LINKING WETLAND MANAGEMENT DECISIONS TO SECRETIVE MARSH BIRD HABITAT USE DURING SPRING MIGRATION AND SUMMER BREEDING ON PUBLIC WETLANDS IN MISSOURI

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by
EVAN B HILL
Dr. Elisabeth Webb, Thesis Supervisor
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The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

LINKING WETLAND MANAGEMENT DECISIONS TO SECRETIVE MARSH BIRD HABITAT USE DURING SPRING MIGRATION AND SUMMER BREEDING ON PUBLIC WETLANDS IN MISSOURI

presented by Evan Hill,

a candidate for the degree of Master of Science,

and hereby certify that, in their opinion, it is worthy of acceptance.

Professor Elisabeth Webb

Doreen Mengel

Professor Frank R. Thompson

Professor Lori Eggert

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ABSTRACT

The extent to which secretive marsh birds rely on wetlands in Missouri during spring migration is relatively unknown. My objective for chapter one was to determine how initial marsh bird occupancy and subsequent colonization and departure probabilities were influenced by wetland management practices, including the duration and initiation date of spring water-level drawdowns, and associated wetland habitat characteristics. We used dynamic occupancy modeling to evaluate factors that influence SMB occupancy and colonization/departure probabilities. Sora and American bittern occupancy models indicated a positive relationship between occupancy probability and duration of drawdown, however the top occupancy model for Virginia rail was the null model. The top colonization/departure model for sora included vegetation density and percent of a site containing emergent vegetation, with both variables having a positive relationship with colonization probability and a negative relationship with departure probability. The top colonization/departure model for Virginia rail included range of water depth and range of vegetation height, both of which had a negative relationship with colonization and departure probability. The top colonization/departure model for American bittern included vegetation interspersion, whereas the top model for least bittern included the percent site inundated and overall area inundated. My objective for chapter two was to determine effects of hydrologic management and habitat characteristics on habitat selection and the daily survival rate (DSR) of least bittern on public wetlands in Missouri at two scales: the entire wetland and the nest point. Least bittern populations have been in decline since the 1970s, most likely due to extensive loss of freshwater emergent wetlands, the primary nesting habitat of least bittern. The decline in nesting habitat emphasizes the need for effective wetland management within the nesting range of least bitterns. The extent to which least bittern rely on wetlands in Missouri during summer nesting efforts is poorly understood. The logistic exposure method was used to evaluate DSR as a function of covariates. At the wetland scale, logistic regression was used to evaluate models composed of combinations of covariates thought to influence least bittern nest site selection. The percent of a wetland covered in emergent vegetation and the average water depth were positively associated with probability of selection at the wetland scale. At the point scale, discrete choice was used to evaluate models composed of combinations of covariates thought to influence least bittern nest site selection. The relative probability of use was positively related with water depth, percent of a site in emergent vegetation, and negatively related with vegetation density. Daily Survival Rate was positively related with average water depth at nest points. These results are important to inform management decisions intended to create wetland conditions favorable to SMBs. Both migrants and breeders are more likely to use wetlands with emergent vegetation interspersed with patches of open water. Drawdown schedules will increase occupancy if they are timed to conform to the life history stage of the target species, providing water for migrants in April-May, and for breeders in June and July. A possible ecological trap will be avoided if drawdowns are complete before least bittern begin nest site selection in mid to late May.

CHAPTER I

USE OF A DYNAMIC OCCUPANCY MODEL TO EVALUATE SECRETIVE MARSH BIRD RESPONSE TO WETLAND MANAGEMENT PRACTICES DURING SPRING MIGRATION.

INTRODUCTION

Over the past two hundred years, approximately half of the original functional wetland area in the continental U.S. has been eliminated (Dahl 1990). Dahl (1990) estimated over 150 million hectares of wetlands in the United States in 1780, with approximately 90 million hectares in the lower 48 states. However, by 1980, over 53% of wetland area in the U.S. had been converted (Dahl 1990). Based on national wetland inventory surveys, wetlands of every category have experienced major declines in area since the 1950s (Shaw and Fredine, 1956, Dahl and Johnson 1991, Dahl 2000). Approximately 24% of freshwater emergent wetland area has been eliminated since the 1950s; more than any other freshwater wetland type (Dahl 2000). Missouri was no exception, eliminating 87% (1,700,000 hectares) of its original wetland area between 1780 and 1980 (Dahl 1990).

Despite heavy wetland losses, many migratory waterbirds rely on the remaining freshwater wetlands in Missouri during migration, and in some cases, for breeding (Sayre and Rundle 1984, Reid 1989, Darrah and Krementz 2011). During migration, waterbirds use Missouri wetlands during brief stopover periods for resting and foraging in order to meet the energetic demands of migration (Baldassarre and Bolen 1994, Skagen and Knopf 1994). If a waterbird's need for rest and forage are not met during these stopover events, the individual's success during the subsequent breeding season could be negatively impacted (Newton 2006). Likewise, the conditions on wetland sites used by waterbirds that breed in Missouri would also have an impact on their subsequent breeding success (Nelson 2003, Moore et al. 2009, Darrah and Krementz 2011).

The elimination of the vast majority of Missouri's wetlands emphasizes the need for efficient and effective management of remaining wetlands to provide wildlife habitat. Wetland management strategies have often used the natural environmental characteristics of an existing wetland to their advantage or have directly manipulated wetland environmental characteristics to achieve specific goals, including creating waterfowl habitat (Baldassarre and Bolen 1994). A common wetland management strategy used to create conditions suitable for migrating waterfowl is moist-soil management, which often involves active hydrologic manipulation and mechanical soil disturbances to provide water depths suitable for foraging waterfowl, an abundance of invertebrate prey, and to encourage the growth of seed-producing annual hydrophytes (Rundle and Fredrickson 1981, Fredrickson and Taylor 1982, Fredrickson 1991, Lane and Jensen 1999). These management strategies emulate the dynamic water conditions of natural wetlands as they change over time, and complexes of wetlands create spatial variation across a managed area (Fredrickson and Taylor 1982). Among managed wetlands with spring water level manipulation, often referred to as a drawdown, the initiation and duration of the drawdown can vary to correspond to the migration phenology of wetland-dependent birds and to the differences in seasonal patterns across the state (Fredrickson and Taylor 1982, Fredrickson 1991). A primary assumption of public wetland management in Missouri is that if the full range of habitat characteristics required by many waterfowl species are provided, these habitats will also meet the life-history needs of the many other species of wetland-dependent wildlife. While studies of wetlands along the Missouri River provided some evidence to support this assumption in regards to shorebirds and wading birds (Raedeke et al. 2003), there are integral gaps in the understanding of how other groups of wetland dependent birds respond to the vegetative and habitat conditions that result when wetlands are managed primarily for migrating waterfowl.

Secretive marsh birds are a group of wetland-dependent birds that use freshwater wetlands for cover, foraging, and breeding (Bent 1926, Eddleman et al. 1988). Secretive marsh birds depend on freshwater wetlands during every stage of their life history (Weller 1999). Extensive wetland habitat loss throughout the United States (Dahl 2011) is believed to have contributed to the subsequent decrease in geographic range of many SMB species, including Virginia rail (*Rallus limicola*), sora (*Porzana carolina*), king rail (*Rallus elegans*), least bittern (*Ixobrychus exilis*), and American bittern (*Botaurus lentiginosus*) (Santisteban et al. 2011, Sauer et al. 2013). While wetland management has typically focused on providing wetland habitat for waterfowl (Rundle and Fredrickson 1981), providing habitat for non-waterfowl species, like SMBs, should be an important goal of wetland management decisions as well. However, studying the response of SMBs to this altered landscape with fewer wetlands is challenging because SMBs use dense emergent vegetation and are rarely detected outside of the breeding season, when they are most vocal (Eddleman et al. 1988, Conway and Gibbs 2011, Steidl et al. 2013).

Depending on the species of SMB and what stage of the annual cycle it is currently in, wetlands in Missouri fulfill different life-history needs for the individual (Nelson 2003, Griffin et al. 2009, Van Der Laar and Krementz 2012). Sora, Virginia rail, and American bittern breed further north than Missouri, but depend on wetlands in Missouri during spring migration for foraging and roosting locations (Robbins and Easterla 1992, Melvin and Gibbs 1996, Lowther et al. 2009). In contrast, king rail and least bittern use Missouri wetlands both as migratory stopover sites or as breeding and nesting destinations (Poole et al. 2009, Pickens and Meanley 2015). During migration, SMBs need emergent vegetation for cover, often foraging along the vegetation-water interface (Weller 1999). During breeding, SMBs need emergent vegetation of a sufficient density and height to protect the nest from predators and inclement weather (Eddleman et al. 1988). Missouri wetlands can provide forage and cover during both life-history stages. Regardless of life history stage, birds use emergent vegetation tall and dense enough to provide sufficient cover, but not so dense as to impede bird movement (Reid 1989). Breeding SMBs are often more abundant on wetlands characterized by an even ratio of open water to emergent vegetation coverage (Weller and Spatcher 1965, Weller 1999) but may also require this ratio throughout the annual life cycle.

Wetland water depth can also affect SMB distribution during different life history stages because of the differences in emergent plant communities associated with different water depths, soil types, differences in prey items available, in nesting behavior, and physical limitations dictated by a species' morphology (Reid 1989, Weller 1999). In general, migrant sora and Virginia rail use wetlands with saturated soil or shallowly flooded sites, and generally use water depths <15cm (Griese et al. 1980, Rundle and Fredrickson 1981, Rundle and Sayre 1983, Sayre and Rundle 1984). In contrast, breeding American bittern and least bittern use more deeply flooded wetlands up to 200cm in depth (Lowther et al. 2009, Poole et al. 2009). Providing deeper water levels is especially important for breeding least bittern, which construct a nest platform in deeper water to avoid terrestrial nest predators (Weller 1961, Poole et al. 2009). King rail will also nest over deep water to avoid terrestrial nest predators, but adults will lead broods to forage in shallow water with similar depths used by sora and Virginia rail (Eddleman et al. 1988, Reid 1989).

Wildlife make habitat selection decisions at multiple spatial scales so it is necessary to determine which variables are most important at each scale (Johnson 1980, Buler et al. 2007, Mayor et al. 2009, Pickens and King 2014). Species presumably make adaptive habitat selection decisions that reflect differences in habitat variables between sites (Jaenike and Holt 1991, Forstmeier and Weiss 2004). First-order habitat selection decisions represent the geographic range of a given species. After a geographic range is selected, particular wetlands are selected and these second-order habitat selection decisions can directly influence an individual's reproductive potential (Schlaepfer et al. 2002, Battin 2004), and this is the scale wetland managers should consider during their management decision-making process.

Wetland management strategies can be implemented at multiple scales that affect the availability of water and vegetation across a wetland complex (Fredrickson and Taylor 1982). Water level drawdowns can affect an entire wetland but water depth microhabitats within the wetland depend on topography (Fredrickson 1991). Mowing or disking a strip through a wetland alters the interspersion of open water to emergent vegetation, creating spatial variation of available habitats across the wetland (Fredrickson and Taylor 1982). In order to determine if these wetland management decisions are providing for the life history needs of SMBs, it is necessary to evaluate the response of

SMB occupancy to differences in wetland habitat characteristics at multiple spatial scales. Evaluating occupancy in different wetlands will inform the decision-making process for wetland management strategies intended to provide habitat for SMBs.

The secretive behavior of many marsh bird species has created difficulties in determining the relationship between occupancy and wetland habitat characteristics (Gibbs and Melvin 1997). Commonly found in dense emergent vegetation that obscures them from view, SMBs are not easily flushed by approaching humans (Bent 1926). Furthermore, SMBs rarely call unless responding to another bird, therefore, researchers have developed survey protocols that include playing recordings of their calls to elicit a response (Glahn 1974, Johnson and Dinsmore 1986, Gibbs and Melvin 1997, Conway and Gibbs 2011). Probability of detecting a SMB can vary depending on the specific survey protocol used and the current life history stage of the focal species (Conway and Gibbs 2011, Steidl et al. 2013). The Breeding Bird Survey (BBS) is considered ineffective for surveying abundance of SMBs because of a low probability of detecting SMBs with passive listening road-side surveys (Conway 2011, Santisteban et al. 2011). As a result of low sample sizes and low detection probabilities, actual marsh bird population trend estimates are likely much different than previously reported, which emphasizes a need for more information, especially during spring migration (Santisteban et al. 2011). Overall, limited distributions combined with low detection probability have resulted in SMBs being among the least studied avian groups and for most species in this group there is limited information on population levels, breeding ecology, migration patterns, and overall habitat requirements (Eddleman et al. 1988, Weller 1999, Valente et al. 2011).

Occupancy estimation provides tools that address the challenges of accounting for SMB presence, because this method accounts for an observer's limited ability to detect an individual (MacKenzie et al. 2003, MacKenzie 2006, Bailey et al. 2014). The probability of detection can be affected by variables inherent to the observer and in the surrounding environment (Gibbs and Melvin 1997, Conway and Gibbs 2011). For example, dense vegetation may shield focal species from view and loud background noise may prevent observers from hearing SMB calls (Conway 2011, Conway and Gibbs 2011). Previous studies assessing SMB habitat associations may have used survey methods designed to increase detection probability without actually accounting for this parameter in their estimates of abundance (Zimmerman 1984, Manci and Rusch 1988, Frederick et al. 1990). The usefulness of occupancy estimation is supported by many studies that use this parameter to determine the response of SMBs to differences in habitat characteristics during breeding (Rehm and Baldassarre 2007, Darrah and Krementz 2009, Pickens and King 2014). By accounting for factors that influence detection, these studies demonstrate how occupancy estimates for a given SMB species can be associated with habitat variables, even if SMBs were not directly detected in these habitats. This approach does have limitations including obtaining occupancy estimates close to zero or one due to low sample sizes when fitting occupancy models (Welsh et al. 2013).

One of the primary assumptions of occupancy estimation is that the surveyed site is closed to changes in occupancy between sampling events (Mackenzie and Royle 2005). However, during migration, SMB species are likely moving into and out of a region as well as among individual wetlands within the region, which likely violates the closure assumption inherent in standard occupancy modeling (Robbins and Easterla 1992, Otto et al. 2013, Rota et al. 2014). The robust model, or dynamic occupancy model, offers an approach that accounts for migration movements by allowing individuals to move into and out of sampled areas between major sampling events, as long as the closure assumption is met during secondary sub-counts (Pollock 1982, Mackenzie and Royle 2005). The dynamic model is appropriate for studying migrating individuals because it estimates not only occupancy, but also colonization and extinction probabilities(MacKenzie et al. 2003, Kéry and Chandler 2012). Colonization and extinction can be thought of as settlement and vacancy of individuals into and out of sampled habitat (MacKenzie et al. 2003, Kéry and Chandler 2012). Assessing probability of colonization and extinction parameters can help determine patterns in habitat use during brief stopover events; this information can then be used to optimize wetland management strategies timed to the migration stage of SMB life history (Betts et al. 2008, Frey et al. 2012, Stodola et al. 2014).

The fluctuating environmental characteristics within wetlands and mid-season habitat alterations resulting from management actions have the potential to create wetland habitat suitable for initial settlement by spring migrants, but which may become unsuitable over time or as SMB life history needs change. Historically, with more wetland area on the landscape, SMBs were able to settle on wetlands with favorable characteristics and vacate wetlands with unfavorable characteristics, depending on the life history stage. However, there is less wetland area in Missouri today, so a given wetland may have to provide for birds during more than one stage of their life history. Wetland management actions early in the spring migration season may attract SMBs to wetlands but later result in altered habitat conditions, which could influence SMB colonization and extinction rates. Therefore, the first objective of my study was to determine how wetland management and habitat characteristics influence SMB occupancy during spring migration. After accounting for detection and initial occupancy, the second objective was to evaluate patterns in wetland use during spring migration stopover events by determining the habitat variables that influenced SMB colonization and extinction rates. High rates of occupancy and nesting effort of these focal species could provide evidence that wetlands in Missouri are providing suitable wetland habitat for SMBs. Implementing the dynamic occupancy model could potentially clarify patterns in SMB stopover habitat use during this poorly understood stage of their life history, thus informing how management strategies influence habitat conditions for this suite of waterbirds.

METHODS

Study Area and Site Selection

My study took place on public wetlands in four regions within Missouri, the northwest, north-central, northeast, and southeast and each region included two Missouri Department of Conservation (MDC) Conservation Areas (CA) and one United States Fish and Wildlife Service (USFWS) National Wildlife Refuge (NWR) for a total of twelve study areas. State Conservation Areas included Bob Brown, Nodaway Valley, Grand Pass, Fountain Grove, Ted Shanks, B.K. Leach, Duck Creek, and Otter Slough, while the four National Wildlife Refuges included Squaw Creek, Swan Lake, Clarence Cannon, and Mingo (Figure 1). I selected these study areas because they included a range of management strategies of interest, and because they included wetlands likely to be used by both migrant and breeding SMBs. I selected five focal SMB species for my study; sora, Virginia rail, king rail, American bittern, and least bittern, because they provided a comprehensive representation of the life history needs of most SMB species using wetlands in Missouri during spring migration and summer breeding (Robbins and Easterla 1992, Conway 1995, Melvin and Gibbs 1996, Lowther et al. 2009, Poole et al. 2009).

Following meetings with area managers and preliminary site assessments, I classified individual wetland units within CAs or NWRs into management categories (active or passive) based on water-level manipulation strategies. Active sites were distinguished from passive sites based on whether area managers manipulated a water control structure with the intent to draw down water levels on a given wetland. Most active sites were expected to be completely dewatered within 2-4 weeks of initial water-level manipulation, whereas water levels in passive sites were not manipulated, but allowed to fluctuate without restriction. Water levels within wetlands in either management category could increase due to rain or flood events, or decrease due to evapotranspiration or percolation through the substrate. However, only active sites had water levels directly manipulated through the use of water control structures before or during the sampling period.

Assuming a minimum detection probability p of 0.4 and an occupancy ψ probability of 0.1, I concluded that a minimum of 60 study sites was necessary to calculate reliable occupancy estimates (Mackenzie et al. 2006). To determine number of study sites, I relied on p and ψ estimates obtained from king rail studies (Darrah and Krementz 2009) because I anticipated king rail would be the rarest species encountered in the study, and thus used conservative estimates of occupancy and detection probability. After categorizing hydrologic management at each potential study site, I selected 26 active and 23 passive wetlands in 2013 and 28 active and 32 passive wetlands in 2014 (Appendix 1). I attempted to choose an equal number of study sites between management categories in each region and study area, but was constrained by availability of sites with differing management categories at each study area and the dynamic nature of management which could alter planned hydrologic management of a given wetland mid-season.

I stratified study sites based on dominant vegetation communities and I placed a SMB survey point within each available habitat type (Rehm and Baldassarre 2007, Budd and Krementz 2010, 2011). Specifically, I used ArcMap to view an aerial photo of each study site and digitized zones of five vegetative communities: persistent emergent vegetation (e.g. *Typha spp*.), non-persistent emergent vegetation (e.g. *Carex spp.),* shrub (e.g. *Salix spp*.), agriculture (e.g. *Zea mays*), and open water. I generated fifty random points within each study site and eliminated points until only a single point in each of the available vegetative communities remained, based on the following criteria: 1) ≥60% of the area within a 50m radius of the survey point consisted of the designated vegetative communities for that survey point, 2) points were located ≥50m from the perimeter of the study site, 3) points were at least 200m apart, and 4) ≥80% of the area within a 50m radius of the survey point was inundated. Area of some study sites was insufficient to maintain the 200m distance between points recommended by the Standardized Marsh Bird Monitoring Protocol (Conway 2011) while also placing a point in each habitat type, in which case, the minimum distance between points was reduced to 150m. If a wetland did not contain all vegetative communities, I placed a survey point in each of the vegetative communities present and then assigned additional survey points randomly in the available vegetative communities, up to a total of 5 points in each site. If vegetative community within a wetland changed over the season (open water transitioned to non-persistent vegetation, etc.), I added points within the wetland to ensure a minimum of 1 survey point in each available habitat type. In addition, inundated area within a wetland varied throughout the season in some sites, so survey points were added if area within a 50m radius of a survey point was ≤20% inundated. As new vegetative communities emerged, such as the growth of patches of non-persistent vegetation, I added points so that at least one point was in each of the available vegetative communities. A minimum of three and a maximum of five survey points at each study site were surveyed for SMB during each primary sampling period.

Marsh Bird Surveys

Marsh bird surveys were conducted using the Standardized Marsh Bird Monitoring Protocol (Conway 2011) to generate detection histories for each focal species at each study site. The survey protocol included a repeated sampling design that used call-broadcast surveys to maximize probability of detecting SMB species (Conway and Gibbs 2011). Six rounds of surveys were conducted from 8 April to 29 June 2013 and from 1 April to 6 June 2014, coinciding with peak migration and breeding times for each of the focal species in Missouri (Robbins and Easterla 1992). Within a round, a minimum of 3 surveys were conducted at each study site during either morning (30 minutes before sunrise to 1000 hours) or evening (1830 hours to 30 minutes after sunset) sampling periods (Conway. 2011). Each survey consisted of a 1-min settling period, a 5-min passive listening period, and a 5-min call-broadcast period. During the settling period, observers remained silent to allow potential disturbance to subside. During the passive listening period, no calls were broadcasted to provoke a response, but any bird detected was recorded, even if it was not one of the five focal species. The passive listening period was followed with a five minute call-broadcast period where 30s segments of calls from each of the five focal SMB species were played separated by 30s of silence (Conway 2011). Observers were trained in visual and aural identification of all SMB species that could occur in Missouri, as well as in distance sampling techniques (Conway 2011, Pickens and King 2014, Glisson et al. 2015).

I assigned a unique name to each survey point and prior to the beginning of each survey the observer recorded the survey point name, time, temperature (in degrees Celsius), and local weather conditions present during the survey. Wind speed was estimated using the Beaufort scale for inland areas (National Weather Service 2013), sky conditions and ambient noise level were estimated using scales described in the Standardized Marsh Bird Monitoring Protocol (Conway 2011). Observers recorded whether a bird was detected visually, aurally, or both, and estimated the direction and distance from the survey point at which the bird was detected, as well as if the bird was within the perimeter of the wetland in which the survey was taking place. The observer's best judgment was used to distinguish between individuals of the same species and whether those two individuals formed a breeding pair (i.e. two individuals calling in response to one another, not the broadcast). Calls from unknown birds were entered into the species column as "unknown" and a short description of the call was entered into the comments section of the datasheet.

Habitat Sampling

I estimated the percentage of five vegetative communities within a 50m radius of each survey point to provide representation of the habitat composition at the survey point level. The five vegetative communities included: persistent emergent vegetation, non-persistent emergent vegetation, shrub vegetation, agricultural crops, and open water (Bolenbaugh et al. 2011). I measured habitat characteristics at each survey point and at 5m from the survey point in each of the 4 cardinal directions. At each point, I quantified water depth (cm), vegetation height (cm) and vegetation density (Robel units) (Table 1). I measured vegetation height from water surface to the full height of the nearest stem touching the measuring device, and vegetation density was measured using a Robel pole, taking the lowest segment not obscured by vegetation when observed from a distance of 1m. If no vegetation was present at a water depth measurement location, the vegetation height was recorded as 0cm and the density as 1 (Robel units).

I characterized water depth, vegetation height, and vegetation density at each study site by calculating an average of measurements taken at each survey point within the study site during a given round of sampling (Table 1). Drawdown duration for each site was quantified as the number of days between when the drawdown was initiated and the site was dewatered (contained <5% water). The drawdown initiation date on active sites was determined based on information obtained from area managers prior to the sampling season. For passive sites, drawdown duration was considered the total number of days between when surveys began and when either the site was dry (contained <5% water) or when surveys ended. To account for evapotranspiration on passive sites, the drawdown initiation was considered ten days after the latest drawdown initiation date within the same region. I calculated degree of vegetative interspersion for each site using the equation developed by Rehm and Baldassarre (2007).

$$\text{Eq.:1 Interspersion} = ((|50\text{-Percent of site in open water}|) * 2)$$

Data Analysis

Detection (p), ψ, colonization (γ), and extinction (ε) probabilities were estimated using a dynamic occupancy model for open populations (MacKenzie et al. 2003). Dynamic occupancy models allow for changes in ψ between seasons or site visits (primary sampling period) but assume ψ does not change within a season or site visit (secondary sampling periods) (Pollock 1982, Mackenzie at al. 2003, Rota et al. 2009, Kéry and Schaub 2012). In my study, the primary sampling periods were the weekly site visits (or sampling rounds), and the surveys conducted within each site during a sampling round were designated as the secondary sampling periods. Dynamic occupancy models are appropriate when the closure assumption can be met for secondary sampling periods but immigration and emigration occur between the primary sampling periods (Pollock 1982, Robbins and Easterla 1992, MacKenzie et al. 2003). I considered that the closure assumption inherent to occupancy modeling to be met because secondary sampling periods in my study all took place during the same time period (morning or evening) of the same day (Betts et al. 2008, Rota et al. 2009, Stodola et al. 2014). All of the focal species were considered migrants through Missouri (with bittern species and king rail being potential breeders), thus it was probable individuals emigrated from sites between primary sampling periods. Although sites were surveyed within a time frame suitable to assume closure, the life-history and migration chronology of the study species would likely have violated the closure assumption between sampling periods necessary for a single-season model (Robbins and Easterla 1992). Wetland sites from 2013 and 2014 were combined to yield 107 study sites.

Occupancy and *p* probability models were fit using the colext function (Kéry and Chandler 2012) in the unmarked package in R 3.1.1 (Fiske and Chandler 2011, R Core Development Team 2015). An initial set of models evaluated the effects of observer, time, and weather conditions on *p* while holding ψ, γ, and ε constant. The top *p* model was then considered the null model in subsequent model sets evaluating ψ, γ, and ε (Hansen et al. 2011, Richmond et al. 2012, Stodola et al. 2014). Covariates used to develop *p* models included observer, ambient noise, time of day, ambient temperature (^{o}C), wind speed, weather condition, and survey round (Conway 2011), whereas covariates used to estimate ψ, γ, and ε probability included habitat characteristics and timing and duration of drawdowns (Table 1). Covariates used to estimate ψ were not allowed to change between primary sampling periods, whereas covariates used to estimate γ and ε were allowed to vary between primary sampling periods, but not between secondary sampling periods (Kéry and Chandler 2012). Covariates used to estimate *p* were allowed to change between both primary and secondary sampling periods (Kéry and Chandler 2012). The relationship between average water depth and ψ may not have been linear for all SMB species, therefore I included linear, quadratic, and logarithmic forms of average water depth in model sets evaluating SMB γ and ε rates (Hansen et al. 2011, Austin and Buhl 2013). The interaction between average water depth and the duration of the drawdown at the time of the survey and the interaction between the vegetation height and the average water depth were also included in model sets evaluating SMB γ and ε rates.

A second and third stage of model selection was necessary because this method reduced the number of models in the candidate set while simultaneously assessing the covariates I thought would explain differences in estimates of ψ, γ, and ε (Franklin et al. 2000, Betts et al. 2008, Hansen et al. 2011, Stodola et al. 2014). The top model from the first model set determined which covariates best predicted p, and was included as the null model in the second and third model sets (Betts et al. 2008, Stodola et al. 2014). The second model set included covariates from the top model in model set 1, and used a variety of covariates to estimate ψ, and set γ and ε to Round-1 (the primary sampling period) for a time-dependent model (Betts et al. 2008). The third model set determined variables that best predicted γ and ε in the context of the variables that best predicted p and ψ probability. The third model set included the covariates from the top model in model sets 1 and 2, and used a variety of covariates to estimate γ and ε (Betts et al. 2008). The various covariates were chosen based on an extensive literature review of what is thought to influence the habitat selection decisions of SMBs during spring migration through Missouri. These variables may have different effects, or more or less of an effect during spring migration, so it is important to evaluate these variables during this portion of the annual cycle. For each occupancy model, I calculated Akaike's Information Criterion (AIC), ΔAIC (the difference in AIC between a given model and the model with the lowest AIC), and AIC weight, which is the weight of evidence that a given model is the best model (Burnham and Anderson 2002, Glisson et al. 2015). I averaged parameter estimates across all models in the 90% AIC confidence set for each species in each of the model sets (Hansen et al. 2011). I considered parameter estimates significant if the 95% confidence interval did not overlap 0, and considered parameters with 95% confidence intervals that marginally overlapped 0 to have modest support for an effect (Glisson et al. 2015).

RESULTS

I completed 1691 surveys in 107 wetlands sites in 2013 and 2014. During spring 2013, flooding caused water to breach levees at Ted Shanks CA and Clarence Cannon NWR and road closures prevented access to these study areas. In 2014, I was able to sample at least one study site within all 12 study areas during each survey round. Middle Marsh at Nodaway Valley CA and MSU1 at Swan Lake NWR, were excluded from analysis because I was only able to conduct a single round of surveys at each of these sites. In 2013, I surveyed 47 sites throughout Missouri, 14 in the central region, 5 in the northeast region, 14 in the northwest region and 14 in the southeast region (Appendix 1). In 2014, I surveyed 60 sites total across Missouri, 15 in each of the four regions (Appendix 1).

All five focal species were detected at least once over the course of the survey period (Table 2). Sora were the most frequently detected species (n=909; p=0.43), followed by least bittern (n=254; p=0.33), American bittern (n=181; p=0.32), Virginia rail (n=99; p=0.21), and king rail (n=9). Too few king rail were detected in order to calculate a reliable p estimate. Nine king rail were detected in both study years, which was insufficient for ψ modeling, thus king rail were excluded from further analysis. Of the four regions, the northwest region had the most detections and the greatest detection rate (n=621; 1.3 detections/survey), followed by the northeast (n=327; 1.1 detections /survey), the north-central (n=266; 0.6 detections/survey), and the southeast (n=238; 0.5 detections /survey) (Table 2). The number of detections of a species per survey in 2013 was greatest for sora in rounds one through three, but greatest for least bittern in rounds four through six (Appendix 2). In 2014, the number of detections of a species per survey was greatest for sora in all six rounds (Appendix 3).

The model that best explained sora *p* included observer as a covariate, thus observer was included in all candidate models predicting sora ψ. For the model set evaluating covariates that best predicted sora ψ, eight models were included in the 90% AIC weight confidence set (Table 3). The top sora ψ model included the covariate for drawdown duration, which was positively related with ψ, and had modest support for an effect (Table 4). Predicted ψ for sora was greatest in sites that had a drawdown duration ≥100 days (Figure 2). In the model set evaluating covariates that best predicted sora γ and ε, three models fell within the 90% AIC weight confidence set, with the most supported model being the top model from the occupancy-oriented model set. The second and third models both included vegetation density and the third model also included the percent of a site in emergent vegetation coverage (Table 5). Sora γ was positively related with vegetation density and percent of a site in emergent vegetation, while ε probability was negatively related with vegetation density and the percent of a site in emergent vegetation (Table 6).

Least bittern *p* was best predicted by the sampling round (primary sampling period) in which a survey took place. Therefore, sampling round was included as a covariate in all candidate models estimating least bittern ψ. In the model set predicting least bittern ψ, the top model included a covariate for drawdown initiation date (Table 7). Least bittern ψ was positively related with drawdown initiation date, with predicted ψ greatest at sites where a drawdown was initiated in mid to late May (Figure 3). The top model in the second model set was the drawdown initiation date, so the ψ parameter was set to the drawdown initiation date in the third model set. Models predicting least bittern γ and ε probability contained two models in the 90% weight confidence set, which included covariates for water depth and the logarithmic transformation of water depth (Table 8). Colonization probability was positively related with the average water depth at a site (Table 10). Extinction estimates for least bittern were negligible at sites that were $\geq$50cm deep (Figure 4).

American bittern *p* was best explained by sky conditions at the time of the survey; therefore, sky condition was included in the null model and in all subsequent models for American bittern. In the model set predicting American bittern ψ, seven models were in the 90% AIC weight confidence set (Table 10), lending a fair amount of uncertainty to this model set. The seven models in the 90% AIC weight confidence set consisted of simple models with only one or two covariates in each parameter, indicating that a more complex model might have fit the data better. However, I was unable to fit complex models, so many of my models include only one or two covariates per parameter. Drawdown duration, drawdown initiation date, water depth and vegetation height were included in the top three models predicting American bittern ψ. American bittern ψ was positively related with the drawdown initiation date and drawdown duration (Table 11). Predicted American bittern ψ was maximized at sites with a July drawdown initiation date or sites with a drawdown duration exceeding 150 days (Figure 5). Finally, American bittern ψ was positively related with water depth. Predicted ψ for American bittern was maximized at sites with a water depth $\geq$150cm (Figure 5). In the model set predicting American bittern γ and ε probability, six models were in the 90% AIC weight confidence set. (Table 12), and the top model included the covariate for interspersion. Vegetative interspersion was negatively related with American bittern γ and significantly positively related with ε probability, meaning that extinction probability was lowest at sites that were in the hemi-marsh condition (e.g. a 50:50 mix of open water to emergent vegetation) (Table 13). An interspersion value of zero indicates a 50:50 mix of open water/emergent vegetation, whereas a value of 100 indicated all open water or all emergent vegetation. American bittern γ and ε probabilities were significantly negatively related with the percent of a site in open water, with negligible ε probability at sites containing ≥80% open water coverage (Figure 7). Therefore, sites at least 80% open water were not likely to be settled, but the individuals that did use these sites were unlikely to leave as a result of the open water conditions. American bittern ε probability was significantly negatively related to water depth and the percent of the site inundated. American bittern ε probability was negligible at sites that had a water depth ≥150cm and at sites that were at least 60% inundated (Figure 8).

Wind conditions during a survey best predicted Virginia rail *p*, thus wind was included in all subsequent model sets for this species. However, because there were six models in the 90% AIC weight confidence set, this model set had some amount of uncertainty. The top model for Virginia rail ψ was the null model, with an AIC weight of 0.99 (Table 14). Therefore, the parameter for ψ was set to constant in the third model set. There were five models in the 90% AIC weight confidence set from models predicting γ and ε (Table 15). The top model included the range of vegetation heights and the range of water depth on a site. Colonization and ε probability were negatively related with the range of vegetation heights, the range of water depths, and the percent of open water at a site (Table 16). Extinction probability was negligible on sites that had a range of vegetation heights ≥100cm (Figure 9) and at sites that had open water coverage ≥70% in (Figure 10). The range in vegetation heights and the percent of open water did not strongly influence settlement, but once a Virginia rail used a site with vegetation height ranges exceeding 100cm or a site that was 70% open water, local vacancy was unlikely.

DISCUSSION

Like other wildlife, SMBs arriving at stopover locations during spring migration likely make adaptive habitat selection decisions that lead to increased fitness of an individual, and reinforce habitat selection patterns (Jaenike and Holt 1991, Martin 1998, Forstmeier and Weiss 2004). Understanding which habitats are selected by SMBs during migration and/or breeding enables wetland managers to determine if they are providing suitable conditions for these different life history events. Of all the wetlands in a managed area, some may be more or less likely to be used by SMBs. Management decisions that result in suitable conditions will only increase the likelihood that wetlands will be used by SMBs, as they may still use less suitable wetlands at some cost to fitness. Public wetland areas in Missouri generally include multiple wetlands characterized by differences in habitats and management strategies that are occupied by SMBs as they arrive in the spring. The wetlands occupied by SMBs and their subsequent migration stopover movements across the wetlands in these public areas likely represent adaptive habitat selection decisions at multiple spatial and temporal scales (Jaenike and Holt 1991, Martin 1998). My study focused on determining patterns in the initial wetland selection of SMBs during spring migration and then assessing the wetland management characteristics and resulting habitat conditions that influenced movements between wetlands at migration stopover sites.

Breeding SMBs, such as the least bittern, use wetlands in Missouri for foraging, pair-formation, and nesting (Nelson 2003, Arnold 2005). While I detected least bittern during spring migration, some of these individuals likely nested in Missouri as well. Least bittern nest in relatively deep water to avoid terrestrial nest predators and can forage over deep water by constructing foraging platforms or by grasping vegetation to catch fish and insects (Poole et al. 2009). Typical nesting vegetation for least bittern includes bulrush (*Scirpus* spp.) and cattail (*Typha* spp.), and least bittern both breeds and forages in wetlands with a high degree of interspersion (Bogner and Baldassarre 2002, Darrah and Krementz 2010). I found 71 least bittern nests, all constructed using either bulrush or cattail. During migration and pair formation, least bittern may not be as restricted to deeper water wetlands, but need deeper water during incubation and brood-rearing.

Migrants, like sora and Virginia rail, use wetlands for foraging and cover during stopover events (Rundle and Fredrickson 1981, Sayre and Rundle 1984). Sora habitat usage during spring migration reflects a more granivorous diet, in that they use wetlands dominated by smartweed, sedges, and other seed producing emergents (Rundle and Sayre 1983). Unlike the least bittern, sora and Virginia rail are associated with relatively shallow water depths (Sayre and Rundle 1984). During migration, sora and Virginia rail do not require vegetation stands as dense as they need during breeding when the vegetation is used to construct sturdy nests that are concealed from above (Melvin and Gibbs 1996). I found a positive relationship between sora γ and vegetation density, but it was not significant, which may indicate this variable is more important later in the annual cycle. Wetlands with some degree of interspersion are important to migrant American bittern and king rail, because they forage along the vegetation-water interface (Lowther et al. 2009, Pickens and Meanley 2015), I found that American bittern were less likely to vacate a wetland that was in the hemi-marsh condition. The larger tarsi of American bittern and king rail allows them to exploit deeper water while foraging, however breeding king rail require shallower water depths to lead their broods to forage. Wetland management strategies that result in habitat suitable for both migrants and breeders likely represent an important component in SMB conservation efforts.

Wetlands with an extended drawdown duration appear to be important predictors of ψ for both migrant and breeding SMB. The drawdown duration length was not an important variable in the colonization and extinction parameters. Drawdown duration was a better predictor of ψ for migrant SMBs than for breeding SMBs, however, migrants and breeders shared a similar response to the timing of hydrologic management. Initially, sora needed water present during the early stage of migration, which was reflected in the positive relationship between sora ψ and drawdown duration. Sora have been found to be associated with a range of water depths, with no strong relationship with any given depth (Sayre and Rundle 1984, Zimmerman 1984, Baschuk et al. 2012). However, in the sora colonization and extinction model sets, the most supported model included the time-dependent covariant whereas the remaining two models in the confidence set included some combination of covariates related to vegetation density and percent of site with emergent vegetation. The latter two models in the confidence set exhibited a positive relationship between colonization and vegetation and negative relationship between extinction and vegetation. This may suggest the birds are responding to increasing vegetative density to a point, at which they then abandon the site, or they leave the site to continue their migration north. This may also suggest that migrant sora are seeking wetlands characterized by dense emergent vegetation because these wetlands shorten total stopover time, allowing them to progress further north in the migratory route. Other studies have found that migrant sora prefer sites with dense emergent vegetation, which was only made available following a drawdown (Sayre and Rundle 1984). Considering all three models suggests that dense emergent vegetation is an important resource for sora during stopover events, but their migration phenology suggests that they will vacate a site eventually, regardless of its characteristics.

American bittern, which I considered a migrant in Missouri, shared a similar response with breeding least bittern to the drawdown initiation date. The American bittern confidence set included eight models, also indicating a fair amount of uncertainty in which covariates best influence American bittern occupancy. However, the top seven models included covariates for water duration, water depth, and drawdown initiation date, indicating that drawdown duration and water depth are important in predicting American bittern occupancy. Both American bittern and least bittern ψ probability were positively related with the initiation day of the drawdown, and results indicated migrant American bittern would be more likely to occupy a site with a drawdown initiated in late-July, and the breeding least bittern would be more likely to occupy a site with a drawdown initiated in mid to late May. These results indicate that having water present on a site during the summer months, even if the site is actively being drawdown, is important in bittern conservation efforts. Previous studies have found that breeding American bittern use wetlands that did not receive intensive hydrologic management, which is similar to my findings. A study by Basckuk et al. (2012) found that breeding American bittern occurred in greater densities in wetlands with no water level manipulation. In addition, Kantrud and Stewart (1984) found a greater abundance of breeding American bittern at semi-permanent wetlands compared to seasonally flooded wetlands.

American bittern shared a similar response with migrant sora to the drawdown duration. Like the American bittern model sets, the sora occupancy and colonization/extinction models sets had a fair amount of uncertainty, which may indicate that a more complex model would be more strongly supported. However, my results indicated that migrant sora and American bittern were more likely to occupy a wetland with a drawdown exceeding 100 days, but the average drawdown length in my study was 45.7 days. The spring migration season extends from April through mid-May (Robbins and Easterla 1992), so the availability of water during this time is important if these wetlands are intended to serve as migration stopover habitat for SMBs. Therefore, while migrant SMBs might have been more likely to occupy wetlands with an extended drawdown duration because these sites were more likely to have standing water present when migrant individuals arrived to make use of the site, the initiation day of the drawdown is important to consider as well. Depending on when drawdowns are initiated, my results indicate water might not be available to spring migrants for the entire April-May migration season (Fredrickson 1991). Similarly, species that were predicted to be more likely to occupy sites with water available until late June also indicated the importance of wetlands with an extended drawdown duration to accommodate both stopover and breeding use by SMB (Reid 1989, Lowther et al. 2009, Poole et al. 2009, Valente et al. 2011).

I found that least bittern were more likely to occupy sites that did not have a drawdown initiated until late May, which correlates with the start of the breeding season for this species. Least bittern spring migration begins in April and the nesting season begins in mid to late-May, extending through July (Poole et. al. 2009). I found that least bittern detections increased during May, peaking in the final round of occupancy surveys in early June. If a drawdown is initiated too early, such as in the first half of March, a site may initially provide hydrologic conditions suitable to migrant least bittern that might also be searching for potential nest sites, but be dry before the end of the breeding period. The abrupt change in hydrologic conditions could result in nest abandonment or increased nest predation rates (Post 1998, Hoover 2006). If least bittern remained with a nest at a dry site, the lack of inundation could put the nest in greater risk of predation while forcing broods and adults to search for inundated foraging grounds far from the nest (Budd and Krementz 2010). I found that the daily survival rate of least bittern nests was positively associated with average water depth. The increased foraging effort might have negative implications in the form of increased energy requirements and unnecessary exposure to predation while foraging. Therefore, if drawdowns are initiated in advance of, or during, the least bitten breeding season, nesting sites could be dry by the time eggs are laid or by the time broods are leaving the nest. The extended drawdown duration important to the migrants could also benefit breeding least bittern by ensuring that nest sites remained inundated for the duration of the breeding season.

While both migrants and breeders shared a similar ψ response to hydrologic management, water depth at a site was important only to migrant American bittern ψ. Previous studies have found that water depth was an important predictor of American bittern nest site selection probability (Lor and Malecki 2006) and nest density (Baschuk et al. 2012) and my results indicate it is important to migrant American bittern ψ as well. Hydrologic management strategies directly influenced wetland habitat characteristics such as water depth and the percent of a wetland inundated at a given time (Fredrickson and Taylor 1982). American bittern were more likely to occupy sites and less likely to go locally extinct at sites with an average water depth of $\geq$100cm. Reid (1989) found that migrant American bittern used relatively deeper water than other SMB species because the larger American bittern is able to take advantage of deeper water than the smaller sora and Virginia rail, which are limited to shallower water depths due to their shorter tarsi lengths. I found a positive relationship between least bittern colonization and average water depth. The greater abundance of fish prey found in wetlands with relatively deeper water levels might also explain the importance of deep water for American bittern (Bouffard and Hanson 1997, Danylchuk and Tonn 2003). American bittern migrating through Missouri selected sites with water present for long durations that also had relatively deep water. However, a completely open water habitat with very little emergent vegetation, such as a lake or reservoir, is not typical migrating or nesting habitat for SMBs (Weller and Spatcher 1965, Eddleman et al. 1988).

Breeding least bittern ε patterns may have been influenced by water depth because as least bittern move through Missouri, they select potential nest site locations suitable for breeding (Poole et al. 2009, Budd and Krementz 2010, Darrah and Krementz

2010). Suitable least bittern breeding wetlands have water depths that effectively render the interior of the site inaccessible to terrestrial nest predators (Weller 1961, Post and Seals 1993, Post 1998). My results for least bittern are consistent with other research that found that water depth is important to breeding least bittern (Bogner and Baldassarre 2002, Baschuk et al. 2012). Breeding pair densities have been found to be greater on wetlands with relatively deeper water (Jobin et al. 2009). In addition, previous studies have found that nest predation increased following a decrease in water depths at wetland sites (Jobin and Picman 1997, Post 1998). My results indicated that least bittern would be more likely to colonize a wetland if the water was $\geq$100cm deep, and less likely to vacate a site with water depth > 50cm. I speculate that water depth ranges between 50-100cm increase the likelihood least bittern would use a wetland site for breeding. If a wetland is intended to provide nesting habitat for least bittern, water levels should be maintained from the nest site selection period in mid to late May, through July, the end of the breeding season. Given that water depths generally decrease throughout the summer, sites that maintain water depths $\geq$50cm through June and July are more likely to provide suitable nesting sites for least bittern. If maintaining water depths through the summer months would require costly continuous pumping, it may not be a feasible option compared to sites that naturally hold water.

Emergent vegetation is known to be important to SMBs at every stage of their life history (Eddleman et al. 1988, Melvin and Gibbs 1996, Weller 1999, Lowther et al. 2009) but is potentially a limited resource during spring migration due to reductions in emergent vegetation coverage over the winter by the actions of ice, snow, and waterfowl use (Rundle and Fredrickson 1981). My results indicated that vegetation characteristics were more important to migrant SMBs than breeding SMBs, as the vegetation characteristics did not appear in the top models for the breeding species, the least bittern. Vegetation characteristics strongly influenced the extinction probability of the migrant species, indicating that migration stopover movements of sora, Virginia rail, and American bittern were influenced by differences in vegetation coverage and density among wetlands.

Early in both field seasons, open water was the primary habitat type in a majority of study wetlands, however as water levels decreased, remnant vegetation emerged and new vegetative growth developed. Given the relatively low availability of remnant vegetative structure in wetlands before the onset of the growing season and the importance of vegetative characteristics in SMB occupancy rates, overwintering wetland vegetation may be a limiting resource for spring migrating SMB. Vegetative structure could be preserved through early spring by flooding only a portion of the wetland during the fall to prevent the flattening of vegetation by snow, ice, and waterfowl use (Sayre and Rundle 1984, Greer et al. 2009). Persistent emergent vegetation, such as bulrush, and cattail, provides early spring cover and summer nesting habitat for breeding SMBs. Non-persistent emergent vegetation, such as pickerelweed and arrowhead, becomes available as the growing season progresses. In Missouri, a slow drawdown in spring is recommended for moist-soil plant germination and establishment (Fredrickson and Taylor 1982, Fredrickson 1991). Therefore, migrant SMBs could be responding to the plant communities available on sites with a long drawdown duration. However, wetlands with low vegetative interspersion (i.e., those dominated by either predominantly open water of vegetation) were less likely to be used by spring migrating SMBs compared to sites with a more even distribution of open water to emergent vegetation. Using mechanical soil disturbances to create an even ratio of open water to emergent vegetation will likely provide the best foraging opportunities for spring migrants. Emergent vegetation dense enough to provide suitable concealment and tall enough to provide adequate nesting habitat for breeders would increase use by both migrant and breeding SMBs (Weller 1999, Lor and Malecki 2006).

Spring migrants arriving at stopover sites sporadically during April and early May require a sufficient density of emergent vegetation to provide suitable concealment for foraging, hiding from predators, and for resting (Bent 1926, Weller 1999). I found that vegetation density appeared in the top extinction models for sora, and previous studies have found that sora are known to use wetlands dominated by dense emergent vegetation during both spring and fall migration (Griese et al. 1980, Rundle and Fredrickson 1981, Sayre and Rundle 1984, Johnson and Dinsmore 1986). My results indicated vegetation density drove migration stopover movements of sora, which corresponds to previous work that found plant species composition was often less important in predicting sora habitat use compared to vegetative structure (Rundle and Fredrickson 1981, Sayre and Rundle 1984).

The ratio of emergent vegetation to open water was an important predictor of ε for migrant Virginia and American bittern, which is consistent with SMB use of wetlands with a 50:50 ratio of open water to emergent vegetation (Weller and Spatcher 1965, Weller and Fredrickson 1973, Murkin et al. 1997). American bittern extinction rate was positively related with interspersion, indicating that American bittern were less likely to go locally extinct at sites that are closest to the hemi-marsh condition. Virginia rail were less likely to go locally extinct at sites characterized by a wide range of vegetation heights, which could have been the result of the patchy distribution of open water and emergent vegetation. My results are consistent with previous research that reported abundance of breeding American bittern and Virginia rail were positively related with interspersion (Rehm and Baldassare 2007). Interspersion is likely important to migrant SMBs as well because it can increase the amount of foraging habitat. American bittern forage along the vegetation-water interface, so hemi-marshes provide the most foraging habitat (Lowther et al. 2009). In addition, the hemi-marsh condition can increase the abundance of aquatic invertebrate prey in the wetland (Voigts 1976, Kaminski and Prince 1981). Migrant SMBs may be seeking out hemi-marshes as they search for prey to restore energy lost during migration and to prepare for courtship and breeding. The length of time migrant SMBs spend on wetlands during stopover migration events might not be directly related to the capacity of that habitat to provide for their needs during this stage of the annual cycle. If wetland characteristics contribute to a higher local extinction rate, it may indicate that individuals have been able to efficiently obtain what they need, allowing them to proceed with migration. However, the reverse may be equally true, as wetlands with a high local extinction rate may reflect poor habitat that individuals vacated in order to find more suitable habitat. My conclusions are based on the latter idea that low local extinction rates indicate that a given wetland characteristic is providing suitable stopover habitat. Further research is needed to determine the average stopover period of SMBs in wetlands considered to be quality spring migration habitat.

The historical reduction in emergent wetland habitat makes managing remaining wetlands very important for conservation efforts targeting wetland-dependent wildlife.

However, it may not be feasible to manage for all wetland-dependent wildlife, including SMBs, on a single wetland. Wetland complexes could provide different water regimes and emergent plant communities within a managed area. Occupancy probabilities will be increased in wetlands with a drawdown schedule that coincides with the life-history stage of the target SMB species. The water manipulation infrastructure present in some wetlands may allow managers better flexibility in the timing and duration of drawdowns and the subsequent emergent plant communities. In contrast, it may be too expensive to inundate certain wetlands every summer, however, these wetlands could possibly provide habitat for other wetland-dependent wildlife. During seasons in which a wetland is dry, emergent vegetation could be disked or mowed to create a hemi-marsh condition for the next period of inundation.

MANAGEMENT IMPLICATIONS

Hydrologic manipulations timed to the provide water for the current life history stage of target SMB species will result in an increased occupancy probability. Drawdowns initiated in early April and that continue through late May will increase occupancy probability for migrant sora, Virginia rail and American bittern. Average drawdown duration on my study wetlands with active water manipulation was 45 days, which encompasses the five week migration period (early April to mid-May) of sora, Virginia rail, and American bittern in Missouri (Robbins and Easterla 1992). In contrast, breeding least bittern would not benefit from a 45 day drawdown initiated earlier than June, because the least bittern breeding season extends from early June through July. If water levels are maintained through late July, this would ensure that water would be on sites for both spring migrants and summer breeders. However, summer breeding may be less successful if drawdowns decrease water depths too swiftly, leaving nesting sites dry before the conclusion of the breeding season in late July. In addition, this lengthy hydroperiod may require costly summer pumping of water, which could render a wetland unsuitable for providing breeding SMB habitat.

Drawdown initiation date on wetlands with an actively manipulated hydrology will affect its suitability for migrant or breeding SMBs. For wetlands intended to provide spring migration habitat for sora, Virginia rail, and American bittern, drawdowns initiated in the 2nd week of April will increase the probability that inundated wetlands will be available throughout the migration period. While the 45 day drawdown is sufficient to provide inundated wetlands for migrants, the breeding phenology of the least bittern indicates a need for drawdowns to be delayed until early June rather than initiated in mid-April. Least bittern begin to lay their first clutch in early June (Poole et al. 2009), and a 45 day drawdown initiated in early June would be sufficient to accommodate the least bittern's 20 day incubation period, six days of brooding, and the 14 days juveniles linger in their natal wetland before fledging (Weller 1961, Poole et al. 2009). Wetland water levels left to fluctuate on their own during spring could also provide sufficient drawdown duration for breeding least bittern, however supplemental summer pumping might be necessary if water levels decrease as a result of draining through the substrate or evapotranspiration.

Presence of water in wetlands at the appropriate times is likely not the only requirement migrating and breeding SMB; the availability of emergent vegetation is also known to be strongly associated with SMB wetland use and should be evenly distributed with open water patches within a wetland. Wetlands that contain primarily open water with little vegetation are unlikely to provide suitable SMB habitat, regardless of drawdown schedule or life-history stage. Wetlands that have substantial emergent vegetation during autumn could be flooded the following March instead of the previous autumn, to preserve the vegetation structure for migrant and breeding SMBs. As some migrants, like the American bittern, arrive as early as March, this remnant vegetation would likely provide the structure that migrants use for foraging and cover during a migration stopover event. Cattails and bulrush, which are the primary nesting vegetation of breeding least bittern, could be maintained in certain wetlands and restricted in others to mitigate the invasive behavior of this vegetation.

My results suggest that migrating and breeding SMB species are selecting similar habitat features and could be managed for within the same Conservation Area or National Wildlife Refuge. However, it is unlikely that a single wetland would be able to provide the habitat features used by both migrant and breeding SMBs. However, many publicly managed wetland areas consists of a complex of several discrete wetlands, which could allow for one wetland could provide habitat for migrant SMBs, while another could provide breeding SMB habitat. Therefore, the managed area as a whole could provide habitat for both spring migrants and summer breeding SMBs.

FUTURE RESEARCH

I found it surprising that I detected so few Virginia rail and king rail during my study despite exhaustive sampling effort. I speculate that, Virginia rail and king rail may use private wetlands during spring migration more heavily than public wetlands, which would explain why, despite such a heavy amount of sampling, I had so few detections of these species. Alternatively, Missouri wetlands, regardless of being public or private, might not be heavily used by either species during spring migration. As I only performed occupancy surveys during spring migration, my detections would not necessarily reflect wetland use during fall migration. Finally, there was a fair amount of model uncertainty in the model set evaluating Virginia rail detection, which may indicate that I was not able to discern what detection variables best predicted Virginia rail detectability. Further research is needed to determine how prevalent Virginia and king rail are on wetlands during spring stopover events, and to determine what habitat characteristics will increase wetland use by these elusive species.

Future research should include radio-tagging individual SMBs to quantify the time individuals spend on a wetland during a stopover event. Tracking SMBs would also elucidate patterns in movement between wetlands within the same public area or to nearby wetlands, including privately owned areas. Privately owned wetlands may also be used by spring migrants, so future SMB research could evaluate the importance of these wetlands as well. Tracking radio-tagged SMBs would also allow for more accurate identification of the exact location of individuals within patches of vegetation within a wetland. For future call-broadcast survey regimes, I recommend monitoring a given wetland each day as opposed to once every 7-10 days. I speculate that I may have missed detecting individuals that used wetlands between my primary sampling periods. In addition, a more intensive sampling effort would lessen the impact of missing surveys on a particular wetland in a given week because of logistic constraints. However, note that the occupancy method does account for unequal survey effort among study sites. I surveyed many wetlands in many areas across Missouri, but a more intensive sampling regime may have to be limited to a single Conservation Area or National Wildlife Refuge.

However, sampling effort could be distributed among several researchers operating independently at multiple Conservation Areas or National Wildlife Refuges on the same day.

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TABLES

Table 1.1 Covariates used in models to predict Occupancy ψ, Colonization γ, Extinction ε, and Detection *p* probabilities of SMBs on public wetlands in Missouri during spring 2013 and 2014.

Parameter	Covariate	Type	Description
Occupancy ψ[1]	Initiation	Continuous	Begin day of drawdown initiation.
	Duration	Continuous	Total duration in days of the drawdown.
	DepthRange	Continuous	Range of water depths across the entire season.
	HeightRange	Continuous	Range of vegetation heights across the entire season.
	Depth	Continuous	Average water depth across the entire season.
	Depth2	Continuous	Quadratic transformation of avg. water depth
	DepthLog	Continuous	Log transformation of avg water depth
	Height	Continuous	Average vegetation height across the entire season.
Colonization γ			
Extinction ε			
	Duration	Continuous	Duration in days of the drawdown.
	Depth	Continuous	Average water depth.
	Depth2	Continuous	Quadratic transformation of avg. water depth
	DepthLog	Continuous	Log transformation of avg water depth
	Range	Continuous	Range in water depths.
	Height	Continuous	Average vegetation height.
	HeightRng	Continuous	Range of vegetation heights.
	IntCov	Continuous	(|(% of site in open water – 50)|*2)
	Flood	Continuous	Percent of the site that was inundated.
	Acres	Continuous	Total site acres inundated.
	Robel	Continuous	Average vegetation density by Robel.
	Emerge	Continuous	Percent of the site in emergent vegetation.
	Ow	Continuous	Percent of the site in open water.
	Shrub	Continuous	Percent of the site in shrub-scrub vegetation.
	Agric	Continuous	Percent of the site in agricultural vegetation.
Detection *p*[3]			
	Obs	Categorical	The observer conducting the call-broadcast survey.
	Time	Categorical	Am or Pm survey timing.
	Temp	Continuous	Degrees Celsius at the time of the survey.
	Wind	Continuous	Beaufort scale reading at the time of the survey.
	Sky	Categorical	National Weather Service sky condition at the time of the survey.
	Noise	Continuous	Background noise level on a scale from 0-4. 0 being no background noise, 4 being intense background noise.
	Round-1	Categorical	The primary sampling period (1-6) that the survey took place in.

1 Occupancy covariates are averaged across all primary sampling periods, and therefore have a single measurement for each site. Initiation and Duration were not averaged.

2 Colonization and extinction covariates have a measurement for each site for each of the 6 primary sampling periods.

3 Detection covariates have a measurement for each secondary sampling period.

Table 1.2 Number of least bittern (*Ixobrychus exilis;* LEBI), sora (*Porzana carolina;* SORA), Virginia rail (*Rallus limicola;* VIRA), king rail (*Rallus elegans;* KIRA), and American bittern (*Botaurus lentiginosus;* AMBI), detected at publicly managed wetland conservation areas in Missouri during spring 2013 and 2014 and the number of surveys conducted at each study area.

Region	Conservation Area	Number of Surveys	LEBI	SORA	VIRA	KIRA	AMBI	Total
North-central	Grand Pass	147	4	44	2	0	4	54
	Fountain Grove	149	21	47	3	1	0	72
	Swan Lake	138	17	95	15	2	11	140
	Total	434	42	186	20	3	15	266
Northwest	Nodaway Valley	190	10	181	22	0	26	239
	Squaw Creek	188	48	166	23	2	44	283
	Bob Brown	101	2	89	4	1	3	99
	Total	479	60	436	49	3	73	621
Northeast	B.K. Leach	143	49	103	7	3	52	214
	Ted Shanks	75	6	71	7	0	7	91
	Clarence Cannon	81	1	19	2	0	0	22
	Total	299	56	193	16	3	59	327
Southeast	Duck Creek	146	10	19	4	0	13	46
	Mingo	167	72	32	3	0	18	125
	Otter Slough	144	14	43	7	0	3	67
	Total	457	96	94	14	0	34	238
	Overall Total	1669	254	909	99	9	181	1452

Table 1.3 Model selection results for 13 dynamic occupancy models (Occupancy ψ, Colonization γ, Extinction ε, Detection p) fit to 2013-2014 sora (*Porzana carolina*) detection data from 107 study sites located on public wetland management areas in Missouri, USA. The model was used to determine the covariates that best predict occupancy rates given the covariate that best predicted sora detection.

Model	K	AIC	delta	-LogLike	AIC weight	cumltv weight
ψ(Duration), γ(Round-1), ε(Round-1), p(Obs)	20	1463.13	0.00	711.56	0.31	0.31
ψ(.), γ(Round-1), ε(Round-1.), p(Obs) (Null)	19	1464.55	1.43	713.28	0.15	0.46
ψ(Height), γ(Round-1), ε(Round-1), p(Obs)	20	1465.43	2.30	712.71	0.10	0.56
ψ(DepthRange), γ(Round-1), ε(Round-1), p(Obs)	20	1466.01	2.89	713.01	0.07	0.63
ψ(HeightRange), γ(Round-1), ε(Round-1), p(Obs)	20	1466.32	3.20	713.16	0.06	0.69
ψ(DepthLog), γ(Round-1), ε(Round-1), p(Obs)	20	1466.35	3.22	713.17	0.06	0.76
ψ(Initiation), γ(Round-1), ε(Round-1), p(Obs)	20	1466.37	3.24	713.18	0.06	0.82
ψ(Depth), γ(Round-1), ε(Round-1), p(Obs)	20	1466.54	3.41	713.27	0.06	0.90
ψ(Depth2), γ(Round-1), ε(Round-1), p(Obs)	20	1466.83	3.71	713.42	0.05	0.92
ψ(Depth + Height), γ(Round-1), ε(Round-1), p(Obs)	21	1467.41	4.28	712.70	0.04	0.96
ψ(DepthRange + HeightRange), γ(Round-1), ε(Round-1), p(Obs)	21	1467.70	4.57	712.85	0.03	0.99
ψ(Depth * Height), γ(Round-1), ε(Round-1), p(Obs)	22	1469.82	6.70	712.91	0.01	1.00
ψ(Duration * Depth), γ(Round-1), ε(Round-1), p(Obs)	22	1648.51	185.38	802.25	0.00	1.00

Note*:* Models were ranked based on Akaike's information criterion (AIC) and weights of evidence (AIC weight). K is the degrees of freedom, delta is the difference in AIC from the top model, -LogLike is the negative log likelihood of the model, AIC weight is the weight of evidence that a given model is the best model, cumltv weight is the cumulative added weight of each model to the models above it on the table, ψ is initial occupancy, ε is extinction probability, γ is colonization probability, and p is detection probability. Detection probability was modeled as a function of the observer.

Table 1.4. Parameter estimates for models within the 90% AIC weight confidence set of models predicting sora (*Porzana carolina*) occupancy at publicly managed wetland areas in during spring 2013 and 2014.

		Model 1		Model 2		Model 3		Model 4		Model 5		Model 6		Model 7		Model 8		Model-Average	
Par	Covariate	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
ψ	Intercept	-2.143	0.964	-0.257	0.399	-1.077	0.766	-0.406	0.416	-1.244	1.658	-0.621	0.589	-0.331	0.652	-1.32	1.24	-1.32	1.24
	Duration	0.027	0.015															**0.027**	**0.015**
	Height			-0.006	0.006													-0.006	0.006
	DepthRng					0.013	0.018											0.013	0.018
	HeightRng							-0.002	0.003									-0.002	0.003
	DepthLog									0.249	0.549							0.249	0.549
	Init											0.006	0.014					0.006	0.014
	Depth													0.002	0.019			0.002	0.019
	Depth2															2E-05	5E-04	2E-05	5E-04

Note: Model-averaged parameter estimates and standard errors were averaged over all 8 models using their AICc weights (Table 3).

Table 1.5. Model selection results for 20 dynamic occupancy models (Occupancy ψ, Colonization γ, Extinction ε, Detection *p*) fit to 2013-2014 sora (*Porzana carolina*) detection data from 107 study sites located on public wetland management areas in Missouri, USA. The model was used to determine the covariates that best predict colonization and extinction rates given the covariate that best predicted sora occupancy.

Model	K	AIC	delta	-LogLike	AIC weight	cumltv weight
ψ(Duration), γ(Round-1), ε(Round-1), *p*(Obs)	20	1463.13	0.00	711.56	0.49	0.49
ψ(Duration), γ(Robel), ε(Robel), *p*(Obs)	14	1464.22	1.09	718.11	0.29	0.78
ψ(Duration), γ(Emerge + Robel), ε(Emerge + Robel), *p*(Obs)	16	1464.85	1.73	716.43	0.21	0.99
ψ(Duration), γ(HgtRng), ε(HgtRng), *p*(Obs)	14	1471.65	8.52	721.82	0.01	0.99
ψ(Duration), γ(Height), ε(Height), *p*(Obs)	14	1473.70	10.57	722.85	0.00	0.99
ψ(Duration), γ(Height + Depth), ε(Height + Depth), *p*(Obs)	16	1474.73	11.60	721.37	0.00	1.00
ψ(Duration), γ(HgtRng + Range), ε(HgtRng + Range), *p*(Obs)	16	1474.78	11.65	721.39	0.00	1.00
ψ(Duration), γ(Shrub), ε(Shrub), *p*(Obs)	14	1476.27	13.14	724.13	0.00	1.00
ψ(Duration), γ(Duration), ε(Duration), *p*(Obs)	14	1476.41	13.28	724.20	0.00	1.00
ψ(Duration), γ(IntCov), ε(IntCov), *p*(Obs)	14	1476.65	13.52	724.33	0.00	1.00
ψ(Duration), γ(Emerge), ε(Emerge), (Obs)	14	1478.36	15.23	725.18	0.00	1.00
ψ(Duration), γ(Ow), ε(Ow), *p*(Obs)	14	1480.72	17.59	726.36	0.00	1.00
ψ(Duration), γ(.), ε(.), *p*(Obs) (null)	12	1480.91	17.78	728.46	0.00	1.00
ψ(Duration), γ(DepthLog), ε(DepthLog), *p*(Obs)	14	1481.09	17.96	726.55	0.00	1.00
ψ(Duration), γ(Agric), ε(Agric), *p*(Obs)	14	1481.14	18.01	726.57	0.00	1.00
ψ(Duration), γ(Depth), ε(Depth), *p*(Obs)	14	1481.26	18.13	726.63	0.00	1.00
ψ(Duration), γ(Depth2), ε(Depth2), *p*(Obs)	14	1481.89	18.77	726.95	0.00	1.00
ψ(Duration), γ(Flood + Acres), ε(Flood + Acres), *p*(Obs)	16	1482.10	18.97	725.05	0.00	1.00
ψ(Duration), γ(Range), ε(Range), *p*(Obs)	14	1483.77	20.64	727.88	0.00	1.00
ψ(Duration), γ(Duration * Depth), ε(Duration * Depth), *p*(Obs)	18	1595.50	132.37	779.75	0.00	1.00
ψ(Duration), γ(Depth * Height), ε(Depth * Height), *p*(Obs)	18	1604.87	141.75	784.44	0.00	1.00

Table 1.6. Model-averaged parameter estimates for models predicting sora (*Porzana carolina*) occupancy, colonization, and extinction probabilities that fell within 90% AIC weight confidence set.

		Model 1		Model 2		Model 3		Model-Average	
Parameter	Covariate	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Occupancy	Intercept	-2.14	0.963	-2.26	0.98	-2.28	0.99	-2.26	0.98
	Duration	0.02	0.01	0.03	0.02	0.03	0.02	0.03	0.02
Colonization	Intercept			-0.91	0.28	-1.04	0.36	-0.94	0.31
	Robel			0.04	0.09	0.01	0.09	0.03	0.09
	Emerge					0.01	0.01	0.01	0.01
Extinction	Intercept			0.56	1.02	1.12	0.96	0.70	1.03
	Robel			-1.11	0.89	-1.02	0.77	-1.09	0.86
	Emerge					-0.02	0.01	-0.02	0.01

Note: Model-averaged parameter estimates and standard errors were averaged over all 3 models using their AICc weights (Table 5).

Table 1.7. Model selection results for 13 dynamic occupancy models (Occupancy ψ, Colonization γ, Extinction ε, Detection p) fit to 2013-2014 least bittern (*Ixobrychus exilis*) detection data from 107 study sites located on public wetland management areas in Missouri, USA. The model was used to determine the covariates that best predict occupancy rates given the covariate that best predicted least bittern detection.

Model	K	AIC	delta	-LogLike	AIC weight	cumltv weight
ψ(Initiation), γ (Round-1), ε (Round-1), p(Round)	18	802.37	0.00	383.18	0.92	0.92
ψ(Height), γ (Round-1), ε (Round-1), p(Round)	18	809.35	6.98	386.68	0.03	0.95
ψ(Depth + Height), γ (Round-1), ε (Round-1), p(Round)	19	811.06	8.70	386.53	0.01	0.97
ψ(DepthRange), γ (Round-1), ε (Round-1), p(Round)	18	811.78	9.41	387.89	0.01	0.97
ψ(Depth), γ (Round-1), ε (Round-1), p(Round)	18	812.91	10.54	388.45	0.00	0.98
ψ(Duration), γ (Round-1), ε (Round-1), p(Round)	18	812.91	10.54	388.46	0.00	0.98
ψ(HeightRange), γ (Round-1), ε (Round-1), p(Round)	18	813.12	10.75	388.56	0.00	0.99
ψ(DepthLog), γ (Round-1), ε (Round-1), p(Round)	18	813.14	10.77	388.57	0.00	0.99
ψ(DepthRange + HeightRange), γ (Round-1), ε (Round-1), p(Round)	19	813.21	10.85	387.61	0.00	1.00
ψ(.), γ(Round-1), ε(Round-1), p(Round) (null)	17	814.44	12.07	390.22	0.00	1.00
ψ(Depth * Height), γ (Round-1), ε (Round-1), p(Round)	20	814.72	12.35	387.36	0.00	1.00
ψ(Duration * Depth), γ(Round-1), ε (Round-1), p(Round)	20	819.31	16.94	389.65	0.00	1.00
ψ(Depth2), γ (Round-1), ε (Round-1), p(Round)	18	820.10	17.73	392.05	0.00	1.00

Note: Models were ranked based on Akaike's information criterion (AIC) and weights of evidence (AIC weight). K is the degrees of freedom, delta is the difference in AIC from the top model, -LogLike is the negative log likelihood of the model, AIC weight is the weight of evidence that a given model is the best model, cumltv weight is the cumulative added weight of each model to the models above it on the table, ψ is initial occupancy, ε is extinction probability, γ is colonization probability, and p is detection probability. Detection probability was modeled as a function of the survey round.

Table 1.8. Model selection results for 20 dynamic occupancy models (Occupancy ψ, Colonization γ, Extinction ε, Detection *p*) fit to 2013-2014 least bittern (*Ixobrychus exilis*) detection data from 107 study sites located on public wetland management areas in Missouri, USA. The model was used to determine the covariates that best predict colonization and extinction rates given the covariate that best predicted least bittern occupancy.

Model	K	AIC	delta	-LogLike	AIC weight	cumltv weight
ψ(.), γ(Depth), ε(Depth), p(Round)	12	777.40	0.00	376.70	0.49	0.49
ψ(.), γ(DepthLog), ε(DepthLog), p(Round)	12	777.75	0.35	376.87	0.41	0.90
ψ(.), γ(Height + Depth), ε(Height + Depth), p(Round)	14	780.77	3.37	376.39	0.09	0.99
ψ(.), γ(Flood + Acres), ε(Flood + Acres) p(Round)	14	785.49	8.09	378.74	0.01	0.99
ψ(.), γ(IntCov), ε(IntCov), p(Round)	12	786.22	8.82	381.11	0.01	1.00
ψ(.), γ(Duration), ε(Duration), p(Round)	12	791.74	14.34	383.87	0.00	1.00
ψ(.), γ(Agric), ε(Agric), p(Round)	12	793.71	16.31	384.86	0.00	1.00
ψ(.), γ(Emerge), ε(Emerge), p(Round)	12	798.83	21.43	387.41	0.00	1.00
ψ(Begin), γ(.), ε(.), p(Round)	10	798.97	21.57	389.49	0.00	1.00
ψ(.), γ(Emerge + Robel), ε(Emerge + Robel), p(Round)	14	801.28	23.88	386.64	0.00	1.00
ψ(.), γ(Range), ε(Range), p(Round)	12	801.49	24.09	388.74	0.00	1.00
ψ(.), γ(Ow), ε(Ow), p(Round)	12	802.04	24.64	389.02	0.00	1.00
ψ(.), γ(Robel), ε(Robel), p(Round)	12	802.07	24.67	389.03	0.00	1.00
ψ(.), γ(Depth2), ε(Depth2), p(Round)	12	802.19	24.79	389.09	0.00	1.00
ψ(.), γ(HgtRng), ε(HgtRng), p(Round)	12	802.22	24.82	389.11	0.00	1.00
ψ(.), γ(HgtRng + Range), ε(HgtRng + Range), p(Round)	14	804.34	26.93	388.17	0.00	1.00
ψ(.), γ(Depth * Height), (Depth * Height), p(Round)	16	811.41	34.01	389.70	0.00	1.00
ψ(.), γ(Shrub), ε(Shrub), p(Round)	12	815.36	37.96	395.68	0.00	1.00
ψ(.), γ(Height), ε(Height), p(Round)	12	923.77	146.37	449.88	0.00	1.00
ψ(.), γ(Duration * Depth), ε(Duration * Depth), p(Round)	16	1018.29	240.89	493.14	0.00	1.00

Note: Models were ranked based on Akaike's information criterion (AIC) and weights of evidence (AIC weight). K is the degrees of freedom, delta is the difference in AIC from the top model, -LogLike is the negative log likelihood of the model, AIC weight is the weight of evidence that a given model is the best model, cumltv weight is the cumulative added weight of each model to the models above it on the table, ψ is initial occupancy, ε is extinction probability, γ is colonization probability, and *p* is detection probability. Occupancy probability was set to constant in this model set.

Table 1.9. Model-averaged parameter estimates for least bittern (*Ixobrychus exilis*) for models in the 90% AIC weight confidence set that assessed the response of colonization and extinction rates to differences in habitat and management characteristics during the spring of 2013 and 2014.

		Model 1		Model 2		Model Average	
Parameter	Covariate	Est	SE	Est	SE	Est	SE
Occupancy	Intercept	-4.14	2.6	-4.17	2.6	-4.15	2.6
	Begin	0.02	0.02	0.02	0.02	0.02	0.02
Colonization	Intercept	-2.61	0.43	-4.6	1.2	-3.6	0.8
	Depth	0.03	0.01			**0.03**	**0.01**
	LogDepth			0.9	0.3		
Extinction	Intercept	1.5	0.79	5.6	2.1	3.55	1.4
	Depth	-0.05	0.02				
	LogDepth			-1.77	0.6	**-1.77**	**0.6**

Note: Model-averaged parameter estimates and standard errors were averaged over the top model using their AICc weights (Table 8).

Table 1.10. Model selection results for 13 dynamic occupancy models (Occupancy ψ, Colonization γ, Extinction ε, Detection *p*) fit to 2013-2014 American bittern (*Botaurus lentiginosus*) detection data from 107 study sites located on public wetland management areas in Missouri, USA.

Model	K	AIC	delta	-LogLike	AIC weight	cumltv weight
ψ(Duration), γ(Round-1), ε(Round-1), *p*(Sky)	14	736.41	0.00	354.21	0.36	0.36
ψ(Depth + Height), γ (Round-1), ε (Round-1), *p*(Sky)	15	737.62	1.21	353.81	0.20	0.56
ψ(Initiation), γ (Round-1), ε (Round-1), *p*(Sky)	14	738.14	1.73	355.07	0.15	0.71
ψ(Depth), γ (Round-1), ε (Round-1), *p*(Sky)	14	739.42	3.01	355.71	0.08	0.79
ψ(DepthLog), γ (Round-1), ε (Round-1), *p*(Sky)	14	740.38	3.97	356.19	0.05	0.84
ψ(Depth2), γ (Round-1), ε (Round-1), *p*(Sky)	14	740.61	4.20	356.30	0.04	0.88
ψ(Height), γ (Round-1), ε (Round-1), *p*(Sky)	14	740.85	4.44	356.43	0.04	0.92
ψ(Depth * Height), γ (Round-1), ε (Round-1), *p*(Sky)	16	741.15	4.74	354.58	0.03	0.96
ψ(.), γ (Round-1), ε (Round-1), *p*(Sky)	13	742.10	5.69	358.05	0.02	0.98
ψ(DepthRange), γ (Round-1), ε (Round-1), *p*(Sky)	14	743.42	7.01	357.71	0.01	0.99
ψ(HeightRange), γ (Round-1), ε (Round-1), *p*(Sky)	14	743.96	7.55	357.98	0.01	1.00
ψ(DepthRange + HeightRange), γ (Round-1), ε (Round-1), *p*(Sky)	15	745.39	8.98	357.69	0.00	1.00
ψ(Duration * Depth), γ (Round-1), ε (Round-1), *p*(Sky)	16	813.36	76.95	390.68	0.00	1.00

Note: Models were ranked based on Akaike's information criterion (AIC) and weights of evidence (AIC weight). K is the degrees of freedom, delta is the difference in AIC from the top model, -LogLike is the negative log likelihood of the model, AIC weight is the weight of evidence that a given model is the best model, cumltv weight is the cumulative added weight of each model to the models above it on the table, ψ is initial occupancy, ε is extinction probability, γ is colonization probability, and *p* is detection probability. Detection probability was modeled as a function of sky condition.

Table 1.11. Model-averaged parameter estimates for American bittern (*Botaurus lentiginosus*) for models in the 90% AIC weight confidence set that assessed the response of occupancy rates to differences in habitat and management characteristics during the spring of 2013 and 2014.

		Model 1		Model 2		Model 3		Model 4 (null)		Model 5		Model 6		Model 7		Model-Average	
Parameter	Covariate	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
Occupancy	Intercept	-6.62	2.28	-2.71	1.06	-9.25	3.92	-1.91	0.40	-3.42	0.95	-6.72	2.85	-3.30	0.84	-4.08	3.16
	Duration	0.07	0.03													**0.07**	**0.03**
	Depth			0.06	0.03					0.05	0.03					**0.05**	**0.03**
	Height			-0.03	0.02									-0.03	0.02	-0.03	0.02
	Initiation					0.06	0.03									**0.06**	**0.03**
	DepthLog											1.46	0.82			1.46	0.82
	Depth2													0.001	0.0006	0.001	0.0006

Note: Model-averaged parameter estimates and standard errors were averaged over the top 7 models using their AICc weights (Table 10).

Table 1.12. Model selection results for 20 dynamic occupancy models (Occupancy ψ, Colonization γ, Extinction ε, Detection *p*) fit to 2013-2014 American bittern (*Botaurus lentiginosus*) detection data from 107 study sites located on public wetland management areas in Missouri, USA. The model was used to determine the covariates that best predict colonization and extinction rates given the covariate that best predicted American bittern occupancy.

Model	K	AIC	delta	-LogLike	AIC weight	cumltv weight
ψ(Duration), γ(IntCov), ε(IntCov), *p*(Sky)	8	728.28	0.00	356.14	0.27	0.27
ψ(Duration), γ(DepthLog), ε(DepthLog), *p*(Sky)	8	728.38	0.10	356.19	0.26	0.53
ψ(Duration), γ(Ow), ε(Ow), *p*(Sky)	8	728.89	0.61	356.45	0.20	0.72
ψ(Duration), γ(Depth), ε(Depth), *p*(Sky)	8	731.00	2.72	357.50	0.07	0.79
ψ(Duration), γ(Flood + Acres), ε(Flood + Acres), *p*(Sky)	10	731.73	3.45	355.86	0.05	0.84
ψ(Duration), γ(Emerge + Robel), ε(Emerge + Robel), *p*(Sky)	10	732.41	4.13	356.20	0.03	0.90
ψ(Duration), γ(Robel), ε(Robel), *p*(Sky)	8	732.47	4.19	358.24	0.03	0.91
ψ(Duration), γ(.), ε(.), *p*(Sky) (null)	6	733.34	5.06	360.67	0.02	0.93
ψ(Duration), γ(Height + Depth), ε(Height + Depth), *p*(Sky)	10	733.98	5.70	356.99	0.02	0.95
ψ(Duration), γ(Emerge), ε(Emerge), *p*(Sky)	8	734.38	6.10	359.19	0.01	0.96
ψ(Duration), γ(Agric), ε(Agric), *p*(Sky)	8	734.86	6.58	359.43	0.01	0.97
ψ(Duration), γ(Duration), ε(Duration), *p*(Sky)	8	735.44	7.16	359.72	0.01	0.98
ψ(Duration), γ(Height), ε(Height), *p*(Sky)	8	735.82	7.54	359.91	0.01	0.98
ψ(Duration), γ(Range), ε(Range), *p*(Sky)	8	735.97	7.69	359.98	0.01	0.99
ψ(Duration), γ(HgtRng), ε(HgtRng), *p*(Sky)	8	736.05	7.78	360.03	0.01	0.99
ψ(Duration), γ(Round-1), ε(Round-1), *p*(Sky)	14	736.41	8.13	354.21	0.00	1.00
ψ(Duration), γ(HgtRng + Range), ε(HgtRng + Range), *p*(Sky)	10	738.91	10.63	359.45	0.00	1.00
ψ(Duration), γ(Depth2), ε(Depth2), *p*(Sky)	8	740.99	12.72	362.50	0.00	1.00
ψ(Duration), γ(Shrub), ε(Shrub), *p*(Sky)	8	742.35	14.07	363.17	0.00	1.00
ψ(Duration), γ(Depth * Height), ε(Depth * Height), *p*(Sky)	12	849.03	120.75	412.52	0.00	1.00
ψ(Duration), γ(Duration * Depth), ε(Duration * Depth), *p*(Sky)	12	850.81	122.53	413.40	0.00	1.00

Note: Models were ranked based on Akaike's information criterion (AIC) and weights of evidence (AIC weight). K is the degrees of freedom, delta is the difference in AIC from the top model, -LogLike is the negative log likelihood of the model, AIC weight is the weight of evidence that a given model is the best model, cumltv weight is the cumulative added weight of each model to the models above it on the table, ψ is initial occupancy, ε is extinction probability, γ is colonization probability, and p is detection probability. Occupancy probability was modeled as a function of drawdown duration.

Table 1.13. Model-averaged parameter estimates for American bittern (*Botaurus lentiginosus*) for models in the 90% AIC weight confidence set that assessed the response of colonization and extinction rates to differences in habitat and management characteristics during the spring of 2013 and 2014.

		Model 1		Model 2		Model 3		Model 4		Model 5		Model 6		Model-Average	
Par	Covariate	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
ψ	Intercept	-6.71	2.31	-6.43	2.24	-6.286	2.21	-6.47	2.26	-6.38	2.27	-6.41	2.24	-6.49	2.26
	Duration	0.075	0.032	0.066	0.031	0.071	0.032	0.068	0.032	0.070	0.031	0.074	0.032	**0.070**	**0.030**
γ	Intercept	-1.63	0.300	-2.81	0.99	-0.75	0.45	-2.05	0.39	-1.97	0.54	-2.39	0.43	-1.85	0.99
	Interspersion	-0.004	0.007											-0.004	0.007
	LogDepth			0.32	0.29									0.32	0.29
	Open Water					-0.023	0.009							-0.023	0.009
	Depth							0.009	0.011					0.009	0.011
	Flood									0.003	0.007			0.003	0.007
	Acres									0.000	0.001			0.000	0.001
	Emerge											0.013	0.008	**0.013**	**0.008**
	Robel											0.039	0.101	0.039	0.101
ε	Intercept	-1.19	0.53	4.66	2.26	1.86	1.14	1.26	0.79	4.76	2.29	-0.14	0.69	1.74	2.82
	Interspersion	0.044	0.019											**0.044**	**0.019**
	LogDepth			-1.43	0.65									**-1.43**	**0.65**
	Open Water					-0.045	0.025							-0.045	0.025
	Depth							-0.044	0.022					**-0.044**	**0.022**
	Flood									-0.048	0.024			**-0.048**	**0.024**
	Acres									-0.006	0.004			-0.006	0.004
	Emerge											0.024	0.014	0.024	0.014
	Robel											-0.409	0.200	-0.409	0.200

Note: Model-averaged parameter estimates and standard errors were averaged over the top 6 models using their AICc weights (Table 12).

Table 1.14. Model selection results for 13 dynamic occupancy models (Occupancy ψ, Colonization γ, Extinction ε, Detection *p*) fit to 2013-2014 Virginia rail (*Rallus limicola*) detection data from 107 study sites located on public wetland management areas in Missouri, USA.

Model	K	AIC	delta	-LogLike	AIC weight	cumltv weight
ψ(.), γ(Round-1), ε(Round-1), *p*(Wind) (null)	5	576.56	0.00	283.28	0.98	0.98
ψ(Depth + Height), γ(Round-1), ε(Round-1), *p*(Wind)	15	586.94	10.38	278.47	0.01	0.99
ψ(Height), γ(Round-1), ε(Round-1),*p*(Wind)	14	588.46	11.91	280.23	0.00	0.99
ψ(Depth2), γ(Round-1), ε(Round-1),*p*(Wind)	14	589.51	12.95	280.75	0.00	0.99
ψ(Depth), γ(Round-1), ε(Round-1),*p*(Wind)	14	589.93	13.38	280.97	0.00	0.99
ψ(Depth * Height), γ(Round-1), ε(Round-1),*p*(Wind)	16	590.60	14.05	279.30	0.00	1.00
ψ(Duration), γ(Round-1), ε(Round-1),*p*(Wind)	14	590.63	14.08	281.32	0.00	1.00
ψ(DepthRange), γ(Round-1), ε(Round-1),*p*(Wind)	14	590.73	14.17	281.36	0.00	1.00
ψ(Initiation), γ(Round-1), ε(Round-1),*p*(Wind)	14	590.86	14.30	281.43	0.00	1.00
ψ(DepthLog), γ(Round-1), ε(Round-1),*p*(Wind)	14	590.99	14.44	281.50	0.00	1.00
ψ(HeightRange), γ(Round-1), ε(Round-1),*p*(Wind)	14	591.57	15.02	281.79	0.00	1.00
ψ(DepthRange + HeightRange), γ(Round-1), ε(Round-1),*p*(Wind)	15	592.17	15.62	281.09	0.00	1.00
ψ(Duration * Depth), γ(Round-1), ε(Round-1),*p*(Wind)	16	594.71	18.15	281.35	0.00	1.00

Models were ranked based on Akaike's information criterion (AIC) and weights of evidence (AIC weight). K is the degrees of freedom, delta is the difference in AIC from the top model, -LogLike is the negative log likelihood of the model, AIC weight is the weight of evidence that a given model is the best model, cumltv weight is the cumulative added weight of each model to the models above it on the table, ψ is initial occupancy, ε is extinction probability, γ is colonization probability, and p is detection probability. Detection probability was modeled as a function of wind speed at the time of the survey.

Table 1.15. Model selection results for 20 dynamic occupancy models (Occupancy ψ, Colonization γ, Extinction ε, and Detection *p*) fit to 2013-2014 Virginia rail (*Rallus limicola*) detection data from 107 study sites located on public wetland management areas in Missouri, USA. The model was used to determine the covariates that best predict colonization and extinction rates given the covariate that best predicted Virginia rail occupancy.

Model	K	AIC	delta	negLogLike	AICwt	cumltvWt
ψ (.) γ (HgtRng + Range), ε(HgtRng + Range), p(Wind)	9	575.11	0.00	278.56	0.38	0.38
ψ(.), γ(.), ε(.), *p*(Wind) (null)	5	576.56	1.44	283.28	0.19	0.57
ψ (.) γ (Ow), ε(Ow), p(Wind)	7	576.88	1.77	281.44	0.16	0.73
ψ (.) γ (Emerge), ε(Emerge), p(Wind)	7	577.14	2.03	281.57	0.14	0.87
ψ (.) γ (Range), ε(Range), p(Wind)	7	578.94	3.82	282.47	0.06	0.93
ψ (.) γ (DepthLog), ε(DepthLog), p(Wind)	7	580.12	5.00	283.06	0.03	0.96
ψ (.) γ (Shrub), ε(Shrub), p(Wind)	7	580.43	5.32	283.22	0.03	0.99
ψ (.) γ (Robel), ε(Robel), p(Wind)	7	582.68	7.57	284.34	0.01	0.99
ψ (.) γ (Height), ε(Height), p(Wind)	7	584.56	9.45	285.28	0.00	1.00
ψ (.) γ (Duration * Depth), (Duration * Depth), p(Wind)	11	586.07	10.96	282.04	0.00	1.00
ψ (.) γ(Emerge + Robel), ε(Emerge + Robel), p(Wind)	9	590.29	15.18	286.15	0.00	1.00
ψ (.) γ (Agric), ε(Agric), p(Wind)	7	591.80	16.68	288.90	0.00	1.00
ψ (.) γ (Depth), ε(Depth), p(Wind)	7	597.49	22.38	291.75	0.00	1.00
ψ (.) γ (Duration), ε(Duration), p(Wind)	7	599.67	24.56	292.84	0.00	1.00
ψ (.) γ (Height + Depth), ε(Height + Depth), p(Wind)	9	602.52	27.40	292.26	0.00	1.00
ψ (.) γ (Depth2), ε(Depth2), p(Wind)	7	602.76	27.64	294.38	0.00	1.00
ψ (.) γ (HgtRng), ε(HgtRng), p(Wind)	7	603.72	28.61	294.86	0.00	1.00
ψ (.) γ (IntCov), ε(IntCov), p(Wind)	7	604.46	29.34	295.23	0.00	1.00
ψ (.) γ (Flood + Acres), ε(Flood + Acres), p(Wind)	9	608.81	33.69	295.40	0.00	1.00
ψ (.) γ (Depth * Height), (Depth * Height), p(Wind)	11	683.08	107.96	330.54	0.00	1.00

Models were ranked based on Akaike's information criterion (AIC) and weights of evidence (AIC weight). K is the degrees of freedom, delta is the difference in AIC from the top model, -LogLike is the negative log likelihood of the model, AIC weight is the weight of evidence that a given model is the best model, cumltv weight is the cumulative added weight of each model to the models above it on the table, ψ is initial occupancy, ε is extinction probability, γ is colonization probability, and p is detection probability. Occupancy probability was set to constant in this model set.

Table 1.16. Model-averaged parameter estimates for Virginia rail (*Rallus limicola*) for models in the 90% AIC weight confidence set that assessed the response of colonization and extinction rates to differences in habitat and management characteristics during the spring of 2013 and 2014.

		Model 1		Model 2 (null)		Model 3		Model 4		Model 5		Model-Average	
Par.	Covariate	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
ψ	Intercept	-1.4	0.46	-1.52	0.43	-1.55	0.41	-1.52	0.44	-1.49	0.43	-1.49	0.44
	(.)	-1.4	0.46	-1.52	0.43	-1.55	0.41	-1.52	0.44	-1.49	0.43	-1.49	0.44
γ	Intercept	-1.04	0.73	-2.02	0.27	-0.93	0.67	-2.76	0.62	-1.38	0.68	-1.61	0.91
	Height Range	-0.0003	0.0025									-0.0003	0.0025
	Depth Range	-0.02	0.02							-0.02	0.02	-0.02	0.02
	Ow					-0.03	0.01					**-0.03**	**0.01**
	Emerge							0.02	0.01			0.02	0.01
ε	Intercept	2.54	1.93	-0.31	0.43	1.58	1.58	-0.32	1.38	-0.21	1.28	0.92	1.93
	Height Range	-0.03	0.02									**-0.03**	**0.15**
	Depth Range	-0.01	0.03							-0.002	.03	-0.01	0.03
	Ow					-0.05	0.04					-0.05	0.04
	Emerge							0.0006	0.03			0.0006	0.03

Note: Model-averaged parameter estimates and standard errors were averaged over the top 5 models using their AICc weights (Table 15).

FIGURES

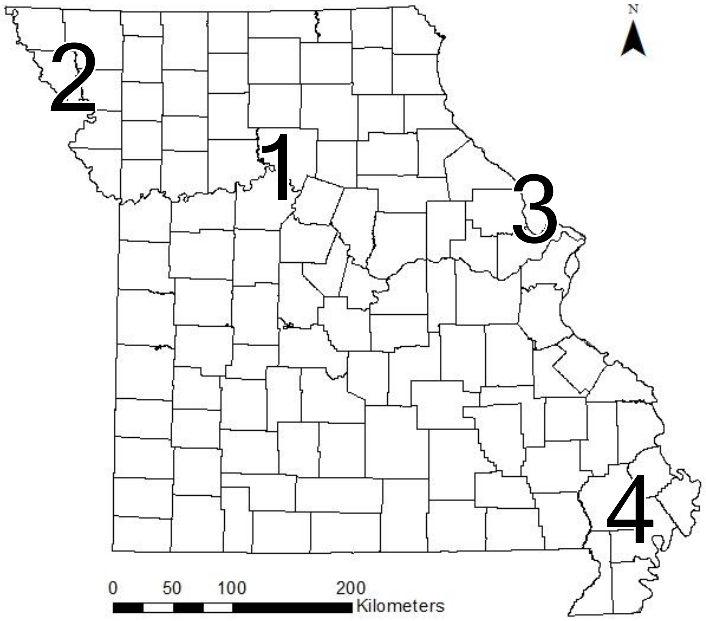

Figure 1.1 Outline of the 4 regions of Missouri where wetlands were located. Occupancy surveys took place in wetlands in these 4 regions during the spring of 2013 and 2014. Region 1 included Swan Lake NWR, Fountain Grove CA, and Grand Pass CA. Region 2 included Squaw Creek NWR, Nodaway Valley CA, and Brown CA. Region 3 included Clarence Cannon NWR, Ted Shanks CA, and BK Leach CA. Finally, region 4 included Mingo NWR, Duck Creek CA, and Otter Slough CA.

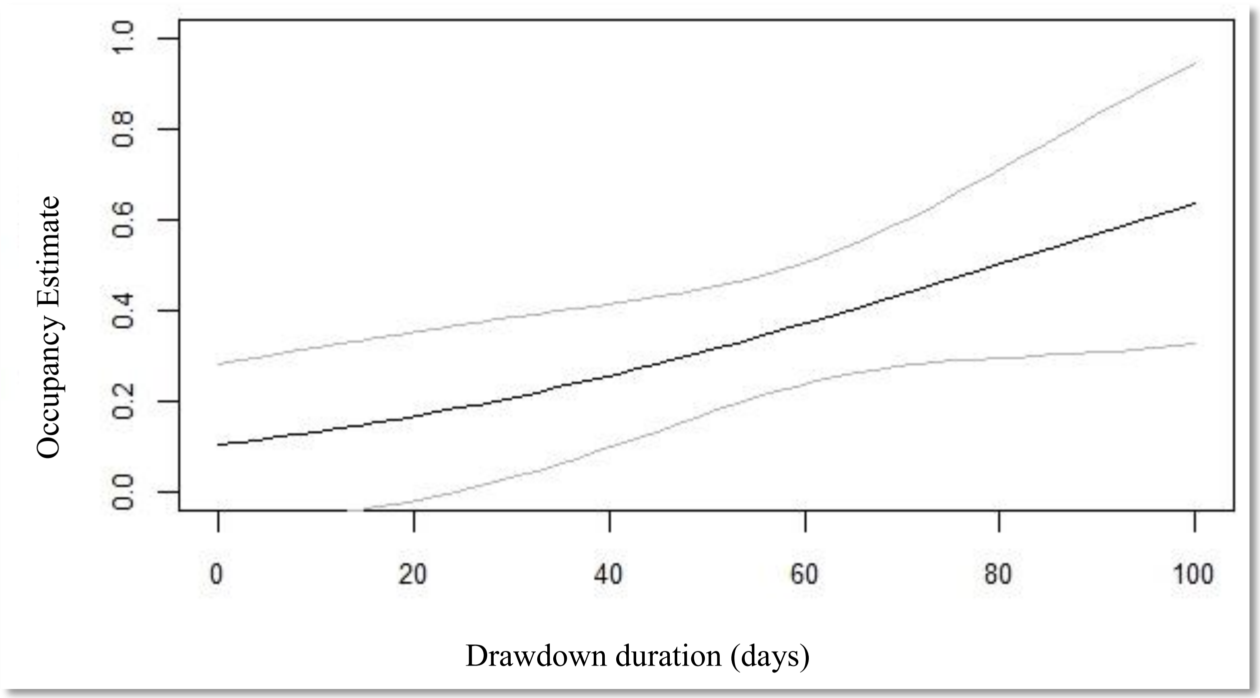

Figure 1.2. Predicted sora (*Porzana carolina*) occupancy estimate as a function of the duration of the drawdown.

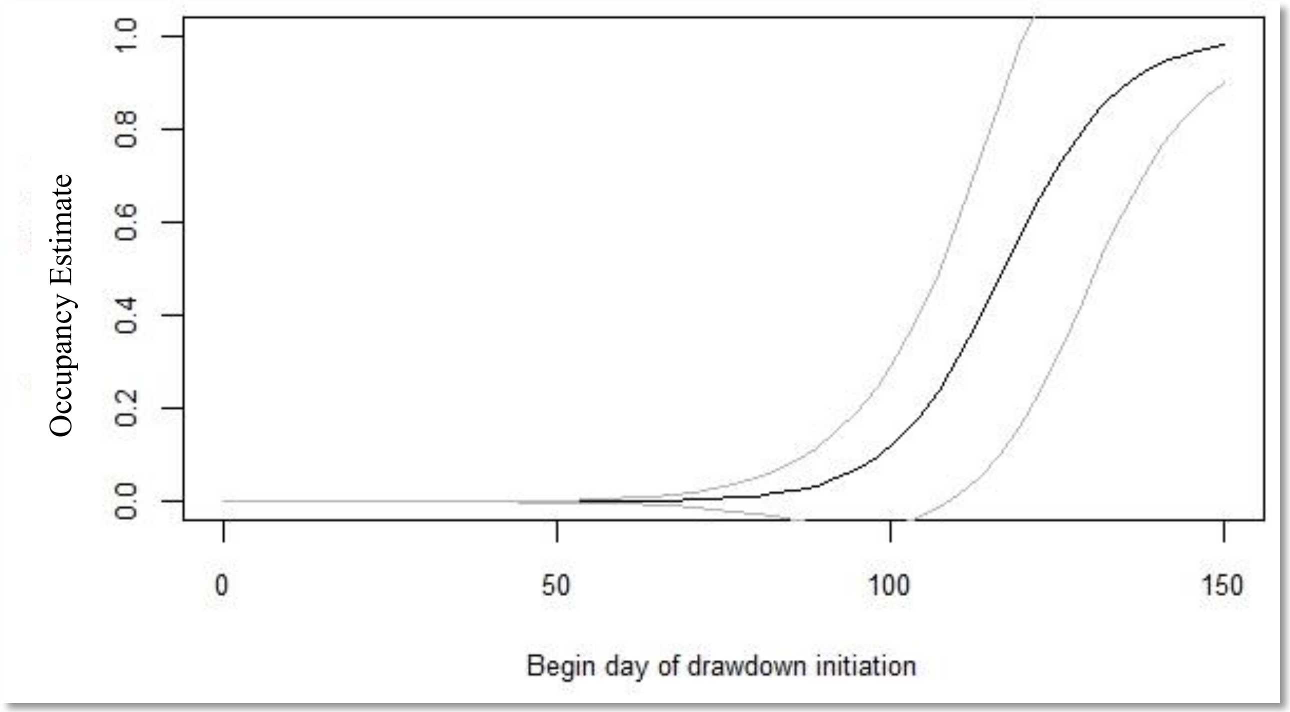

Figure 1.3. Predicted initial least bittern (*Ixobrychus exilis*) occupancy estimate as a function of the initiation date of the drawdown initiation.

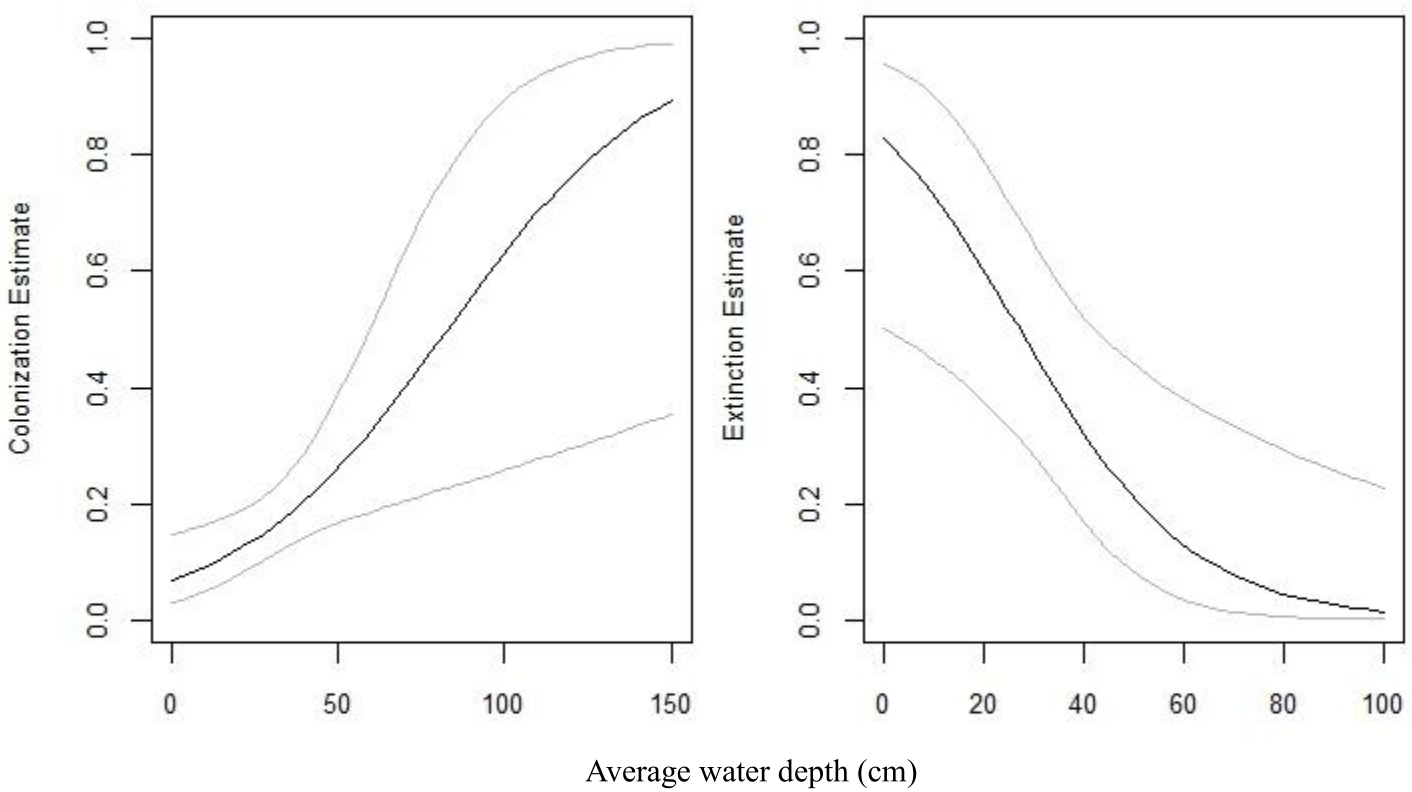

Figure 1.4. Predicted colonization and extinction estimates of least bittern (*Ixobrychus exilis*) as a function of the average water depth at a wetland site.

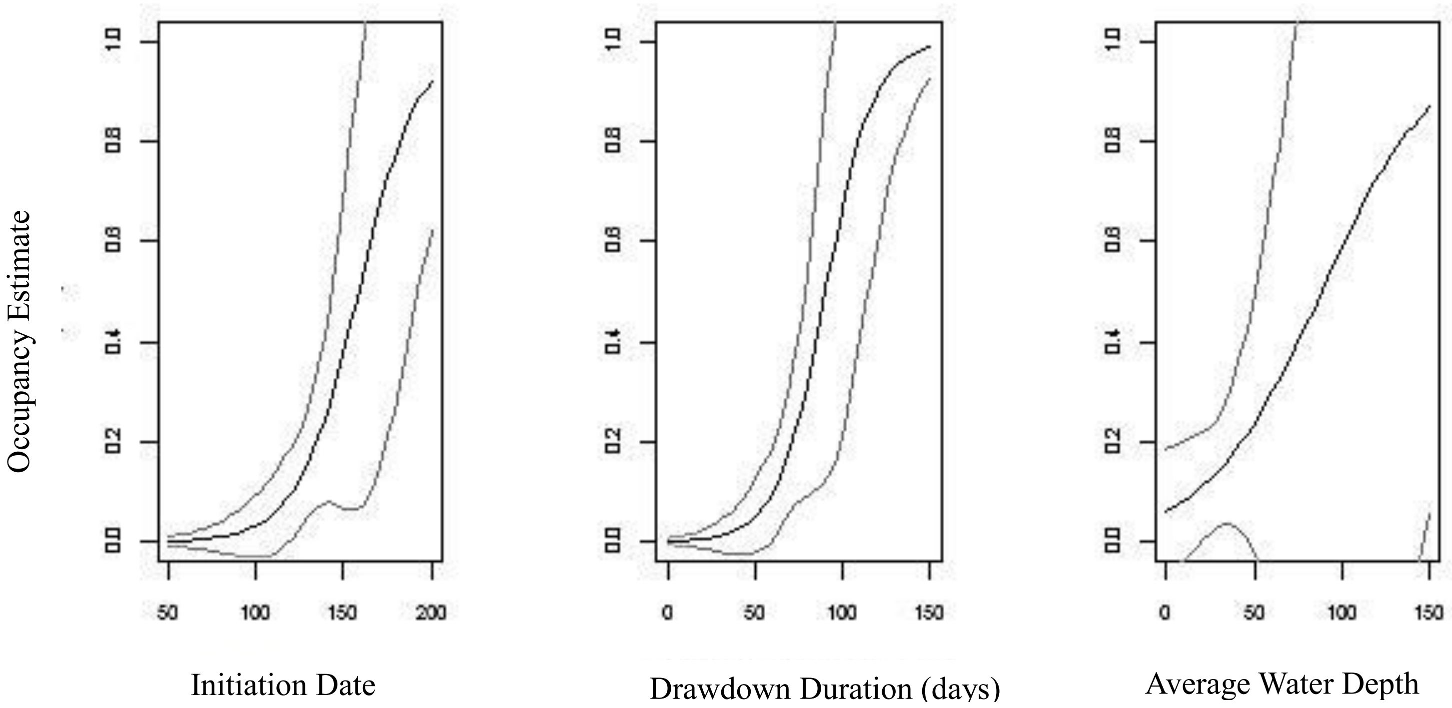

Figure 1.5. Predicted initial American bittern (*Botaurus lentiginosus*) occupancy estimate as a function of the initiation date, the drawdown duration, and the average water depth at a site.

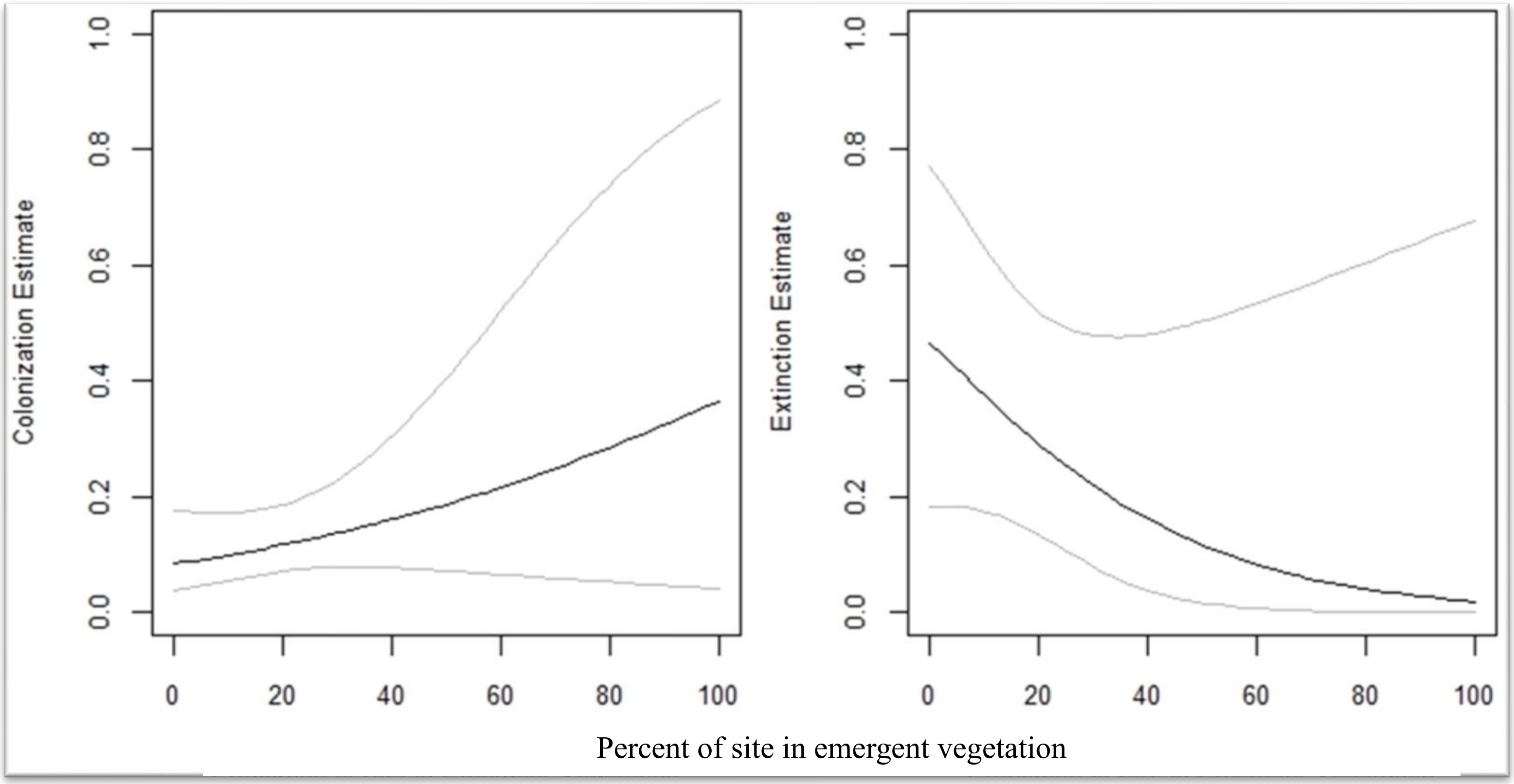

Figure 1.6. Predicted American bittern (*Botaurus lentiginosus*) colonization and extinction estimates as a function of the percent of a site in emergent vegetation coverage.

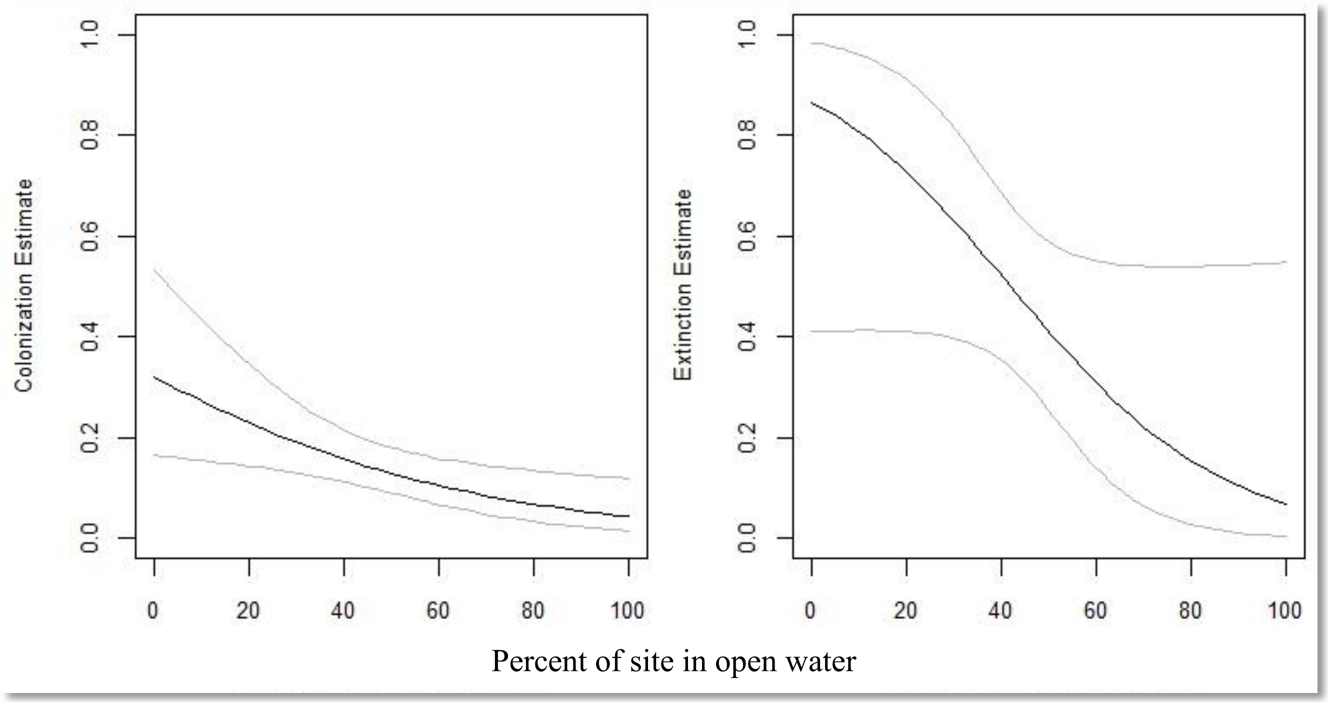

Figure 1.7. Predicted American bittern (*Botaurus lentiginosus*) colonization and extinction estimates as a function of the percent of a site in open water coverage.

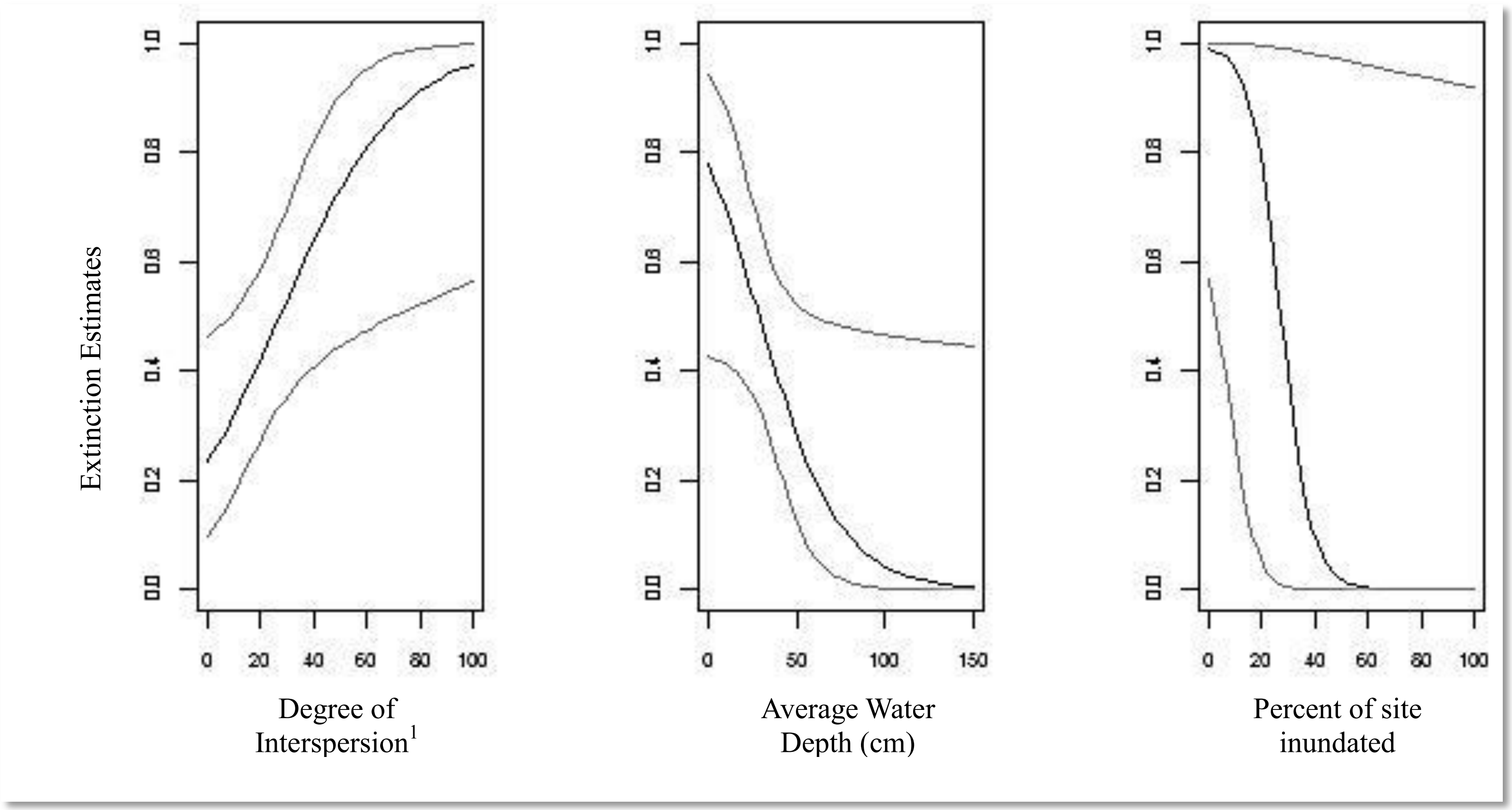

Figure 1.8. Predicted American bittern (*Botaurus lentiginosus*) extinction estimate as a function of the degree of interspersion at a site, the average water depth at a site, and the percent of a site that is inundated. [1]Interspersion of 0=50:50 mix of open water/emergent vegetation; 100=all open water or all emergent vegetation.

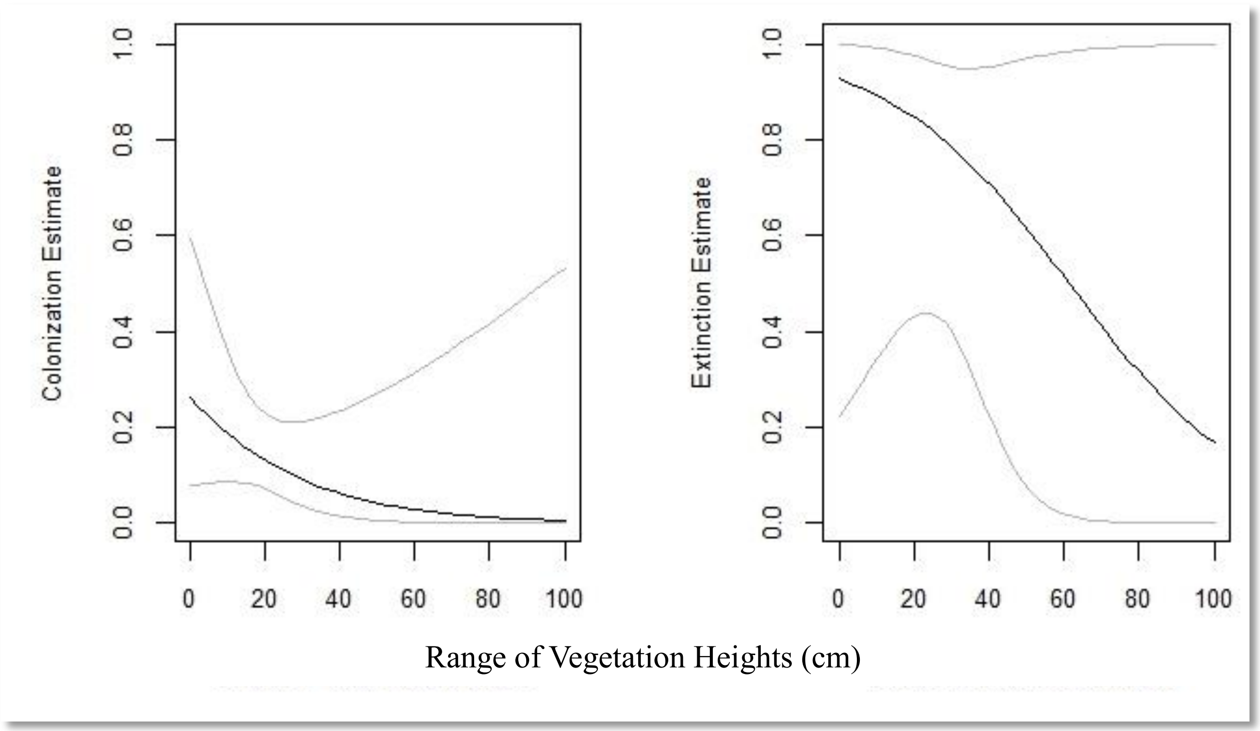

Figure 1.9. Predicted Virginia rail (*Rallus limicola*) colonization and extinction estimates as a function of the range of vegetation heights (cm) at sites.

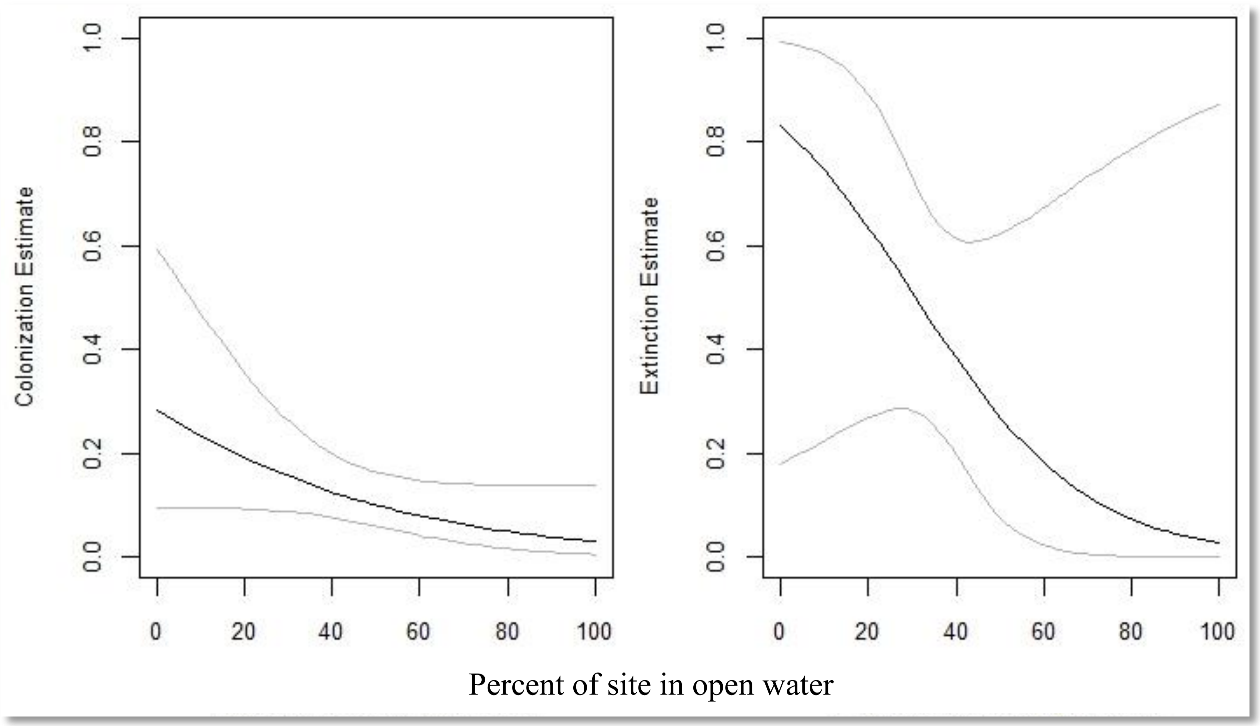

Figure 1.10. Predicted Virginia rail (*Rallus limicola*) colonization and extinction estimates as a function of the percent of a site in open water coverage.

CHAPTER II

LINKING WETLAND MANAGEMENT PRACTICES TO LEAST BITTERN NEST SITE SELECTION AND BREEDING SUCCESS AT MULTIPLE SPATIAL SCALES.

INTRODUCTION

Natural selection is assumed to drive habitat selection decisions of breeding avian species with the reproductive success of an individual being influenced by habitats used during courtship, incubation, and brood rearing (Johnson and Dinsmore 1985, Yerkes 2000, Mayor et al. 2009, Darrah and Krementz 2011). Therefore, habitats selected by breeding birds should be adaptive and nonrandom, and increase the probability of a successful breeding effort (Schlaepfer et al. 2002). In general, a nest is defined as successful if at least one of the eggs hatches during a given nesting attempt (Mayfield 1975, Johnson 1979, Farnsworth et al. 2000, Dinsmore et al. 2002, Rotella et al. 2004). However, environmental variables can influence the likelihood that at least one egg within a given nest will hatch (Caccamise 1977, Rodewald and Yahner 2001, Pierluissi and King 2008). Accordingly, breeding individuals should make nesting habitat selection decisions that increase the probability of nest success during a given nesting attempt.

Birds likely make nesting habitat selection decisions at multiple spatial scales; Johnson (1980) describes the orders of hierarchical habitat selection. First-order habitat selection defines a species' geographic range and within these geographic ranges are forests, prairies, wetlands, and other patches of habitat available for use. A habitat patch, such as a wetland, selected by an individual for a nesting site or breeding territory is an example of second-order selection. Reproductive success of shorebirds and songbirds has been linked to second-order habitat selection decisions (Martin 1998, Alves et al. 2013). Once an individual selects a habitat patch within which to nest, specific microhabitats distributed within this habitat patch are selected as a location to construct a nest (Johnson 1980, Martin 1998, Schlaepfer et al. 2002, Mayor et al. 2009). For example, selection of a particular vegetation type within a wetland in which to establish a breeding territory or to use for foraging would be third-order habitat selection. Many studies have specifically explored the relationship between waterbird nest success and third-order habitat selection (Warnock and Takekawa 1995, Becker and Beissinger 2003, Stephens et al. 2005). These studies demonstrate the usefulness of understanding the relationship between nest success and habitat selection at multiple spatial scales in order to recognize the importance of different habitat types for breeding waterbirds.

Secretive marsh birds are a group of wetland dependent birds commonly associated with dense emergent vegetation throughout the annual life cycle (Bent 1926, Weller 1999) resulting in low detection probabilities and low sample sizes in many studies (Conway and Gibbs 2011). Among the SMB species known to use wetland habitats in Missouri, only the king rail (*Rallus elegans*) and least bittern (*Ixobrychus exilis*) are regular breeders in the state (Poole et al. 2009, Darrah and Krementz 2011). Although king rail are known to breed in Missouri, they are extremely rare and their nests are challenging to find; therefore, my study focuses on the relationship between least bittern nest habitat characteristics and nest success.

Least bittern are members of the heron family (Ardeidae) and occur in Missouri as both migrants and breeders (Weller 1961, Poole et al. 2009). Least bittern breed throughout Missouri in wetlands characterized by emergent vegetation (Poole et al. 2009, Darrah and Krementz 2011). Least bittern often go undetected in large-scale monitoring efforts because of their small size, secretive nature, and preference for occupying dense stands of tall emergent vegetation (Conway and Gibbs 2011, Steidl et al. 2013). As a result, population trends of least bittern are poorly understood and often contradictory due to a lack of available data and low detection probability (Poole et al. 2009). However, Santisteban et al (2011) reported that least bittern populations have declined across their range in the U.S.A. from 1999 to 2009. Even so, these estimates were derived from Breeding Bird Surveys, which are not as useful for detecting SMBs as more recent protocols. Given a potentially declining least bittern population, and studies exploring the relationship between nest success and nesting habitat selection at multiple spatial scales are important to identify those habitats with the potential to reverse population declines. These efforts benefit from development of call-broadcast monitoring protocols that increase the probability of detecting least bittern and other secretive marsh birds (Conway and Gibbs 2011, Steidl et al. 2013).

Nesting habitat selection decisions and nest success of least bittern can be evaluated in the context of wetland management strategies on public wetlands in Missouri. Missouri is located in the western edge of the breeding range of the least bittern, which encompasses the entire eastern half of the U.S. and extends north to the U.S. and Canada border and south to the Gulf of Mexico (Poole et al. 2009). Therefore, some least bittern passing through Missouri during migration will migrate further north to Iowa and Minnesota to breed, but some birds will breed in wetland habitat in Missouri (Robbins and Easterla 1992, Poole et al. 2009). Breeding least bittern may be basing nest site selection on habitat characteristics present during the migration period and the pair-formation phase in late May. However, wetlands are highly dynamic systems and habitat conditions encountered by least bittern on public wetlands in Missouri could fluctuate between when nest site selection decisions are made and the conclusion of the incubation period. Wetland management strategies applied to public wetlands often determine when and how rapidly wetland habitat conditions change over time, which has an effect on subsequent habitat selection decisions.

On many publicly managed wetlands, managers can manipulate wetland hydrology to mimic historical seasonal water levels by pumping water to inundate a site or drawing water off of the site, commonly referred to as a drawdown (Meeks 1969, Van der Valk 1981, Fredrickson 1991). The timing and duration of water level drawdown can alter wetland habitat conditions encountered by least bittern during spring migration and summer breeding season (Fredrickson 1991). The area of inundated habitat and water depths available throughout the breeding season vary depending on both the initiation date and duration of water level drawdown. Wetlands that initially contained water depths attractive to least bittern selecting nesting locations may have much shallower water depth by the time the incubation period ends. Changing wetland habitat conditions have the potential to decouple least bittern nest site selection decisions from nest success on publicly managed wetlands in Missouri.

Wetland vegetation characteristics, including height and density, many contribute to least bittern nest success. Least bittern typically construct nests within stands of robust emergent vegetation, such as cattails (*Typha spp.*) or bulrush (*Scirpus spp.*) and occasionally in woody vegetation (*Salix spp.*) (Weller 1961, Post 1998, Moore et al. 2009). Sedges (*Carex spp.*), arrowhead (*Sagittaria spp.*), and common reed (*Phragmites* *australis*) are also potential nesting vegetation for least bittern (Poole et al. 2009). Least bittern typically build nests in vegetation at least 1m in height (Weller 1961, Post 1998). Although numerous studies have examined the influence of stem density on nest success in upland habitats (Keppie and Herzog 1978, Murphy 1983, Martin and Roper 1988, Kelly 1993, Rush and Stutchbury 2008), there is relatively little information on the relationship between stem density and nest success in wetland habitats used by least bittern (Caccamise and Caccamise 1977). Although height and density of emergent vegetation may be important components in nest site selection and construction, vegetative cover patterns, (i.e. the ratio of open water and emergent vegetation) within a wetland could also be important to breeding least bittern. Studies indicate that optimal least bittern nesting habitat often includes open water coverage in addition to emergent vegetation coverage (Bogner and Baldassarre 2002*b*, Budd and Krementz 2010). Patches of open water likely prevent some terrestrial nest-predators from locating least bittern nests and provide foraging habitat for nesting adults (Weller and Spatcher 1965).

Least bittern generally nest over standing water and water depth beneath the nest varies with the topography of the wetland site and with fluctuating water levels (Weller 1961, Post and Seals 1993, Post 1998, Winstead and King 2006, Poole et al. 2009). While least bittern require at least some standing water below and surrounding the nest, there is little information on how specific water depths influence nest site selection or success (Post 1998, Bogner and Baldassarre 2002, Moore et al. 2009). Water depth is very relevant on intensively managed wetlands, because hydrologic management can substantially alter water levels over a relatively brief span of time (Fredrickson and Taylor 1982, Fredrickson 1991).

Although breeding least bittern require dense, tall emergent vegetation interspersed with patches of open water (Weller 1961, Poole et al. 2009), it is unclear how differences in these vegetation and hydrologic characteristics affect nesting habitat selection and nest success. Furthermore, it is unclear whether habitat induced changes caused by spring water-level management may result in a decoupling of least bittern nest success from nest site selection. The objectives of my study were to examine least bittern nest site selection patterns on public wetlands in Missouri and to evaluate whether the same factors that influenced nest site selection were important predictors of least bittern nest success.

METHODS

Study Site Selection and Nest Searches

I selected study sites as part of my larger marsh bird project that took place on publicly managed wetlands in four regions within Missouri, the northwest, north-central, northeast, and southeast. Within each of the four regions, I selected two state Conservation Areas and one USFWS National Wildlife Refuge, for 12 study areas (Appendix 1). Study areas included wetland complexes composed of numerous individual wetlands and I conducted repeated marsh bird occupancy surveys within a subset of the available sites within each area. I selected wetlands to search for nests based on results of six rounds of spring call-broadcast surveys designed to increase detection of secretive marsh birds (Conway 2011). Specifically, I searched for nests at wetlands where least bittern or king rail were detected at least once during spring occupancy surveys and that were inundated during the final round of occupancy surveys.

I searched available wetlands for SMB nests following completion of occupancy surveys conducted during spring migration period 2013 and 2014. Wetlands were considered available to nesting least bittern if at least one least bittern was detected during spring occupancy surveys and if the site was at least 25% inundated during the final round of spring occupancy surveys. Sites were not considered available if they were less than 25% inundated, even if at least one least bittern was detected during spring occupancy surveys. I conducted nest searches by foot and searched flooded stands of available emergent vegetation known from previous studies to be used by least bittern as nesting material (Nelson 2003, Arnold 2005, Poole et al. 2009). I considered available emergent vegetation to be either persistent or non-persistent emergent vegetation or scrub-shrub vegetation. Persistent vegetation remained standing following the end of the growing season and could include such species as cattail (*Typha spp.*) or bulrush (*Scirpus spp.*), while non-persistent vegetation, such as arrowhead (*Sagittaria latifolia*), fell below the surface of the water at the end of the growing season (Cowardin et al. 1979). Shrub-scrub vegetation included woody vegetation, such as willow (*Salix spp.*) or buttonbush (*Cephalanthus occidentalis*).

Nests were located by a 1-3 person search team walking approximately 3-10m apart through flooded vegetation (Bogner and Baldassarre 2002, Pierluissi and King 2008). Starting at one edge of a patch of flooded vegetation, the search team moved through the vegetation until reaching the edge of the patch of flooded vegetation or a levee. The individual on the leading edge of the search path used a handheld GPS device set to track movement in order to create a line transect. A handheld GPS device was also used to mark the location of any least bittern or king rail nests.

I monitored nests every 4-7 days to determine nest fate, returning to nests at least three times, until nest fate was conclusive. If eggs or fledglings were found during the revisit, the nest successfully survived the exposure period, otherwise it was deemed failed (Rotella et al. 2004, Shaffer 2004). A nest might fail if it was physically destroyed, if damaged eggs were found in the nest, or if dead young were found in the nest. If a nest platform was empty on the first visit, and still empty on the third revisit, I considered the nest failed.

Habitat Sampling

I assessed least bittern nest site selection by comparing used and available points at two spatial scales; the wetland scale, which included the wetland in which a nest was located and the point scale, which included area immediately surrounding nests. At the point scale, habitat conditions were evaluated within a 50 m radius of a nest or available point. Available points were survey points used during spring call-back surveys within the same wetland located at least 100m away from any nest location. Available points were used to determine if birds were selecting certain wetland habitats for nesting disproportionately to their availability. Habitat characteristics measured at nest points and available points included water depth, vegetation height and vegetation density. I also visually estimated percent of the surrounding 50m radius that was inundated, contained open water, and contained emergent vegetation. I measured each habitat variable at five locations; immediately adjacent to the nest and at 5m from the nest in each cardinal direction. Habitat measurements were recorded during each nest visit and were subsequently averaged prior to analysis. I collected the same habitat measurements at available points; however habitat variables at each point represented an average of measurements taken during the fifth and sixth round of call-broadcast surveys. I used a Robel pole to quantify vegetative characteristics, including vegetation height and density. Vegetation height was the tallest stem touching the pole, while vegetation density was assessed as the lowest Robel increment visible from 1m away.

I evaluated nest site selection at the wetland scale by comparing habitat characteristics at used and available wetland units. Only a subset of the available wetlands were used by nesting least bittern. Available wetlands were all wetlands that I surveyed during the nest searching process. At used wetlands, water depth, vegetation height, and vegetation density, were estimated as the average of all measurements recorded at nests over the course of the nest searching period. I estimated the percent of a wetland site inundated, covered in open water, and covered emergent vegetation during the fifth and sixth rounds of call broadcast surveys and averaged these values. At available wetlands, I measured the same variables, except all values were averaged across the fifth and sixth round of occupancy surveys. The 5th and 6th rounds took place in early to mid-June, corresponding to the time during which least bittern were likely making nest site selection decisions in Missouri (Robbins and Easterla 1992, Poole et al. 2009). I also determined water level drawdown initiation date and duration at the wetland scale.

Following meetings with area managers and preliminary site assessments, all wetland units were classified into active or passive management categories based on water level manipulation strategies. Active sites were distinguished from passive sites based on whether area managers manipulated a water control structure with the intent to drawdown the water level on a given wetland. The drawdown duration was quantified as the number of days between when the drawdown was initiated and the site was dewatered (contained <5% water). The drawdown initiation date on active sites was determined based on information collected from area managers prior to the sampling season. For passive sites, drawdown duration was considered the total number of days between when surveys began and when either the site was dry (contained <5% water) or when surveys ended. To account for evapotranspiration on passive sites, the drawdown initiation was considered ten days after the latest drawdown initiation date within the same region.

Data Analysis

I used discrete choice modeling to assess least bittern nest site selection at the point scale. Discrete choice models assess nest site selection as a series of predicted decisions of nest site habitat use from a set of possible alternatives from a given choice set (Cooper and Millspaugh 1999). I paired least bittern nest point locations with 4 available points within the same study area that were at least 50m from a nest point (Conservation Area or National Wildlife Refuge). I assessed nest point selection using mixed logit discrete choice models in a Bayesian framework to model the probability that a breeding least bittern would choose the used nest point versus an random point when offered the choice between the two (Beatty et al. 2014, Rota et al. 2014). Choice sets were described as four circular areas of wetland habitat with a radius of 50m within the breeding range of least bittern *j*; the used nest point and an available nest point of equal area. I modeled the utility of the used wetland points in the *i*th choice set of least bittern *j* as a linear function of wetland habitat characteristics (Hardy 2013, Rota et al. 2014).

$$U_{ij}^{used} = ß_{1j}DEPTH_{ij}^{used} + ß_{1j}HEIGHT_{ij}^{used} + ß_{1j}ROBEL_{ij}^{used} + ß_{1j}EMERGE_{ij}^{used} + ß_{1j}OW_{ij}^{used}$$

I calculated the relative probability of a least bittern selecting a used nest point as:

$$\psi_{ij}^{used} = (\exp(U_{ij}^{used})/(\exp(U_{ij}^{used}) + \exp(U_{ij}^{avail}))$$

Regression coefficients explain how a one unit change in the value of a corresponding habitat variable changes the 'utility' of a point for least bittern *j*, with greater utility leading to a higher relative probability of use (Rota et al. 2014). I used vague prior distributions for all model parameters and fitted the discrete choice models using the r2jags package (Su and Yajima 2012), which allows users to code for JAGS models in R version 3.1.1 (Plummer 2003). I used three Markov chains to simulate the posterior distributions of all model parameters. I ran each chain for 25,000 iterations, discarding the first 15000 as burn-in. Discarding the initial draws as burn-in is necessary because initial draws on the posterior distribution are not independent of the starting values, and thus do not represent the equilibrium distribution of the Markov Chain (Kery 2010). I retained every 50th iteration after the initial burn-in period, resulting in a total of 600 random draws on the posterior distribution of the model parameters (Rota et al. 2014). A Brooks–Gelman–Rubin convergence diagnostic of <1.01 indicated adequate convergence for all covariates (Brooks and Gelman 1998). I assessed nine models with various combinations of covariates and ranked models according to their Deviance Information Criterion (DIC) (McCarthy 2007, Link and Barker 2009, Kery 2010, Hardy 2013). Ranking models based on DIC produces equivalent results compared to other Bayesian model ranking methods such as Watanabe-Akaike's Information Criterion (WAIC) (Gelman et al. 2013). The top model was considered the model with the lowest DIC

(Hardy 2013, Glisson et al. 2015). Parameters for which the 95% credible interval (CRI) did not overlap zero were considered to have significant effects on relative probability of use.

I did not use discrete choice modeling at the wetland scale because of the nature of how the wetlands were selected. As part of a larger study, I selected wetlands because of the hydrologic management taking place there, as opposed to prior assumptions on a wetland's potential as nesting habitat. Therefore, at the wetland scale, I evaluated least bittern nest site selection using a logistic regression (Pierluissi 2006, Darrah and Krementz 2011). Used sites, in which I detected a nest, were assigned a value of one, whereas unused sites were assigned a value of zero. In this analysis, site was defined as a discrete wetland impoundment within a publicly managed wetland area. I evaluated the effect of several habitat and hydrologic management characteristics on the probability that a site would be selected by breeding least bittern, comparing across 16 models and ranking models using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002). A null model containing no covariates was included in the candidate set (Weatherhead et al. 2010, Darrah and Krementz 2011, Murray and Best 2014). I calculated model-averaged parameter estimates for all models in the 90% AIC confidence set (Hansen 2007). I considered parameter estimates to have significant effects on selection if the 95% confidence interval did not overlap zero (Glisson et al. 2015). I fit all models using the AICmodavg package in R version 3.1.1 (Mazerolle 2015, R Core Team 2015).

Nest Success

I used the logistic exposure method to determine the effect of habitat characteristics on the daily survival rate (DSR) of least bittern nests. The logistic exposure method allows use of generalized linear mixed models to evaluate the DSR of a nest during a given nest-check interval as a function of covariates (Rotella et al. 2004, Shaffer 2004, Jones and Geupel 2007). I used the logistic exposure method because of its flexibility, specifically, and because it allows for the simultaneous evaluation of categorical, continuous, and time-specific variables in complex, mixed models (Rotella et al. 2004, Shaffer 2004, Jones and Geupel 2007). In addition, in the logistic exposure model, nest survival does not need to be constant from day to day and failure dates can be unknown (Shaffer 2004). The daily survival rate is modeled in terms of x through a predictor function with a value between zero and one (Shaffer 2004). The exposure method uses the same logistic function as is used in logistic regression.

$s(x) = e^{ß0}+^{ß1x} / 1 + e^{ß0}+^{ß1x}$

The function $g(\theta)=\log_e(\theta^{(1/t)}/1- \theta^{(1/t)})$ is the link function for the logistic exposure method, and is the main difference between logistic regression and the logistic exposure methods (Rotella et al. 2004). The exponent (1/t) in the numerator and denominator accounts for the fact that probability of surviving an interval depends on interval length (Shaffer 2004).

I compared 14 models comprised of various combinations of variables to determine the best predictors of daily survival probability for least bittern nests based on their AIC_c ranking (Burnham and Anderson 2002). A null model containing no covariates was included in the candidate set (Weatherhead et al. 2010, Darrah and Krementz 2011, Murray and Best 2014). The same habitat characteristics measured in the 50m radius surrounding nest points were evaluated in the daily nest survival analysis. I averaged parameter coefficients across all models in the 90% AIC confidence set (Hansen 2007). I considered parameter estimates to have significant effects on selection if the 95% CRI did not overlap zero (Glisson et al. 2015), and fit all models using the AICmodavg package in R version 3.1.1 (Mazerolle 2015, R Core Development Team 2015).

RESULTS

In 2013, I searched 18 wetlands, and found 40 nests at Fountain Grove CA, Swan Lake NWR, Squaw Creek NWR, and BK Leach CA. In 2014, I searched 16 wetlands, and found 43 nests at Fountain Grove CA, BK Leach CA, and Squaw Creek NWR. No king rail nests were found, so all further analyses involved only least bittern. In both years combined I found a total of 83 least bittern nests, which was reduced to 71 nests after removing nests for which I could not determine fate, nests that were determined to be abandoned prior to the start of the nest search period and nests determined to be remnant nests from a previous breeding season. Of the 71 nests monitored in both years, all were built within either bulrush (*Scirpus spp.*) or cattail (*Typha spp.*) and 46 (65%) fledged at least one young.

At the wetland level, least bittern nested in 8 out of 39 available sites (Table 2.1). There were significant differences in habitat characteristics between used and available wetlands. The percent of emergent vegetation at a site (t-test $p<0.05$) was significantly greater at used sites than available sites. Out of 17 total models for wetland selection, eight models were in the 90% confidence set (Table 2.2). The top model included covariates for water depth and percent of the site covered in emergent vegetation, which were both positively related with selection probability (Table 2.3). The top model had a strong fit, with a χ^2 of $p<0.01$, however, only water depth had a significant relationship with nest selection probability at the wetland scale (Figure 2.1).

At the nest point scale, I found more variables that influenced probability of use than compared to the wetland scale. Water depth (t-test $p<0.01$), vegetation height (t-test $p<0.01$), and the percent of a point covered in emergent vegetation (t-test $p<0.05$), were significantly greater at used points than at available points. Among the eight competing models to predict nest site selection at the point scale, the top model included covariates for water depth, the quadratic transformation of water depth, vegetation height, vegetation density, and percent emergent vegetation coverage (Table 2.4). The Brooks–Gelman–Rubin convergence diagnostic (Brooks and Gelman 1998) indicated adequate convergence for all hyperparameters (Rhat=1). Relative probability of use had a significant positive relationship with water depth and vegetation height (Figure 2.2). Vegetation density had a significant negative relationship with the relative probability of use (Figure 2.2). There was not a strong relationship between relative probability of use and either the quadratic transformation of water depth or the percent a nest point surrounded by emergent vegetation.

The logistic exposure regression of habitat characteristics between failed and successful nests resulted in 5 of 14 models in the 90% confidence set, and the top model included only the covariate for water depth surrounding nest locations (Table 2.5). Water depth had a significant positive relationship with daily nest survival rate (Table 2.6), and water depth between 50-80cm at a nest site generally predicted that a nest would survive an interval (Figure 2.3). Four models competed with the top model in the 90%

confidence set, and each of these competing models included the covariate for water depth surrounding nest locations. Water depth was positively related with daily survival rate in all competing models. The vegetation height and the percent of a nest point covered in open water habitat were also positively related with daily survival rate. The vegetation density and the percent of a nest point covered in emergent vegetation habitat were negatively related with daily survival rate.

DISCUSSION

My results indicate breeding least bittern made habitat selection decisions at the wetland level based on two factors: emergent vegetation cover and water depth. Historically, least bittern are known to use tall emergent vegetation during breeding (Bent 1926, Weller 1961, Zeibell 1990, Post and Seals 1993). My results are consistent with other studies that also found a similar relationship between emergent vegetation and least bittern breeding effort. A study by Bogner and Baldassarre (2002) reported the majority of least bittern nested in wetlands characterized by tall emergent vegetation and Post (1998) found that the availability of patches of tall emergent vegetation was the main requirement for a successful least bittern breeding attempt. However, my study provides evidence that least bittern are actively selecting for tall emergent vegetation over other available wetland habitat. The availability of typical nesting vegetation such as cattail and bulrush, is likely a requirement for breeding bittern (Bent 1926, Weller 1961). Furthermore, emergent vegetation provides foraging microhabitat because least bittern typically forage by clinging to emergent vegetation compared to the larger king rail and American bittern that forage while wading (Weller and Spatcher 1965, Reid 1989, Lowther et al. 2009, Poole et al. 2009).

More habitat characteristics were important in predicting selection at the point scale than at the wetland scale, indicating that least bittern may be responding to more detailed characteristics of the vegetation in the local area surrounding the nest location. The water depths surrounding least bittern nest locations range from 34 – 107 cm (Post 1998, Rodgers Jr. and Schwikert 1999, Bogner and Baldassarre 2002, Lor and Malecki 2006), however, my study is one of the first to demonstrate nest point selection based on water depth. The top model for nest point selection indicated that wetlands with depths of ≥70cm were more likely to be selected by least bittern, whereas water depths ≤40cm were less likely to be selected. Although the presence of emergent vegetation structure is likely static and unlikely to change within the time span of the least bittern breeding season, water depths can be more dynamic (Kushlan 1986, Bolduc and Afton 2008). Spring drawdowns on active wetlands were complete by the start of the nest-searching period, but water levels in some wetlands sites decreased over the course of the nest monitoring period regardless of whether the site had actively or passively manipulated water levels, because of natural evapotranspiration and draining. Water level manipulations are a common management strategy for seasonal wetlands in Missouri (Fredrickson 1991) with potential to influence breeding efforts of least bittern. Water levels are commonly drawn down in the spring (Fredrickson 1991), coinciding with least bittern nest site selection and potentially leaving sites dry when broods hatch in June and July (Poole et al. 2009). If a spring drawdown is applied to a wetland, I speculate that it should be completed by the end of May so that it is dry when least bittern are making nest-site selection decisions in order to prevent the bitterns from nesting in wetlands that would become dry before the end of the nesting period. The majority of nests were found on passively managed wetlands rather than actively managed wetlands. Even so, some passively managed sites had decreased water levels either from percolation through the soil or evapotranspiration.

Given that both water depth and percent of a wetland containing emergent vegetation were important factors in determining nest site selection at the wetland scale, least bittern nesting effort may be increased on wetlands characterized by both habitat characteristics. Presence of emergent vegetation was likely not relevant to nest site selection if a wetland was not inundated because least bittern nest over water, further indicating that both variables are important predictors of least bittern nest site selection (Bent 1926, Weller 1961, Poole et al. 2009). If an available site had suitable water levels, but was sparsely vegetated, it would not serve as important nesting habitat. Likewise, if a site was dry, but had a sufficient area of emergent vegetation, it may be avoided by breeding least bittern. If wetland managers provide wetlands with emergent vegetation that are flooded to at least 70cm during the nest-site selection process in late May and early June, these sites would likely be selected by breeding least bittern. However, unless water levels are held above 40cm for the duration of incubation and brood rearing, the daily survival rate of least bittern nests may decrease as a result.

Like other wetland nesting birds, after least bittern select a wetland in which to construct a nest, they presumably use more detailed cues in the next stage of habitat selection when deciding in which particular patch of vegetation to nest. Many other studies have found that habitat characteristics at small spatial scales can significantly influence nesting effort and success (Martin 1998, Rodewald and Yahner 2001, Mezquida and Marone 2002, Fernández-Juricic et al. 2005, Barg et al. 2006). My results indicated that there were more factors involved in the nest point selection process than in the nest site selection process. The top model for nest point selection included the same covariates as the wetland model, but also included covariates for vegetation height and density, and the quadratic transformation for depth, which may not be detectable until the individual has entered the wetland. At the coarser wetland scale, least bittern appear to be selecting inundated wetlands, while at the finer nest point scale, the importance of vegetation characteristics becomes apparent. Wetlands intended to provide least bittern breeding habitat should consider the specific microhabitats within inundated wetlands.

While the presence of emergent vegetation was an important predictor of wetland and nest point selection, I found that the vegetation height and vegetation stem density were only important predictors of nest point selection. Tall vegetation could allow a nest to be constructed further above the water, in order to protect the nest from sudden increases in water levels. Taller vegetation could also potentially increase concealment from above, screening the nest from nest predators and shielding least bittern chicks from intense sunlight (Post 1998). My results indicated average vegetation height at nest points (47.9 ± 59.9 cm) was consistent with Lor and Malecki (2006), who observed least bittern nesting in vegetation averaging 42.4 cm. In general, least bittern are known to nest in tall emergent vegetation, such as cattail and bulrush (Bent 1926, Weller 1961, Poole et al. 2009). All least bittern nests in my study were constructed in either cattail (*Typha* spp.) or bulrush (*Scirpus* spp.), which was consistent with other studies of least bittern breeding ecology (Post 1998, Rodgers Jr. and Schwikert 1999, Bogner and Baldassarre 2002, Nelson 2003, Lor and Malecki 2006).

Although I expected vegetation density to be an important factor in nest site selection at the point level, I did not anticipate that the relationship between vegetation density and nest site selection probability would be negative. The negative relationship between nest site selection and vegetation density could have been the result of the vegetation density surrounding nest sites impeding adults' movement to and from the nest and may have contributed to greater nest site selection in areas with lower vegetation density (Reid 1989). Alternatively, if the area immediately adjacent to a nest consisted of patches of emergent vegetation interspersed with open water, my sampling protocols required that some density measurements be taken over open water, which likely reduced the average stem density metric from that nest. Least bittern may be selecting for wetlands characterized by a patchy distribution of emergent vegetation and open water, which could provide ready access to open water for foraging adjacent to the nest. Previous studies have found least bittern build their nests in microhabitat near the vegetation water interface (Post and Seals 1993, Post 1998, Bogner and Baldassarre 2002, Lor and Malecki 2006). Least bittern, like other marsh birds, forage primarily along the vegetation water interface (Sutton 1936, Bogner and Baldassarre 2002, Poole et al. 2009). While my vegetation density results may indicate the importance of a patchy distribution of open water and emergent vegetation, more research is needed to determine the response of least bittern habitat selection to stem density.

While Least bittern require nesting areas that provide ready access to foraging habitat along the vegetation-water interface, nesting habitat selection also reflects an avoidance of areas that are accessible from terrestrial predators (Bent 1926, Post 1990, 1998). Deep water under and around nests would inhibit access by terrestrial nest predators, and this is considered one of the main reasons least bittern and other marsh birds exploit wetland habitat as nesting sites (Eddleman et al. 1988, Weller 1999). My results indicated that the single most important factor affecting daily survival rate at the nest point scale was the average water depth. Similarly, Jobin et al. (2009) reported least bittern breeding pair densities were positively related with water depth. Furthermore, many studies have found nest predation increased in a wetland following a drawdown (Jobin and Picman 1997, Post 1998), emphasizing that drawdowns have the potential to negatively impact nest success of least bittern. While my results indicated that daily nest survival rate was maximized at water depths of 80cm, a range of 50-80cm would be likely be effective in increasing survivability. However, many publicly managed wetlands in Missouri do not maintain 50-80cm of water throughout the breeding season and may be functioning as an ecological trap if water depths assessed by least bitterns during nest site selection are not maintained throughout the entirety of the breeding season.

MANAGEMENT IMPLICATIONS

Wetland loss, wetland isolation, and infrastructure limitations all contribute to the challenge of providing breeding habitat for least bittern, and other secretive marsh birds. I speculate that it is unrealistic to attempt to manage a single wetland impoundment to provide suitable habitat for all species of secretive marsh bird. Rather, the habitat characteristics of the wetland site need to be evaluated to determine if it is feasible to target management decisions to the needs of breeding least bittern. Some wetlands may require extensive water and vegetation manipulation in order to provide least bittern breeding habitat, which may not be economically viable because of infrastructure limitations and limitations imposed by the natural drainage characteristics of the site.

Despite these limitations, the availability of water in wetlands with tall emergent vegetation is necessary to support high breeding densities of least bittern (Bent 1926, Weller 1961, Weller and Spatcher 1965, Poole et al. 2009). Many previous studies of least bittern have focused on evaluating how water depth influences breeding least bittern habitat use and subsequent nest success, however, many of these studies did not take place on wetlands subject to water level manipulations (Post 1998, Rodgers Jr. and Schwikert 1999, Lor 2000, Bogner and Baldassarre 2002, Lor and Malecki 2006). Providing breeding habitat for least bittern on public wetlands in Missouri requires water to be available throughout the summer breeding season. However, the typical cycle of hydrologic management includes flooding in the fall and reducing water levels in the spring (Fredrickson and Taylor 1982). In the spring, wetlands may have water deep enough to attract breeding least bittern searching for suitable breeding grounds, but an ecological trap may occur if these water depths encountered by least bittern in the spring are not maintained for the entire breeding season.

Water depth was also the strongest factor influencing the daily nest survival rate, emphasizing that decreasing water levels encountered during summer breeding months could have a negative impact on marsh birds breeding on these wetlands. Publicly managed wetland complexes in Missouri can provide breeding habitat if some wetlands in the complex are allowed to remain inundated at appropriate water depths throughout the summer breeding season. The availability of water is not the only requirement; the typical nesting vegetation must be available as well. Managing the timing and duration of a wetland's drawdown duration will take into consideration how these water manipulations will alter the available vegetation in order to provide cattail, bulrush, and other typical nesting vegetation (Bellrose 1945, Brinson et al. 1981). Therefore, a wetland may not provide suitable least bittern breeding habitat every year due to management decisions that result in suitable water depths and vegetation compositions in subsequent years.

I speculate that it may be challenging to provide the habitat conditions that maximize least bittern nest survival on wetlands with shorter spring hydroperiods or with soils that do not maintain water depths of 50-80cm throughout the breeding season. Continuously pumping water into wetlands that naturally drain to a dry state during the summer may be inefficient and cost prohibitive. Some wetlands may have soils that drain swiftly following flooding, which would necessitate the need for continuous pumping. I recommend focusing wetland management targeted on breeding least bittern to wetlands with suitable vegetative characteristics that can maintain water depths between 50-80cm during June and July without the need for extensive supplemental water addition. The wetland areas I surveyed during my study were complexes of several smaller wetlands, which may differ in the amount of management required to create conditions suitable for breeding least bittern. These wetland areas are also part of a landscape that includes privately managed wetland areas. Although my study focuses on publicly managed wetlands, these private wetland areas may provide additional wetland suitable for breeding least bittern.

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TABLES

Table 2.1. Mean (±SD) habitat characteristics associated with both available random points and used successful and used failed least bittern (*Ixobrychus exilis*) nest sites located on public wetlands during the 2013 and 2014 breeding seasons in Missouri, USA.

Scale	Variable	Available	Used		
Wetland Level[1]			Overall	Successful	Failed
		n=39	n=8	n=3	n=5
	Depth	25.31	38.82	51.29	31.35
		14.72	19.46	23.42	14.22
	Height	61.34	57.69	57.02	58.10
		39.41	28.47	36.53	27.41
	Robel	1.61	1.45	1.61	1.36
		0.9	0.33	0.53	0.16
	Ow	35.25	38.01	42.50	35.33
		12.36	10.17	16.22	5.05
	Emerge	48.2	58.53	56.94	59.50
		19.93	9.82	15.60	6.65
	Initiation	55	73	72.33	73.40
		20.48	8.28	9.23	8.76
	Duration	118.78	136.25	135.67	136.60
		20.43	7.24	8.08	7.67
Point Level[2]		Available	Overall	Successful	Failed
		n=284	n=71	n=46	n=25
	Depth	37.26	61.85	69.97	46.88
		25.29	18.23	13.45	16.45
	Height	47.81	117.80	117.09	119.09
		59.92	42.56	45.23	37.99
	Robel	2.24	2.38	2.12	2.86
		2.47	1.67	1.49	1.89
	Ow	45.86	37.35	42.39	28.08
		38.63	21.57	20.78	20.21
	Emerge	50.74	62.51	57.6	71.52
		38.26	21.42	20.78	19.9
	Initiation	66.80	75.11	77.08	71.48
		22.64	8.06	7.80	7.33
	Duration	132.88	138.10	139.8	134.92
		14.37	7.05	6.83	6.41

[1] At the wetland scale, variables were measured for the entire wetland

[2] At the local scale, variables were measured within a 50m radius of a central point or nest

Depth: average water depth (cm)
Height: average vegetation height (cm)
Robel: vegetation density measured using a Robel pole
% Open water: percent of open water coverage
% emergents: percent of emergent vegetation coverage
Initiation: Julian day of drawdown initiation
Duration: duration of drawdown in days

Table 2.2. Logistic regression model selection results for 16 wetland selection models examining differences in habitat characteristics between 8 sites used by breeding least bittern (*Ixobrychus exilis*) and 31 available wetlands during the 2013 and 2014 breeding seasons in Missouri, USA.

Model	K	AICc	ΔAICc	ModelLik	AICcWt	LL	Cum.Wt
Depth+Emerge	3	38.26	0.00	1.00	0.37	-15.80	0.37
Depth	2	40.20	1.94	0.38	0.14	-17.94	0.52
Depth+Emerge+(Depth*Emerge)	4	40.72	2.46	0.29	0.11	-15.79	0.62
Depth+Flood	3	41.91	3.65	0.16	0.06	-17.62	0.68
Emerge	2	42.08	3.82	0.15	0.06	-18.88	0.74
Depth+Robel	3	42.19	3.93	0.14	0.05	-17.76	0.79
Depth+Ow	3	42.24	3.98	0.14	0.05	-17.79	0.84
Depth+Depth^2	3	42.53	4.27	0.12	0.04	-17.93	0.90
Depth+Height	3	42.54	4.28	0.12	0.04	-17.94	0.93
Ow	2	43.90	5.64	0.06	0.02	-19.79	0.95
Height	2	44.29	6.03	0.05	0.02	-19.98	0.97
Depth+Height+Robel	4	44.65	6.39	0.04	0.02	-17.75	0.99
Depth+Height+(Depth*Height)	4	45.00	6.74	0.03	0.01	-17.93	1.00
Duration	2	57.19	18.93	0.00	0.00	-26.54	1.00
Initiation	2	57.59	19.33	0.00	0.00	-26.74	1.00
Flood	2	58.05	19.79	0.00	0.00	-26.97	1.00
Null	1	59.53	21.27	0.00	0.00	-28.75	1.00

Note: Models were ranked based on Akaike's information criterion (AIC) and weights of evidence (AIC weight). K is the degrees of freedom, ΔAICc is the difference in AICc from the top model, ModelLik is the log likelihood of the model, AICcWt is the weight of evidence that a given model is the best model, LL is the negative log likelihood of the model, and Cum. Wt is the cumulative added weight of each model to the models above it on the table.

Table 2.3. Model-averaged parameter estimates from all models in the 90% AIC weight confidence set from the logistic regression of 16 models examining differences in habitat characteristics between 34 publicly managed wetlands selected used by breeding least bittern (*Ixobrychus exilis*) and available sites in Missouri during the 2013 and 2014 breeding seasons.

	Model1		Model2		Model3		Model4		Model5		Model6		Model7		Model 8		Model-Avg	
Cov.	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
Depth	0.06	0.03	0.05	0.02	0.08	0.090.025	0.04	0.03			0.05	0.03	0.06	0.03	0.06	0.1	**0.06**	**0.03**
Depth* Emerge					-0.0002	0.0015											-0.0002	0.0015
Depth^2															-.0001	0.001	-.0001	0.001
Robel											-0.336	0.594					-0.35	0.59
Emerge	0.05	0.03			0.04	0.03			0.038	0.027							0.05	0.03
Ow													-0.02	0.04			-0.02	0.04
Flood							0.02	0.02									0.02	0.02

Note: Model-averaged parameter estimates and standard errors were averaged over the models in the 90% AIC weight confidence set.

Table 2.4. Eight discrete choice model rankings based on DIC value for least bittern (*Ixobrychus exilis*) nest site selection at the point level within publicly managed wetland areas during the 2013 and 2014 breeding seasons in Missouri, USA.. The point level refers to a 50m area surrounding a nest or random point.

Model	DIC
Depth+Height+Robel+Emerge+Depth^2	60
Depth+Height+Robel+Emerge	62.7
Depth+Height+Robel	63.5
Depth+Height+Depth^2	72.7
Depth+Height+Emerge	73.2
Depth	156.2
Depth+Robel	156.4
Depth+Depth^2	157.7

Depth: average water depth (cm)
Height: average vegetation height (cm)
Robel: vegetation density measured using a Robel pole
% Open water: percent of open water coverage
% Emergents: percent of emergent vegetation coverage
Begin: Julian day of drawdown initiation
Duration: duration of drawdown in days

Table 2.5. Logistic exposure AIC model selection results for 14 models examining differences in habitat characteristics surrounding 71 least bittern (*Ixobrychus exilis*) nests found on publicly managed wetland areas in Missouri, USA during the 2013 and 2014 breeding seasons.

Model	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
Depth	2	298.20	0.00	1.00	0.31	-147.07	0.31
Depth+Depth^2	3	298.94	0.74	0.69	0.22	-146.41	0.53
Depth+Height+Robel+Emerge	5	299.81	1.61	0.45	0.14	-144.74	0.67
Depth+Height+Robel+Ow	5	299.81	1.62	0.45	0.14	-144.75	0.81
Depth+Emerge	3	300.01	1.81	0.40	0.13	-146.94	0.94
Depth+Height+Robel+Ow+Emerge	6	301.84	3.64	0.16	0.05	-144.69	0.99
Depth*Emerge	2	305.44	7.25	0.03	0.01	-150.69	1.00
Depth*Ow	2	313.95	15.75	0.00	0.00	-154.94	1.00
Null	1	314.07	15.88	0.00	0.00	-156.03	1.00
Height*Robel	2	315.12	16.92	0.00	0.00	-155.53	1.00
Robel	2	315.49	17.30	0.00	0.00	-155.72	1.00
Emerge	2	315.72	17.53	0.00	0.00	-155.83	1.00
Height	2	315.77	17.58	0.00	0.00	-155.86	1.00
Height+Robel+Emerge	4	317.93	19.73	0.00	0.00	-154.86	1.00

Note: Models were ranked based on Akaike's information criterion (AIC) and weights of evidence (AIC weight). K is the degrees of freedom, ΔAICc is the difference in AICc from the top model, ModelLik is the log likelihood of the model, AICcWt is the weight of evidence that a given model is the best model, LL is the negative log likelihood of the model, and Cum. Wt is the cumulative added weight of each model to the models above it on the table.

Table 2.6. Model-averaged parameter estimates from all models in the 90% AIC weight confidence set from the logistic exposure regression of 13 models examining differences in habitat characteristics surrounding 71 least bittern (*Ixobrychus exilis*) nests found on publicly managed wetland areas in Missouri during the 2013 and 2014 breeding seasons.

	Model1		Model2		Model3		Model4		Model5		Model-Avg	
Covariate	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
Depth	0.0335	0.0088			0.0373	0.0101	0.0372	0.0101	0.0341	0.0094	**0.0351**	**0.0096**
Depth^2			-0.0004	0.0004							-0.0004	0.0004
Height					0.0104	0.0051	0.0103	0.0050			0.0103	0.0051
Robel					-0.0778	0.1020	-0.0783	0.1019			-0.0780	0.1019
Emerge					-0.0017	0.0096			0.0036	0.0081	0.0008	0.0093
Ow							0.0015	0.0095			0.0015	0.0095

Note: Model-averaged parameter estimates and standard errors were averaged over the models in the 90% AIC weight confidence set.

FIGURES

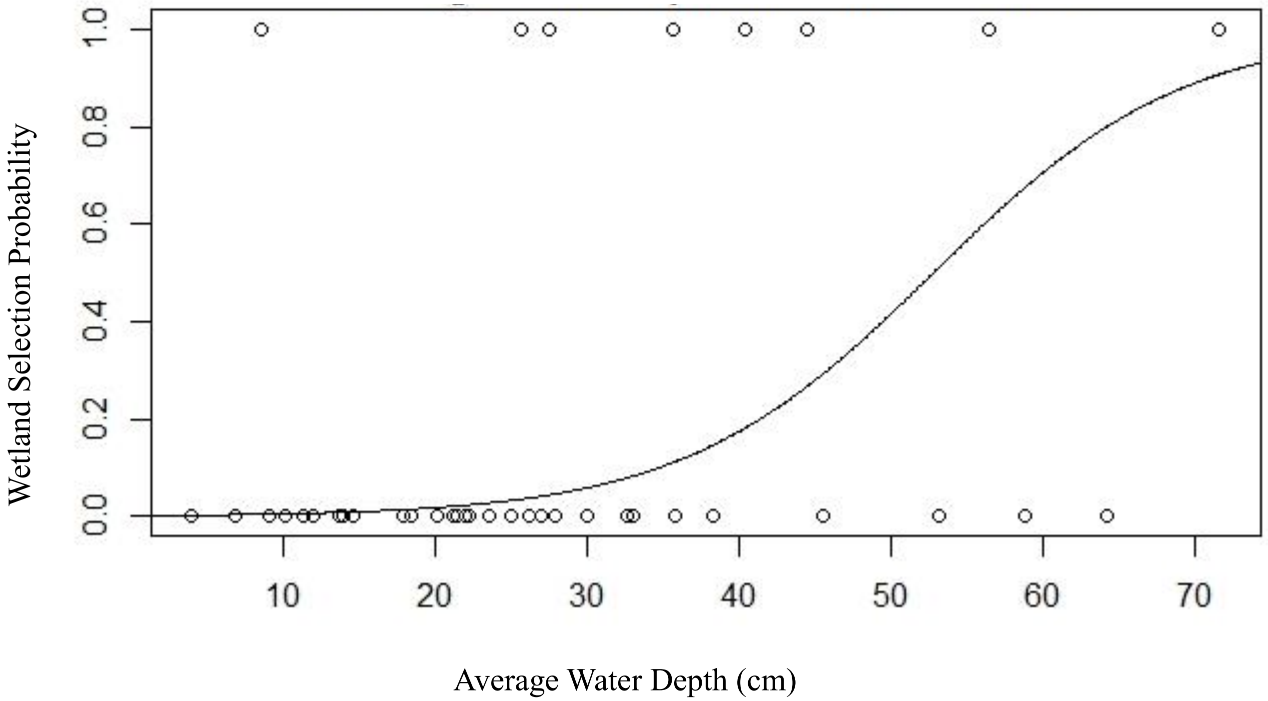


Figure 2.1. Effect of the average water depth on the relative probability a site would be selected by breeding least bitterns (*Ixobrychus exilis*) as a nesting wetland during the 2013 and 2014 breeding seasons in Missouri, USA.

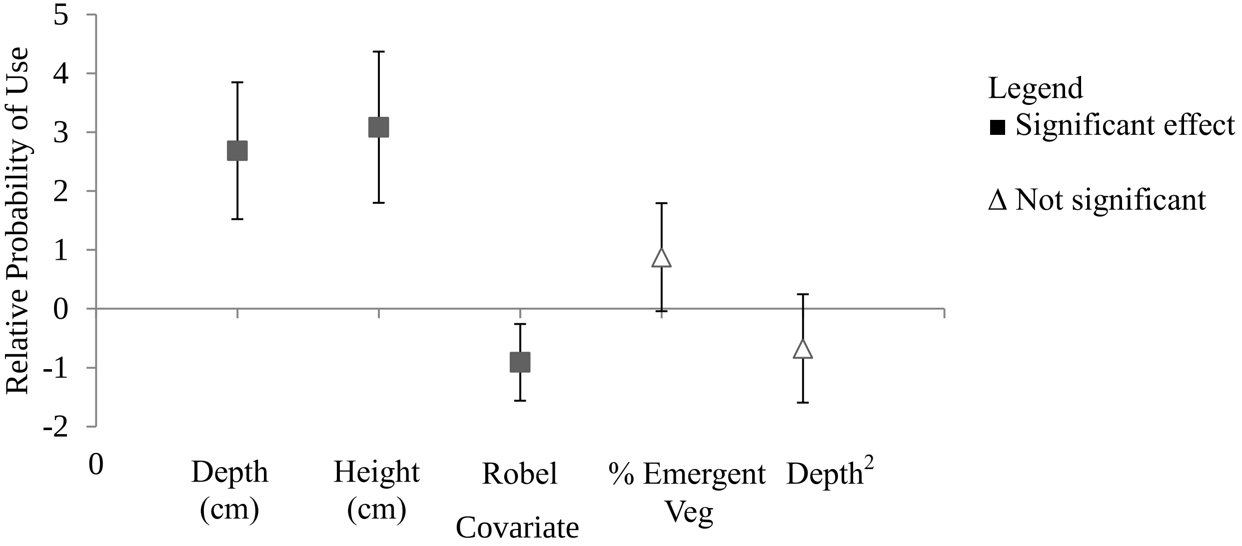


Figure 2.2. Model-averaged parameter estimates and associated 95 % credible intervals for the top discrete choice model that examined relative probability of use of habitat characteristics by breeding least bittern (*Ixobrychus exilis*) within managed public wetland areas during the 2013 and 2014 breeding seasons in Missouri, USA.

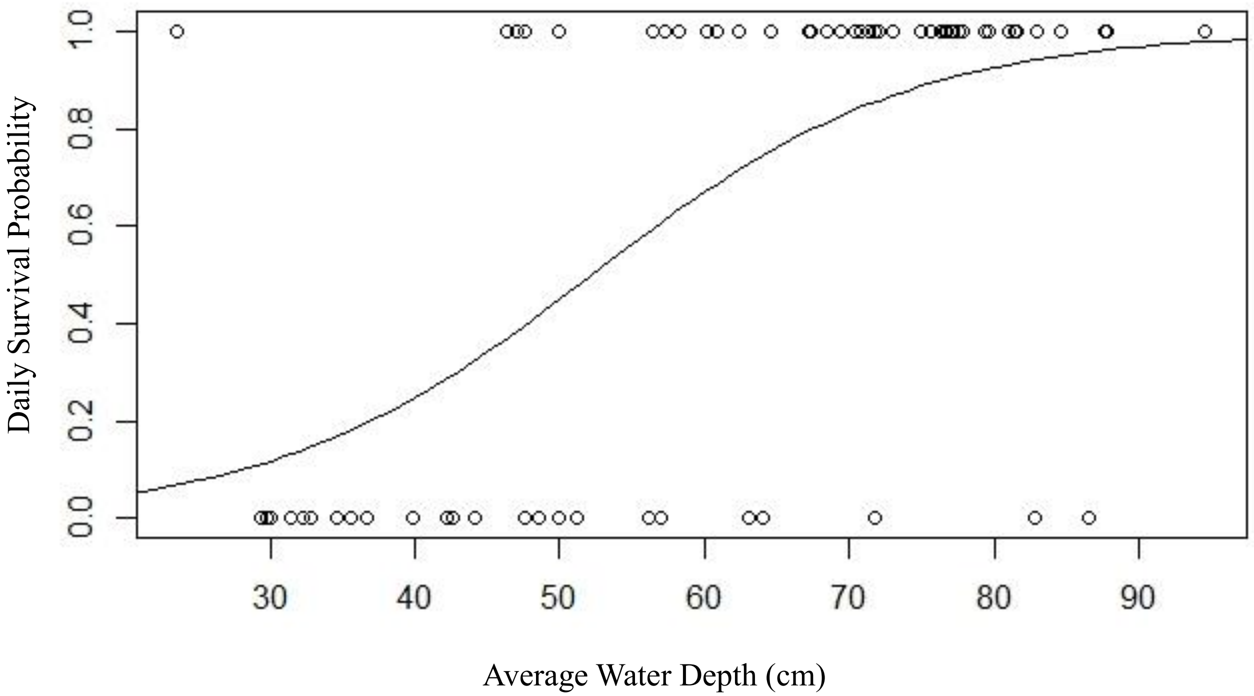


Figure 2.3. Effect of the average water depth surrounding least bittern (*Ixobrychus* exilis) nest locations on the predicted daily survival probability of those nests found on publicly managed wetlands in Missouri during the 2013 and 2014 breeding seasons.

APPENDICES

Appendix 1. Water management strategy of each study site where SMB surveys were conducted during spring 2013 and 2014 and their corresponding study areas and regions in Missouri, USA.

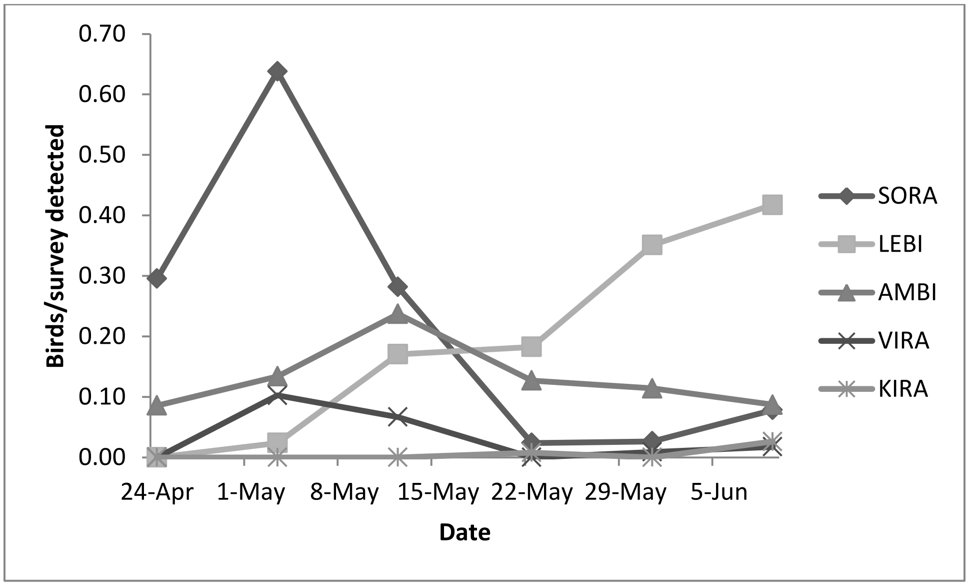
Region	Study Area	Site	Type
Central	Fountain Grove	Boardwalk	passive[1]
		Pool 2	active[2]
		Pool 3	active
		Stinson Marsh	active
		West Parsons	passive
	Grand Pass	Wellhead	active
		Tetesau Lake	passive
		Pool 1	active
		Pool 7N	active
		Pool 8	active
	Swan Lake	M6	passive
		M2	active
		M10	active
		M12	active
		M17	passive
Northeast	BK Leach	Bittern Basin 3	passive
		Bittern Basin 1	passive
		King's Lake 5	passive
		King's Lake 6	active
		King's Lake 9	passive
Northeast	Clarence Cannon	14B	active
		Big Pond	passive
		Msu 4	active
		Msu 5	active
		Msu 9	passive
	Ted Shanks	Pool 2	active
		Pool 3D	active
		Pool 11A	passive
		Nose Slough	active
		Salt Pits	passive

1 Water levels in sites classified as passive were not manipulated but allowed to fluctuate without restriction.

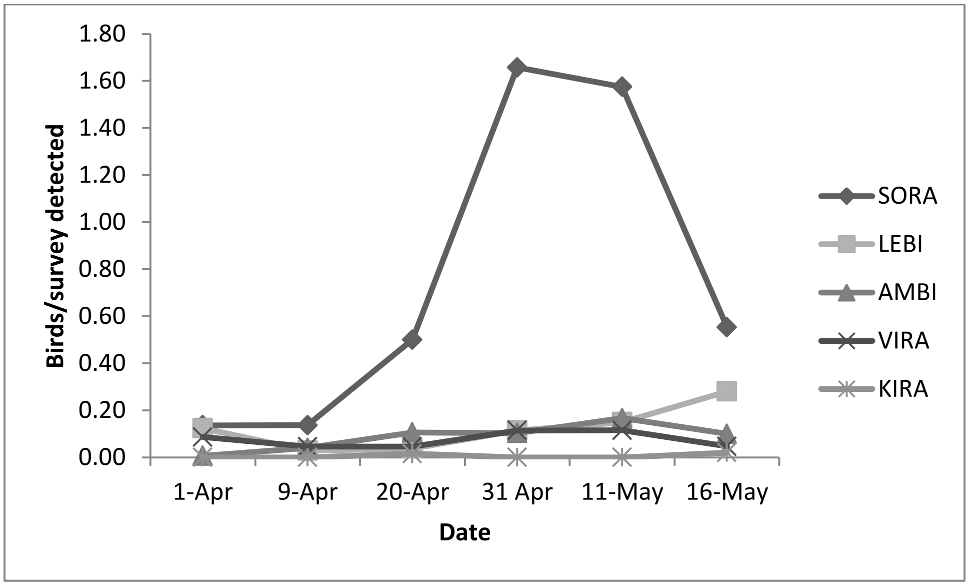
2 Active sites experienced a drawdown during the spring migration season, with most sites expected to be completely drawn down within 2-4 weeks.

Appendix 1 cont. Water management strategy of each study site where SMB surveys were conducted during spring 2013 and 2014 and their corresponding study areas and regions in Missouri, USA.

Region	Study Area	Site	Type
Northwest	Bob Brown	Ringneck	passive
		Sandpiper flats	passive
		Iowa Point	passive
	Nodaway Valley	Ash Grove	passive
		Cattail Ditch	active
		Mike Keller	passive
		Redhead North	passive
		Redhead South	passive
		Sanctuary	passive
	Squaw Creek	MSU 3	active
		North Pintail	passive
		Snow Goose A	active
		Mallard North	active
		Mallard South	passive
		Pelican	passive
Southeast	Mingo	Red Mill	passive
		MS 4S	active
		MS 7N	active
		MS 8E	passive
		MS 9	active
	Duck Creek	11	active
		20	active
		22	active
		23	active
		54	active
	Otter Slough	13	passive
		17	active
		30	active
		32	active
		Plover Pond	passive



Appendix 2. Detections of each species per call-broadcast survey in 2013 on publicly managed wetlands in Missouri, USA. The species evaluated are: sora (*Porzana carolina*), least bittern (*Ixobrychus exilis*), American bittern (*Botaurus lentiginosus*), Virginia rail (*Rallus limicola*), and king rail (*Rallus elegans*).



Appendix 3. Detections of each species per call-broadcast survey in 2014 on publicly managed wetlands in Missouri, USA. The species evaluated are : sora (*Porzana carolina*), least bittern (*Ixobrychus exilis*), American bittern (*Botaurus lentiginosus*), Virginia rail (*Rallus limicola*), and king rail (*Rallus elegans*).

Appendix 4. AIC model selection results for 8 detection models in the 90% AIC weight confidence set, examining differences in observer and environmental characteristics that would influence detection rates of sora (*Porzana carolina*) on publicly managed wetland areas in Missouri, USA during the 2013 and 2014 spring migration seasons.

Model	K	AIC	delta	-LogLike	AICwt	cumltv
ψ(.)+γ(.)+ε(.)+*p*(Observer)	11	1482.03	0.00	730.02	1.00	1
ψ(.)+γ(.)+ε(.)+*p*(Round)	9	1513.22	31.19	747.61	0.00	1
ψ(.)+γ(.)+ε(.)+*p*(Sky)	5	1525.59	43.56	757.80	0.00	1
ψ(.)+γ(.)+ε(.)+*p*(Noise)	5	1532.24	50.21	761.12	0.00	1
ψ(.)+γ(.)+ε(.)+*p*(Noise+Wind)	6	1533.61	51.58	760.80	0.00	1
ψ(.)+γ(.)+ε(.)+*p*(Wind)	5	1534.66	52.63	762.33	0.00	1
ψ(.)+γ(.)+ε(.)+*p*(Start)	5	1535.26	53.23	762.63	0.00	1
ψ(.)+γ(.)+ε(.)+*p*(Temp)	5	1536.44	54.41	763.22	0.00	1

Note: Models were ranked based on Akaike's information criterion (AIC) and weights of evidence (AIC weight). K is the degrees of freedom, delta is the difference in AIC from the top model, -LogLike is the negative log likelihood of the model, AICwt is the weight of evidence that a given model is the best model, cumltv is the cumulative added weight of each model to the models above it on the table, ψ is initial occupancy, ε is extinction probability, γ is colonization probability, and *p* is detection probability.

Appendix 5. AIC model selection results for 8 detection models in the 90% AIC weight confidence set, examining differences in observer and environmental characteristics that would influence detection rates of least bittern (*Ixobrychus exilis*) on publicly managed wetland areas in Missouri, USA during the 2013 and 2014 spring migration seasons.

Model	K	AIC	delta	-LogLike	AICwt	cumltv
$\psi(.)+\gamma(.)+\varepsilon(.)+p$(Round)	9	798.7	0	390.35	0.9	0.9
$\psi(.)+\gamma(.)+\varepsilon(.)+p$(Temp)	5	803.26	4.55	396.63	0.09	1.00
$\psi(.)+\gamma(.)+\varepsilon(.)+p$(Wind)	5	811.66	12.96	400.83	0.00	1.00
$\psi(.)+\gamma(.)+\varepsilon(.)+p$(Noise+Wind)	6	813.58	14.87	400.79	0.00	1.00
$\psi(.)+\gamma(.)+\varepsilon(.)+p$(Sky)	5	815.11	16.41	402.56	0.00	1.00
$\psi(.)+\gamma(.)+\varepsilon(.)+p$(Start)	5	815.42	16.71	402.71	0.00	1.00
$\psi(.)+\gamma(.)+\varepsilon(.)+p$(Noise)	5	815.51	16.80	402.76	0.00	1.00
$\psi(.)+\gamma(.)+\varepsilon(.)+p$(Obs)	11	818.34	19.64	398.17	0.00	1.00

Note: Models were ranked based on Akaike's information criterion (AIC) and weights of evidence (AIC weight). K is the degrees of freedom, delta is the difference in AIC from the top model, -LogLike is the negative log likelihood of the model, AICwt is the weight of evidence that a given model is the best model, cumltv is the cumulative added weight of each model to the models above it on the table, ψ is initial occupancy, ε is extinction probability, γ is colonization probability, and p is detection probability.

Appendix 6. AIC model selection results for 8 detection models in the 90% AIC weight confidence set, examining differences in observer and environmental characteristics that would influence detection rates of American bittern (*Botaurus lentiginosus*) on publicly managed wetland areas in Missouri, USA during the 2013 and 2014 spring migration seasons.

Model	K	AIC	delta	-LogLike	AICwt	cumltv
$\psi(.)+\gamma(.)+\varepsilon(.)+p(\text{Sky})$	5	739.01	0.00	364.50	0.45	0.45
$\psi(.)+\gamma(.)+\varepsilon(.)+p(\text{Obs})$	11	741.50	2.49	359.75	0.13	0.57
$\psi(.)+\gamma(.)+\varepsilon(.)+p(\text{Start})$	5	741.80	2.80	365.90	0.11	0.69
$\psi(.)+\gamma(.)+\varepsilon(.)+p(\text{Temp})$	5	742.14	3.13	366.07	0.09	0.78
$\psi(.)+\gamma(.)+\varepsilon(.)+p(\text{Noise})$	5	742.23	3.22	366.11	0.09	0.87
$\psi(.)+\gamma(.)+\varepsilon(.)+p(\text{Wind})$	5	742.24	3.23	366.12	0.09	0.96
$\psi(.)+\gamma(.)+\varepsilon(.)+p(\text{Noise+Wind})$	6	744.01	5.00	366.01	0.04	0.99
$\psi(.)+\gamma(.)+\varepsilon(.)+p(\text{Round})$	9	747.24	8.24	364.62	0.01	1.00

Note: Models were ranked based on Akaike's information criterion (AIC) and weights of evidence (AIC weight). K is the degrees of freedom, delta is the difference in AIC from the top model, -LogLike is the negative log likelihood of the model, AICwt is the weight of evidence that a given model is the best model, cumltv is the cumulative added weight of each model to the models above it on the table, ψ is initial occupancy, ε is extinction probability, γ is colonization probability, and p is detection probability.

Appendix 7. AIC model selection results for 8 detection models in the 90% AIC weight confidence set, examining differences in observer and environmental characteristics that would influence detection rates of Virginia rail (*Rallus limicola*) on publicly managed wetland areas in Missouri, USA during the 2013 and 2014 spring migration seasons.

Model	K	AIC	delta	-LogLike	AICwt	cumltv
ψ(.)+γ(.)+ε(.)+*p*(Wind)	5	576.56	0.00	283.2781	0.22	0.22
ψ(.)+γ(.)+ε(.)+*p*(Observer)	11	576.56	0.01	277.2807	0.21	0.43
ψ(.)+γ(.)+ε(.)+*p*(Sky)	5	577.21	0.65	283.6045	0.16	0.58
ψ(.)+γ(.)+ε(.)+*p*(Noise)	5	577.61	1.06	283.8068	0.13	0.71
ψ(.)+γ(.)+ε(.)+*p*(Noise+Wind)	6	577.97	1.42	282.9869	0.11	0.82
ψ(.)+γ(.)+ε(.)+*p*(Start)	5	578.09	1.53	284.0452	0.10	0.92
ψ(.)+γ(.)+ε(.)+*p*(Temp)	5	578.65	2.09	284.32	0.08	0.99
ψ(.)+γ(.)+ε(.)+*p*(Round)	9	583.41	6.85	282.70	0.01	1.00

Note: Models were ranked based on Akaike’s information criterion (AIC) and weights of evidence (AIC weight). K is the degrees of freedom, delta is the difference in AIC from the top model, -LogLike is the negative log likelihood of the model, AICwt is the weight of evidence that a given model is the best model, cumltv is the cumulative added weight of each model to the models above it on the table, ψ is initial occupancy, ε is extinction probability, γ is colonization probability, and *p* is detection probability.