.55	29641
Facultative	MODO	Detection Visit 1	0.40	0.04	0.32	0.47	187128
Matrix	NOFL	Detection Visit 1	0.01	0.01	0.00	0.05	160389
Facultative	NOMO	Detection Visit 1	0.39	0.04	0.31	0.47	72972
Facultative	NRWS	Detection Visit 1	0.04	0.04	0.01	0.14	153008
Matrix	NUWO	Detection Visit 1	0.02	0.01	0.00	0.04	299400
Facultative	OATI	Detection Visit 1	0.02	0.01	0.00	0.04	201527
Matrix	OSPR	Detection Visit 1	0.03	0.05	0.00	0.19	88626
Matrix	RNPH	Detection Visit 1	0.10	0.05	0.03	0.22	299400
Facultative	RSHA	Detection Visit 1	0.06	0.04	0.01	0.16	134607
Facultative	RTHA	Detection Visit 1	0.03	0.02	0.01	0.09	61234
Obligate	RWBL	Detection Visit 1	0.52	0.03	0.46	0.58	299400
Facultative	SOSP	Detection Visit 1	0.54	0.04	0.46	0.63	186467
Matrix	SPTO	Detection Visit 1	0.37	0.10	0.20	0.58	81590

Matrix	SWHA	Detection Visit 1	0.02	0.04	0.00	0.10	299400
Facultative	TRSW	Detection Visit 1	0.30	0.04	0.23	0.37	299400
Obligate	VIRA	Detection Visit 1	0.09	0.04	0.03	0.18	167995
Matrix	WBNU	Detection Visit 1	0.01	0.01	0.00	0.04	299400
Matrix	WEBL	Detection Visit 1	0.03	0.02	0.01	0.07	27683
Facultative	WEKI	Detection Visit 1	0.74	0.03	0.67	0.79	299400
Matrix	WEME	Detection Visit 1	0.20	0.05	0.12	0.30	272596
Matrix	WEWP	Detection Visit 1	0.37	0.07	0.23	0.51	200733
Obligate	WIFL	Detection Visit 1	0.04	0.05	0.00	0.19	299400
Obligate	WISN	Detection Visit 1	0.19	0.07	0.09	0.34	299400
Matrix	WITU	Detection Visit 1	0.10	0.04	0.05	0.18	299400
Obligate	WODU	Detection Visit 1	0.10	0.06	0.03	0.25	65361
Facultative	WREN	Detection Visit 1	0.04	0.03	0.00	0.13	173644
Obligate	YBCH	Detection Visit 1	0.38	0.07	0.25	0.52	59925
Obligate	YWAR	Detection Visit 1	0.37	0.10	0.19	0.56	299400
Matrix	ACWO	Detection Visit 2	0.42	0.04	0.35	0.49	89621
Obligate	AMBI	Detection Visit 2	0.21	0.04	0.14	0.29	299400
Matrix	AMCR	Detection Visit 2	0.20	0.05	0.12	0.30	299400
Matrix	AMGO	Detection Visit 2	0.02	0.02	0.00	0.07	60228
Matrix	AMKE	Detection Visit 2	0.07	0.03	0.02	0.15	296974
Matrix	AMRO	Detection Visit 2	0.21	0.04	0.13	0.31	64251
Facultative	ANHU	Detection Visit 2	0.05	0.03	0.01	0.12	42775
Facultative	ATFL	Detection Visit 2	0.01	0.01	0.00	0.04	47265
Facultative	BASW	Detection Visit 2	0.01	0.01	0.00	0.03	299400
Obligate	BEKI	Detection Visit 2	0.03	0.01	0.01	0.06	299400
Facultative	BEWR	Detection Visit 2	0.03	0.02	0.00	0.08	28799
Facultative	BHCO	Detection Visit 2	0.29	0.03	0.23	0.36	299400
Matrix	BHGR	Detection Visit 2	0.11	0.08	0.02	0.30	272200
Obligate	BLPH	Detection Visit 2	0.29	0.03	0.23	0.36	133261
Obligate	BLRA	Detection Visit 2	0.14	0.06	0.05	0.27	141034
Facultative	BRBL	Detection Visit 2	0.05	0.08	0.00	0.29	129027
Facultative	BUOR	Detection Visit 2	0.20	0.04	0.14	0.28	97892
Facultative	BUSH	Detection Visit 2	0.18	0.05	0.10	0.29	186843
Obligate	CANG	Detection Visit 2	0.04	0.02	0.01	0.09	299400
Matrix	CAQU	Detection Visit 2	0.55	0.03	0.49	0.62	299400
Matrix	CASJ	Detection Visit 2	0.20	0.03	0.15	0.27	115588
Matrix	CATO	Detection Visit 2	0.26	0.04	0.19	0.33	93486
Matrix	CEDW	Detection Visit 2	0.03	0.05	0.00	0.19	50857
Facultative	CLSW	Detection Visit 2	0.07	0.06	0.01	0.24	95468
Obligate	COMO	Detection Visit 2	0.16	0.05	0.07	0.28	299400
Matrix	CORA	Detection Visit 2	0.05	0.05	0.01	0.18	36915
Obligate	COYE	Detection Visit 2	0.62	0.10	0.41	0.78	106554
Matrix	DEJU	Detection Visit 2	0.25	0.10	0.08	0.47	299400
Matrix	DOWO	Detection Visit 2	0.04	0.03	0.01	0.12	65637

Matrix	EUCD	Detection Visit 2	0.24	0.08	0.10	0.42	299400
Facultative	EUST	Detection Visit 2	0.22	0.04	0.15	0.30	148918
Obligate	GBHE	Detection Visit 2	0.05	0.04	0.01	0.17	108583
Facultative	GHOW	Detection Visit 2	0.02	0.02	0.00	0.06	299400
Obligate	GREG	Detection Visit 2	0.09	0.11	0.00	0.43	100315
Obligate	GRHE	Detection Visit 2	0.09	0.11	0.01	0.43	115977
Matrix	GRSP	Detection Visit 2	0.42	0.11	0.22	0.65	111200
Facultative	GTGR	Detection Visit 2	0.09	0.11	0.00	0.41	62406
Matrix	HOFI	Detection Visit 2	0.02	0.01	0.00	0.05	299400
Matrix	HOSP	Detection Visit 2	0.22	0.10	0.05	0.45	299400
Facultative	HOWR	Detection Visit 2	0.21	0.05	0.12	0.32	260233
Facultative	KILL	Detection Visit 2	0.16	0.05	0.08	0.26	148908
Matrix	LASP	Detection Visit 2	0.10	0.05	0.03	0.22	155966
Facultative	LAZB	Detection Visit 2	0.02	0.01	0.00	0.05	299400
Matrix	LEGO	Detection Visit 2	0.17	0.03	0.12	0.24	299400
Obligate	MALL	Detection Visit 2	0.18	0.05	0.09	0.29	299400
Obligate	MAWR	Detection Visit 2	0.41	0.08	0.30	0.61	33232
Facultative	MODO	Detection Visit 2	0.30	0.03	0.24	0.37	299400
Matrix	NOFL	Detection Visit 2	0.03	0.03	0.00	0.10	135447
Facultative	NOMO	Detection Visit 2	0.39	0.04	0.31	0.48	299400
Facultative	NRWS	Detection Visit 2	0.03	0.03	0.00	0.11	73508
Matrix	NUWO	Detection Visit 2	0.11	0.03	0.06	0.19	69935
Facultative	OATI	Detection Visit 2	0.21	0.03	0.15	0.29	299400
Matrix	OSPR	Detection Visit 2	0.04	0.06	0.00	0.21	299400
Matrix	RNPH	Detection Visit 2	0.06	0.03	0.01	0.15	299400
Facultative	RSHA	Detection Visit 2	0.29	0.07	0.16	0.45	299400
Facultative	RTHA	Detection Visit 2	0.02	0.02	0.00	0.07	57550
Obligate	RWBL	Detection Visit 2	0.77	0.03	0.71	0.82	299400
Facultative	SOSP	Detection Visit 2	0.35	0.04	0.27	0.43	299400
Matrix	SPTO	Detection Visit 2	0.22	0.07	0.10	0.39	129125
Matrix	SWHA	Detection Visit 2	0.06	0.10	0.00	0.33	68648
Facultative	TRSW	Detection Visit 2	0.37	0.04	0.30	0.45	299400
Obligate	VIRA	Detection Visit 2	0.14	0.05	0.06	0.25	99154
Matrix	WBNU	Detection Visit 2	0.24	0.07	0.13	0.40	299400
Matrix	WEBL	Detection Visit 2	0.02	0.01	0.00	0.05	22238
Facultative	WEKI	Detection Visit 2	0.46	0.03	0.39	0.52	299400
Matrix	WEME	Detection Visit 2	0.32	0.06	0.22	0.44	103989
Matrix	WEWP	Detection Visit 2	0.27	0.07	0.15	0.41	299400
Obligate	WIFL	Detection Visit 2	0.05	0.06	0.00	0.20	272573
Obligate	WISN	Detection Visit 2	0.04	0.03	0.01	0.11	85249
Matrix	WITU	Detection Visit 2	0.11	0.04	0.05	0.20	54717
Obligate	WODU	Detection Visit 2	0.08	0.05	0.02	0.21	51999
Facultative	WREN	Detection Visit 2	0.30	0.09	0.16	0.50	299400
Obligate	YBCH	Detection Visit 2	0.30	0.06	0.19	0.44	110202

Obligate	YWAR	Detection Visit 2	0.33	0.09	0.16	0.52	238725
Matrix	ACWO	Detection Visit 3	0.50	0.04	0.43	0.57	299400
Obligate	AMBI	Detection Visit 3	0.13	0.03	0.07	0.19	299400
Matrix	AMCR	Detection Visit 3	0.09	0.03	0.04	0.15	94788
Matrix	AMGO	Detection Visit 3	0.03	0.03	0.00	0.10	24010
Matrix	AMKE	Detection Visit 3	0.02	0.01	0.00	0.06	268897
Matrix	AMRO	Detection Visit 3	0.13	0.04	0.07	0.21	299400
Facultative	ANHU	Detection Visit 3	0.09	0.04	0.03	0.20	44849
Facultative	ATFL	Detection Visit 3	0.01	0.01	0.00	0.04	299400
Facultative	BASW	Detection Visit 3	0.02	0.02	0.00	0.07	299400
Obligate	BEKI	Detection Visit 3	0.05	0.02	0.02	0.10	60838
Facultative	BEWR	Detection Visit 3	0.01	0.01	0.00	0.03	78831
Facultative	BHCO	Detection Visit 3	0.39	0.03	0.32	0.46	299400
Matrix	BHGR	Detection Visit 3	0.08	0.06	0.01	0.24	299400
Obligate	BLPH	Detection Visit 3	0.27	0.03	0.21	0.34	168026
Obligate	BLRA	Detection Visit 3	0.35	0.09	0.19	0.53	166279
Facultative	BRBL	Detection Visit 3	0.14	0.15	0.00	0.55	299400
Facultative	BUOR	Detection Visit 3	0.20	0.04	0.13	0.28	209000
Facultative	BUSH	Detection Visit 3	0.16	0.04	0.09	0.27	299400
Obligate	CANG	Detection Visit 3	0.13	0.03	0.07	0.21	189282
Matrix	CAQU	Detection Visit 3	0.60	0.03	0.53	0.66	299400
Matrix	CASJ	Detection Visit 3	0.18	0.03	0.13	0.24	239732
Matrix	CATO	Detection Visit 3	0.21	0.03	0.15	0.28	279629
Matrix	CEDW	Detection Visit 3	0.03	0.05	0.00	0.18	54174
Facultative	CLSW	Detection Visit 3	0.02	0.02	0.00	0.07	299400
Obligate	COMO	Detection Visit 3	0.17	0.06	0.08	0.30	299400
Matrix	CORA	Detection Visit 3	0.03	0.04	0.00	0.13	103041
Obligate	COYE	Detection Visit 3	0.76	0.08	0.58	0.88	299400
Matrix	DEJU	Detection Visit 3	0.20	0.09	0.06	0.41	299400
Matrix	DOWO	Detection Visit 3	0.03	0.02	0.00	0.10	96296
Matrix	EUCD	Detection Visit 3	0.13	0.06	0.05	0.27	299400
Facultative	EUST	Detection Visit 3	0.28	0.04	0.20	0.36	299400
Obligate	GBHE	Detection Visit 3	0.02	0.03	0.00	0.09	140426
Facultative	GHOW	Detection Visit 3	0.01	0.01	0.00	0.03	299400
Obligate	GREG	Detection Visit 3	0.03	0.06	0.00	0.21	48337
Obligate	GRHE	Detection Visit 3	0.02	0.04	0.00	0.14	299400
Matrix	GRSP	Detection Visit 3	0.36	0.10	0.17	0.58	299400
Facultative	GTGR	Detection Visit 3	0.15	0.14	0.01	0.56	93741
Matrix	HOFI	Detection Visit 3	0.05	0.02	0.02	0.10	137429
Matrix	HOSP	Detection Visit 3	0.17	0.09	0.03	0.38	174432
Facultative	HOWR	Detection Visit 3	0.27	0.06	0.17	0.38	272625
Facultative	KILL	Detection Visit 3	0.20	0.05	0.11	0.31	131191
Matrix	LASP	Detection Visit 3	0.16	0.07	0.05	0.31	59481
Facultative	LAZB	Detection Visit 3	0.02	0.02	0.01	0.06	299400

Matrix	LEGO	Detection Visit 3	0.12	0.03	0.07	0.17	221982
Obligate	MALL	Detection Visit 3	0.16	0.05	0.08	0.27	289264
Obligate	MAWR	Detection Visit 3	0.38	0.07	0.27	0.55	16394
Facultative	MODO	Detection Visit 3	0.32	0.03	0.25	0.39	101705
Matrix	NOFL	Detection Visit 3	0.02	0.03	0.00	0.10	115556
Facultative	NOMO	Detection Visit 3	0.38	0.04	0.30	0.46	299400
Facultative	NRWS	Detection Visit 3	0.01	0.01	0.00	0.04	235840
Matrix	NUWO	Detection Visit 3	0.11	0.03	0.06	0.18	102577
Facultative	OATI	Detection Visit 3	0.19	0.03	0.13	0.26	188006
Matrix	OSPR	Detection Visit 3	0.09	0.11	0.00	0.43	215899
Matrix	RNPH	Detection Visit 3	0.04	0.03	0.01	0.12	299400
Facultative	RSHA	Detection Visit 3	0.39	0.08	0.24	0.56	299400
Facultative	RTHA	Detection Visit 3	0.02	0.02	0.00	0.07	59530
Obligate	RWBL	Detection Visit 3	0.80	0.03	0.75	0.85	135856
Facultative	SOSP	Detection Visit 3	0.42	0.04	0.34	0.51	154315
Matrix	SPTO	Detection Visit 3	0.12	0.05	0.04	0.25	299400
Matrix	SWHA	Detection Visit 3	0.06	0.10	0.00	0.32	116366
Facultative	TRSW	Detection Visit 3	0.20	0.03	0.14	0.26	299400
Obligate	VIRA	Detection Visit 3	0.16	0.06	0.07	0.29	32833
Matrix	WBNU	Detection Visit 3	0.18	0.06	0.09	0.31	229498
Matrix	WEBL	Detection Visit 3	0.02	0.01	0.00	0.05	39651
Facultative	WEKI	Detection Visit 3	0.34	0.03	0.28	0.40	299400
Matrix	WEME	Detection Visit 3	0.47	0.06	0.36	0.59	299400
Matrix	WEWP	Detection Visit 3	0.41	0.07	0.27	0.55	299400
Obligate	WIFL	Detection Visit 3	0.07	0.08	0.01	0.29	299400
Obligate	WISN	Detection Visit 3	0.08	0.04	0.03	0.17	107904
Matrix	WITU	Detection Visit 3	0.06	0.03	0.02	0.13	299400
Obligate	WODU	Detection Visit 3	0.06	0.04	0.01	0.17	53299
Facultative	WREN	Detection Visit 3	0.15	0.06	0.06	0.29	160754
Obligate	YBCH	Detection Visit 3	0.17	0.05	0.09	0.28	112149
Obligate	YWAR	Detection Visit 3	0.18	0.08	0.06	0.35	248141
Matrix	ACWO	Julian Date	0.08	0.22	-0.35	0.51	277360
Obligate	AMBI	Julian Date	-6.56	1.34	-9.19	-3.90	34000
Matrix	AMCR	Julian Date	0.78	0.47	-0.15	1.71	285258
Matrix	AMGO	Julian Date	-0.68	1.15	-3.04	1.46	172125
Matrix	AMKE	Julian Date	0.99	0.54	-0.10	2.03	299400
Matrix	AMRO	Julian Date	1.22	0.43	0.34	2.05	267933
Facultative	ANHU	Julian Date	0.53	0.72	-0.87	1.97	299400
Facultative	ATFL	Julian Date	0.29	0.65	-0.99	1.57	299400
Facultative	BASW	Julian Date	-0.92	1.03	-2.99	1.07	166549
Obligate	BEKI	Julian Date	1.73	0.48	0.79	2.68	299400
Facultative	BEWR	Julian Date	-2.29	1.09	-4.54	-0.28	169120
Facultative	BHCO	Julian Date	0.01	0.20	-0.38	0.40	299400
Matrix	BHGR	Julian Date	0.36	1.35	-2.18	3.21	114945

Obligate	BLPH	Julian Date	0.38	0.23	-0.07	0.83	299400
Obligate	BLRA	Julian Date	-1.19	0.56	-2.32	-0.13	196473
Facultative	BRBL	Julian Date	-0.02	2.04	-4.22	4.02	299400
Facultative	BUOR	Julian Date	-0.37	0.33	-1.02	0.27	299400
Facultative	BUSH	Julian Date	0.07	0.37	-0.65	0.80	299400
Obligate	CANG	Julian Date	-2.21	0.79	-3.84	-0.75	159216
Matrix	CAQU	Julian Date	-0.45	0.18	-0.80	-0.09	299400
Matrix	CASJ	Julian Date	1.07	0.24	0.59	1.55	48139
Matrix	CATO	Julian Date	-0.23	0.26	-0.74	0.27	299400
Matrix	CEDW	Julian Date	-0.06	1.75	-3.69	3.45	77610
Facultative	CLSW	Julian Date	0.57	0.87	-1.25	2.16	299400
Obligate	COMO	Julian Date	-0.74	0.73	-2.17	0.74	133040
Matrix	CORA	Julian Date	0.87	0.92	-1.04	2.59	299400
Obligate	COYE	Julian Date	1.66	0.84	0.05	3.33	299400
Matrix	DEJU	Julian Date	-1.67	1.12	-3.82	0.55	299400
Matrix	DOWO	Julian Date	1.15	0.88	-0.60	2.90	71989
Matrix	EUCD	Julian Date	-0.15	0.76	-1.64	1.35	159164
Facultative	EUST	Julian Date	-0.47	0.30	-1.06	0.10	256450
Obligate	GBHE	Julian Date	-0.83	1.21	-3.20	1.63	220324
Facultative	GHOW	Julian Date	-1.81	1.09	-4.07	0.20	299400
Obligate	GREG	Julian Date	0.33	1.81	-3.03	4.20	299400
Obligate	GRHE	Julian Date	-0.57	1.67	-3.69	3.03	299400
Matrix	GRSP	Julian Date	1.41	1.37	-1.20	4.17	299400
Facultative	GTGR	Julian Date	-0.43	1.82	-3.81	3.41	98692
Matrix	HOFI	Julian Date	-0.14	0.62	-1.41	1.02	101652
Matrix	HOSP	Julian Date	-2.82	1.52	-5.78	0.16	205406
Facultative	HOWR	Julian Date	-0.96	0.38	-1.70	-0.23	299400
Facultative	KILL	Julian Date	-0.99	0.49	-2.00	-0.07	299400
Matrix	LASP	Julian Date	-1.13	0.93	-2.95	0.72	155942
Facultative	LAZB	Julian Date	0.62	0.77	-0.96	2.09	90009
Matrix	LEGO	Julian Date	0.20	0.32	-0.42	0.83	51387
Obligate	MALL	Julian Date	-0.99	0.63	-2.30	0.19	53967
Obligate	MAWR	Julian Date	-5.20	1.46	-8.01	-2.33	18555
Facultative	MODO	Julian Date	0.04	0.23	-0.39	0.51	299400
Matrix	NOFL	Julian Date	1.23	0.96	-0.76	3.03	126286
Facultative	NOMO	Julian Date	1.12	0.24	0.66	1.59	130736
Facultative	NRWS	Julian Date	0.83	0.89	-0.91	2.67	299400
Matrix	NUWO	Julian Date	0.06	0.41	-0.76	0.85	67857
Facultative	OATI	Julian Date	0.75	0.30	0.17	1.33	74904
Matrix	OSPR	Julian Date	-0.23	1.83	-4.01	3.45	299400
Matrix	RNPH	Julian Date	-0.79	0.94	-2.65	1.11	299400
Facultative	RSHA	Julian Date	0.70	1.00	-1.21	2.69	299400
Facultative	RTHA	Julian Date	-0.52	0.84	-2.29	1.02	149264
Obligate	RWBL	Julian Date	-1.37	0.20	-1.76	-0.99	268999

Facultative	SOSP	Julian Date	0.50	0.25	0.01	0.99	299400
Matrix	SPTO	Julian Date	1.17	0.81	-0.50	2.68	199143
Matrix	SWHA	Julian Date	1.96	0.97	-0.09	3.75	82324
Facultative	TRSW	Julian Date	-1.73	0.32	-2.36	-1.12	250439
Obligate	VIRA	Julian Date	-1.07	0.50	-2.09	-0.13	299400
Matrix	WBNU	Julian Date	0.27	0.85	-1.46	1.86	127654
Matrix	WEBL	Julian Date	0.56	0.70	-0.88	1.88	108104
Facultative	WEKI	Julian Date	0.05	0.18	-0.31	0.41	299358
Matrix	WEME	Julian Date	-0.58	0.52	-1.55	0.51	299400
Matrix	WEWP	Julian Date	-0.84	0.61	-2.01	0.38	206813
Obligate	WIFL	Julian Date	0.58	1.53	-2.63	3.70	299400
Obligate	WISN	Julian Date	0.68	0.49	-0.30	1.64	299400
Matrix	WITU	Julian Date	-0.17	0.57	-1.30	0.95	106574
Obligate	WODU	Julian Date	-1.60	1.25	-4.06	0.87	48801
Facultative	WREN	Julian Date	1.59	1.22	-0.95	3.92	299400
Obligate	YBCH	Julian Date	0.11	0.67	-1.19	1.41	63278
Obligate	YWAR	Julian Date	-1.85	0.73	-3.37	-0.50	299400
Matrix	ACWO	Intercept	5.17	1.68	1.96	8.53	180842
Obligate	AMBI	Intercept	-0.58	1.89	-4.32	3.12	12466
Matrix	AMCR	Intercept	3.50	1.79	0.10	7.12	19964
Matrix	AMGO	Intercept	0.89	2.26	-3.44	5.38	3473
Matrix	AMKE	Intercept	1.95	1.93	-1.81	5.78	32518
Matrix	AMRO	Intercept	2.83	1.64	-0.31	6.09	61644
Facultative	ANHU	Intercept	0.76	2.02	-3.09	4.83	299400
Facultative	ATFL	Intercept	2.35	1.94	-1.39	6.24	21407
Facultative	BASW	Intercept	0.43	2.28	-3.90	5.02	8390
Obligate	BEKI	Intercept	2.86	2.02	-1.05	6.87	174342
Facultative	BEWR	Intercept	0.62	2.08	-3.38	4.76	78707
Facultative	BHCO	Intercept	5.50	1.70	2.19	8.86	61677
Matrix	BHGR	Intercept	0.18	1.92	-3.51	4.02	31295
Obligate	BLPH	Intercept	4.44	1.56	1.44	7.55	15048
Obligate	BLRA	Intercept	-1.86	1.69	-5.16	1.45	31986
Facultative	BRBL	Intercept	-1.51	2.24	-5.75	3.09	88023
Facultative	BUOR	Intercept	3.10	1.64	-0.07	6.36	6558
Facultative	BUSH	Intercept	2.01	1.88	-1.52	5.85	6196
Obligate	CANG	Intercept	1.52	1.88	-2.13	5.24	38636
Matrix	CAQU	Intercept	5.33	1.66	2.12	8.63	55675
Matrix	CASJ	Intercept	3.28	1.66	0.11	6.61	8170
Matrix	CATO	Intercept	4.50	1.46	1.71	7.42	48691
Matrix	CEDW	Intercept	-0.51	2.38	-5.01	4.34	16909
Facultative	CLSW	Intercept	0.59	2.11	-3.44	4.81	30277
Obligate	COMO	Intercept	-0.26	1.81	-3.77	3.33	13214
Matrix	CORA	Intercept	0.16	2.20	-4.09	4.53	5925
Obligate	COYE	Intercept	-1.47	1.70	-4.86	1.82	299400

Matrix	DEJU	Intercept	-2.34	1.84	-5.97	1.25	22993
Matrix	DOWO	Intercept	1.86	2.05	-2.08	5.95	14025
Matrix	EUCD	Intercept	0.99	1.67	-2.24	4.30	207064
Facultative	EUST	Intercept	2.82	1.67	-0.43	6.11	27133
Obligate	GBHE	Intercept	0.14	2.15	-4.02	4.39	11783
Facultative	GHOW	Intercept	1.49	2.22	-2.72	5.92	21090
Obligate	GREG	Intercept	-0.61	2.26	-4.90	3.96	73884
Obligate	GRHE	Intercept	-0.30	2.17	-4.45	4.04	25483
Matrix	GRSP	Intercept	-1.92	1.74	-5.38	1.43	37690
Facultative	GTGR	Intercept	-1.14	2.06	-5.12	2.97	20578
Matrix	HOFI	Intercept	2.63	2.09	-1.42	6.80	183721
Matrix	HOSP	Intercept	-1.35	1.90	-5.05	2.40	137589
Facultative	HOWR	Intercept	1.19	1.44	-1.58	4.08	62168
Facultative	KILL	Intercept	-0.21	1.65	-3.44	3.05	10985
Matrix	LASP	Intercept	-0.01	1.66	-3.20	3.31	11948
Facultative	LAZB	Intercept	2.04	2.20	-2.21	6.41	299400
Matrix	LEGO	Intercept	3.36	1.86	-0.14	7.12	17017
Obligate	MALL	Intercept	-0.22	1.64	-3.42	3.01	42683
Obligate	MAWR	Intercept	-0.58	1.84	-4.21	3.02	42904
Facultative	MODO	Intercept	3.19	1.68	-0.02	6.55	23065
Matrix	NOFL	Intercept	0.68	2.27	-3.69	5.19	26784
Facultative	NOMO	Intercept	2.52	1.43	-0.26	5.36	15185
Facultative	NRWS	Intercept	0.79	2.27	-3.58	5.33	22978
Matrix	NUWO	Intercept	2.55	1.88	-1.07	6.32	69860
Facultative	OATI	Intercept	1.87	1.87	-1.67	5.70	25728
Matrix	OSPR	Intercept	-0.49	2.26	-4.79	4.08	38224
Matrix	RNPH	Intercept	0.79	1.87	-2.85	4.50	112932
Facultative	RSHA	Intercept	1.20	1.59	-1.92	4.29	61523
Facultative	RTHA	Intercept	1.28	2.21	-2.95	5.70	299400
Obligate	RWBL	Intercept	4.91	1.57	1.89	8.04	55544
Facultative	SOSP	Intercept	2.41	1.30	-0.10	4.98	3832
Matrix	SPTO	Intercept	-2.12	1.71	-5.51	1.23	26108
Matrix	SWHA	Intercept	-0.69	2.30	-5.08	3.91	24642
Facultative	TRSW	Intercept	3.62	1.49	0.74	6.59	7076
Obligate	VIRA	Intercept	1.43	1.71	-1.81	4.93	45697
Matrix	WBNU	Intercept	0.47	1.71	-2.89	3.82	115887
Matrix	WEBL	Intercept	1.47	2.23	-2.81	5.93	8296
Facultative	WEKI	Intercept	4.66	1.59	1.60	7.82	25938
Matrix	WEME	Intercept	0.44	1.56	-2.55	3.56	299400
Matrix	WEWP	Intercept	0.83	1.42	-1.98	3.61	49701
Obligate	WIFL	Intercept	-0.04	2.16	-4.11	4.38	90397
Obligate	WISN	Intercept	0.80	1.78	-2.63	4.32	124153
Matrix	WITU	Intercept	2.49	1.81	-0.99	6.12	13305
Obligate	WODU	Intercept	0.19	1.91	-3.52	3.96	79137

Facultative	WREN	Intercept	-1.09	1.81	-4.65	2.47	22669
Obligate	YBCH	Intercept	-1.14	1.52	-4.12	1.87	94570
Obligate	YWAR	Intercept	-0.73	1.64	-3.95	2.47	26574
Matrix	ACWO	Area	0.88	1.01	-1.02	2.96	83817
Obligate	AMBI	Area	0.29	1.59	-2.82	3.46	146827
Matrix	AMCR	Area	-0.85	1.47	-3.93	1.85	90064
Matrix	AMGO	Area	1.10	2.16	-3.12	5.37	69564
Matrix	AMKE	Area	1.56	1.78	-1.85	5.16	299400
Matrix	AMRO	Area	0.05	1.04	-2.09	2.02	299400
Facultative	ANHU	Area	1.48	1.60	-1.67	4.64	69969
Facultative	ATFL	Area	-1.83	1.93	-5.61	1.98	271169
Facultative	BASW	Area	0.29	2.01	-3.57	4.37	43614
Obligate	BEKI	Area	1.17	2.07	-2.86	5.28	19608
Facultative	BEWR	Area	-1.00	2.01	-4.95	2.96	242048
Facultative	BHCO	Area	0.31	1.55	-2.44	3.64	299400
Matrix	BHGR	Area	1.35	1.84	-2.34	4.91	63498
Obligate	BLPH	Area	-0.79	1.07	-2.78	1.48	116445
Obligate	BLRA	Area	1.47	1.15	-0.70	3.82	122803
Facultative	BRBL	Area	0.64	2.06	-3.45	4.64	299400
Facultative	BUOR	Area	-0.33	1.18	-2.65	2.06	143357
Facultative	BUSH	Area	0.22	1.36	-2.17	3.29	299400
Obligate	CANG	Area	0.59	1.68	-2.59	4.05	187203
Matrix	CAQU	Area	0.80	1.54	-2.07	3.97	299400
Matrix	CASJ	Area	1.44	1.29	-0.99	4.10	299400
Matrix	CATO	Area	0.75	0.80	-0.77	2.39	85298
Matrix	CEDW	Area	-0.43	2.07	-4.52	3.64	41108
Facultative	CLSW	Area	-1.14	1.97	-4.97	2.78	294266
Obligate	COMO	Area	1.30	1.41	-1.36	4.23	299400
Matrix	CORA	Area	1.05	2.05	-2.98	5.10	299400
Obligate	COYE	Area	1.54	0.97	-0.35	3.47	42683
Matrix	DEJU	Area	0.97	1.81	-2.64	4.45	185361
Matrix	DOWO	Area	-0.42	2.07	-4.47	3.67	157717
Matrix	EUCD	Area	-0.37	1.33	-3.08	2.13	238170
Facultative	EUST	Area	0.47	1.27	-1.96	3.04	299400
Obligate	GBHE	Area	2.15	2.00	-1.79	6.04	187645
Facultative	GHOW	Area	0.11	1.81	-3.40	3.76	299400
Obligate	GREG	Area	-0.01	2.12	-4.15	4.20	113993
Obligate	GRHE	Area	0.36	1.99	-3.49	4.33	116804
Matrix	GRSP	Area	0.36	1.67	-3.03	3.52	229996
Facultative	GTGR	Area	0.49	1.89	-3.26	4.16	69255
Matrix	HOFI	Area	-0.63	1.89	-4.28	3.22	118363
Matrix	HOSP	Area	0.29	1.57	-2.81	3.36	163104
Facultative	HOWR	Area	1.33	0.93	-0.43	3.24	299400
Facultative	KILL	Area	2.12	1.36	-0.42	4.98	23934

Matrix	LASP	Area	-1.94	1.27	-4.50	0.49	222523
Facultative	LAZB	Area	0.24	1.95	-3.52	4.18	223889
Matrix	LEGO	Area	0.32	1.45	-2.48	3.28	299400
Obligate	MALL	Area	-0.23	1.31	-2.84	2.32	287415
Obligate	MAWR	Area	3.27	1.58	0.28	6.49	299400
Facultative	MODO	Area	1.78	1.13	-0.24	4.21	176446
Matrix	NOFL	Area	0.39	2.15	-3.81	4.66	50472
Facultative	NOMO	Area	-0.14	0.86	-1.82	1.54	299400
Facultative	NRWS	Area	-0.04	2.15	-4.19	4.29	41848
Matrix	NUWO	Area	0.11	1.79	-3.32	3.75	239199
Facultative	OATI	Area	-0.04	1.50	-2.91	3.09	172027
Matrix	OSPR	Area	0.48	2.09	-3.64	4.59	74926
Matrix	RNPH	Area	0.50	1.67	-2.70	3.90	299400
Facultative	RSHA	Area	0.66	1.48	-2.28	3.54	144337
Facultative	RTHA	Area	-1.52	2.13	-5.65	2.71	40752
Obligate	RWBL	Area	0.76	0.98	-1.08	2.79	132920
Facultative	SOSP	Area	1.51	0.70	0.19	2.91	141006
Matrix	SPTO	Area	2.60	1.11	0.48	4.83	299400
Matrix	SWHA	Area	-0.17	2.04	-4.19	3.84	133813
Facultative	TRSW	Area	-0.87	1.06	-2.90	1.26	191212
Obligate	VIRA	Area	0.90	1.31	-1.51	3.67	110505
Matrix	WBNU	Area	-1.78	1.78	-5.34	1.64	295826
Matrix	WEBL	Area	0.36	2.08	-3.70	4.49	82221
Facultative	WEKI	Area	-0.34	0.91	-2.12	1.47	299400
Matrix	WEME	Area	0.47	1.16	-1.68	2.88	299400
Matrix	WEWP	Area	1.93	1.03	-0.01	4.03	260552
Obligate	WIFL	Area	0.88	1.99	-3.12	4.76	299400
Obligate	WISN	Area	0.58	1.59	-2.40	3.95	166105
Matrix	WITU	Area	-2.01	1.73	-5.46	1.34	185120
Obligate	WODU	Area	2.10	1.58	-0.95	5.27	107815
Facultative	WREN	Area	-1.36	1.70	-4.79	1.82	299400
Obligate	YBCH	Area	0.52	0.95	-1.38	2.38	217430
Obligate	YWAR	Area	0.80	1.14	-1.47	3.02	299400
Matrix	ACWO	Elevation	0.22	1.55	-2.58	3.51	265296
Obligate	AMBI	Elevation	-2.34	1.99	-6.31	1.52	196179
Matrix	AMCR	Elevation	-0.11	1.37	-2.71	2.68	27814
Matrix	AMGO	Elevation	-0.87	2.19	-5.13	3.49	90064
Matrix	AMKE	Elevation	-2.04	1.98	-5.95	1.85	54586
Matrix	AMRO	Elevation	0.65	1.19	-1.60	3.07	65664
Facultative	ANHU	Elevation	-0.56	1.92	-4.22	3.39	100460
Facultative	ATFL	Elevation	1.84	1.87	-1.73	5.62	77401
Facultative	BASW	Elevation	-1.92	2.12	-6.02	2.34	79988
Obligate	BEKI	Elevation	-0.41	1.85	-3.96	3.32	10799
Facultative	BEWR	Elevation	0.81	2.18	-3.40	5.10	141051

Facultative	BHCO	Elevation	0.29	1.41	-2.34	3.22	299400
Matrix	BHGR	Elevation	-0.59	1.77	-4.02	2.99	53740
Obligate	BLPH	Elevation	1.60	1.59	-1.32	4.90	299400
Obligate	BLRA	Elevation	-2.71	1.49	-5.76	0.08	299400
Facultative	BRBL	Elevation	0.25	1.97	-3.64	4.12	71185
Facultative	BUOR	Elevation	1.17	1.42	-1.35	4.28	299400
Facultative	BUSH	Elevation	-1.89	1.64	-4.85	1.79	299400
Obligate	CANG	Elevation	-2.45	1.88	-6.18	1.23	20242
Matrix	CAQU	Elevation	-1.21	1.16	-3.53	1.04	299400
Matrix	CASJ	Elevation	0.80	1.62	-2.24	4.10	142869
Matrix	CATO	Elevation	-0.20	1.18	-2.33	2.35	14468
Matrix	CEDW	Elevation	0.26	2.09	-3.79	4.43	139797
Facultative	CLSW	Elevation	-2.44	2.03	-6.41	1.58	39170
Obligate	COMO	Elevation	-2.06	1.65	-5.39	1.07	120232
Matrix	CORA	Elevation	-1.36	2.10	-5.50	2.77	64435
Obligate	COYE	Elevation	-2.60	1.72	-6.13	0.61	299400
Matrix	DEJU	Elevation	-0.05	1.63	-3.25	3.18	299400
Matrix	DOWO	Elevation	-0.38	2.09	-4.40	3.87	247096
Matrix	EUCD	Elevation	1.26	1.34	-1.26	3.99	299400
Facultative	EUST	Elevation	-3.11	1.25	-5.64	-0.70	299400
Obligate	GBHE	Elevation	-1.35	2.13	-5.54	2.83	299400
Facultative	GHOW	Elevation	-2.17	2.21	-6.36	2.32	18510
Obligate	GREG	Elevation	-1.09	2.11	-5.26	3.07	145588
Obligate	GRHE	Elevation	-1.17	2.12	-5.35	2.99	299400
Matrix	GRSP	Elevation	2.55	1.34	-0.02	5.25	299400
Facultative	GTGR	Elevation	-1.10	2.05	-5.16	2.87	204000
Matrix	HOFI	Elevation	-0.66	1.96	-4.42	3.31	65522
Matrix	HOSP	Elevation	0.76	1.58	-2.24	3.97	299400
Facultative	HOWR	Elevation	-1.41	1.04	-3.52	0.57	96839
Facultative	KILL	Elevation	-0.35	1.30	-2.90	2.22	54258
Matrix	LASP	Elevation	-2.24	1.35	-4.93	0.37	154982
Facultative	LAZB	Elevation	-0.74	2.32	-5.22	3.87	41054
Matrix	LEGO	Elevation	-0.34	1.90	-3.77	3.74	52667
Obligate	MALL	Elevation	0.66	1.44	-2.20	3.48	299400
Obligate	MAWR	Elevation	-1.75	1.86	-5.51	1.78	70892
Facultative	MODO	Elevation	1.29	1.43	-1.35	4.24	56648
Matrix	NOFL	Elevation	0.16	2.04	-3.79	4.23	55240
Facultative	NOMO	Elevation	-2.94	1.07	-5.09	-0.91	188603
Facultative	NRWS	Elevation	-1.18	2.18	-5.38	3.22	84375
Matrix	NUWO	Elevation	1.21	1.88	-2.36	5.01	299400
Facultative	OATI	Elevation	-0.19	2.14	-4.02	4.43	149643
Matrix	OSPR	Elevation	-0.98	2.11	-5.08	3.21	146990
Matrix	RNPH	Elevation	-0.16	1.65	-3.35	3.13	66290
Facultative	RSHA	Elevation	1.43	1.22	-0.85	3.95	64585

Facultative	RTHA	Elevation	-0.32	2.07	-4.32	3.84	299400
Obligate	RWBL	Elevation	0.04	1.01	-1.92	2.06	299400
Facultative	SOSP	Elevation	0.73	0.88	-0.97	2.48	35605
Matrix	SPTO	Elevation	-0.27	1.27	-2.79	2.22	171954
Matrix	SWHA	Elevation	-1.39	2.09	-5.47	2.78	299400
Facultative	TRSW	Elevation	0.56	1.03	-1.40	2.64	102790
Obligate	VIRA	Elevation	-0.42	1.49	-3.15	2.74	70375
Matrix	WBNU	Elevation	2.80	1.53	-0.01	5.95	299400
Matrix	WEBL	Elevation	0.11	2.24	-4.19	4.57	70095
Facultative	WEKI	Elevation	-0.70	1.31	-3.12	2.06	176044
Matrix	WEME	Elevation	-1.71	1.15	-4.01	0.52	296447
Matrix	WEWP	Elevation	0.54	1.00	-1.37	2.55	299400
Obligate	WIFL	Elevation	0.29	1.94	-3.39	4.27	136779
Obligate	WISN	Elevation	0.60	1.38	-2.02	3.41	17552
Matrix	WITU	Elevation	0.56	1.54	-2.30	3.75	299400
Obligate	WODU	Elevation	-2.01	2.03	-6.01	1.98	49666
Facultative	WREN	Elevation	1.22	1.47	-1.59	4.16	143409
Obligate	YBCH	Elevation	-1.31	1.09	-3.55	0.73	197835
Obligate	YWAR	Elevation	-0.91	1.15	-3.17	1.35	299400
Matrix	ACWO	Juncus	-0.73	1.11	-2.96	1.45	101303
Obligate	AMBI	Juncus	-0.14	1.64	-3.36	3.08	57867
Matrix	AMCR	Juncus	-0.84	1.32	-3.48	1.78	58264
Matrix	AMGO	Juncus	0.66	2.04	-3.32	4.69	299400
Matrix	AMKE	Juncus	-0.65	1.88	-4.24	3.13	13518
Matrix	AMRO	Juncus	-3.54	1.20	-6.04	-1.35	123609
Facultative	ANHU	Juncus	1.68	1.80	-1.87	5.21	159698
Facultative	ATFL	Juncus	1.42	1.70	-1.90	4.78	26104
Facultative	BASW	Juncus	0.27	1.78	-3.20	3.83	22098
Obligate	BEKI	Juncus	1.51	1.93	-2.24	5.36	18248
Facultative	BEWR	Juncus	0.23	1.85	-3.36	3.89	6399
Facultative	BHCO	Juncus	1.31	1.47	-1.46	4.35	299400
Matrix	BHGR	Juncus	-2.50	1.89	-6.20	1.24	22111
Obligate	BLPH	Juncus	0.13	1.07	-1.92	2.30	299400
Obligate	BLRA	Juncus	3.63	1.27	1.26	6.25	101860
Facultative	BRBL	Juncus	-0.74	1.99	-4.65	3.17	84920
Facultative	BUOR	Juncus	-0.54	1.24	-2.98	1.95	11514
Facultative	BUSH	Juncus	-0.17	1.52	-3.07	3.06	299400
Obligate	CANG	Juncus	1.06	1.53	-1.95	4.09	100400
Matrix	CAQU	Juncus	1.51	1.29	-0.86	4.26	42751
Matrix	CASJ	Juncus	2.22	1.57	-0.57	5.60	173265
Matrix	CATO	Juncus	-1.03	0.83	-2.73	0.55	53431
Matrix	CEDW	Juncus	0.18	1.98	-3.68	4.12	299400
Facultative	CLSW	Juncus	-0.63	1.87	-4.25	3.10	12496
Obligate	COMO	Juncus	0.30	1.39	-2.44	3.04	129379

Matrix	CORA	Juncus	0.86	1.91	-2.87	4.64	83760
Obligate	COYE	Juncus	0.43	1.12	-1.76	2.63	86356
Matrix	DEJU	Juncus	0.67	1.60	-2.53	3.78	134148
Matrix	DOWO	Juncus	-0.76	1.92	-4.45	3.11	113912
Matrix	EUCD	Juncus	-0.98	1.23	-3.37	1.45	99603
Facultative	EUST	Juncus	1.79	1.12	-0.32	4.09	122643
Obligate	GBHE	Juncus	0.63	1.89	-3.11	4.31	54416
Facultative	GHOW	Juncus	0.45	1.91	-3.18	4.40	55686
Obligate	GREG	Juncus	-1.44	2.07	-5.47	2.72	12540
Obligate	GRHE	Juncus	-1.71	2.09	-5.72	2.49	37010
Matrix	GRSP	Juncus	-0.63	1.38	-3.36	2.06	42231
Facultative	GTGR	Juncus	-2.02	1.94	-5.83	1.81	90494
Matrix	HOFI	Juncus	0.62	1.98	-3.18	4.60	19472
Matrix	HOSP	Juncus	-0.12	1.40	-2.89	2.65	299400
Facultative	HOWR	Juncus	1.39	0.90	-0.30	3.24	299400
Facultative	KILL	Juncus	-0.32	1.18	-2.59	2.05	35663
Matrix	LASP	Juncus	0.78	1.21	-1.54	3.24	299400
Facultative	LAZB	Juncus	1.08	2.04	-2.88	5.13	27168
Matrix	LEGO	Juncus	-1.03	1.63	-4.07	2.38	19577
Obligate	MALL	Juncus	-0.83	1.17	-3.15	1.47	86867
Obligate	MAWR	Juncus	-1.58	1.66	-4.87	1.64	132216
Facultative	MODO	Juncus	0.10	1.09	-1.99	2.30	116703
Matrix	NOFL	Juncus	0.76	2.00	-3.14	4.73	20719
Facultative	NOMO	Juncus	1.47	0.78	-0.03	3.04	182475
Facultative	NRWS	Juncus	1.06	1.89	-2.68	4.76	38056
Matrix	NUWO	Juncus	0.53	1.85	-2.83	4.38	15911
Facultative	OATI	Juncus	1.41	1.64	-1.72	4.74	25924
Matrix	OSPR	Juncus	-1.55	2.03	-5.49	2.50	12972
Matrix	RNPH	Juncus	-0.94	1.69	-4.27	2.37	299400
Facultative	RSHA	Juncus	-0.16	1.22	-2.57	2.22	89292
Facultative	RTHA	Juncus	0.73	1.84	-2.87	4.39	35259
Obligate	RWBL	Juncus	-0.23	0.91	-2.05	1.54	98463
Facultative	SOSP	Juncus	0.82	0.66	-0.46	2.13	224669
Matrix	SPTO	Juncus	2.17	1.34	-0.37	4.88	50619
Matrix	SWHA	Juncus	-0.22	1.96	-4.04	3.66	85065
Facultative	TRSW	Juncus	0.59	0.83	-1.03	2.25	299400
Obligate	VIRA	Juncus	1.44	1.13	-0.69	3.80	32436
Matrix	WBNU	Juncus	-0.09	1.29	-2.63	2.45	130753
Matrix	WEBL	Juncus	2.42	1.97	-1.46	6.30	28903
Facultative	WEKI	Juncus	1.42	0.95	-0.42	3.33	132550
Matrix	WEME	Juncus	-1.55	0.93	-3.46	0.21	93697
Matrix	WEWP	Juncus	0.11	0.92	-1.69	1.93	299400
Obligate	WIFL	Juncus	-0.18	1.88	-3.81	3.60	11065
Obligate	WISN	Juncus	-0.77	1.48	-3.76	2.07	11477

Matrix	WITU	Juncus	-1.31	1.48	-4.29	1.58	109273
Obligate	WODU	Juncus	-2.53	1.87	-6.14	1.24	15918
Facultative	WREN	Juncus	0.36	1.46	-2.51	3.22	48843
Obligate	YBCH	Juncus	1.55	0.92	-0.23	3.40	219741
Obligate	YWAR	Juncus	-1.24	1.19	-3.57	1.13	299400
Matrix	ACWO	Typha	-1.60	1.10	-3.89	0.44	65048
Obligate	AMBI	Typha	0.85	1.63	-2.34	4.06	50900
Matrix	AMCR	Typha	-1.46	1.31	-4.17	0.98	118465
Matrix	AMGO	Typha	1.10	1.97	-2.73	5.01	20403
Matrix	AMKE	Typha	-0.71	1.76	-4.08	2.83	299400
Matrix	AMRO	Typha	0.68	1.09	-1.41	2.87	28325
Facultative	ANHU	Typha	-0.25	1.65	-3.46	3.06	38528
Facultative	ATFL	Typha	-0.34	1.86	-3.93	3.38	116323
Facultative	BASW	Typha	1.72	1.85	-1.94	5.38	17051
Obligate	BEKI	Typha	0.12	2.10	-3.79	4.43	13270
Facultative	BEWR	Typha	-0.23	1.71	-3.55	3.21	35360
Facultative	BHCO	Typha	-0.36	1.32	-2.76	2.47	273700
Matrix	BHGR	Typha	0.14	1.70	-3.22	3.49	33541
Obligate	BLPH	Typha	0.51	1.00	-1.43	2.52	126893
Obligate	BLRA	Typha	0.05	1.03	-2.02	2.05	299400
Facultative	BRBL	Typha	-0.87	1.96	-4.74	2.97	103965
Facultative	BUOR	Typha	-0.39	0.97	-2.29	1.54	94651
Facultative	BUSH	Typha	0.15	1.17	-2.20	2.49	21672
Obligate	CANG	Typha	-0.74	1.42	-3.55	2.03	199671
Matrix	CAQU	Typha	0.71	1.15	-1.45	3.13	299400
Matrix	CASJ	Typha	0.51	1.46	-2.23	3.54	270220
Matrix	CATO	Typha	-0.61	0.74	-2.08	0.83	120228
Matrix	CEDW	Typha	-0.12	1.97	-3.91	3.85	168453
Facultative	CLSW	Typha	-1.77	1.81	-5.26	1.89	299400
Obligate	COMO	Typha	-0.03	1.34	-2.64	2.65	40006
Matrix	CORA	Typha	-0.79	1.93	-4.52	3.07	42774
Obligate	COYE	Typha	0.25	1.13	-1.91	2.52	76120
Matrix	DEJU	Typha	0.01	1.48	-2.95	2.88	299400
Matrix	DOWO	Typha	-0.10	1.91	-3.76	3.73	11479
Matrix	EUCD	Typha	-0.73	1.14	-3.02	1.48	20977
Facultative	EUST	Typha	-1.76	1.11	-4.12	0.25	170718
Obligate	GBHE	Typha	0.17	1.91	-3.55	3.95	95307
Facultative	GHOW	Typha	1.09	1.86	-2.37	4.94	100324
Obligate	GREG	Typha	-0.42	2.00	-4.31	3.56	91555
Obligate	GRHE	Typha	-0.72	1.94	-4.50	3.13	91365
Matrix	GRSP	Typha	-0.86	1.34	-3.52	1.76	299400
Facultative	GTGR	Typha	-1.32	1.84	-4.94	2.28	299400
Matrix	HOFI	Typha	1.82	1.98	-2.05	5.74	21104
Matrix	HOSP	Typha	-0.42	1.48	-3.41	2.43	41588

Facultative	HOWR	Typha	-0.63	0.90	-2.58	0.99	70034
Facultative	KILL	Typha	2.43	1.25	-0.04	4.89	299400
Matrix	LASP	Typha	0.49	1.06	-1.59	2.59	44926
Facultative	LAZB	Typha	1.20	2.00	-2.67	5.17	24489
Matrix	LEGO	Typha	2.66	1.59	-0.48	5.82	59889
Obligate	MALL	Typha	2.16	1.34	-0.42	4.82	141594
Obligate	MAWR	Typha	1.28	1.60	-1.83	4.43	299400
Facultative	MODO	Typha	1.40	0.98	-0.41	3.45	177739
Matrix	NOFL	Typha	-1.33	2.14	-5.38	3.07	48471
Facultative	NOMO	Typha	-1.65	0.82	-3.34	-0.10	299400
Facultative	NRWS	Typha	1.51	1.90	-2.19	5.27	16839
Matrix	NUWO	Typha	-0.11	1.65	-3.23	3.28	60421
Facultative	OATI	Typha	1.40	1.37	-1.32	4.11	78287
Matrix	OSPR	Typha	0.03	1.91	-3.72	3.81	151948
Matrix	RNPH	Typha	0.81	1.61	-2.33	3.99	299400
Facultative	RSHA	Typha	-2.59	1.12	-4.85	-0.46	299400
Facultative	RTHA	Typha	0.51	1.89	-3.15	4.28	12668
Obligate	RWBL	Typha	0.20	0.77	-1.34	1.70	299400
Facultative	SOSP	Typha	1.13	0.60	-0.03	2.34	56827
Matrix	SPTO	Typha	0.03	1.21	-2.38	2.37	68972
Matrix	SWHA	Typha	-0.24	1.92	-3.98	3.58	137937
Facultative	TRSW	Typha	0.34	0.74	-1.10	1.81	143662
Obligate	VIRA	Typha	-0.32	1.16	-2.53	2.11	45087
Matrix	WBNU	Typha	0.31	1.32	-2.17	3.00	92075
Matrix	WEBL	Typha	-0.35	2.11	-4.29	3.98	27260
Facultative	WEKI	Typha	-0.25	0.92	-2.09	1.53	192109
Matrix	WEME	Typha	0.08	0.93	-1.76	1.88	299400
Matrix	WEWP	Typha	0.97	0.85	-0.66	2.68	181020
Obligate	WIFL	Typha	0.11	1.79	-3.37	3.70	20235
Obligate	WISN	Typha	1.34	1.38	-1.32	4.09	299400
Matrix	WITU	Typha	0.67	1.44	-2.15	3.55	29021
Obligate	WODU	Typha	0.14	1.66	-3.13	3.40	235808
Facultative	WREN	Typha	-0.75	1.43	-3.61	2.00	164849
Obligate	YBCH	Typha	-0.35	0.81	-2.00	1.21	24503
Obligate	YWAR	Typha	0.53	1.07	-1.53	2.66	299400
Matrix	ACWO	Slope	0.04	1.53	-2.98	3.03	126083
Obligate	AMBI	Slope	-3.34	1.88	-7.07	0.33	41324
Matrix	AMCR	Slope	-0.50	1.62	-3.72	2.66	22022
Matrix	AMGO	Slope	-1.21	2.13	-5.34	3.04	27712
Matrix	AMKE	Slope	-2.10	1.95	-5.93	1.72	46300
Matrix	AMRO	Slope	-0.57	1.48	-3.45	2.37	33323
Facultative	ANHU	Slope	-1.32	1.85	-4.93	2.34	26471
Facultative	ATFL	Slope	-1.51	1.95	-5.20	2.47	15134
Facultative	BASW	Slope	-1.37	2.11	-5.45	2.84	46982

Obligate	BEKI	Slope	-0.53	2.03	-4.45	3.51	299400
Facultative	BEWR	Slope	1.19	1.97	-2.69	5.06	91670
Facultative	BHCO	Slope	-1.06	1.71	-4.34	2.36	58976
Matrix	BHGR	Slope	-2.20	1.96	-6.06	1.63	239033
Obligate	BLPH	Slope	0.36	1.48	-2.50	3.31	32742
Obligate	BLRA	Slope	-1.04	1.50	-4.00	1.89	34575
Facultative	BRBL	Slope	-2.80	2.14	-7.02	1.41	105221
Facultative	BUOR	Slope	-0.97	1.46	-3.84	1.89	41431
Facultative	BUSH	Slope	0.38	1.69	-2.90	3.76	78583
Obligate	CANG	Slope	-1.80	1.83	-5.35	1.81	85724
Matrix	CAQU	Slope	-1.15	1.60	-4.30	1.96	29860
Matrix	CASJ	Slope	-0.44	1.65	-3.70	2.80	16051
Matrix	CATO	Slope	-0.57	1.26	-3.07	1.87	43783
Matrix	CEDW	Slope	-3.10	2.21	-7.34	1.39	14916
Facultative	CLSW	Slope	-1.97	2.01	-5.87	2.02	42015
Obligate	COMO	Slope	-1.42	1.69	-4.85	1.82	19975
Matrix	CORA	Slope	-2.05	2.04	-6.04	1.97	53329
Obligate	COYE	Slope	-3.33	1.64	-6.58	-0.16	52455
Matrix	DEJU	Slope	-2.66	1.82	-6.26	0.86	20130
Matrix	DOWO	Slope	-2.58	2.05	-6.52	1.53	56948
Matrix	EUCD	Slope	-0.25	1.60	-3.38	2.88	299400
Facultative	EUST	Slope	0.31	1.58	-2.75	3.45	58027
Obligate	GBHE	Slope	-3.17	2.14	-7.36	1.06	60376
Facultative	GHOW	Slope	-1.12	2.08	-5.11	3.04	263462
Obligate	GREG	Slope	-2.47	2.19	-6.76	1.82	96544
Obligate	GRHE	Slope	-2.60	2.18	-6.88	1.68	38085
Matrix	GRSP	Slope	-0.49	1.67	-3.74	2.81	38626
Facultative	GTGR	Slope	-2.55	2.11	-6.75	1.55	150893
Matrix	HOFI	Slope	-0.39	2.08	-4.41	3.76	58141
Matrix	HOSP	Slope	0.17	1.78	-3.28	3.71	21217
Facultative	HOWR	Slope	-1.54	1.25	-4.00	0.93	163366
Facultative	KILL	Slope	-0.89	1.59	-4.01	2.25	45448
Matrix	LASP	Slope	-2.16	1.52	-5.15	0.83	17629
Facultative	LAZB	Slope	-0.54	2.19	-4.82	3.76	64729
Matrix	LEGO	Slope	0.04	1.78	-3.40	3.58	11519
Obligate	MALL	Slope	-3.75	1.62	-6.97	-0.61	102913
Obligate	MAWR	Slope	-3.22	1.82	-6.85	0.30	84706
Facultative	MODO	Slope	-0.21	1.53	-3.34	2.70	68219
Matrix	NOFL	Slope	-0.56	2.11	-4.66	3.59	299400
Facultative	NOMO	Slope	0.07	1.31	-2.52	2.61	13142
Facultative	NRWS	Slope	-2.45	2.15	-6.58	1.89	299400
Matrix	NUWO	Slope	1.39	1.92	-2.43	5.14	299400
Facultative	OATI	Slope	0.77	1.73	-2.66	4.14	140503
Matrix	OSPR	Slope	-2.86	2.15	-7.04	1.39	71045

Matrix	RNPH	Slope	-1.10	1.88	-4.75	2.62	299400
Facultative	RSHA	Slope	-1.08	1.60	-4.22	2.04	23563
Facultative	RTHA	Slope	-0.77	2.09	-4.80	3.43	64852
Obligate	RWBL	Slope	-1.54	1.40	-4.36	1.14	20087
Facultative	SOSP	Slope	-2.71	1.15	-5.00	-0.48	8375
Matrix	SPTO	Slope	-1.46	1.55	-4.51	1.59	34189
Matrix	SWHA	Slope	-1.20	2.04	-5.20	2.80	25483
Facultative	TRSW	Slope	-2.00	1.31	-4.62	0.52	14641
Obligate	VIRA	Slope	-1.11	1.61	-4.25	2.10	12899
Matrix	WBNU	Slope	-1.10	1.61	-4.30	2.02	36383
Matrix	WEBL	Slope	0.56	2.11	-3.58	4.71	130517
Facultative	WEKI	Slope	-0.26	1.50	-3.22	2.67	49373
Matrix	WEME	Slope	-1.81	1.41	-4.66	0.90	234181
Matrix	WEWP	Slope	-1.61	1.34	-4.21	1.02	254775
Obligate	WIFL	Slope	-1.50	2.02	-5.38	2.55	22806
Obligate	WISN	Slope	-0.42	1.63	-3.60	2.82	26939
Matrix	WITU	Slope	-2.72	1.75	-6.23	0.63	19503
Obligate	WODU	Slope	-3.16	2.03	-7.21	0.75	134045
Facultative	WREN	Slope	-4.20	1.74	-7.65	-0.83	60807
Obligate	YBCH	Slope	-1.32	1.35	-3.99	1.33	287377
Obligate	YWAR	Slope	-2.43	1.55	-5.50	0.61	26553
Matrix	ACWO	Impoundment	-0.96	2.01	-4.89	3.01	22247
Obligate	AMBI	Impoundment	1.19	2.21	-3.15	5.53	81751
Matrix	AMCR	Impoundment	-0.36	2.28	-4.85	4.10	16980
Matrix	AMGO	Impoundment	-0.20	2.38	-4.86	4.48	22319
Matrix	AMKE	Impoundment	-0.83	2.46	-5.63	4.02	47004
Matrix	AMRO	Impoundment	-1.87	2.31	-6.45	2.62	49651
Facultative	ANHU	Impoundment	-0.41	2.32	-4.96	4.15	229520
Facultative	ATFL	Impoundment	-1.85	2.40	-6.56	2.86	34723
Facultative	BASW	Impoundment	0.61	2.39	-4.11	5.27	55077
Obligate	BEKI	Impoundment	-0.53	2.39	-5.19	4.18	53997
Facultative	BEWR	Impoundment	-1.51	2.42	-6.29	3.21	299400
Facultative	BHCO	Impoundment	0.56	2.31	-3.97	5.08	40468
Matrix	BHGR	Impoundment	-1.62	2.43	-6.37	3.13	299400
Obligate	BLPH	Impoundment	-1.13	2.04	-5.19	2.84	55102
Obligate	BLRA	Impoundment	-1.50	2.11	-5.64	2.64	42058
Facultative	BRBL	Impoundment	-1.50	2.45	-6.31	3.29	76201
Facultative	BUOR	Impoundment	-1.61	2.34	-6.26	2.91	62467
Facultative	BUSH	Impoundment	-1.09	2.30	-5.69	3.34	141113
Obligate	CANG	Impoundment	0.10	2.33	-4.49	4.68	81160
Matrix	CAQU	Impoundment	-0.21	2.36	-4.80	4.44	70907
Matrix	CASJ	Impoundment	-2.03	2.32	-6.49	2.66	156299
Matrix	CATO	Impoundment	0.48	2.04	-3.52	4.57	47105
Matrix	CEDW	Impoundment	-1.37	2.46	-6.18	3.45	35654

Facultative	CLSW	Impoundment	-0.24	2.35	-4.87	4.38	155042
Obligate	COMO	Impoundment	-2.53	2.30	-6.91	2.15	59800
Matrix	CORA	Impoundment	-1.61	2.52	-6.52	3.36	164858
Obligate	COYE	Impoundment	-0.23	1.91	-3.98	3.52	19101
Matrix	DEJU	Impoundment	-1.90	2.36	-6.54	2.72	65702
Matrix	DOWO	Impoundment	-1.35	2.49	-6.23	3.52	69632
Matrix	EUCD	Impoundment	-2.84	2.19	-7.17	1.41	299400
Facultative	EUST	Impoundment	-2.78	2.03	-6.80	1.19	124671
Obligate	GBHE	Impoundment	0.13	2.39	-4.58	4.83	60610
Facultative	GHOW	Impoundment	0.16	2.36	-4.50	4.77	55686
Obligate	GREG	Impoundment	-0.37	2.41	-5.09	4.35	30987
Obligate	GRHE	Impoundment	0.11	2.35	-4.49	4.72	290473
Matrix	GRSP	Impoundment	-1.36	2.43	-6.16	3.39	63643
Facultative	GTGR	Impoundment	-1.92	2.33	-6.44	2.72	299400
Matrix	HOFI	Impoundment	-0.89	2.40	-5.60	3.82	299400
Matrix	HOSP	Impoundment	-2.78	2.25	-7.22	1.62	47533
Facultative	HOWR	Impoundment	-3.34	2.05	-7.43	0.63	29917
Facultative	KILL	Impoundment	-1.98	2.04	-5.97	2.03	71721
Matrix	LASP	Impoundment	-2.70	2.19	-7.02	1.57	105615
Facultative	LAZB	Impoundment	-1.33	2.50	-6.22	3.56	131738
Matrix	LEGO	Impoundment	-1.71	2.34	-6.24	2.94	14446
Obligate	MALL	Impoundment	1.24	2.17	-3.02	5.49	81366
Obligate	MAWR	Impoundment	0.30	2.23	-4.03	4.71	81364
Facultative	MODO	Impoundment	1.20	2.06	-2.97	5.12	55390
Matrix	NOFL	Impoundment	-1.27	2.49	-6.14	3.61	53374
Facultative	NOMO	Impoundment	-1.27	1.95	-5.18	2.48	23580
Facultative	NRWS	Impoundment	-1.42	2.48	-6.27	3.46	31674
Matrix	NUWO	Impoundment	-1.71	2.41	-6.43	2.99	179735
Facultative	OATI	Impoundment	-2.77	2.31	-7.31	1.73	172865
Matrix	OSPR	Impoundment	-1.42	2.46	-6.25	3.42	22076
Matrix	RNPH	Impoundment	0.52	2.34	-4.08	5.09	28133
Facultative	RSHA	Impoundment	-1.81	2.38	-6.49	2.83	61563
Facultative	RTHA	Impoundment	-1.53	2.44	-6.33	3.24	90167
Obligate	RWBL	Impoundment	0.09	2.23	-4.24	4.53	67301
Facultative	SOSP	Impoundment	-0.54	1.80	-4.06	3.02	21406
Matrix	SPTO	Impoundment	-1.96	2.32	-6.53	2.57	33606
Matrix	SWHA	Impoundment	-1.39	2.50	-6.28	3.56	299400
Facultative	TRSW	Impoundment	-0.24	2.15	-4.38	4.07	66309
Obligate	VIRA	Impoundment	-0.24	2.16	-4.45	4.02	299400
Matrix	WBNU	Impoundment	-1.68	2.36	-6.34	2.92	41926
Matrix	WEBL	Impoundment	-1.42	2.49	-6.28	3.47	96804
Facultative	WEKI	Impoundment	-0.64	1.88	-4.36	3.00	39540
Matrix	WEME	Impoundment	-1.74	2.31	-6.34	2.73	167335
Matrix	WEWP	Impoundment	-2.28	2.25	-6.74	2.11	48203

Obligate	WIFL	Impoundment	-1.48	2.45	-6.29	3.32	65349
Obligate	WISN	Impoundment	-0.23	2.18	-4.49	4.08	119959
Matrix	WITU	Impoundment	0.54	2.30	-3.98	5.03	44254
Obligate	WODU	Impoundment	-0.13	2.24	-4.52	4.29	50454
Facultative	WREN	Impoundment	-1.58	2.41	-6.31	3.14	72314
Obligate	YBCH	Impoundment	-1.78	2.30	-6.33	2.66	47687
Obligate	YWAR	Impoundment	-1.95	2.30	-6.51	2.54	168793
Matrix	ACWO	Fringe	-0.52	1.57	-3.55	2.62	71714
Obligate	AMBI	Fringe	-2.02	1.96	-5.90	1.78	29799
Matrix	AMCR	Fringe	-0.86	1.78	-4.31	2.70	39071
Matrix	AMGO	Fringe	-1.76	2.32	-6.25	2.87	50441
Matrix	AMKE	Fringe	-1.28	2.06	-5.31	2.79	38277
Matrix	AMRO	Fringe	-2.18	1.64	-5.43	1.03	21487
Facultative	ANHU	Fringe	-0.48	1.97	-4.30	3.44	101991
Facultative	ATFL	Fringe	1.62	2.04	-2.41	5.61	30154
Facultative	BASW	Fringe	-2.49	2.32	-6.87	2.23	73362
Obligate	BEKI	Fringe	-1.40	2.23	-5.70	3.06	93880
Facultative	BEWR	Fringe	-2.71	2.22	-6.99	1.75	26291
Facultative	BHCO	Fringe	0.06	1.68	-3.26	3.34	32921
Matrix	BHGR	Fringe	-0.63	2.01	-4.53	3.37	113774
Obligate	BLPH	Fringe	-1.88	1.59	-4.89	1.42	19740
Obligate	BLRA	Fringe	-1.18	1.61	-4.40	1.92	54787
Facultative	BRBL	Fringe	-1.87	2.19	-6.18	2.43	64282
Facultative	BUOR	Fringe	-2.26	1.51	-5.24	0.70	10669
Facultative	BUSH	Fringe	-1.50	1.68	-4.74	1.89	52723
Obligate	CANG	Fringe	-1.11	1.79	-4.64	2.39	58489
Matrix	CAQU	Fringe	1.42	1.88	-2.18	5.21	33320
Matrix	CASJ	Fringe	-0.12	1.68	-3.40	3.22	16084
Matrix	CATO	Fringe	-2.43	1.32	-5.07	0.13	24247
Matrix	CEDW	Fringe	0.03	2.10	-4.08	4.17	83190
Facultative	CLSW	Fringe	-2.01	2.18	-6.29	2.28	121466
Obligate	COMO	Fringe	1.25	1.70	-2.08	4.60	17632
Matrix	CORA	Fringe	0.19	2.09	-3.93	4.28	37688
Obligate	COYE	Fringe	-0.58	1.57	-3.64	2.49	35217
Matrix	DEJU	Fringe	-1.60	1.82	-5.19	1.93	23432
Matrix	DOWO	Fringe	-0.15	2.10	-4.22	4.03	32087
Matrix	EUCD	Fringe	-0.12	1.64	-3.34	3.06	299400
Facultative	EUST	Fringe	-0.52	1.65	-3.73	2.73	68328
Obligate	GBHE	Fringe	-0.66	2.15	-4.86	3.58	91722
Facultative	GHOW	Fringe	-1.22	2.19	-5.43	3.22	175059
Obligate	GREG	Fringe	-1.77	2.24	-6.16	2.65	147293
Obligate	GRHE	Fringe	-1.76	2.24	-6.16	2.64	25190
Matrix	GRSP	Fringe	-2.42	1.96	-6.38	1.30	115598
Facultative	GTGR	Fringe	-0.52	2.03	-4.55	3.42	57125

Matrix	HOFI	Fringe	-0.41	2.21	-4.70	3.94	76563
Matrix	HOSP	Fringe	-2.32	2.00	-6.35	1.52	15142
Facultative	HOWR	Fringe	-1.25	1.38	-3.95	1.47	53982
Facultative	KILL	Fringe	-3.97	1.79	-7.57	-0.54	11738
Matrix	LASP	Fringe	-1.93	1.58	-4.98	1.21	22031
Facultative	LAZB	Fringe	0.02	2.23	-4.35	4.40	299400
Matrix	LEGO	Fringe	0.71	1.94	-3.04	4.60	26580
Obligate	MALL	Fringe	0.84	1.60	-2.27	4.00	20883
Obligate	MAWR	Fringe	-0.93	1.84	-4.52	2.68	19128
Facultative	MODO	Fringe	1.00	1.63	-2.24	4.20	36381
Matrix	NOFL	Fringe	-1.59	2.29	-6.07	2.92	10372
Facultative	NOMO	Fringe	-0.10	1.38	-2.82	2.60	13858
Facultative	NRWS	Fringe	-0.32	2.15	-4.45	3.95	14516
Matrix	NUWO	Fringe	-0.86	1.92	-4.57	2.98	15062
Facultative	OATI	Fringe	0.93	1.78	-2.52	4.49	25959
Matrix	OSPR	Fringe	-1.83	2.21	-6.16	2.55	58085
Matrix	RNPH	Fringe	-1.91	2.00	-5.87	1.99	27566
Facultative	RSHA	Fringe	-0.25	1.63	-3.41	2.96	22462
Facultative	RTHA	Fringe	0.05	2.14	-4.12	4.27	299400
Obligate	RWBL	Fringe	0.39	1.58	-2.68	3.52	40194
Facultative	SOSP	Fringe	-2.20	1.18	-4.53	0.10	8633
Matrix	SPTO	Fringe	-1.20	1.59	-4.32	1.90	20818
Matrix	SWHA	Fringe	-1.85	2.22	-6.19	2.53	186657
Facultative	TRSW	Fringe	-0.92	1.40	-3.67	1.81	12786
Obligate	VIRA	Fringe	-1.38	1.61	-4.57	1.76	85635
Matrix	WBNU	Fringe	-0.02	1.69	-3.33	3.31	35864
Matrix	WEBL	Fringe	-1.96	2.34	-6.47	2.72	51362
Facultative	WEKI	Fringe	-0.34	1.58	-3.37	2.82	31521
Matrix	WEME	Fringe	-2.16	1.56	-5.25	0.87	80593
Matrix	WEWP	Fringe	-2.77	1.40	-5.55	-0.02	299400
Obligate	WIFL	Fringe	-0.70	2.01	-4.63	3.25	15479
Obligate	WISN	Fringe	-0.72	1.77	-4.20	2.74	41841
Matrix	WITU	Fringe	-0.19	1.93	-3.86	3.73	23969
Obligate	WODU	Fringe	0.00	1.89	-3.70	3.71	47167
Facultative	WREN	Fringe	-1.83	1.82	-5.42	1.73	65884
Obligate	YBCH	Fringe	-1.11	1.42	-3.92	1.66	91335
Obligate	YWAR	Fringe	-2.03	1.66	-5.33	1.18	44749
Matrix	ACWO	Fluvial	-0.15	1.79	-3.50	3.57	54040
Obligate	AMBI	Fluvial	-2.06	2.16	-6.35	2.11	33421
Matrix	AMCR	Fluvial	0.44	1.84	-3.13	4.10	23914
Matrix	AMGO	Fluvial	-1.70	2.34	-6.26	2.92	41306
Matrix	AMKE	Fluvial	0.54	2.02	-3.39	4.55	24643
Matrix	AMRO	Fluvial	0.68	1.66	-2.49	4.05	52558
Facultative	ANHU	Fluvial	-2.69	2.21	-6.97	1.72	299400

Facultative	ATFL	Fluvial	-1.47	2.03	-5.41	2.59	36188
Facultative	BASW	Fluvial	-1.97	2.29	-6.43	2.55	35438
Obligate	BEKI	Fluvial	-0.39	2.20	-4.69	3.96	36621
Facultative	BEWR	Fluvial	-2.02	2.28	-6.46	2.49	36453
Facultative	BHCO	Fluvial	0.04	1.78	-3.45	3.55	52042
Matrix	BHGR	Fluvial	-1.01	2.06	-5.04	3.03	34266
Obligate	BLPH	Fluvial	-0.29	1.59	-3.40	2.85	27077
Obligate	BLRA	Fluvial	-2.40	1.68	-5.78	0.84	31107
Facultative	BRBL	Fluvial	-1.05	2.17	-5.34	3.19	42712
Facultative	BUOR	Fluvial	1.02	1.86	-2.49	4.83	36068
Facultative	BUSH	Fluvial	-0.50	1.90	-4.15	3.36	31356
Obligate	CANG	Fluvial	-1.26	2.06	-5.27	2.79	298941
Matrix	CAQU	Fluvial	-0.70	1.74	-4.09	2.75	31583
Matrix	CASJ	Fluvial	-1.21	1.97	-4.91	2.85	19273
Matrix	CATO	Fluvial	-1.02	1.52	-3.89	2.11	25048
Matrix	CEDW	Fluvial	-1.82	2.30	-6.31	2.71	20724
Facultative	CLSW	Fluvial	-0.73	2.09	-4.83	3.37	100535
Obligate	COMO	Fluvial	-2.41	2.05	-6.52	1.50	58633
Matrix	CORA	Fluvial	-2.08	2.26	-6.48	2.40	38016
Obligate	COYE	Fluvial	-2.85	1.93	-6.77	0.79	93803
Matrix	DEJU	Fluvial	-1.90	1.88	-5.58	1.78	28122
Matrix	DOWO	Fluvial	0.23	2.10	-3.88	4.35	74708
Matrix	EUCD	Fluvial	-1.19	1.82	-4.76	2.40	32303
Facultative	EUST	Fluvial	0.15	1.66	-3.08	3.43	21025
Obligate	GBHE	Fluvial	-1.93	2.27	-6.37	2.56	299400
Facultative	GHOW	Fluvial	-2.03	2.34	-6.55	2.65	213513
Obligate	GREG	Fluvial	-1.70	2.28	-6.18	2.77	14234
Obligate	GRHE	Fluvial	-1.77	2.28	-6.25	2.71	145267
Matrix	GRSP	Fluvial	-3.07	1.99	-7.06	0.77	33091
Facultative	GTGR	Fluvial	-1.80	2.23	-6.23	2.53	22259
Matrix	HOFI	Fluvial	-1.39	2.23	-5.70	3.08	128755
Matrix	HOSP	Fluvial	-2.11	2.16	-6.40	2.06	26222
Facultative	HOWR	Fluvial	-2.41	1.47	-5.30	0.47	299400
Facultative	KILL	Fluvial	1.31	1.86	-2.27	5.05	67930
Matrix	LASP	Fluvial	-1.05	1.71	-4.34	2.39	42081
Facultative	LAZB	Fluvial	-1.85	2.40	-6.50	2.93	145648
Matrix	LEGO	Fluvial	-1.53	2.05	-5.43	2.63	13161
Obligate	MALL	Fluvial	-3.21	1.93	-7.10	0.49	36027
Obligate	MAWR	Fluvial	-2.17	2.10	-6.39	1.86	62899
Facultative	MODO	Fluvial	-1.49	1.64	-4.78	1.65	18235
Matrix	NOFL	Fluvial	-1.69	2.32	-6.24	2.86	299400
Facultative	NOMO	Fluvial	-3.00	1.46	-5.92	-0.19	16780
Facultative	NRWS	Fluvial	-0.72	2.16	-4.95	3.55	96142
Matrix	NUWO	Fluvial	-1.53	2.18	-5.65	2.95	56770

Facultative	OATI	Fluvial	-1.71	1.98	-5.55	2.23	54848
Matrix	OSPR	Fluvial	-0.08	2.10	-4.19	4.07	53817
Matrix	RNPH	Fluvial	-2.31	2.15	-6.56	1.88	86335
Facultative	RSHA	Fluvial	-1.18	1.69	-4.50	2.11	31895
Facultative	RTHA	Fluvial	-2.15	2.36	-6.69	2.58	159068
Obligate	RWBL	Fluvial	-0.37	1.63	-3.52	2.88	28612
Facultative	SOSP	Fluvial	-2.03	1.29	-4.57	0.48	12033
Matrix	SPTO	Fluvial	-2.78	1.82	-6.44	0.71	78981
Matrix	SWHA	Fluvial	-1.98	2.24	-6.38	2.43	299400
Facultative	TRSW	Fluvial	-0.13	1.49	-3.05	2.81	9175
Obligate	VIRA	Fluvial	-0.73	1.72	-4.10	2.67	48027
Matrix	WBNU	Fluvial	-1.92	1.86	-5.59	1.74	110344
Matrix	WEBL	Fluvial	-1.43	2.33	-5.94	3.21	278058
Facultative	WEKI	Fluvial	0.01	1.70	-3.31	3.35	59102
Matrix	WEME	Fluvial	0.82	1.59	-2.30	3.95	43641
Matrix	WEWP	Fluvial	-1.29	1.46	-4.16	1.57	76288
Obligate	WIFL	Fluvial	-2.09	2.22	-6.44	2.28	238712
Obligate	WISN	Fluvial	-3.37	2.00	-7.33	0.56	35246
Matrix	WITU	Fluvial	-0.38	1.96	-4.16	3.55	36859
Obligate	WODU	Fluvial	-2.16	2.18	-6.48	2.07	68026
Facultative	WREN	Fluvial	0.90	1.77	-2.56	4.40	25091
Obligate	YBCH	Fluvial	-0.92	1.49	-3.84	2.01	263586
Obligate	YWAR	Fluvial	-0.01	1.66	-3.24	3.28	39265
Matrix	ACWO	% Wet	0.29	1.30	-2.53	2.59	226334
Obligate	AMBI	% Wet	-1.47	1.67	-4.78	1.78	68325
Matrix	AMCR	% Wet	-0.08	1.23	-2.63	2.22	299400
Matrix	AMGO	% Wet	0.36	2.21	-4.05	4.61	80413
Matrix	AMKE	% Wet	-2.99	1.66	-6.31	0.23	299400
Matrix	AMRO	% Wet	0.79	0.99	-1.08	2.80	299400
Facultative	ANHU	% Wet	0.44	1.88	-3.32	4.10	118304
Facultative	ATFL	% Wet	0.37	1.48	-2.66	3.20	143917
Facultative	BASW	% Wet	-0.39	1.92	-4.23	3.35	125555
Obligate	BEKI	% Wet	-0.15	2.27	-4.69	4.21	299400
Facultative	BEWR	% Wet	0.09	2.09	-4.07	4.12	171613
Facultative	BHCO	% Wet	-0.39	1.20	-2.95	1.82	163055
Matrix	BHGR	% Wet	-0.09	1.92	-3.98	3.62	163399
Obligate	BLPH	% Wet	1.47	1.01	-0.60	3.40	299400
Obligate	BLRA	% Wet	-0.60	1.02	-2.57	1.45	285463
Facultative	BRBL	% Wet	-0.38	1.99	-4.30	3.55	299400
Facultative	BUOR	% Wet	-0.44	1.01	-2.53	1.48	137980
Facultative	BUSH	% Wet	0.20	1.73	-3.88	3.11	31357
Obligate	CANG	% Wet	-1.95	1.64	-5.27	1.20	299400
Matrix	CAQU	% Wet	-1.90	1.31	-4.69	0.44	62535
Matrix	CASJ	% Wet	-2.00	1.69	-5.57	1.04	87172

Matrix	CATO	% Wet	-1.91	0.88	-3.78	-0.31	234695
Matrix	CEDW	% Wet	0.33	2.07	-3.78	4.39	118490
Facultative	CLSW	% Wet	-0.85	1.85	-4.61	2.73	67116
Obligate	COMO	% Wet	1.59	1.40	-1.03	4.49	299400
Matrix	CORA	% Wet	-1.28	1.91	-5.11	2.44	82921
Obligate	COYE	% Wet	0.63	1.06	-1.37	2.79	208990
Matrix	DEJU	% Wet	-0.75	1.62	-3.93	2.43	299400
Matrix	DOWO	% Wet	-3.17	1.70	-6.48	0.24	156621
Matrix	EUCD	% Wet	0.75	1.12	-1.42	3.00	56040
Facultative	EUST	% Wet	-1.91	1.34	-4.65	0.57	299400
Obligate	GBHE	% Wet	-0.03	1.99	-4.00	3.84	45681
Facultative	GHOW	% Wet	0.32	1.95	-3.64	4.13	299400
Obligate	GREG	% Wet	0.68	2.10	-3.54	4.73	62044
Obligate	GRHE	% Wet	-1.67	1.99	-5.57	2.29	17882
Matrix	GRSP	% Wet	-0.82	1.17	-3.18	1.43	57022
Facultative	GTGR	% Wet	-0.61	1.88	-4.34	3.11	176298
Matrix	HOFI	% Wet	-0.75	1.92	-4.61	2.96	145930
Matrix	HOSP	% Wet	0.56	1.44	-2.26	3.43	299400
Facultative	HOWR	% Wet	-0.49	0.82	-2.11	1.12	64575
Facultative	KILL	% Wet	-0.44	1.22	-2.91	1.94	41489
Matrix	LASP	% Wet	1.18	1.17	-1.04	3.57	212777
Facultative	LAZB	% Wet	0.88	2.25	-3.61	5.21	299400
Matrix	LEGO	% Wet	-2.30	1.63	-5.65	0.77	68083
Obligate	MALL	% Wet	-2.36	1.18	-4.74	-0.11	43972
Obligate	MAWR	% Wet	0.01	1.57	-3.05	3.10	161882
Facultative	MODO	% Wet	-0.54	1.07	-2.90	1.30	44643
Matrix	NOFL	% Wet	0.72	2.19	-3.66	4.94	57809
Facultative	NOMO	% Wet	-1.05	0.81	-2.74	0.47	88992
Facultative	NRWS	% Wet	-0.20	2.00	-4.18	3.73	15664
Matrix	NUWO	% Wet	-1.37	1.73	-4.91	1.89	39093
Facultative	OATI	% Wet	-1.08	1.84	-4.83	2.36	299400
Matrix	OSPR	% Wet	-0.70	2.04	-4.73	3.31	91282
Matrix	RNPH	% Wet	-2.38	1.41	-5.22	0.36	194377
Facultative	RSHA	% Wet	1.02	1.10	-1.14	3.21	161178
Facultative	RTHA	% Wet	-1.74	1.89	-5.48	1.99	83378
Obligate	RWBL	% Wet	-0.24	0.76	-1.76	1.23	256700
Facultative	SOSP	% Wet	0.37	0.58	-0.75	1.52	299400
Matrix	SPTO	% Wet	-0.54	1.10	-2.62	1.73	160540
Matrix	SWHA	% Wet	-0.94	2.00	-4.96	2.95	37610
Facultative	TRSW	% Wet	1.76	0.90	0.03	3.57	299400
Obligate	VIRA	% Wet	1.88	1.30	-0.45	4.71	67730
Matrix	WBNU	% Wet	-1.17	1.46	-4.08	1.60	204551
Matrix	WEBL	% Wet	-0.93	1.99	-4.88	2.95	24502
Facultative	WEKI	% Wet	-0.38	0.84	-2.09	1.24	243358

Matrix	WEME	% Wet	1.99	1.04	0.05	4.14	299400
Matrix	WEWP	% Wet	0.58	0.88	-1.07	2.38	213809
Obligate	WIFL	% Wet	-0.30	1.80	-3.84	3.32	51121
Obligate	WISN	% Wet	0.69	1.16	-1.56	3.02	79764
Matrix	WITU	% Wet	1.63	1.48	-1.23	4.62	240060
Obligate	WODU	% Wet	-0.33	1.65	-3.69	2.87	126711
Facultative	WREN	% Wet	-0.91	1.32	-3.52	1.69	299400
Obligate	YBCH	% Wet	-0.79	0.80	-2.37	0.79	61927
Obligate	YWAR	% Wet	1.54	1.21	-0.73	4.04	223394
Matrix	ACWO	Natural	-0.16	1.51	-3.08	2.90	45322
Obligate	AMBI	Natural	-3.67	1.94	-7.57	0.02	299400
Matrix	AMCR	Natural	-1.84	1.55	-4.86	1.27	98706
Matrix	AMGO	Natural	-3.01	2.23	-7.33	1.43	151071
Matrix	AMKE	Natural	-3.28	2.08	-7.40	0.76	180522
Matrix	AMRO	Natural	-2.55	1.42	-5.38	0.20	264796
Facultative	ANHU	Natural	-2.96	1.94	-6.79	0.85	299400
Facultative	ATFL	Natural	-1.00	1.87	-4.55	2.80	107464
Facultative	BASW	Natural	-0.48	2.02	-4.47	3.47	145968
Obligate	BEKI	Natural	-3.66	2.27	-7.96	0.98	23554
Facultative	BEWR	Natural	-0.66	1.88	-4.35	3.05	84276
Facultative	BHCO	Natural	-1.60	1.84	-4.97	2.29	299400
Matrix	BHGR	Natural	-1.53	1.91	-5.28	2.22	149557
Obligate	BLPH	Natural	-1.01	1.51	-3.86	2.09	150923
Obligate	BLRA	Natural	-2.54	1.41	-5.33	0.22	36135
Facultative	BRBL	Natural	-2.77	2.15	-7.02	1.42	299400
Facultative	BUOR	Natural	-1.49	1.43	-4.22	1.41	100679
Facultative	BUSH	Natural	-2.14	1.67	-5.47	1.08	18586
Obligate	CANG	Natural	-2.71	1.78	-6.24	0.74	39420
Matrix	CAQU	Natural	-1.49	1.57	-4.49	1.71	91215
Matrix	CASJ	Natural	-2.89	1.66	-6.27	0.27	299400
Matrix	CATO	Natural	-2.65	1.19	-5.01	-0.34	37943
Matrix	CEDW	Natural	-2.99	2.18	-7.24	1.36	299400
Facultative	CLSW	Natural	-2.21	2.00	-6.09	1.74	64702
Obligate	COMO	Natural	0.40	1.54	-2.62	3.42	299400
Matrix	CORA	Natural	-3.02	2.15	-7.22	1.22	194922
Obligate	COYE	Natural	-4.00	1.80	-7.67	-0.61	75335
Matrix	DEJU	Natural	-2.52	1.90	-6.33	1.11	165505
Matrix	DOWO	Natural	-1.34	2.04	-5.30	2.69	31049
Matrix	EUCD	Natural	-4.05	1.54	-7.16	-1.12	89253
Facultative	EUST	Natural	1.20	1.75	-2.10	4.74	299400
Obligate	GBHE	Natural	-2.90	2.16	-7.16	1.33	88342
Facultative	GHOW	Natural	-1.95	2.08	-5.98	2.20	41393
Obligate	GREG	Natural	-2.69	2.18	-7.00	1.58	255077
Obligate	GRHE	Natural	-2.78	2.17	-7.03	1.46	299400

Matrix	GRSP	Natural	-1.90	1.60	-5.08	1.20	256601
Facultative	GTGR	Natural	-2.97	2.10	-7.14	1.11	230965
Matrix	HOFI	Natural	-0.79	2.18	-5.02	3.52	99671
Matrix	HOSP	Natural	-4.14	1.83	-7.85	-0.67	95028
Facultative	HOWR	Natural	-0.85	1.20	-3.27	1.47	23594
Facultative	KILL	Natural	-4.62	1.57	-7.80	-1.66	299400
Matrix	LASP	Natural	-1.10	1.45	-3.95	1.75	68279
Facultative	LAZB	Natural	-1.70	2.19	-5.93	2.66	229543
Matrix	LEGO	Natural	-0.01	1.91	-3.74	3.77	94861
Obligate	MALL	Natural	-1.26	1.45	-4.12	1.58	41793
Obligate	MAWR	Natural	-1.64	1.77	-5.14	1.79	73423
Facultative	MODO	Natural	-0.22	1.65	-3.29	3.23	39052
Matrix	NOFL	Natural	-2.72	2.22	-7.06	1.65	178115
Facultative	NOMO	Natural	-1.95	1.13	-4.18	0.26	52133
Facultative	NRWS	Natural	-0.45	1.97	-4.31	3.42	210862
Matrix	NUWO	Natural	-2.93	1.94	-6.57	1.11	45494
Facultative	OATI	Natural	-1.92	1.71	-5.23	1.50	172492
Matrix	OSPR	Natural	-2.97	2.15	-7.19	1.27	100781
Matrix	RNPH	Natural	-4.19	1.85	-7.90	-0.63	299400
Facultative	RSHA	Natural	-3.91	1.66	-7.27	-0.77	299400
Facultative	RTHA	Natural	-0.69	1.99	-4.57	3.23	256032
Obligate	RWBL	Natural	-0.05	1.29	-2.56	2.50	148522
Facultative	SOSP	Natural	-1.04	1.05	-3.16	0.98	19918
Matrix	SPTO	Natural	-1.30	1.45	-4.16	1.53	299400
Matrix	SWHA	Natural	-2.76	2.15	-7.01	1.45	142257
Facultative	TRSW	Natural	-1.67	1.16	-3.96	0.59	69382
Obligate	VIRA	Natural	-2.50	1.52	-5.54	0.44	13837
Matrix	WBNU	Natural	-2.20	1.53	-5.20	0.82	299400
Matrix	WEBL	Natural	-2.47	2.16	-6.60	1.88	28636
Facultative	WEKI	Natural	0.51	1.68	-2.64	3.96	299400
Matrix	WEME	Natural	0.43	1.23	-1.94	2.88	55108
Matrix	WEWP	Natural	-1.52	1.14	-3.79	0.71	111973
Obligate	WIFL	Natural	-3.43	2.06	-7.46	0.65	133567
Obligate	WISN	Natural	-4.80	1.62	-7.99	-1.66	41708
Matrix	WITU	Natural	-0.83	1.64	-4.02	2.43	115915
Obligate	WODU	Natural	-1.25	1.86	-4.89	2.38	128389
Facultative	WREN	Natural	-3.49	1.96	-7.45	0.23	299400
Obligate	YBCH	Natural	-0.80	1.19	-3.14	1.54	234124
Obligate	YWAR	Natural	-4.53	1.72	-8.05	-1.34	97936
Matrix	ACWO	Irrigation	-0.97	1.46	-3.84	1.89	64886
Obligate	AMBI	Irrigation	-0.28	1.86	-3.91	3.38	299400
Matrix	AMCR	Irrigation	-2.79	1.52	-5.77	0.21	134820
Matrix	AMGO	Irrigation	-0.67	2.08	-4.72	3.44	21568
Matrix	AMKE	Irrigation	-1.41	1.91	-5.15	2.34	104634

Matrix	AMRO	Irrigation	-2.09	1.32	-4.69	0.47	176603
Facultative	ANHU	Irrigation	-0.06	1.86	-3.64	3.65	107122
Facultative	ATFL	Irrigation	-1.02	1.84	-4.61	2.63	46512
Facultative	BASW	Irrigation	-1.99	2.13	-6.04	2.36	299400
Obligate	BEKI	Irrigation	-1.06	2.04	-5.00	3.03	44953
Facultative	BEWR	Irrigation	-1.92	1.93	-5.65	1.95	22888
Facultative	BHCO	Irrigation	-0.86	1.75	-4.23	2.66	108613
Matrix	BHGR	Irrigation	-2.92	2.02	-6.91	1.04	115437
Obligate	BLPH	Irrigation	-2.13	1.57	-5.09	1.10	59479
Obligate	BLRA	Irrigation	-3.09	1.43	-5.92	-0.30	136787
Facultative	BRBL	Irrigation	-2.89	2.15	-7.09	1.32	299400
Facultative	BUOR	Irrigation	-2.15	1.47	-5.13	0.66	158839
Facultative	BUSH	Irrigation	-0.27	1.64	-3.45	3.04	52696
Obligate	CANG	Irrigation	0.80	1.76	-2.61	4.30	15191
Matrix	CAQU	Irrigation	-0.83	1.51	-3.73	2.19	250560
Matrix	CASJ	Irrigation	-0.03	1.83	-3.50	3.67	66943
Matrix	CATO	Irrigation	-1.32	1.27	-3.74	1.24	18973
Matrix	CEDW	Irrigation	-0.90	2.03	-4.90	3.07	287655
Facultative	CLSW	Irrigation	-0.13	1.91	-3.85	3.64	65551
Obligate	COMO	Irrigation	-1.66	1.63	-4.89	1.52	74766
Matrix	CORA	Irrigation	-1.94	2.05	-5.92	2.13	299400
Obligate	COYE	Irrigation	-0.67	1.59	-3.79	2.45	43436
Matrix	DEJU	Irrigation	-3.27	1.83	-6.88	0.27	169846
Matrix	DOWO	Irrigation	-2.27	2.06	-6.28	1.80	299400
Matrix	EUCD	Irrigation	-2.04	1.43	-4.85	0.78	88248
Facultative	EUST	Irrigation	-2.81	1.45	-5.68	0.00	299400
Obligate	GBHE	Irrigation	-1.77	2.12	-5.91	2.41	299400
Facultative	GHOW	Irrigation	-0.71	1.99	-4.53	3.30	65338
Obligate	GREG	Irrigation	-1.70	2.14	-5.88	2.50	299400
Obligate	GRHE	Irrigation	-1.35	2.09	-5.47	2.73	299400
Matrix	GRSP	Irrigation	-4.23	1.80	-7.88	-0.83	299400
Facultative	GTGR	Irrigation	-1.72	2.06	-5.78	2.29	163267
Matrix	HOFI	Irrigation	-1.02	2.09	-5.10	3.12	21295
Matrix	HOSP	Irrigation	-0.97	1.62	-4.15	2.20	138576
Facultative	HOWR	Irrigation	-1.60	1.27	-4.16	0.81	28936
Facultative	KILL	Irrigation	-0.57	1.45	-3.36	2.32	299400
Matrix	LASP	Irrigation	-0.79	1.45	-3.66	2.03	41107
Facultative	LAZB	Irrigation	-1.37	2.17	-5.62	2.91	26784
Matrix	LEGO	Irrigation	-1.05	1.84	-4.71	2.58	52178
Obligate	MALL	Irrigation	-2.78	1.67	-6.14	0.40	91301
Obligate	MAWR	Irrigation	-1.17	1.86	-4.82	2.47	299400
Facultative	MODO	Irrigation	-2.81	1.49	-5.76	0.08	49751
Matrix	NOFL	Irrigation	-0.10	2.04	-4.10	3.92	66797
Facultative	NOMO	Irrigation	-1.24	1.17	-3.50	1.09	299400

Facultative	NRWS	Irrigation	-3.42	2.19	-7.61	1.02	130337
Matrix	NUWO	Irrigation	-2.89	1.99	-6.75	1.05	10690
Facultative	OATI	Irrigation	-1.58	1.84	-5.19	2.04	177229
Matrix	OSPR	Irrigation	-2.65	2.16	-6.91	1.59	105051
Matrix	RNPH	Irrigation	-0.35	1.82	-3.84	3.31	299400
Facultative	RSHA	Irrigation	-5.46	1.70	-8.82	-2.18	142184
Facultative	RTHA	Irrigation	-3.68	2.20	-7.87	0.80	14953
Obligate	RWBL	Irrigation	-1.64	1.21	-4.02	0.71	148569
Facultative	SOSP	Irrigation	-1.83	1.10	-4.03	0.27	45196
Matrix	SPTO	Irrigation	-1.41	1.42	-4.20	1.37	299400
Matrix	SWHA	Irrigation	-2.97	2.15	-7.20	1.25	137148
Facultative	TRSW	Irrigation	-2.38	1.20	-4.77	-0.04	73236
Obligate	VIRA	Irrigation	-2.28	1.59	-5.44	0.79	12469
Matrix	WBNU	Irrigation	-3.69	1.63	-6.91	-0.53	223787
Matrix	WEBL	Irrigation	-1.52	2.06	-5.48	2.60	247500
Facultative	WEKI	Irrigation	-3.06	1.36	-5.76	-0.40	176912
Matrix	WEME	Irrigation	-1.50	1.32	-4.10	1.07	74912
Matrix	WEWP	Irrigation	-4.51	1.40	-7.33	-1.86	110502
Obligate	WIFL	Irrigation	-0.61	1.92	-4.35	3.18	27891
Obligate	WISN	Irrigation	-0.38	1.75	-3.68	3.17	248634
Matrix	WITU	Irrigation	-3.10	1.72	-6.49	0.27	74994
Obligate	WODU	Irrigation	-1.44	1.99	-5.34	2.44	299400
Facultative	WREN	Irrigation	0.19	1.62	-3.00	3.35	72175
Obligate	YBCH	Irrigation	-0.61	1.22	-3.01	1.76	299400
Obligate	YWAR	Irrigation	0.61	1.37	-2.04	3.33	286412
Matrix	ACWO	Natural + Irrigation	-0.12	1.56	-3.12	3.00	120237
Obligate	AMBI	Natural + Irrigation	-3.08	2.01	-7.11	0.77	80633
Matrix	AMCR	Natural + Irrigation	-0.30	1.57	-3.30	2.86	77897
Matrix	AMGO	Natural + Irrigation	-2.77	2.28	-7.17	1.79	56061
Matrix	AMKE	Natural + Irrigation	0.61	1.85	-3.00	4.28	183145
Matrix	AMRO	Natural + Irrigation	-1.52	1.47	-4.41	1.36	103079
Facultative	ANHU	Natural + Irrigation	-2.35	1.94	-6.14	1.50	42137
Facultative	ATFL	Natural + Irrigation	-3.64	2.07	-7.56	0.63	55277
Facultative	BASW	Natural + Irrigation	-3.22	2.18	-7.42	1.16	184987
Obligate	BEKI	Natural + Irrigation	0.00	2.01	-3.90	3.98	299400
Facultative	BEWR	Natural + Irrigation	-3.68	2.16	-7.80	0.72	45228
Facultative	BHCO	Natural + Irrigation	-1.42	1.60	-4.54	1.75	191114
Matrix	BHGR	Natural + Irrigation	-2.42	1.96	-6.26	1.44	92808
Obligate	BLPH	Natural + Irrigation	-1.50	1.51	-4.42	1.52	79436
Obligate	BLRA	Natural + Irrigation	-0.87	1.51	-3.80	2.15	299400
Facultative	BRBL	Natural + Irrigation	-1.96	2.10	-6.11	2.14	247382
Facultative	BUOR	Natural + Irrigation	-0.94	1.53	-3.93	2.09	299400
Facultative	BUSH	Natural + Irrigation	-0.07	1.75	-3.44	3.47	30858
Obligate	CANG	Natural + Irrigation	-2.46	1.82	-6.04	1.08	23787

Matrix	CAQU	Natural + Irrigation	-1.04	1.65	-4.22	2.26	299400
Matrix	CASJ	Natural + Irrigation	-0.89	1.85	-4.36	2.94	47160
Matrix	CATO	Natural + Irrigation	-1.97	1.29	-4.51	0.55	21096
Matrix	CEDW	Natural + Irrigation	-2.75	2.20	-7.04	1.63	59140
Facultative	CLSW	Natural + Irrigation	-3.11	2.11	-7.25	1.03	93312
Obligate	COMO	Natural + Irrigation	-3.96	1.80	-7.53	-0.48	299400
Matrix	CORA	Natural + Irrigation	-1.21	2.02	-5.17	2.80	79212
Obligate	COYE	Natural + Irrigation	-2.54	1.65	-5.83	0.65	89210
Matrix	DEJU	Natural + Irrigation	-1.49	1.75	-4.91	1.94	195472
Matrix	DOWO	Natural + Irrigation	-1.36	2.04	-5.31	2.69	80658
Matrix	EUCD	Natural + Irrigation	-1.66	1.56	-4.75	1.40	41407
Facultative	EUST	Natural + Irrigation	-2.06	1.60	-5.13	1.15	65031
Obligate	GBHE	Natural + Irrigation	-1.59	2.08	-5.67	2.51	107600
Facultative	GHOW	Natural + Irrigation	-2.15	2.15	-6.29	2.18	181018
Obligate	GREG	Natural + Irrigation	-2.54	2.19	-6.84	1.75	58361
Obligate	GRHE	Natural + Irrigation	-2.53	2.19	-6.85	1.76	87943
Matrix	GRSP	Natural + Irrigation	-3.23	1.92	-7.13	0.39	299400
Facultative	GTGR	Natural + Irrigation	-2.65	2.14	-6.88	1.51	62808
Matrix	HOFI	Natural + Irrigation	-2.53	2.30	-6.86	2.14	123508
Matrix	HOSP	Natural + Irrigation	-3.43	1.91	-7.29	0.22	63995
Facultative	HOWR	Natural + Irrigation	0.05	1.40	-2.62	2.88	49992
Facultative	KILL	Natural + Irrigation	-1.55	1.54	-4.56	1.47	207868
Matrix	LASP	Natural + Irrigation	-2.10	1.56	-5.20	0.94	20848
Facultative	LAZB	Natural + Irrigation	-1.23	2.20	-5.47	3.13	16161
Matrix	LEGO	Natural + Irrigation	-1.33	1.96	-5.01	2.69	44288
Obligate	MALL	Natural + Irrigation	-2.92	1.72	-6.31	0.43	110832
Obligate	MAWR	Natural + Irrigation	-3.64	1.98	-7.57	0.18	141651
Facultative	MODO	Natural + Irrigation	-1.96	1.50	-4.90	0.98	11785
Matrix	NOFL	Natural + Irrigation	-2.73	2.22	-7.06	1.67	81374
Facultative	NOMO	Natural + Irrigation	-1.07	1.32	-3.64	1.55	299400
Facultative	NRWS	Natural + Irrigation	-1.48	2.06	-5.43	2.66	223186
Matrix	NUWO	Natural + Irrigation	0.82	1.98	-3.02	4.74	43321
Facultative	OATI	Natural + Irrigation	0.15	1.83	-3.35	3.84	299400
Matrix	OSPR	Natural + Irrigation	-1.01	2.03	-4.99	3.00	200707
Matrix	RNPH	Natural + Irrigation	-3.60	2.00	-7.57	0.29	299400
Facultative	RSHA	Natural + Irrigation	-1.93	1.51	-4.89	1.04	100323
Facultative	RTHA	Natural + Irrigation	-0.87	2.04	-4.84	3.18	76080
Obligate	RWBL	Natural + Irrigation	0.09	1.38	-2.59	2.83	274386
Facultative	SOSP	Natural + Irrigation	-0.70	1.18	-3.03	1.58	31421
Matrix	SPTO	Natural + Irrigation	-2.63	1.56	-5.76	0.35	197660
Matrix	SWHA	Natural + Irrigation	-1.18	2.03	-5.17	2.81	299400
Facultative	TRSW	Natural + Irrigation	-2.05	1.28	-4.58	0.44	113515
Obligate	VIRA	Natural + Irrigation	-0.49	1.64	-3.61	2.85	66085
Matrix	WBNU	Natural + Irrigation	-3.63	1.68	-6.96	-0.36	299400

Matrix	WEBL	Natural + Irrigation	-0.70	2.10	-4.83	3.43	299400
Facultative	WEKI	Natural + Irrigation	-2.11	1.55	-5.05	1.05	299400
Matrix	WEME	Natural + Irrigation	-3.05	1.47	-5.98	-0.20	89016
Matrix	WEWP	Natural + Irrigation	-1.56	1.29	-4.12	0.97	299400
Obligate	WIFL	Natural + Irrigation	-3.39	2.10	-7.48	0.80	299400
Obligate	WISN	Natural + Irrigation	-3.49	1.67	-6.79	-0.24	74114
Matrix	WITU	Natural + Irrigation	-1.37	1.75	-4.81	2.05	299400
Obligate	WODU	Natural + Irrigation	-3.34	2.03	-7.37	0.62	42183
Facultative	WREN	Natural + Irrigation	-2.21	1.77	-5.70	1.23	89359
Obligate	YBCH	Natural + Irrigation	-0.40	1.30	-2.95	2.13	299400
Obligate	YWAR	Natural + Irrigation	-1.82	1.50	-4.82	1.08	142339
Matrix	ACWO	Developed 100m	-0.09	1.36	-2.56	2.79	299400
Obligate	AMBI	Developed 100m	-0.58	1.77	-4.25	2.68	267124
Matrix	AMCR	Developed 100m	0.09	1.50	-2.67	3.28	299400
Matrix	AMGO	Developed 100m	1.12	2.00	-2.76	5.11	53652
Matrix	AMKE	Developed 100m	-1.36	2.05	-5.34	2.71	54744
Matrix	AMRO	Developed 100m	1.99	1.41	-0.55	4.93	45152
Facultative	ANHU	Developed 100m	2.17	1.49	-0.72	5.13	73329
Facultative	ATFL	Developed 100m	-0.28	1.61	-3.21	3.20	222262
Facultative	BASW	Developed 100m	-1.36	2.09	-5.37	2.95	19738
Obligate	BEKI	Developed 100m	-0.24	2.08	-4.30	3.91	18211
Facultative	BEWR	Developed 100m	-0.07	1.80	-3.41	3.77	72659
Facultative	BHCO	Developed 100m	1.89	1.61	-1.12	5.21	50586
Matrix	BHGR	Developed 100m	0.89	1.76	-2.52	4.42	299400
Obligate	BLPH	Developed 100m	-1.57	1.59	-4.17	2.32	74861
Obligate	BLRA	Developed 100m	1.06	1.17	-1.29	3.31	299400
Facultative	BRBL	Developed 100m	-0.68	2.03	-4.65	3.37	196370
Facultative	BUOR	Developed 100m	1.84	1.47	-0.74	5.02	31614
Facultative	BUSH	Developed 100m	0.72	1.57	-2.00	4.18	145265
Obligate	CANG	Developed 100m	3.23	1.45	0.56	6.24	299400
Matrix	CAQU	Developed 100m	-0.68	1.17	-2.90	1.73	81046
Matrix	CASJ	Developed 100m	-0.31	1.38	-2.89	2.56	105012
Matrix	CATO	Developed 100m	-0.81	0.95	-2.59	1.10	22126
Matrix	CEDW	Developed 100m	-0.69	2.11	-4.81	3.55	72069
Facultative	CLSW	Developed 100m	0.68	1.79	-2.78	4.26	70849
Obligate	COMO	Developed 100m	0.73	1.15	-1.51	3.03	82355
Matrix	CORA	Developed 100m	-0.44	2.05	-4.46	3.63	299400
Obligate	COYE	Developed 100m	-0.77	1.63	-4.17	2.22	208924
Matrix	DEJU	Developed 100m	-0.60	1.66	-4.02	2.48	96098
Matrix	DOWO	Developed 100m	-0.77	2.15	-4.86	3.58	19342
Matrix	EUCD	Developed 100m	0.44	1.34	-2.13	3.18	264963
Facultative	EUST	Developed 100m	1.18	1.54	-1.59	4.47	57237
Obligate	GBHE	Developed 100m	-0.31	2.06	-4.38	3.74	299400
Facultative	GHOW	Developed 100m	-0.78	2.10	-4.83	3.51	31999

Obligate	GREG	Developed 100m	-0.43	2.12	-4.61	3.73	135287
Obligate	GRHE	Developed 100m	-0.60	2.09	-4.72	3.51	257163
Matrix	GRSP	Developed 100m	-1.28	1.66	-4.73	1.78	41844
Facultative	GTGR	Developed 100m	-0.58	1.99	-4.56	3.26	154535
Matrix	HOFI	Developed 100m	0.40	1.95	-3.36	4.29	299400
Matrix	HOSP	Developed 100m	-1.52	1.78	-5.22	1.75	299400
Facultative	HOWR	Developed 100m	0.66	0.94	-1.12	2.57	10599
Facultative	KILL	Developed 100m	0.81	1.27	-1.67	3.34	96171
Matrix	LASP	Developed 100m	-1.19	1.24	-3.52	1.36	31958
Facultative	LAZB	Developed 100m	-1.00	2.30	-5.37	3.62	75991
Matrix	LEGO	Developed 100m	0.08	1.66	-2.89	3.66	128590
Obligate	MALL	Developed 100m	-2.70	1.66	-6.17	0.28	69564
Obligate	MAWR	Developed 100m	-1.06	1.75	-4.70	2.13	39226
Facultative	MODO	Developed 100m	1.55	1.31	-0.77	4.41	96725
Matrix	NOFL	Developed 100m	0.35	2.15	-3.89	4.58	102690
Facultative	NOMO	Developed 100m	-0.88	0.90	-2.67	0.85	281555
Facultative	NRWS	Developed 100m	-0.22	2.18	-4.41	4.17	49147
Matrix	NUWO	Developed 100m	-0.44	1.80	-3.69	3.48	88764
Facultative	OATI	Developed 100m	0.71	1.66	-2.58	3.97	26870
Matrix	OSPR	Developed 100m	-0.65	2.08	-4.77	3.46	34530
Matrix	RNPH	Developed 100m	-0.95	1.84	-4.67	2.57	154481
Facultative	RSHA	Developed 100m	0.23	1.31	-2.33	2.88	299400
Facultative	RTHA	Developed 100m	0.78	1.68	-2.35	4.28	49079
Obligate	RWBL	Developed 100m	2.34	1.38	-0.18	5.22	84832
Facultative	SOSP	Developed 100m	-0.34	0.77	-1.83	1.20	28961
Matrix	SPTO	Developed 100m	-2.24	1.43	-5.17	0.45	186147
Matrix	SWHA	Developed 100m	-0.60	2.13	-4.80	3.56	27354
Facultative	TRSW	Developed 100m	-0.45	0.85	-2.08	1.28	22859
Obligate	VIRA	Developed 100m	1.04	1.18	-1.20	3.49	43668
Matrix	WBNU	Developed 100m	-1.62	1.40	-4.38	1.18	65692
Matrix	WEBL	Developed 100m	-0.49	2.10	-4.50	3.77	253245
Facultative	WEKI	Developed 100m	-0.66	1.35	-3.05	2.28	162206
Matrix	WEME	Developed 100m	0.70	1.06	-1.31	2.86	87162
Matrix	WEWP	Developed 100m	0.60	0.90	-1.15	2.38	23591
Obligate	WIFL	Developed 100m	-0.96	2.05	-5.00	3.07	24978
Obligate	WISN	Developed 100m	-0.26	1.55	-3.40	2.72	42217
Matrix	WITU	Developed 100m	0.89	1.67	-1.99	4.58	166896
Obligate	WODU	Developed 100m	-0.87	1.79	-4.44	2.72	163460
Facultative	WREN	Developed 100m	-1.37	1.72	-4.86	1.87	111749
Obligate	YBCH	Developed 100m	0.70	0.97	-1.20	2.65	87359
Obligate	YWAR	Developed 100m	0.69	1.12	-1.55	2.85	299400
Matrix	ACWO	Forest 100m	0.48	1.88	-3.12	4.26	69413
Obligate	AMBI	Forest 100m	-2.86	2.09	-7.03	1.16	65853
Matrix	AMCR	Forest 100m	0.26	1.94	-3.49	4.13	49901

Matrix	AMGO	Forest 100m	-1.67	2.27	-6.12	2.82	35795
Matrix	AMKE	Forest 100m	-2.11	2.17	-6.30	2.24	111872
Matrix	AMRO	Forest 100m	-1.34	1.73	-4.79	2.02	25347
Facultative	ANHU	Forest 100m	0.13	2.14	-4.06	4.34	30657
Facultative	ATFL	Forest 100m	-1.57	2.18	-5.75	2.79	73616
Facultative	BASW	Forest 100m	-2.85	2.25	-7.29	1.55	27181
Obligate	BEKI	Forest 100m	-2.64	2.32	-7.11	2.01	30300
Facultative	BEWR	Forest 100m	-1.20	2.15	-5.43	3.03	18858
Facultative	BHCO	Forest 100m	-5.79	1.75	-9.29	-2.42	21243
Matrix	BHGR	Forest 100m	0.06	2.12	-4.04	4.29	37589
Obligate	BLPH	Forest 100m	-2.28	1.93	-5.74	1.93	42592
Obligate	BLRA	Forest 100m	-1.92	1.76	-5.43	1.50	17477
Facultative	BRBL	Forest 100m	-0.89	2.14	-5.09	3.34	38706
Facultative	BUOR	Forest 100m	-2.11	1.67	-5.42	1.15	19405
Facultative	BUSH	Forest 100m	-0.70	2.00	-4.47	3.43	28226
Obligate	CANG	Forest 100m	-3.75	2.04	-7.77	0.25	28674
Matrix	CAQU	Forest 100m	-1.84	1.70	-5.18	1.50	61268
Matrix	CASJ	Forest 100m	-0.54	2.16	-4.73	3.71	64700
Matrix	CATO	Forest 100m	-0.96	1.55	-4.04	2.03	10564
Matrix	CEDW	Forest 100m	-1.94	2.28	-6.37	2.58	24430
Facultative	CLSW	Forest 100m	-2.54	2.20	-6.86	1.77	26763
Obligate	COMO	Forest 100m	-0.71	1.81	-4.27	2.84	10638
Matrix	CORA	Forest 100m	-1.23	2.18	-5.48	3.06	64896
Obligate	COYE	Forest 100m	-3.85	1.78	-7.44	-0.45	50744
Matrix	DEJU	Forest 100m	1.25	1.89	-2.40	4.99	84651
Matrix	DOWO	Forest 100m	-0.88	2.27	-5.25	3.64	144911
Matrix	EUCD	Forest 100m	-2.70	1.80	-6.25	0.80	16122
Facultative	EUST	Forest 100m	-1.74	1.63	-4.96	1.47	15008
Obligate	GBHE	Forest 100m	-0.78	2.15	-5.01	3.44	68548
Facultative	GHOW	Forest 100m	-1.03	2.19	-5.31	3.26	88804
Obligate	GREG	Forest 100m	-2.12	2.26	-6.55	2.33	133485
Obligate	GRHE	Forest 100m	-2.23	2.24	-6.62	2.17	24446
Matrix	GRSP	Forest 100m	-2.72	1.99	-6.70	1.12	79928
Facultative	GTGR	Forest 100m	-2.19	2.17	-6.49	2.03	91369
Matrix	HOFI	Forest 100m	-2.24	2.28	-6.67	2.29	26331
Matrix	HOSP	Forest 100m	-2.50	2.05	-6.59	1.46	108477
Facultative	HOWR	Forest 100m	-0.29	1.56	-3.29	2.81	11343
Facultative	KILL	Forest 100m	-2.36	1.85	-6.03	1.20	23279
Matrix	LASP	Forest 100m	-1.66	1.69	-4.95	1.71	23150
Facultative	LAZB	Forest 100m	-1.20	2.28	-5.64	3.31	33350
Matrix	LEGO	Forest 100m	-0.01	2.05	-4.01	4.03	21830
Obligate	MALL	Forest 100m	-2.37	1.82	-5.98	1.14	25119
Obligate	MAWR	Forest 100m	-3.27	2.04	-7.35	0.64	45857
Facultative	MODO	Forest 100m	-1.85	1.63	-5.11	1.29	22849

Matrix	NOFL	Forest 100m	-0.95	2.29	-5.42	3.56	7349
Facultative	NOMO	Forest 100m	-0.67	1.44	-3.50	2.14	27234
Facultative	NRWS	Forest 100m	-1.13	2.25	-5.52	3.31	77615
Matrix	NUWO	Forest 100m	-0.46	1.90	-4.16	3.30	38229
Facultative	OATI	Forest 100m	0.70	2.02	-3.18	4.71	25715
Matrix	OSPR	Forest 100m	-2.13	2.26	-6.55	2.31	19918
Matrix	RNPH	Forest 100m	-3.14	2.09	-7.25	0.98	69285
Facultative	RSHA	Forest 100m	0.52	1.70	-2.78	3.89	70763
Facultative	RTHA	Forest 100m	-1.81	2.22	-6.16	2.56	34475
Obligate	RWBL	Forest 100m	-2.97	1.54	-6.01	0.04	52883
Facultative	SOSP	Forest 100m	-2.78	1.34	-5.44	-0.16	13505
Matrix	SPTO	Forest 100m	0.10	1.83	-3.34	3.85	18552
Matrix	SWHA	Forest 100m	-2.13	2.27	-6.59	2.31	26584
Facultative	TRSW	Forest 100m	-4.35	1.58	-7.47	-1.27	20347
Obligate	VIRA	Forest 100m	-2.97	1.87	-6.50	0.89	46740
Matrix	WBNU	Forest 100m	1.19	1.80	-2.31	4.76	33062
Matrix	WEBL	Forest 100m	-1.51	2.28	-5.95	2.99	187335
Facultative	WEKI	Forest 100m	-3.42	1.50	-6.36	-0.48	23632
Matrix	WEME	Forest 100m	-2.78	1.77	-6.29	0.65	52492
Matrix	WEWP	Forest 100m	-2.12	1.62	-5.31	1.03	12408
Obligate	WIFL	Forest 100m	-0.04	2.01	-4.02	3.88	13668
Obligate	WISN	Forest 100m	-3.94	1.97	-7.86	-0.11	194572
Matrix	WITU	Forest 100m	-1.41	1.88	-5.07	2.30	121973
Obligate	WODU	Forest 100m	-1.38	1.95	-5.17	2.48	53753
Facultative	WREN	Forest 100m	-0.21	1.90	-3.82	3.61	46389
Obligate	YBCH	Forest 100m	-1.20	1.66	-4.39	2.15	76457
Obligate	YWAR	Forest 100m	-0.64	1.68	-3.91	2.66	25493
Matrix	ACWO	Open 100m	-1.05	2.01	-4.99	2.91	35387
Obligate	AMBI	Open 100m	-2.95	2.18	-7.25	1.30	41518
Matrix	AMCR	Open 100m	-2.68	2.11	-6.88	1.42	72280
Matrix	AMGO	Open 100m	-2.99	2.38	-7.69	1.63	30160
Matrix	AMKE	Open 100m	-2.73	2.32	-7.33	1.76	61335
Matrix	AMRO	Open 100m	-1.23	2.06	-5.28	2.81	13207
Facultative	ANHU	Open 100m	-4.16	2.29	-8.68	0.31	9176
Facultative	ATFL	Open 100m	-1.92	2.25	-6.37	2.48	13377
Facultative	BASW	Open 100m	-2.22	2.35	-6.83	2.38	63094
Obligate	BEKI	Open 100m	-1.98	2.43	-6.77	2.75	24591
Facultative	BEWR	Open 100m	-1.60	2.35	-6.17	3.03	17374
Facultative	BHCO	Open 100m	-0.94	2.07	-5.01	3.13	23875
Matrix	BHGR	Open 100m	-3.32	2.30	-7.86	1.15	23965
Obligate	BLPH	Open 100m	-1.87	2.02	-5.86	2.05	13163
Obligate	BLRA	Open 100m	-1.14	2.03	-5.12	2.85	15570
Facultative	BRBL	Open 100m	-2.86	2.33	-7.44	1.68	31080
Facultative	BUOR	Open 100m	-1.34	2.08	-5.41	2.74	12869

Facultative	BUSH	Open 100m	-1.28	2.11	-5.47	2.81	15229
Obligate	CANG	Open 100m	-3.38	2.20	-7.72	0.91	24621
Matrix	CAQU	Open 100m	-3.03	2.10	-7.16	1.07	51733
Matrix	CASJ	Open 100m	-2.34	2.20	-6.71	1.94	19445
Matrix	CATO	Open 100m	-2.27	1.93	-6.14	1.44	8330
Matrix	CEDW	Open 100m	-1.59	2.41	-6.37	3.10	66992
Facultative	CLSW	Open 100m	-2.95	2.29	-7.46	1.55	52569
Obligate	COMO	Open 100m	-4.18	2.12	-8.38	-0.04	19609
Matrix	CORA	Open 100m	-3.60	2.35	-8.24	0.99	49059
Obligate	COYE	Open 100m	-3.86	1.87	-7.55	-0.24	19826
Matrix	DEJU	Open 100m	-3.77	2.16	-8.03	0.46	24538
Matrix	DOWO	Open 100m	-2.08	2.45	-6.93	2.68	10967
Matrix	EUCD	Open 100m	-2.32	2.03	-6.30	1.65	27782
Facultative	EUST	Open 100m	-1.23	1.98	-5.10	2.66	11868
Obligate	GBHE	Open 100m	-4.08	2.34	-8.68	0.49	27269
Facultative	GHOW	Open 100m	-3.19	2.29	-7.68	1.31	45711
Obligate	GREG	Open 100m	-3.41	2.32	-7.99	1.13	26618
Obligate	GRHE	Open 100m	-3.48	2.31	-8.03	1.05	39461
Matrix	GRSP	Open 100m	-1.02	2.23	-5.36	3.39	18322
Facultative	GTGR	Open 100m	-2.88	2.27	-7.36	1.52	132320
Matrix	HOFI	Open 100m	-2.41	2.29	-6.88	2.08	16709
Matrix	HOSP	Open 100m	-1.64	2.16	-5.88	2.63	22667
Facultative	HOWR	Open 100m	-1.39	1.94	-5.18	2.41	6551
Facultative	KILL	Open 100m	-0.23	1.93	-4.04	3.53	21390
Matrix	LASP	Open 100m	-1.27	2.03	-5.26	2.70	26562
Facultative	LAZB	Open 100m	-1.93	2.38	-6.62	2.73	22431
Matrix	LEGO	Open 100m	-1.84	2.27	-6.42	2.49	34593
Obligate	MALL	Open 100m	-2.79	2.07	-6.85	1.25	19595
Obligate	MAWR	Open 100m	-2.98	2.17	-7.26	1.25	29015
Facultative	MODO	Open 100m	-1.23	1.91	-5.00	2.50	10975
Matrix	NOFL	Open 100m	-2.81	2.42	-7.55	1.95	30762
Facultative	NOMO	Open 100m	-0.73	1.82	-4.32	2.83	27046
Facultative	NRWS	Open 100m	-2.69	2.36	-7.32	1.92	26063
Matrix	NUWO	Open 100m	-1.80	2.19	-6.12	2.51	13912
Facultative	OATI	Open 100m	-2.64	2.20	-6.97	1.66	10399
Matrix	OSPR	Open 100m	-1.47	2.38	-6.14	3.18	94499
Matrix	RNPH	Open 100m	-2.57	2.21	-6.92	1.72	21422
Facultative	RSHA	Open 100m	-4.08	2.10	-8.19	0.03	45969
Facultative	RTHA	Open 100m	-1.51	2.38	-6.21	3.14	17108
Obligate	RWBL	Open 100m	-3.18	2.02	-7.16	0.74	108524
Facultative	SOSP	Open 100m	-4.70	1.73	-8.13	-1.35	15784
Matrix	SPTO	Open 100m	-2.61	2.10	-6.75	1.49	24158
Matrix	SWHA	Open 100m	-2.02	2.42	-6.81	2.70	11708
Facultative	TRSW	Open 100m	-3.00	1.95	-6.83	0.82	12831

Obligate	VIRA	Open 100m	-1.28	2.08	-5.46	2.73	11838
Matrix	WBNU	Open 100m	-3.64	2.09	-7.75	0.45	28904
Matrix	WEBL	Open 100m	-2.00	2.40	-6.72	2.68	24646
Facultative	WEKI	Open 100m	-2.73	1.73	-6.14	0.66	25963
Matrix	WEME	Open 100m	-0.26	2.10	-4.34	3.87	18681
Matrix	WEWP	Open 100m	-1.87	2.01	-5.81	2.09	13786
Obligate	WIFL	Open 100m	-2.47	2.30	-7.00	2.01	17477
Obligate	WISN	Open 100m	-1.79	2.18	-6.07	2.47	174657
Matrix	WITU	Open 100m	-2.78	2.16	-7.07	1.41	39937
Obligate	WODU	Open 100m	-4.34	2.17	-8.64	-0.13	33091
Facultative	WREN	Open 100m	-2.15	2.18	-6.43	2.08	30305
Obligate	YBCH	Open 100m	-2.26	2.01	-6.21	1.66	17201
Obligate	YWAR	Open 100m	-1.88	2.06	-5.92	2.16	20465
Matrix	ACWO	Wetland 100m	-1.17	1.59	-4.30	1.94	25751
Obligate	AMBI	Wetland 100m	-0.72	1.88	-4.35	3.05	42180
Matrix	AMCR	Wetland 100m	-1.81	1.94	-5.63	2.02	268456
Matrix	AMGO	Wetland 100m	-0.48	2.29	-4.93	4.02	192510
Matrix	AMKE	Wetland 100m	1.04	2.10	-3.05	5.17	98476
Matrix	AMRO	Wetland 100m	-2.48	1.95	-6.38	1.27	32321
Facultative	ANHU	Wetland 100m	-0.77	2.19	-5.01	3.56	299400
Facultative	ATFL	Wetland 100m	-0.48	2.10	-4.64	3.62	28921
Facultative	BASW	Wetland 100m	-0.44	2.19	-4.65	3.92	22137
Obligate	BEKI	Wetland 100m	-0.20	2.28	-4.69	4.27	9916
Facultative	BEWR	Wetland 100m	-2.13	2.19	-6.46	2.13	18250
Facultative	BHCO	Wetland 100m	-0.36	1.86	-3.96	3.35	97481
Matrix	BHGR	Wetland 100m	-1.04	2.17	-5.29	3.22	61232
Obligate	BLPH	Wetland 100m	1.77	1.66	-1.51	5.05	12535
Obligate	BLRA	Wetland 100m	-2.52	1.72	-5.94	0.80	35071
Facultative	BRBL	Wetland 100m	-0.43	2.21	-4.79	3.89	39001
Facultative	BUOR	Wetland 100m	-1.79	1.82	-5.44	1.74	50397
Facultative	BUSH	Wetland 100m	-0.51	1.91	-4.27	3.27	40303
Obligate	CANG	Wetland 100m	0.77	2.08	-3.25	4.91	192066
Matrix	CAQU	Wetland 100m	0.42	2.05	-3.55	4.48	64196
Matrix	CASJ	Wetland 100m	-1.68	2.07	-5.58	2.60	97690
Matrix	CATO	Wetland 100m	-0.93	1.63	-4.05	2.36	22348
Matrix	CEDW	Wetland 100m	-1.28	2.26	-5.72	3.16	49062
Facultative	CLSW	Wetland 100m	-1.35	2.33	-5.76	3.37	51654
Obligate	COMO	Wetland 100m	2.28	1.82	-1.24	5.91	145290
Matrix	CORA	Wetland 100m	1.39	2.21	-2.96	5.74	36151
Obligate	COYE	Wetland 100m	-0.90	1.41	-3.67	1.89	42250
Matrix	DEJU	Wetland 100m	-1.09	2.05	-5.12	2.90	28694
Matrix	DOWO	Wetland 100m	-1.48	2.28	-5.92	3.01	15168
Matrix	EUCD	Wetland 100m	-1.65	1.88	-5.34	2.05	66970
Facultative	EUST	Wetland 100m	-1.13	1.61	-4.34	2.00	33877

Obligate	GBHE	Wetland 100m	0.31	2.24	-4.02	4.75	21211
Facultative	GHOW	Wetland 100m	-2.13	2.56	-6.74	3.19	47951
Obligate	GREG	Wetland 100m	0.43	2.18	-3.81	4.73	51438
Obligate	GRHE	Wetland 100m	-0.02	1.99	-3.79	4.03	85203
Matrix	GRSP	Wetland 100m	-1.33	2.15	-5.61	2.83	278774
Facultative	GTGR	Wetland 100m	0.08	2.09	-3.93	4.27	75446
Matrix	HOFI	Wetland 100m	-1.26	2.27	-5.60	3.32	25312
Matrix	HOSP	Wetland 100m	0.92	1.84	-2.70	4.51	44307
Facultative	HOWR	Wetland 100m	-1.77	1.65	-5.04	1.45	16247
Facultative	KILL	Wetland 100m	0.41	1.64	-2.88	3.57	20089
Matrix	LASP	Wetland 100m	0.00	1.74	-3.44	3.38	21904
Facultative	LAZB	Wetland 100m	-1.26	2.33	-5.80	3.34	15816
Matrix	LEGO	Wetland 100m	-1.06	1.98	-4.93	2.86	34855
Obligate	MALL	Wetland 100m	0.19	1.78	-3.25	3.74	78426
Obligate	MAWR	Wetland 100m	0.30	1.95	-3.49	4.17	50222
Facultative	MODO	Wetland 100m	-0.74	1.51	-3.73	2.23	63747
Matrix	NOFL	Wetland 100m	-0.85	2.33	-5.42	3.74	25582
Facultative	NOMO	Wetland 100m	-0.80	1.50	-3.71	2.22	18642
Facultative	NRWS	Wetland 100m	-0.44	2.27	-4.90	4.01	118286
Matrix	NUWO	Wetland 100m	-2.02	2.08	-6.13	2.01	33854
Facultative	OATI	Wetland 100m	-1.11	1.98	-5.02	2.74	61159
Matrix	OSPR	Wetland 100m	-1.28	2.24	-5.69	3.12	40141
Matrix	RNPH	Wetland 100m	-1.08	2.36	-5.59	3.61	54595
Facultative	RSHA	Wetland 100m	0.16	1.91	-3.61	3.89	139145
Facultative	RTHA	Wetland 100m	-1.79	2.24	-6.18	2.61	71169
Obligate	RWBL	Wetland 100m	0.37	1.79	-3.09	3.95	48062
Facultative	SOSP	Wetland 100m	-3.04	1.39	-5.79	-0.33	22081
Matrix	SPTO	Wetland 100m	-1.11	1.90	-4.89	2.57	81973
Matrix	SWHA	Wetland 100m	-0.45	2.28	-4.89	4.08	25575
Facultative	TRSW	Wetland 100m	1.94	1.69	-1.32	5.33	90533
Obligate	VIRA	Wetland 100m	-0.37	1.81	-3.95	3.16	9251
Matrix	WBNU	Wetland 100m	-0.30	2.00	-4.29	3.57	28556
Matrix	WEBL	Wetland 100m	-0.99	2.32	-5.52	3.56	54996
Facultative	WEKI	Wetland 100m	-1.30	1.36	-3.97	1.35	29554
Matrix	WEME	Wetland 100m	-2.52	1.89	-6.28	1.11	98157
Matrix	WEWP	Wetland 100m	-0.19	1.79	-3.74	3.29	74284
Obligate	WIFL	Wetland 100m	-1.78	2.23	-6.12	2.63	30587
Obligate	WISN	Wetland 100m	-1.28	2.02	-5.13	2.86	74103
Matrix	WITU	Wetland 100m	-0.11	2.01	-4.07	3.83	91847
Obligate	WODU	Wetland 100m	-1.26	2.25	-5.35	3.46	15292
Facultative	WREN	Wetland 100m	-1.89	2.13	-6.10	2.23	79564
Obligate	YBCH	Wetland 100m	-1.33	1.79	-4.89	2.13	28706
Obligate	YWAR	Wetland 100m	-2.20	1.94	-6.10	1.50	75280
Matrix	ACWO	Developed 500m	1.72	1.29	-0.65	4.42	299400

Obligate	AMBI	Developed 500m	-1.46	1.82	-5.08	2.02	102270
Matrix	AMCR	Developed 500m	-0.81	1.60	-3.81	2.43	178195
Matrix	AMGO	Developed 500m	1.13	2.10	-3.03	5.23	299400
Matrix	AMKE	Developed 500m	-0.46	1.86	-4.06	3.25	67208
Matrix	AMRO	Developed 500m	-0.12	1.13	-2.43	2.03	299400
Facultative	ANHU	Developed 500m	-1.37	2.10	-5.18	3.09	48149
Facultative	ATFL	Developed 500m	-2.07	1.99	-5.91	1.97	98918
Facultative	BASW	Developed 500m	-0.11	2.10	-4.28	3.97	20787
Obligate	BEKI	Developed 500m	-0.45	2.03	-4.36	3.65	63940
Facultative	BEWR	Developed 500m	-0.26	2.02	-4.20	3.77	33760
Facultative	BHCO	Developed 500m	2.72	1.57	-0.09	6.02	293051
Matrix	BHGR	Developed 500m	0.08	1.99	-3.76	4.08	299400
Obligate	BLPH	Developed 500m	2.97	1.39	0.30	5.76	299400
Obligate	BLRA	Developed 500m	-0.16	1.27	-2.69	2.32	70402
Facultative	BRBL	Developed 500m	2.36	1.74	-1.13	5.74	82350
Facultative	BUOR	Developed 500m	1.48	1.06	-0.50	3.70	216620
Facultative	BUSH	Developed 500m	1.29	1.44	-1.37	4.39	41156
Obligate	CANG	Developed 500m	-0.18	1.74	-3.55	3.30	127182
Matrix	CAQU	Developed 500m	0.71	1.41	-1.77	3.76	299400
Matrix	CASJ	Developed 500m	0.21	1.43	-2.50	3.19	299400
Matrix	CATO	Developed 500m	1.99	1.03	0.13	4.16	177157
Matrix	CEDW	Developed 500m	1.21	2.07	-2.91	5.24	32009
Facultative	CLSW	Developed 500m	-0.96	2.03	-4.95	3.01	299400
Obligate	COMO	Developed 500m	-1.91	1.66	-5.26	1.25	299400
Matrix	CORA	Developed 500m	1.06	1.95	-2.78	4.90	299400
Obligate	COYE	Developed 500m	-0.83	1.48	-3.87	1.93	56461
Matrix	DEJU	Developed 500m	-1.08	2.02	-4.75	3.07	88396
Matrix	DOWO	Developed 500m	-0.02	2.06	-4.04	4.07	299400
Matrix	EUCD	Developed 500m	-1.62	1.52	-4.73	1.22	147221
Facultative	EUST	Developed 500m	1.15	1.48	-1.65	4.17	40730
Obligate	GBHE	Developed 500m	-0.51	2.09	-4.58	3.63	71113
Facultative	GHOW	Developed 500m	-1.12	2.11	-5.22	3.08	149576
Obligate	GREG	Developed 500m	-0.35	2.13	-4.56	3.81	105362
Obligate	GRHE	Developed 500m	-0.51	2.13	-4.73	3.66	270995
Matrix	GRSP	Developed 500m	-0.70	1.72	-4.23	2.46	162902
Facultative	GTGR	Developed 500m	-0.40	2.06	-4.48	3.61	192059
Matrix	HOFI	Developed 500m	-1.30	2.30	-5.67	3.35	66669
Matrix	HOSP	Developed 500m	0.06	1.62	-3.19	3.15	182720
Facultative	HOWR	Developed 500m	-0.98	1.05	-3.15	0.98	36731
Facultative	KILL	Developed 500m	0.17	1.33	-2.47	2.78	79704
Matrix	LASP	Developed 500m	2.85	1.04	0.87	4.97	299400
Facultative	LAZB	Developed 500m	0.29	2.19	-4.00	4.61	65734
Matrix	LEGO	Developed 500m	-0.68	2.05	-4.37	3.59	299400
Obligate	MALL	Developed 500m	-1.33	1.58	-4.56	1.63	119323

Obligate	MAWR	Developed 500m	-1.69	1.82	-5.36	1.76	71988
Facultative	MODO	Developed 500m	-1.73	1.12	-4.06	0.34	151655
Matrix	NOFL	Developed 500m	-0.45	2.16	-4.68	3.85	35726
Facultative	NOMO	Developed 500m	0.06	0.97	-1.89	1.92	299400
Facultative	NRWS	Developed 500m	0.43	2.11	-3.70	4.61	56330
Matrix	NUWO	Developed 500m	1.48	1.48	-1.35	4.54	95857
Facultative	OATI	Developed 500m	0.31	1.53	-2.51	3.53	268503
Matrix	OSPR	Developed 500m	-0.35	2.12	-4.54	3.79	230385
Matrix	RNPH	Developed 500m	-1.56	1.89	-5.33	2.09	78839
Facultative	RSHA	Developed 500m	-1.55	1.43	-4.38	1.39	65722
Facultative	RTHA	Developed 500m	-0.64	2.18	-4.85	3.73	39095
Obligate	RWBL	Developed 500m	-0.68	0.83	-2.31	0.98	36584
Facultative	SOSP	Developed 500m	-0.11	0.74	-1.53	1.38	68149
Matrix	SPTO	Developed 500m	1.37	1.08	-0.72	3.54	117091
Matrix	SWHA	Developed 500m	-1.00	2.06	-5.07	3.04	299400
Facultative	TRSW	Developed 500m	1.65	0.92	-0.04	3.56	247035
Obligate	VIRA	Developed 500m	1.19	1.53	-1.49	4.58	185025
Matrix	WBNU	Developed 500m	0.19	1.33	-2.46	2.81	299400
Matrix	WEBL	Developed 500m	1.21	1.83	-2.41	4.79	299400
Facultative	WEKI	Developed 500m	1.77	1.19	-0.31	4.35	64730
Matrix	WEME	Developed 500m	-0.52	1.30	-3.13	1.97	87842
Matrix	WEWP	Developed 500m	0.97	1.00	-0.91	3.02	54736
Obligate	WIFL	Developed 500m	-1.52	2.01	-5.49	2.43	299400
Obligate	WISN	Developed 500m	-0.85	1.54	-3.91	2.18	66896
Matrix	WITU	Developed 500m	2.44	1.70	-0.87	5.76	134884
Obligate	WODU	Developed 500m	-0.10	1.99	-4.03	3.80	222032
Facultative	WREN	Developed 500m	-0.18	1.84	-3.53	3.52	96768
Obligate	YBCH	Developed 500m	-1.81	1.10	-4.10	0.20	299400
Obligate	YWAR	Developed 500m	0.15	1.21	-2.34	2.47	299400
Matrix	ACWO	Forest 500m	6.29	2.12	2.20	10.51	12984
Obligate	AMBI	Forest 500m	1.69	2.31	-2.84	6.20	19671
Matrix	AMCR	Forest 500m	3.94	2.13	-0.20	8.15	11909
Matrix	AMGO	Forest 500m	3.12	2.50	-1.76	8.04	38646
Matrix	AMKE	Forest 500m	3.34	2.27	-1.09	7.82	48017
Matrix	AMRO	Forest 500m	3.44	2.03	-0.52	7.44	20079
Facultative	ANHU	Forest 500m	4.77	2.20	0.49	9.12	40099
Facultative	ATFL	Forest 500m	3.53	2.18	-0.70	7.87	70414
Facultative	BASW	Forest 500m	1.37	2.44	-3.37	6.19	35535
Obligate	BEKI	Forest 500m	3.09	2.42	-1.63	7.86	93152
Facultative	BEWR	Forest 500m	3.72	2.45	-1.04	8.55	49700
Facultative	BHCO	Forest 500m	2.28	2.07	-1.77	6.38	35129
Matrix	BHGR	Forest 500m	5.63	2.24	1.26	10.06	24528
Obligate	BLPH	Forest 500m	4.53	2.11	0.45	8.75	24348
Obligate	BLRA	Forest 500m	2.63	2.03	-1.36	6.59	15290

Facultative	BRBL	Forest 500m	3.77	2.38	-0.89	8.47	25200
Facultative	BUOR	Forest 500m	2.75	2.00	-1.14	6.70	17250
Facultative	BUSH	Forest 500m	4.99	2.16	0.83	9.30	10007
Obligate	CANG	Forest 500m	2.01	2.28	-2.46	6.51	11654
Matrix	CAQU	Forest 500m	1.35	2.01	-2.59	5.32	14903
Matrix	CASJ	Forest 500m	3.60	2.19	-0.65	7.93	23935
Matrix	CATO	Forest 500m	2.39	1.97	-1.38	6.38	16697
Matrix	CEDW	Forest 500m	3.74	2.45	-1.04	8.57	34123
Facultative	CLSW	Forest 500m	1.47	2.38	-3.20	6.15	23581
Obligate	COMO	Forest 500m	2.37	2.14	-1.83	6.57	11617
Matrix	CORA	Forest 500m	2.68	2.43	-2.05	7.48	13362
Obligate	COYE	Forest 500m	3.13	2.13	-1.08	7.28	20220
Matrix	DEJU	Forest 500m	5.67	2.15	1.49	9.94	16979
Matrix	DOWO	Forest 500m	4.34	2.31	-0.14	8.90	13335
Matrix	EUCD	Forest 500m	1.80	2.10	-2.32	5.93	46686
Facultative	EUST	Forest 500m	2.06	2.00	-1.86	6.01	10827
Obligate	GBHE	Forest 500m	2.59	2.45	-2.19	7.45	36383
Facultative	GHOW	Forest 500m	2.50	2.48	-2.31	7.43	99801
Obligate	GREG	Forest 500m	2.70	2.45	-2.08	7.53	38413
Obligate	GRHE	Forest 500m	2.56	2.44	-2.22	7.35	16102
Matrix	GRSP	Forest 500m	3.27	2.13	-0.91	7.47	34866
Facultative	GTGR	Forest 500m	2.69	2.40	-2.02	7.39	33022
Matrix	HOFI	Forest 500m	2.04	2.48	-2.77	6.96	21322
Matrix	HOSP	Forest 500m	2.55	2.26	-1.90	6.96	24679
Facultative	HOWR	Forest 500m	4.59	1.89	0.93	8.33	15128
Facultative	KILL	Forest 500m	1.53	2.09	-2.59	5.61	14599
Matrix	LASP	Forest 500m	4.62	2.03	0.67	8.64	22722
Facultative	LAZB	Forest 500m	2.91	2.55	-2.02	7.96	31054
Matrix	LEGO	Forest 500m	4.59	2.23	0.26	9.02	37513
Obligate	MALL	Forest 500m	0.38	2.12	-3.76	4.55	26177
Obligate	MAWR	Forest 500m	1.28	2.25	-3.16	5.68	23694
Facultative	MODO	Forest 500m	4.31	2.01	0.44	8.30	16537
Matrix	NOFL	Forest 500m	3.86	2.36	-0.74	8.52	17833
Facultative	NOMO	Forest 500m	2.29	1.82	-1.28	5.86	13936
Facultative	NRWS	Forest 500m	3.26	2.43	-1.50	8.05	74379
Matrix	NUWO	Forest 500m	3.24	2.24	-1.08	7.74	21071
Facultative	OATI	Forest 500m	5.91	2.19	1.67	10.26	14280
Matrix	OSPR	Forest 500m	2.79	2.45	-2.02	7.61	194982
Matrix	RNPH	Forest 500m	1.76	2.19	-2.52	6.07	32578
Facultative	RSHA	Forest 500m	3.67	2.09	-0.41	7.78	19325
Facultative	RTHA	Forest 500m	2.12	2.48	-2.69	7.05	17979
Obligate	RWBL	Forest 500m	2.05	1.90	-1.67	5.80	18179
Facultative	SOSP	Forest 500m	2.27	1.74	-1.14	5.70	18363
Matrix	SPTO	Forest 500m	4.82	2.04	0.88	8.88	11412

Matrix	SWHA	Forest 500m	2.47	2.43	-2.28	7.26	15858
Facultative	TRSW	Forest 500m	1.40	1.89	-2.29	5.12	16563
Obligate	VIRA	Forest 500m	4.26	2.02	0.35	8.29	12359
Matrix	WBNU	Forest 500m	3.94	2.25	-0.36	8.46	94936
Matrix	WEBL	Forest 500m	4.07	2.40	-0.62	8.78	299400
Facultative	WEKI	Forest 500m	4.01	1.93	0.25	7.83	15344
Matrix	WEME	Forest 500m	1.66	2.05	-2.34	5.68	20509
Matrix	WEWP	Forest 500m	5.02	1.95	1.23	8.89	25915
Obligate	WIFL	Forest 500m	3.03	2.36	-1.52	7.72	18049
Obligate	WISN	Forest 500m	1.04	2.09	-3.07	5.17	22047
Matrix	WITU	Forest 500m	3.82	2.22	-0.50	8.23	25018
Obligate	WODU	Forest 500m	3.25	2.28	-1.17	7.77	23337
Facultative	WREN	Forest 500m	5.62	2.13	1.50	9.85	20926
Obligate	YBCH	Forest 500m	5.25	1.96	1.46	9.14	14640
Obligate	YWAR	Forest 500m	4.38	2.00	0.47	8.33	14430
Matrix	ACWO	Open 500m	3.06	2.15	-1.14	7.32	11649
Obligate	AMBI	Open 500m	2.23	2.34	-2.34	6.85	21468
Matrix	AMCR	Open 500m	2.74	2.26	-1.68	7.20	20841
Matrix	AMGO	Open 500m	2.40	2.58	-2.66	7.49	24299
Matrix	AMKE	Open 500m	2.66	2.48	-2.20	7.53	11419
Matrix	AMRO	Open 500m	4.29	2.21	0.00	8.66	9635
Facultative	ANHU	Open 500m	2.17	2.33	-2.41	6.74	38534
Facultative	ATFL	Open 500m	4.78	2.34	0.20	9.39	276127
Facultative	BASW	Open 500m	3.47	2.47	-1.38	8.32	67735
Obligate	BEKI	Open 500m	2.80	2.53	-2.15	7.80	32502
Facultative	BEWR	Open 500m	3.78	2.56	-1.20	8.83	20134
Facultative	BHCO	Open 500m	2.23	2.22	-2.11	6.60	27096
Matrix	BHGR	Open 500m	2.05	2.42	-2.67	6.82	22447
Obligate	BLPH	Open 500m	2.11	2.18	-2.15	6.42	19945
Obligate	BLRA	Open 500m	4.03	2.15	-0.16	8.27	14094
Facultative	BRBL	Open 500m	2.49	2.48	-2.36	7.36	27166
Facultative	BUOR	Open 500m	5.28	2.23	0.97	9.68	24370
Facultative	BUSH	Open 500m	3.25	2.23	-1.08	7.66	13300
Obligate	CANG	Open 500m	2.84	2.36	-1.78	7.46	19568
Matrix	CAQU	Open 500m	4.15	2.24	-0.21	8.55	25426
Matrix	CASJ	Open 500m	3.43	2.31	-1.14	7.93	18020
Matrix	CATO	Open 500m	2.15	2.10	-1.88	6.37	12752
Matrix	CEDW	Open 500m	2.95	2.54	-2.00	7.95	13908
Facultative	CLSW	Open 500m	3.78	2.41	-0.93	8.52	33818
Obligate	COMO	Open 500m	3.78	2.27	-0.72	8.23	47014
Matrix	CORA	Open 500m	3.91	2.56	-1.15	8.91	102631
Obligate	COYE	Open 500m	3.65	2.03	-0.32	7.66	23853
Matrix	DEJU	Open 500m	2.08	2.35	-2.50	6.70	20456
Matrix	DOWO	Open 500m	3.03	2.48	-1.81	7.91	16812

Matrix	EUCD	Open 500m	4.28	2.22	-0.03	8.68	38595
Facultative	EUST	Open 500m	4.81	2.17	0.59	9.11	9982
Obligate	GBHE	Open 500m	2.39	2.49	-2.51	7.28	33573
Facultative	GHOW	Open 500m	3.01	2.51	-1.91	7.95	13698
Obligate	GREG	Open 500m	2.23	2.48	-2.64	7.10	14451
Obligate	GRHE	Open 500m	2.49	2.51	-2.43	7.40	33597
Matrix	GRSP	Open 500m	3.24	2.32	-1.27	7.84	29612
Facultative	GTGR	Open 500m	2.67	2.45	-2.13	7.49	33954
Matrix	HOFI	Open 500m	4.52	2.51	-0.42	9.44	43970
Matrix	HOSP	Open 500m	5.07	2.34	0.55	9.70	20305
Facultative	HOWR	Open 500m	3.97	2.10	-0.09	8.14	17432
Facultative	KILL	Open 500m	5.11	2.17	0.92	9.44	44604
Matrix	LASP	Open 500m	3.22	2.20	-1.07	7.58	27451
Facultative	LAZB	Open 500m	4.21	2.62	-0.93	9.35	34326
Matrix	LEGO	Open 500m	2.95	2.29	-1.54	7.43	48603
Obligate	MALL	Open 500m	3.23	2.20	-1.07	7.57	33442
Obligate	MAWR	Open 500m	1.78	2.29	-2.70	6.29	32997
Facultative	MODO	Open 500m	3.65	2.07	-0.43	7.71	9323
Matrix	NOFL	Open 500m	3.13	2.48	-1.70	8.00	9398
Facultative	NOMO	Open 500m	4.55	2.02	0.62	8.55	11243
Facultative	NRWS	Open 500m	3.76	2.54	-1.23	8.73	29180
Matrix	NUWO	Open 500m	4.54	2.37	-0.07	9.20	30826
Facultative	OATI	Open 500m	3.32	2.27	-1.11	7.80	14536
Matrix	OSPR	Open 500m	4.04	2.52	-0.89	9.00	16836
Matrix	RNPH	Open 500m	2.09	2.37	-2.52	6.78	17950
Facultative	RSHA	Open 500m	3.98	2.28	-0.48	8.49	19018
Facultative	RTHA	Open 500m	4.44	2.53	-0.50	9.41	21810
Obligate	RWBL	Open 500m	2.83	2.10	-1.27	6.97	18207
Facultative	SOSP	Open 500m	2.16	1.91	-1.57	5.92	21010
Matrix	SPTO	Open 500m	3.12	2.23	-1.21	7.51	24641
Matrix	SWHA	Open 500m	2.85	2.54	-2.10	7.86	101840
Facultative	TRSW	Open 500m	2.07	2.07	-1.97	6.12	17807
Obligate	VIRA	Open 500m	1.97	2.14	-2.22	6.20	15963
Matrix	WBNU	Open 500m	3.56	2.39	-1.12	8.23	26747
Matrix	WEBL	Open 500m	3.11	2.49	-1.73	8.03	20853
Facultative	WEKI	Open 500m	3.46	1.95	-0.35	7.30	15383
Matrix	WEME	Open 500m	5.58	2.25	1.23	10.05	16912
Matrix	WEWP	Open 500m	3.03	2.18	-1.21	7.36	23018
Obligate	WIFL	Open 500m	4.41	2.48	-0.49	9.25	23694
Obligate	WISN	Open 500m	3.57	2.30	-0.88	8.13	26367
Matrix	WITU	Open 500m	1.72	2.35	-2.90	6.36	24045
Obligate	WODU	Open 500m	1.01	2.40	-3.66	5.75	17056
Facultative	WREN	Open 500m	2.02	2.33	-2.54	6.60	30604
Obligate	YBCH	Open 500m	3.62	2.17	-0.60	7.91	20603

Obligate	YWAR	Open 500m	3.85	2.20	-0.42	8.22	13275
Matrix	ACWO	Wetland 500m	-0.05	1.76	-3.55	3.37	14326
Obligate	AMBI	Wetland 500m	2.83	2.11	-1.24	7.03	82278
Matrix	AMCR	Wetland 500m	2.09	1.86	-1.55	5.78	138623
Matrix	AMGO	Wetland 500m	1.34	2.37	-3.25	6.02	18678
Matrix	AMKE	Wetland 500m	2.89	2.09	-1.17	7.02	124330
Matrix	AMRO	Wetland 500m	1.15	1.95	-2.74	4.89	87455
Facultative	ANHU	Wetland 500m	0.11	2.29	-4.30	4.68	15476
Facultative	ATFL	Wetland 500m	-0.25	2.20	-4.57	4.09	299400
Facultative	BASW	Wetland 500m	1.55	2.34	-2.96	6.20	127429
Obligate	BEKI	Wetland 500m	2.14	2.26	-2.27	6.59	91101
Facultative	BEWR	Wetland 500m	-0.16	2.28	-4.64	4.29	299400
Facultative	BHCO	Wetland 500m	2.33	2.04	-1.56	6.43	126704
Matrix	BHGR	Wetland 500m	0.00	2.27	-4.46	4.44	50953
Obligate	BLPH	Wetland 500m	1.05	1.78	-2.36	4.65	44162
Obligate	BLRA	Wetland 500m	2.44	1.87	-1.25	6.10	53798
Facultative	BRBL	Wetland 500m	0.99	2.29	-3.52	5.46	78203
Facultative	BUOR	Wetland 500m	-1.27	2.06	-5.36	2.71	62027
Facultative	BUSH	Wetland 500m	0.24	2.01	-3.67	4.21	20926
Obligate	CANG	Wetland 500m	2.33	2.19	-1.89	6.68	135042
Matrix	CAQU	Wetland 500m	1.74	2.13	-2.36	5.98	92708
Matrix	CASJ	Wetland 500m	2.09	1.93	-1.70	5.88	52048
Matrix	CATO	Wetland 500m	0.97	1.68	-2.23	4.42	34602
Matrix	CEDW	Wetland 500m	0.56	2.33	-4.01	5.16	163853
Facultative	CLSW	Wetland 500m	1.45	2.26	-2.93	5.94	87432
Obligate	COMO	Wetland 500m	3.02	1.96	-0.82	6.88	275497
Matrix	CORA	Wetland 500m	1.29	2.34	-3.25	5.96	21128
Obligate	COYE	Wetland 500m	0.62	1.63	-2.60	3.81	92520
Matrix	DEJU	Wetland 500m	0.20	2.16	-4.10	4.37	54684
Matrix	DOWO	Wetland 500m	0.26	2.31	-4.26	4.85	38731
Matrix	EUCD	Wetland 500m	3.02	1.87	-0.63	6.71	299400
Facultative	EUST	Wetland 500m	1.45	1.73	-1.94	4.87	16522
Obligate	GBHE	Wetland 500m	2.45	2.23	-1.86	6.88	66463
Facultative	GHOW	Wetland 500m	1.00	2.38	-3.58	5.80	14186
Obligate	GREG	Wetland 500m	1.98	2.30	-2.49	6.52	31859
Obligate	GRHE	Wetland 500m	1.62	2.39	-2.96	6.40	249212
Matrix	GRSP	Wetland 500m	1.21	2.17	-3.12	5.38	94875
Facultative	GTGR	Wetland 500m	3.34	2.06	-0.71	7.38	49870
Matrix	HOFI	Wetland 500m	0.71	2.35	-3.84	5.40	299400
Matrix	HOSP	Wetland 500m	0.82	2.06	-3.27	4.82	72996
Facultative	HOWR	Wetland 500m	1.71	1.70	-1.65	5.02	52678
Facultative	KILL	Wetland 500m	1.94	1.70	-1.37	5.31	39035
Matrix	LASP	Wetland 500m	0.42	1.99	-3.52	4.29	113754
Facultative	LAZB	Wetland 500m	0.21	2.41	-4.47	4.99	64581

Matrix	LEGO	Wetland 500m	1.20	2.15	-3.00	5.43	47715
Obligate	MALL	Wetland 500m	2.88	2.01	-0.96	6.92	272458
Obligate	MAWR	Wetland 500m	3.43	2.16	-0.73	7.72	76104
Facultative	MODO	Wetland 500m	1.68	1.72	-1.63	5.10	299400
Matrix	NOFL	Wetland 500m	0.68	2.36	-3.94	5.33	67034
Facultative	NOMO	Wetland 500m	1.40	1.64	-1.79	4.64	40643
Facultative	NRWS	Wetland 500m	0.44	2.33	-4.11	5.06	50651
Matrix	NUWO	Wetland 500m	-0.43	2.23	-4.81	3.92	76637
Facultative	OATI	Wetland 500m	-0.37	2.03	-4.35	3.59	42412
Matrix	OSPR	Wetland 500m	0.61	2.30	-3.91	5.13	100076
Matrix	RNPH	Wetland 500m	2.81	2.10	-1.26	7.00	36084
Facultative	RSHA	Wetland 500m	0.72	2.10	-3.48	4.76	47456
Facultative	RTHA	Wetland 500m	1.51	2.16	-2.74	5.73	169261
Obligate	RWBL	Wetland 500m	2.12	1.92	-1.55	5.98	27499
Facultative	SOSP	Wetland 500m	1.10	1.45	-1.74	3.96	59181
Matrix	SPTO	Wetland 500m	-1.63	2.13	-5.85	2.49	142512
Matrix	SWHA	Wetland 500m	3.42	2.16	-0.84	7.64	96389
Facultative	TRSW	Wetland 500m	2.39	2.30	-1.82	7.08	97398
Obligate	VIRA	Wetland 500m	0.87	1.89	-2.87	4.58	31789
Matrix	WBNU	Wetland 500m	0.36	2.09	-3.81	4.41	32149
Matrix	WEBL	Wetland 500m	0.12	2.39	-4.50	4.88	150485
Facultative	WEKI	Wetland 500m	0.99	1.54	-2.01	4.04	47111
Matrix	WEME	Wetland 500m	0.31	2.03	-3.74	4.23	131660
Matrix	WEWP	Wetland 500m	0.02	2.03	-4.02	3.93	221003
Obligate	WIFL	Wetland 500m	0.02	2.29	-4.46	4.52	150606
Obligate	WISN	Wetland 500m	1.27	2.16	-2.84	5.67	167264
Matrix	WITU	Wetland 500m	0.59	2.15	-3.61	4.83	76356
Obligate	WODU	Wetland 500m	2.00	2.15	-2.12	6.32	44959
Facultative	WREN	Wetland 500m	-0.26	2.20	-4.63	3.98	30662
Obligate	YBCH	Wetland 500m	-2.10	2.00	-6.11	1.74	58092
Obligate	YWAR	Wetland 500m	-1.35	2.12	-5.56	2.76	142629

Table S2.3. Visit detection probability derived from multispecies occupancy model parameter estimates, including the probability of detecting a species at least once if present during nine visits (P*).

Guild	Species	Mean	Lower CI	Upper CI	P* (9 visits)
Obligate	RWBL	0.697	0.029	0.752	1.000
Obligate	COYE	0.652	0.092	0.808	1.000
Facultative	WEKI	0.510	0.032	0.573	0.998
Matrix	CAQU	0.469	0.031	0.530	0.997
Facultative	SOSP	0.439	0.042	0.521	0.994
Matrix	GRSP	0.415	0.109	0.642	0.992
Matrix	ACWO	0.395	0.035	0.464	0.989
Obligate	MAWR	0.387	0.075	0.570	0.988
Facultative	NOMO	0.385	0.041	0.468	0.987
Matrix	WEWP	0.351	0.070	0.492	0.979
Facultative	MODO	0.338	0.036	0.410	0.975
Matrix	WEME	0.333	0.054	0.444	0.974
Matrix	CATO	0.299	0.039	0.379	0.959
Obligate	YEWA	0.293	0.089	0.478	0.956
Facultative	TRSW	0.290	0.035	0.361	0.954
Obligate	YBCH	0.285	0.061	0.413	0.951
Obligate	BLPH	0.285	0.033	0.353	0.951
Facultative	BHCO	0.253	0.028	0.311	0.928
Facultative	RSHA	0.250	0.065	0.389	0.925
Facultative	HOWR	0.245	0.053	0.354	0.920
Matrix	SPTO	0.237	0.076	0.408	0.912
Facultative	BUOR	0.231	0.039	0.312	0.906
Matrix	AMRO	0.217	0.045	0.315	0.890
Obligate	MALL	0.204	0.056	0.328	0.872
Obligate	BLRA	0.204	0.066	0.347	0.871
Obligate	AMBI	0.203	0.037	0.283	0.871
Matrix	DEJU	0.202	0.094	0.410	0.869
Facultative	EUST	0.200	0.035	0.273	0.866
Matrix	CASJ	0.179	0.029	0.241	0.831
Facultative	KILL	0.165	0.046	0.267	0.803
Facultative	WREN	0.165	0.060	0.305	0.802
Matrix	LASP	0.157	0.064	0.297	0.784
Matrix	HOSP	0.152	0.084	0.348	0.774
Matrix	WBNU	0.144	0.046	0.251	0.753
Matrix	EUCD	0.142	0.058	0.275	0.749
Facultative	OATI	0.142	0.026	0.197	0.748
Obligate	COMO	0.132	0.048	0.245	0.721
Facultative	BUSH	0.131	0.038	0.218	0.717

Obligate	VIRA	0.128	0.048	0.239	0.708
Matrix	AMCR	0.125	0.034	0.200	0.699
Matrix	LEGO	0.118	0.025	0.172	0.678
Obligate	WISN	0.104	0.043	0.208	0.627
Facultative	GTGR	0.093	0.101	0.382	0.585
Matrix	WITU	0.092	0.033	0.170	0.580
Obligate	CANG	0.084	0.026	0.145	0.548
Matrix	NUWO	0.080	0.024	0.135	0.527
Facultative	BRBL	0.079	0.100	0.369	0.523
Obligate	WODU	0.078	0.051	0.212	0.518
Matrix	BHGR	0.066	0.054	0.209	0.461
Matrix	RNPH	0.066	0.037	0.161	0.459
Obligate	WIFL	0.054	0.062	0.226	0.391
Matrix	OSPR	0.052	0.076	0.279	0.382
Obligate	GREG	0.051	0.076	0.280	0.373
Facultative	ANHU	0.050	0.026	0.115	0.370
Facultative	ATFL	0.048	0.019	0.093	0.359
Facultative	CLSW	0.048	0.048	0.181	0.357
Matrix	SWHA	0.048	0.076	0.252	0.357
Obligate	GRHE	0.045	0.063	0.231	0.342
Matrix	CEDW	0.043	0.069	0.250	0.324
Matrix	AMKE	0.039	0.022	0.094	0.303
Facultative	BEWR	0.037	0.023	0.096	0.291
Matrix	CORA	0.033	0.034	0.124	0.258
Facultative	BASW	0.032	0.027	0.106	0.257
Obligate	GBHE	0.032	0.031	0.114	0.256
Obligate	BEKI	0.030	0.015	0.066	0.239
Matrix	HOFI	0.030	0.014	0.065	0.238
Facultative	GHOW	0.029	0.027	0.106	0.235
Matrix	DOWO	0.029	0.022	0.086	0.230
Facultative	NRWS	0.027	0.026	0.095	0.218
Facultative	RTHA	0.026	0.019	0.076	0.211
Matrix	WEBL	0.021	0.014	0.057	0.172
Matrix	NOFL	0.020	0.025	0.080	0.166
Matrix	AMGO	0.018	0.020	0.069	0.150
Facultative	LAZB	0.015	0.011	0.043	0.129

Table S2.4. Significant occupancy hyperparameter and individual species parameter estimates from a multispecies occupancy model.

Parameter Category	Assemblage	Species	Parameter	Estimate	SD	Lower CI	Upper CI
Water Source	All		Natural	-2.05	0.58	-3.18	-0.92
	All		Irrigated	-1.69	0.58	-2.84	-0.55
	All		Natural + Irrigated	-1.85	0.62	-3.08	-0.63
Landscape	All		Open [100m]	-2.37	1.11	-4.57	-0.24
	All		Forest [500m]	3.21	1.26	0.78	5.73
	All		Open [500m]	3.27	1.42	0.54	6.11
Detection	Obligate	AMBI	Julian Date	-6.56	1.34	-9.19	-3.90
	Obligate	BEKI	Julian Date	1.73	0.48	0.79	2.68
	Obligate	BLRA	Julian Date	-1.19	0.56	-2.32	-0.13
	Obligate	CANG	Julian Date	-2.21	0.79	-3.84	-0.75
	Obligate	COYE	Julian Date	1.66	0.84	0.05	3.33
	Obligate	MAWR	Julian Date	-5.20	1.46	-8.01	-2.33
	Obligate	RWBL	Julian Date	-1.37	0.20	-1.76	-0.99
	Obligate	VIRA	Julian Date	-1.07	0.50	-2.09	-0.13
	Obligate	YEWA	Julian Date	-1.85	0.73	-3.37	-0.50
	Facultative	BEWR	Julian Date	-2.29	1.09	-4.54	-0.28
	Facultative	HOWR	Julian Date	-0.96	0.38	-1.70	-0.23
	Facultative	KILL	Julian Date	-0.99	0.49	-2.00	-0.07
	Facultative	NOMO	Julian Date	1.12	0.24	0.66	1.59
	Facultative	OATI	Julian Date	0.75	0.30	0.17	1.33
	Facultative	SOSP	Julian Date	0.50	0.25	0.01	0.99
	Facultative	TRSW	Julian Date	-1.73	0.32	-2.36	-1.12
	Matrix	AMRO	Julian Date	1.22	0.43	0.34	2.05
	Matrix	CAQU	Julian Date	-0.45	0.18	-0.80	-0.09
	Matrix	CASJ	Julian Date	1.07	0.24	0.59	1.55
Vegetation	Obligate	BLRA	Juncus	3.63	1.27	1.26	6.25
	Matrix	AMRO	Juncus	-3.54	1.20	-6.04	-1.35
	Facultative	NOMO	Typha	-1.65	0.82	-3.34	-0.10
	Facultative	RSHA	Typha	-2.59	1.12	-4.85	-0.46
Geomorphology	Facultative	KILL	Fringe	-3.97	1.79	-7.57	-0.54
	Matrix	WEWP	Fringe	-2.77	1.40	-5.55	-0.02
	Facultative	NOMO	Fluvial	-3.00	1.46	-5.92	-0.19
	Obligate	COYE	Slope	-3.33	1.64	-6.58	-0.16
	Obligate	MALL	Slope	-3.75	1.62	-6.97	-0.61
	Facultative	SOSP	Slope	-2.71	1.15	-5.00	-0.48
	Facultative	WREN	Slope	-4.20	1.74	-7.65	-0.83
Water Source	Obligate	COYE	Natural	-4.00	1.80	-7.67	-0.61
	Obligate	WISN	Natural	-4.80	1.62	-7.99	-1.66

	Obligate	YEWA	Natural	-4.53	1.72	-8.05	-1.34
	Facultative	KILL	Natural	-4.62	1.57	-7.80	-1.66
	Facultative	RSHA	Natural	-3.91	1.66	-7.27	-0.77
	Matrix	CATO	Natural	-2.65	1.19	-5.01	-0.34
	Matrix	EUCD	Natural	-4.05	1.54	-7.16	-1.12
	Matrix	HOSP	Natural	-4.14	1.83	-7.85	-0.67
	Matrix	RNPH	Natural	-4.19	1.85	-7.90	-0.63
	Obligate	BLRA	Irrigation	-3.09	1.43	-5.92	-0.30
	Facultative	EUST	Irrigation	-2.81	1.45	-5.68	0.00
	Facultative	RSHA	Irrigation	-5.46	1.70	-8.82	-2.18
	Facultative	TRSW	Irrigation	-2.38	1.20	-4.77	-0.04
	Facultative	WEKI	Irrigation	-3.06	1.36	-5.76	-0.40
	Matrix	GRSP	Irrigation	-4.23	1.80	-7.88	-0.83
	Matrix	WBNU	Irrigation	-3.69	1.63	-6.91	-0.53
	Matrix	WEWP	Irrigation	-4.51	1.40	-7.33	-1.86
	Obligate	COMO	Natural + Irrigation	-3.96	1.80	-7.53	-0.48
	Obligate	WISN	Natural + Irrigation	-3.49	1.67	-6.79	-0.24
	Matrix	WBNU	Natural + Irrigation	-3.63	1.68	-6.96	-0.36
	Matrix	WEME	Natural + Irrigation	-3.05	1.47	-5.98	-0.20
Biogeographic	Obligate	MAWR	Area	3.27	1.58	0.28	6.49
	Facultative	SOSP	Area	1.51	0.70	0.19	2.91
	Matrix	SPTO	Area	2.60	1.11	0.48	4.83
	Facultative	EUST	Elevation	-3.11	1.25	-5.64	-0.70
	Facultative	NOMO	Elevation	-2.94	1.07	-5.09	-0.91
	Obligate	MALL	% Wet	-2.36	1.18	-4.74	-0.11
	Facultative	TRSW	% Wet	1.76	0.90	0.03	3.57
	Matrix	CATO	% Wet	-1.91	0.88	-3.78	-0.31
	Matrix	WEME	% Wet	1.99	1.04	0.05	4.14
Landscape	Obligate	CANG	Developed 100m	3.23	1.45	0.56	6.24
	Obligate	COYE	Forest 100m	-3.85	1.78	-7.44	-0.45
	Obligate	WISN	Forest 100m	-3.94	1.97	-7.86	-0.11
	Facultative	BHCO	Forest 100m	-5.79	1.75	-9.29	-2.42
	Facultative	SOSP	Forest 100m	-2.78	1.34	-5.44	-0.16
	Facultative	TRSW	Forest 100m	-4.35	1.58	-7.47	-1.27
	Facultative	WEKI	Forest 100m	-3.42	1.50	-6.36	-0.48
	Obligate	COMO	Open 100m	-4.18	2.12	-8.38	-0.04
	Obligate	COYE	Open 100m	-3.86	1.87	-7.55	-0.24
	Obligate	WODU	Open 100m	-4.34	2.17	-8.64	-0.13

Facultative	SOSP	Open 100m	-4.70	1.73	-8.13	-1.35
Facultative	SOSP	Wetland 100m	-3.04	1.39	-5.79	-0.33
Obligate	BLPH	Developed 500m	2.97	1.39	0.30	5.76
Matrix	CATO	Developed 500m	1.99	1.03	0.13	4.16
Matrix	LASP	Developed 500m	2.85	1.04	0.87	4.97
Obligate	BLPH	Forest 500m	4.53	2.11	0.45	8.75
Obligate	VIRA	Forest 500m	4.26	2.02	0.35	8.29
Obligate	YBCH	Forest 500m	5.25	1.96	1.46	9.14
Obligate	YEWA	Forest 500m	4.38	2.00	0.47	8.33
Facultative	ANHU	Forest 500m	4.77	2.20	0.49	9.12
Facultative	BUSH	Forest 500m	4.99	2.16	0.83	9.30
Facultative	HOWR	Forest 500m	4.59	1.89	0.93	8.33
Facultative	MODO	Forest 500m	4.31	2.01	0.44	8.30
Facultative	OATI	Forest 500m	5.91	2.19	1.67	10.26
Facultative	WEKI	Forest 500m	4.01	1.93	0.25	7.83
Facultative	WREN	Forest 500m	5.62	2.13	1.50	9.85
Matrix	ACWO	Forest 500m	6.29	2.12	2.20	10.51
Matrix	BHGR	Forest 500m	5.63	2.24	1.26	10.06
Matrix	DEJU	Forest 500m	5.67	2.15	1.49	9.94
Matrix	LASP	Forest 500m	4.62	2.03	0.67	8.64
Matrix	LEGO	Forest 500m	4.59	2.23	0.26	9.02
Matrix	SPTO	Forest 500m	4.82	2.04	0.88	8.88
Matrix	WEWP	Forest 500m	5.02	1.95	1.23	8.89
Facultative	ATFL	Open 500m	4.78	2.34	0.20	9.39
Facultative	BUOR	Open 500m	5.28	2.23	0.97	9.68
Facultative	EUST	Open 500m	4.81	2.17	0.59	9.11
Facultative	KILL	Open 500m	5.11	2.17	0.92	9.44
Facultative	NOMO	Open 500m	4.55	2.02	0.62	8.55
Matrix	AMRO	Open 500m	4.29	2.21	0.00	8.66
Matrix	HOSP	Open 500m	5.07	2.34	0.55	9.70
Matrix	WEME	Open 500m	5.58	2.25	1.23	10.05

Appendix S3.1: Supplementary information for Chapter 3

Table S3.1. AIC Table comparing different methods of characterizing and summarizing wetlands with a null model. Δ AIC Null denotes the AIC difference between the null model and each parameterized model.

Species	Year	Character.	Summariz.	AIC	Δ AIC Null	Δ AIC	AIC Wt.	Log Like.
Black Rail	2009	Full Wetland	50% Threshold	171.23	-4.64	0.00	0.27	-82.61
		50 m Radius	50% Threshold	171.57	-4.30	0.34	0.23	-82.78
		50 m Radius	60% Threshold	172.02	-3.85	0.79	0.18	-83.01
		Full Wetland	60% Threshold	173.13	-2.74	1.90	0.11	-83.57
		25 m Radius	50% Threshold	173.27	-2.60	2.04	0.10	-83.63
		25 m Radius	60% Threshold	174.60	-1.27	3.37	0.05	-84.30
		Null	Null	175.87	0.00	4.64	0.03	-85.93
		Full Wetland	Mean Probability	177.57	1.71	6.35	0.01	-85.79
		25 m Radius	Mean Probability	177.86	1.99	6.63	0.01	-85.93
		50 m Radius	Mean Probability	177.87	2.00	6.64	0.01	-85.93
	2010	25 m Radius	50% Threshold	138.92	-28.19	0.00	0.47	-66.46
		50 m Radius	50% Threshold	139.83	-27.27	0.91	0.30	-66.92
		50 m Radius	60% Threshold	141.24	-25.86	2.32	0.15	-67.62
		Full Wetland	50% Threshold	142.48	-24.62	3.56	0.08	-68.24
		Full Wetland	Mean Probability	152.12	-14.99	13.20	0.00	-73.06
		25 m Radius	60% Threshold	163.44	-3.67	24.52	0.00	-78.72
		25 m Radius	Mean Probability	166.31	-0.79	27.40	0.00	-80.16
		Null	Null	167.11	0.00	28.19	0.00	-81.55
		50 m Radius	Mean Probability	168.24	1.14	29.33	0.00	-81.12
		Full Wetland	Mean Probability	169.09	1.99	30.17	0.00	-81.55
	2012	25 m Radius	50% Threshold	209.97	-2.39	0.00	0.27	-101.99
		Full Wetland	Mean Probability	211.46	-0.91	1.48	0.13	-102.73
		25 m Radius	Mean Probability	211.58	-0.78	1.61	0.12	-102.79
		Full Wetland	60% Threshold	211.88	-0.48	1.91	0.10	-102.94
		50 m Radius	Mean Probability	212.05	-0.31	2.08	0.10	-103.03

	Null	Null	212.36	0.00	2.39	0.08	-104.18
	50 m Radius	50% Threshold	212.69	0.33	2.72	0.07	-103.35
	25 m Radius	60% Threshold	213.56	1.20	3.59	0.05	-103.78
	50 m Radius	60% Threshold	213.76	1.40	3.79	0.04	-103.88
	Full Wetland	50% Threshold	214.02	1.65	4.05	0.04	-104.01
2014	50 m Radius	60% Threshold	161.37	-18.97	0.00	0.43	-77.69
	Full Wetland	60% Threshold	162.35	-17.99	0.98	0.26	-78.18
	Full Wetland	50% Threshold	163.64	-16.71	2.27	0.14	-78.82
	25 m Radius	50% Threshold	164.24	-16.10	2.87	0.10	-79.12
	50 m Radius	50% Threshold	164.95	-15.40	3.57	0.07	-79.47
	25 m Radius	60% Threshold	178.55	-1.80	17.18	0.00	-86.27
	Null	Null	180.35	0.00	18.97	0.00	-88.17
	Full Wetland	Mean Probability	182.09	1.74	20.71	0.00	-88.04
	25 m Radius	Mean Probability	182.29	1.95	20.92	0.00	-88.15
	50 m Radius	Mean Probability	182.33	1.98	20.96	0.00	-88.16
2016	25 m Radius	60% Threshold	193.48	-30.18	0.00	0.78	-93.74
	Full Wetland	50% Threshold	197.80	-25.85	4.32	0.09	-95.90
	25 m Radius	50% Threshold	198.21	-25.44	4.73	0.07	-96.11
	50 m Radius	50% Threshold	198.65	-25.00	5.18	0.06	-96.33
	Full Wetland	Mean Probability	207.04	-16.62	13.56	0.00	-100.52
	50 m Radius	60% Threshold	213.22	-10.43	19.75	0.00	-103.61
	Full Wetland	Mean Probability	221.79	-1.86	28.32	0.00	-107.90
	Null	Null	223.65	0.00	30.18	0.00	-109.83
	25 m Radius	Mean Probability	223.73	0.07	30.25	0.00	-108.86
	50 m Radius	Mean Probability	224.23	0.57	30.75	0.00	-109.11
2018	Full Wetland	60% Threshold	290.08	-71.38	0.00	0.91	-142.04
	50 m Radius	60% Threshold	295.55	-65.91	5.47	0.06	-144.77
	Full Wetland	50% Threshold	297.99	-63.46	7.91	0.02	-146.00
	25 m Radius	50% Threshold	298.98	-62.48	8.90	0.01	-146.49
	50 m Radius	50% Threshold	300.18	-61.27	10.10	0.01	-147.09
	25 m Radius	60% Threshold	346.08	-15.37	56.00	0.00	-170.04
	Full Wetland	Mean Probability	349.26	-12.20	59.18	0.00	-171.63
	50 m Radius	Mean Probability	355.40	-6.05	65.32	0.00	-174.70
	25 m Radius	Mean Probability	355.88	-5.58	65.80	0.00	-174.94

		Null	Null	361.45	0.00	71.38	0.00	-178.73
	2009	25 m Radius	50% Threshold	199.59	-23.99	0.00	0.36	-96.80
		50 m Radius	50% Threshold	200.23	-23.35	0.64	0.26	-97.12
		25 m Radius	60% Threshold	200.82	-22.77	1.22	0.19	-97.41
		50 m Radius	60% Threshold	201.40	-22.19	1.80	0.15	-97.70
		Full Wetland	50% Threshold	204.64	-18.95	5.05	0.03	-99.32
		Full Wetland	60% Threshold	206.18	-17.41	6.58	0.01	-100.09
		50 m Radius	Mean Probability	219.26	-4.33	19.66	0.00	-106.63
		25 m Radius	Mean Probability	219.76	-3.82	20.17	0.00	-106.88
		Null	Null	223.59	0.00	23.99	0.00	-109.79
		Full Wetland	Mean Probability	223.62	0.04	24.03	0.00	-108.81
Virginia Rail	2010	50 m Radius	50% Threshold	203.29	-38.10	0.00	0.76	-98.64
		25 m Radius	50% Threshold	206.00	-35.39	2.72	0.20	-100.00
		50 m Radius	60% Threshold	210.30	-31.09	7.02	0.02	-102.15
		25 m Radius	60% Threshold	211.50	-29.89	8.21	0.01	-102.75
		Full Wetland	50% Threshold	212.17	-29.22	8.89	0.01	-103.09
		Full Wetland	60% Threshold	216.03	-25.36	12.74	0.00	-105.02
		Full Wetland	Mean Probability	240.55	-0.84	37.26	0.00	-117.27
		Null	Null	241.39	0.00	38.10	0.00	-118.69
		25 m Radius	Mean Probability	241.75	0.36	38.47	0.00	-117.88
		50 m Radius	Mean Probability	242.68	1.29	39.39	0.00	-118.34
	2012	25 m Radius	50% Threshold	219.73	-44.06	0.00	0.80	-106.86
		50 m Radius	50% Threshold	222.84	-40.95	3.11	0.17	-108.42
		Full Wetland	50% Threshold	226.74	-37.05	7.01	0.02	-110.37
		25 m Radius	60% Threshold	231.40	-32.39	11.67	0.00	-112.70
		50 m Radius	60% Threshold	233.04	-30.75	13.31	0.00	-113.52
		Full Wetland	60% Threshold	234.34	-29.45	14.61	0.00	-114.17
		25 m Radius	Mean Probability	253.41	-10.37	33.68	0.00	-123.71
		50 m Radius	Mean Probability	254.85	-8.93	35.12	0.00	-124.43
		Full Wetland	Mean Probability	255.63	-8.15	35.90	0.00	-124.82
		Null	Null	263.78	0.00	44.06	0.00	-129.89
	2014	25 m Radius	50% Threshold	192.25	-50.77	0.00	0.54	-93.12

	50 m Radius	50% Threshold	193.82	-49.20	1.57	0.25	-93.91
	25 m Radius	Mean Probability	194.87	-48.15	2.62	0.15	-94.44
	50 m Radius	Mean Probability	197.50	-45.52	5.26	0.04	-95.75
	Full Wetland	50% Threshold	198.47	-44.55	6.22	0.02	-96.24
	Full Wetland	60% Threshold	204.91	-38.11	12.66	0.00	-99.45
	50 m Radius	Mean Probability	226.86	-16.16	34.62	0.00	-110.43
	25 m Radius	Mean Probability	228.45	-14.57	36.20	0.00	-111.23
	Full Wetland	Mean Probability	230.01	-13.01	37.76	0.00	-112.01
	Null	Null	243.02	0.00	50.77	0.00	-119.51
2016	25 m Radius	60% Threshold	255.59	-44.66	0.00	0.52	-124.79
	50 m Radius	60% Threshold	257.55	-42.69	1.97	0.19	-125.78
	25 m Radius	50% Threshold	258.38	-41.86	2.80	0.13	-126.19
	50 m Radius	50% Threshold	259.55	-40.69	3.96	0.07	-126.77
	Full Wetland	60% Threshold	260.46	-39.78	4.87	0.05	-127.23
	Full Wetland	50% Threshold	260.87	-39.37	5.28	0.04	-127.43
	25 m Radius	Mean Probability	291.96	-8.28	36.37	0.00	-142.98
	50 m Radius	Mean Probability	293.52	-6.72	37.93	0.00	-143.76
	Full Wetland	Mean Probability	295.10	-5.14	39.52	0.00	-144.55
	Null	Null	300.24	0.00	44.66	0.00	-148.12
2018	Full Wetland	50% Threshold	404.04	-59.16	0.00	0.95	-199.02
	25 m Radius	50% Threshold	410.95	-52.25	6.91	0.03	-202.48
	50 m Radius	50% Threshold	412.46	-50.75	8.42	0.01	-203.23
	Full Wetland	60% Threshold	418.35	-44.86	14.30	0.00	-206.17
	25 m Radius	60% Threshold	422.47	-40.73	18.43	0.00	-208.24
	50 m Radius	60% Threshold	423.90	-39.30	19.86	0.00	-208.95
	Full Wetland	Mean Probability	456.97	-6.23	52.93	0.00	-225.49
	25 m Radius	Mean Probability	458.99	-4.21	54.95	0.00	-226.49
	50 m Radius	Mean Probability	459.66	-3.54	55.62	0.00	-226.83
	Null	Null	463.20	0.00	59.16	0.00	-229.60

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