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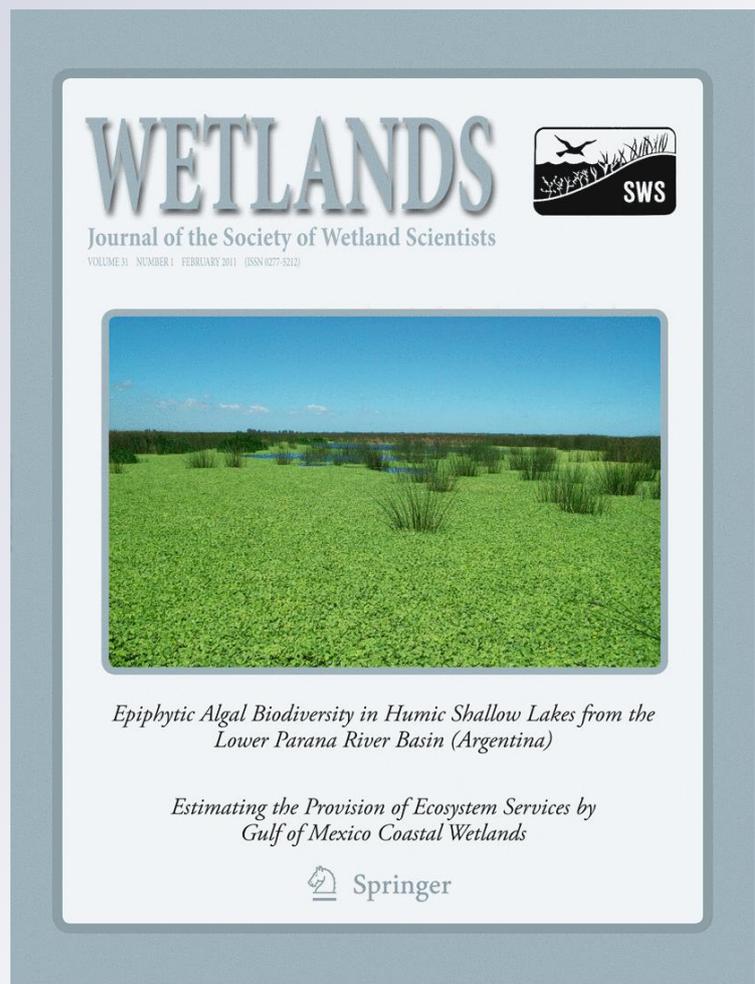
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Distribution and Habitat Associations of Breeding Secretive Marsh Birds in Louisiana's Mississippi Alluvial Valley

Jonathon J. Valente · Sammy L. King ·
R. Randy Wilson

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Abstract Populations of many North American secretive marsh birds (SMBs) have declined in recent decades, partially as a function of wetland loss. Protecting and restoring appropriate habitat for these species is contingent upon understanding the habitat features they utilize. We investigated breeding distributions of SMBs in northeast Louisiana at 118 wetlands in 2007 and 2008 and modeled species occupancy (ψ) as a function of habitat variables measured at local (≤ 100 m) and landscape (≤ 1 km) scales. Common Moorhens (*Gallinula chloropus*), Least Bitterns (*Ixobrychus exilis*), and Purple Gallinules (*Porphyrola martinica*) were the most commonly detected species, whereas breeding King Rails (*Rallus elegans*) and American Coots (*Fulica americana*) were rare. Local habitat features consistently played a greater role in predicting ψ than landscape features for the three most common species. The

proportion of local wetland area dominated by robust emergent vegetation (i.e., *Typha* spp. and *Zizaniopsis miliacea*) positively influenced ψ for all species, while other wetland vegetation types tended to have a minimal or negative effect. Our results suggest the habitat characteristics preferred by breeding SMBs differ from those used by migrating shorebirds and wintering waterfowl and management and restoration objectives for those species may be inadequate for enhancing SMB habitat.

Keywords Bittern · Rail · Wetland

Introduction

Wetlands are some of the most ecologically important habitats in the world, providing valuable ecosystem services, and supporting diverse floral and faunal communities. Yet wetland area has been dramatically declining in the conterminous United States for more than 200 years, from an estimated 89.4 million hectares before European settlement, to approximately 42.1 million hectares by 1980 (Dahl 1990). The rate of destruction has been particularly severe in the Southeast, which contains nearly half of the country's wetland area, yet accounted for 89% of net wetland loss (105,000 hectares/yr) between the mid-1970s and the mid-1980s (Hefner et al. 1994). Consequently, wetland protection and restoration has become a primary conservation objective in this region for a variety of ecological, cultural, and economic reasons (Hefner et al. 1994; King et al. 2006). The Natural Resources Conservation Service, for instance, has spent more than \$95 million to date restoring and managing more than 52,000 hectares of wetland habitat in Louisiana as part of its Wetlands Reserve Program (WRP; NRCS 2010).

J. J. Valente (✉)
School of Renewable Natural Resources,
Louisiana State University,
Baton Rouge, LA 70803, USA
e-mail: Jonathon.J.Valente@gmail.com

S. L. King
U.S. Geological Survey, Louisiana Cooperative Fish and Wildlife
Research Unit, 124 School of Renewable Natural Resources,
Louisiana State University,
Baton Rouge, LA 70803, USA

R. R. Wilson
U.S. Fish and Wildlife Service,
6578 Dogwood View Parkway Suite B,
Jackson, MS 39213, USA

Present Address:
J. J. Valente
Environmental Laboratory, US Army Engineer
Research and Development Center,
Louisville, KY 40204, USA

The Lower Mississippi Valley Joint Venture (LMVJV) is a partnership developed among private, state, and federal agencies that focuses on implementing the objectives of national and international bird conservation plans in the Mississippi Alluvial Valley (MAV). The LMVJV has set specific wetland management and restoration objectives for both wintering waterfowl (Loesch et al. 1994) and migrating shorebirds (Elliott and McKnight 2000), but currently lacks the information it needs to create effective strategies for supporting populations of breeding secretive marsh birds (SMBs). SMBs are a group of marsh-dependent species that includes all rails, bitterns, moorhens, and gallinules (Conway 2005). Although populations of these birds are broadly distributed across North America, SMBs remain one of the most poorly studied avian groups. For most species we lack basic information on population size, distribution, breeding and foraging ecology, migration patterns, and habitat requirements (Eddleman et al. 1988). Evidence suggests that many SMB species have suffered drastic population declines in recent decades (Eddleman et al. 1988; Timmermans et al. 2008), which may be primarily attributable to wetland loss (Eddleman et al. 1988; Conway et al. 1994). Indeed, the emergent palustrine and riverine wetlands utilized by SMBs continue to be among the most threatened (Eddleman et al. 1988, Dahl 2006), and there is no indication that population sizes of SMB species have benefitted from increased wetland restoration and conservation efforts. One possible explanation for this is that we are not protecting and restoring wetlands that exhibit habitat characteristics appropriate for breeding SMBs. Consequently, it is important to develop a thorough understanding of the habitat resources these birds prefer in various stages of their life cycles.

Numerous studies have investigated SMB nest site characteristics, describing the impacts of vegetation cover, water depth, vegetation height, and vegetation composition around active nests, yet speculation over the relative importance of these variables continues (Flores and Eddleman 1995; Popper and Stern 2000; Robert et al. 2000; Lor and Malecki 2006). For example, Lor and Malecki (2006) found a general trend indicating a higher probability of encountering a nest of five SMB species at sites with increased emergent vegetation, horizontal cover and shallow water depths, whereas Rehm and Baldassarre (2007) investigated the abundance of these same five species in some of the same locations and discovered that interspersed, as measured by edge density, was the best predictor of abundance for four out of those five species. Moreover, avian habitat selection is a multi-phase process (Johnson 1980; Burger 1985; Kristan 2006), and multi-scale habitat selection models are therefore more useful for predicting organism locations (Kristan 2006; Meyer and Thuiller 2006). Yet, few studies have evaluated the

influence of landscape context on wetland occupancy by SMBs, and even fewer have explicitly investigated habitat selection by these species at multiple spatial scales simultaneously, or compared the relative importance of those scales in the decision making process (but see Naugle et al. 2001; Rehm and Baldassarre 2007; Pierluissi and King 2008).

To our knowledge the only data that have been collected to date regarding breeding distributions of SMBs in Louisiana's MAV come from the Louisiana Breeding Bird Atlas (Wiedenfeld and Swan 2000). However, emergent wetland communities are generally not adequately sampled by most bird surveys (Robbins et al. 1986; Gibbs and Melvin 1993), and recent studies suggest that many SMB species are very difficult to detect without utilizing callback recordings to elicit responses (Allen et al. 2004; Conway 2005; Conway and Gibbs 2005). Other researchers have found that Purple Gallinules (*Porphyrio martinica*), King Rails (*Rallus elegans*), Common Moorhens (*Gallinula chloropus*), and Least Bitterns (*Ixobrychus exilis*) nest successfully and in relatively high densities along Louisiana's coast in landscapes dominated by vast complexes of agricultural wetlands (Helm et al. 1987; Hohman et al. 1994; Pierluissi 2006). Yet, wetlands in the MAV were predominantly created by the Mississippi River and are located in landscapes dominated by non-wetland agricultural crops and remnant tracts of bottomland hardwood forest. Thus, wetlands of Louisiana's MAV may differ greatly from coastal wetlands in terms of hydrologic characteristics, vegetation structure, composition, and landscape context. Our research objectives were 1) to identify which of six secretive marsh bird species (King Rail, Purple Gallinule, Common Moorhen, Least Bittern, American Bittern [*Botaurus lentiginosus*], and American Coot [*Fulica Americana*]) breed in the MAV of northeast Louisiana, 2) to model site occupancy as a function of habitat variables at multiple spatial scales for each breeding species, and 3) to provide information that can be used to improve restored and managed wetland habitats for breeding SMBs.

Methods

Study Area

Our study area encompassed most of the MAV in Louisiana north of 31°12" north latitude and east of 92°10'15" west longitude (Fig. 1). Most wetlands in this area were created by the Mississippi River, yet today, an extensive levee system has predominantly decoupled them from its hydrologic influence. The landscape was once dominated by dense bottomland hardwood forest but >80% has been converted to agriculture in the past 200 years (TNC 2009).

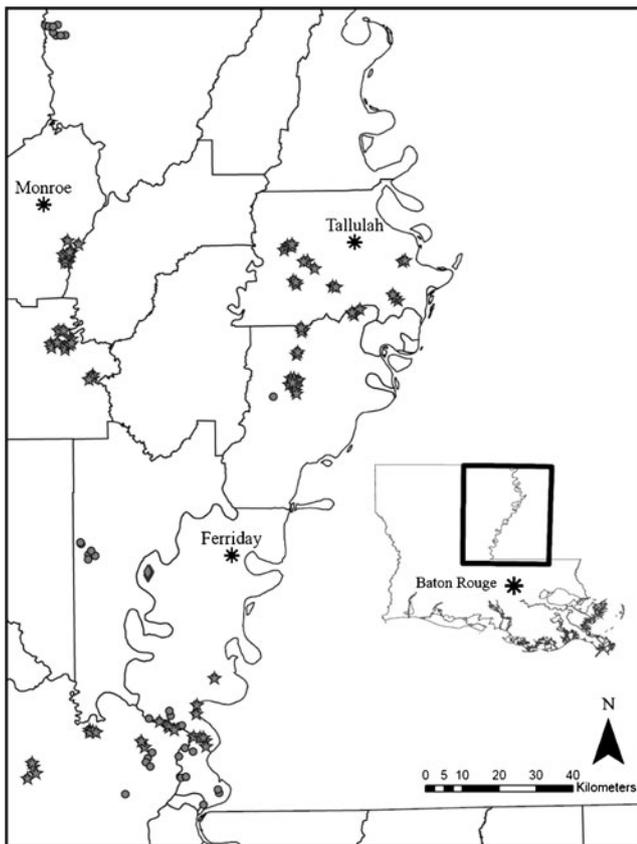


Fig. 1 Locations of 118 wetland sites situated in Louisiana's Mississippi Alluvial Valley which were sampled for secretive marsh birds during the breeding seasons of 2007 and 2008. Circles indicate wetlands which were only sampled in 2007, diamonds indicate those which were only sampled in 2008 and stars indicate wetlands sampled in both years. Several towns are marked with an asterisk for reference

Our study included 49 wetlands on six Louisiana Department of Wildlife and Fisheries Wildlife Management Areas (WMAs; Boeuf, Buckhorn, Ouachita, Pomme de Terre, Red River and Three Rivers), 27 wetlands on four U.S. Fish and Wildlife Service National Wildlife Refuges (NWRs; Catahoula Lake, Grand Cote, Tensas and Upper Ouachita), and 57 wetlands on 25 WRP easements operated by the U.S. Department of Agriculture Natural Resources Conservation Service in six Parishes (Avoyelles, Caldwell, Catahoula, Concordia, Madison and Tensas). Forested wetlands were excluded from consideration because they are not suitable breeding habitat for our study species. Characteristics of our study wetlands varied greatly in terms of vegetation, hydrologic features, landscape context, and size; the largest wetland was >240 ha, but most were <1 ha. Common wetland plants in the region included alligatorweed (*Alternanthera philoxeroides*), water primrose (*Ludwigia* spp.), smartweed (*Polygonum* spp.) sedges (Cyperaceae), arrowhead (*Sagittaria* spp.), needle-rush (*Juncus effuses*), cattail (*Typha* spp.), spikerush (*Eleocharis* spp.), and willow (*Salix nigra*).

Site Selection

We digitized each wetland ($n=318$) on all WMAs, NWRs, and WRP easements we were granted access to using ArcMap 9.1 (ESRI Corporation, Redlands, CA). We used an ArcMap™ tool to randomly place one point on the land-water interface of each wetland with the stipulation that all points had to be at least 700 m apart. Though this spacing is more conservative than the 400 m separation recommended by Conway (2005), we wanted to be absolutely certain we would not detect the same individual bird at multiple sites. Approximately one third of the sample sites were eliminated for logistical reasons (e.g., location relative to other sites, distance from nearest lodging, etc.). From the remaining subset we randomly selected 114 wetlands to sample in 2007. When selected points were found to be inaccessible in the field, they were moved to an accessible spot as close to the original point as possible, while still maintaining the 700 m minimum distance from other sampling points. Our goal in 2008 was to completely replicate our study, but due to large scale flooding throughout much of the spring, we were only able to replicate the surveys at 79 (69.3%) of the original 114 sites; four sites were also added in 2008 to fill in a large geographic gap in Concordia Parish (Fig. 1).

Marsh Bird Sampling

Four observers conducted morning and evening callback surveys for marsh birds at each wetland site between 18 March 2007 and 25 June 2007; three observers conducted surveys between 5 April 2008 and 17 June 2008. We began sampling later in 2008 because the presence of migrants throughout March in the first year confounded our ability to determine which individual birds were breeding. We attempted to survey sites once or twice approximately every 15 days (sampling period), and survey procedures followed those outlined by the Standardized North American Marsh Bird Monitoring Protocols (Conway 2005). Each survey included a 1-min "settling" period, a 5-min passive period, and a 6-min callback period. The callback period consisted of playing 30 s of calls from six secretive marsh bird species (Least Bittern, King Rail, American Bittern, Common Moorhen, Purple Gallinule and American Coot sequentially) followed by 30 s of silence. Pierluissi (2006) found that the American Bittern call elicits responses from King Rails, so we incorporated it into the study design despite the fact that Louisiana is outside its breeding range. Sora calls were not played but Sora detections were recorded. Calls were played from an RP2700A portable CD player (RCA, Paris, France) and broadcast through 40-1434 portable folding speakers (RadioShack, Fort Worth, TX). Observers measured the

distance from the sampling point to the approximate (because many detections were aural) location of each individual bird detected using Yardage Pro Sport 450 range finders (Bushnell, Overland Park, KS).

Habitat Sampling

In both years we conducted one local habitat survey at each site, recording wetland and upland habitat characteristics within a 100 m radius circle centered on the survey point. All habitat surveys were conducted between 1 June 2007 and 11 June 2007, and between 6 June 2008 and 27 June 2008. We recorded the proportion of the survey circle covered by water, and broke the upland habitat down into four categories, defined by the structure of the dominant vegetation type: agriculture, grass and weeds, trees <3 m tall, and trees ≥ 3 m tall. We further characterized wetland vegetation within the associated flooded area by recording each plant species present, the proportion of the wetland it covered, and its mean height. Submerged areas that were not covered by floating or emergent vegetation were considered open water. While we acknowledge that structurally insignificant floating plants such as lesser duckweed (*Lemna minor*) and mosquito fern (*Azolla caroliniana*) may be important food resources for some SMBs, it was difficult to quantify availability of these plants in the field, and thus flooded areas dominated by such species were considered open water.

We also collected landscape scale habitat information by drawing a 1-km circle around each sampling point over digital orthophotos taken in 2007 as part of the U.S. Department of Agriculture's National Agriculture Imagery Program. We printed the image of each site and classified all parts of the landscape into one of five categories in the field: agriculture; residential, grassland, or pasture; wetland or permanent water; young reforested (i.e., dominated by trees ≤ 3 m); or forest (i.e., dominated by trees > 3 m). We then digitized these landscapes using ArcMap™ and calculated the proportion that was comprised of each habitat feature.

Data Analyses

We used a likelihood-based approach to model site occupancy (ψ) for each species separately as a function of measured habitat variables while simultaneously accounting for detection probabilities (p ; MacKenzie et al. 2002). We truncated all surveys conducted prior to 28 April to avoid including migrating birds in our analyses; this eliminated one site sampled in 2008 because all surveys were conducted there prior to this date. If a wetland ever went dry or endured drastic habitat alterations (e.g., draining or disking), all surveys conducted at the site from that point on

were discounted. Finally, sites were also eliminated if they had no water within 100 m at the time of the vegetation survey (as this would provide misleading information about the habitat birds were using; 2007 $n=8$; 2008 $n=6$), if no habitat data were collected (2008 $n=4$), or if we only conducted one bird survey (2007 $n=1$).

For the habitat models, we only considered a site occupied by a species if that species was ever detected within 100 m of the survey point (i.e., the local vegetation survey radius). If the species was never detected within 100 m, the site was considered to be unoccupied during every survey conducted there. If, however, the species was detected within 100 m during any breeding survey at a given site, then all detections ≤ 300 m were included as part of that site's detection history. This ensures that the habitat models are applicable to sites where the species was indeed using that particular habitat, yet relaxes the assumption that a species detected within 100 m must always be within 100 m.

The development of habitat models required several steps and all covariates were standardized prior to this process. All modeling analyses were conducted using program PRESENCE (version 2.2; United States Geological Survey, Patuxent Wildlife Research Center, Laurel, MD). We first held ψ constant and modeled p as a function of all possible combinations of four survey-specific covariates: observer, Julian date, minutes before or after sunrise or sunset, and whether the survey was conducted in the morning or evening. We distinguished among these models using Akaike's Information Criterion corrected for small sample sizes (AIC_C ; Burnham and Anderson 2002:66). The variables included in the top model for each species were used to account for p in all remaining occupancy models, regardless of whether or not there was substantial support for other variable combinations.

Next we combined the habitat information we recorded into 14 local variables and four landscape-scale variables that we thought could plausibly influence SMB site occupancy based on previously published accounts and our own field observations (Table 1). To reduce the number of variables to be considered for each species we constructed models which included the effects of year, wetland area within the survey circle, and each of the habitat variables individually on ψ (models of interest), then compared them to a reduced model containing only the year and wetland area variables. If the AIC_C value associated with a model of interest was not improved by ≥ 2 units over the reduced model (i.e., if there was substantial support for the reduced model being the better explanation), then the habitat variable was eliminated from further consideration. When two of the retained variables were highly correlated (i.e., Pearson correlation coefficient $r \geq |0.7|$), we also eliminated the variable with the larger AIC_C value.

Table 1 The change in AIC_C^a values resulting from individually adding local (within 100 m) and landscape (within 1 km) habitat variables to a reduced model^b accounting for occupancy of three secretive marsh bird species encountered in northeast Louisiana in 2007 and 2008

Variables	Proportion of the area dominated by:	Description of habitat	Common Moorhen	Least Bittern	Purple Gallinule
Local Wetland					
OPEN	Water with no structurally significant vegetation cover	Open water, <i>Lemna minor</i> , and <i>Azolla caroliniana</i> , etc.	0.98	-1.10	-0.06
OPEN ²	Water with no structurally significant vegetation cover	Model investigated a quadratic relationship between occupancy and OPEN	1.78	1.17	1.77
ROBUST	Robust emergent vegetation	Only <i>Typha</i> spp. and <i>Zizaniopsis miliacea</i>	-6.55	-44.36	-6.86
NR_TALLHERB	Non-robust herbaceous emergent vegetation ≥ 0.75 m	<i>Carex</i> spp., <i>Juncus effuses</i> , <i>Rhynchospora</i> spp., etc.	-1.22	-0.01	-3.08
NR_SHORTHERB	Non-robust herbaceous emergent vegetation < 0.75 m tall	<i>Ludwigia</i> spp., <i>Alternanthera philoxeroides</i> , <i>Carex</i> spp., <i>Sagittaria</i> spp., etc.	2.11	-3.02*	2.12
TALLHERB	All herbaceous emergent vegetation ≥ 0.75 m	Sum of ROBUST and NR_TALLHERB	-1.34	-22.05*	-1.79
HERB	All herbaceous emergent vegetation	Sum of TALLHERB and NR_SHORTHERB	0.16	-0.66	0.51
SHORTWOODY	Woody emergent vegetation < 3 m	<i>Salix nigra</i> , <i>Brunnichia</i> spp., <i>Campsis radicans</i> , etc.	2.08	2.21	0.28
TALLWOODY	Woody emergent vegetation ≥ 3 m	<i>Salix nigra</i> , <i>Taxodium distichum</i> , <i>Quercus</i> spp., etc.	-3.14	-0.31	-2.07*
WOODY	All woody emergent vegetation	Sum of TALLWOODY and SHORTWOODY	-1.80	0.28	-4.21
NR_HERB	All non-robust herbaceous emergent vegetation	Sum of NR_TALLHERB and NR_SHORTHERB	1.94	-5.23	1.17
FLOAT	Structurally significant floating vegetation	<i>Nelumbo lutea</i> , <i>Eichornia crassipes</i> , <i>Potamogeton</i> spp., <i>Utricularia</i> spp., etc.	-0.34	-1.01	-6.04
Local Upland					
TALLTREES100M	Trees ≥ 3 m	Predominantly mature forest	-1.22	-1.71	-1.98
TREES100M	All trees	Mature forest and young reforested areas	2.11	-1.42	-3.72
AG100M	Agriculture	All active and fallow agricultural fields	1.17	1.11	0.70
Landscape					
WATER1KM	Water	Lakes, rivers, streams, and wetlands	2.05	-5.61	1.59
TALLTREES1KM	Trees ≥ 3 m	Predominantly mature forest	2.11	1.71	2.17
TREES1KM	All trees	Mature forest and young reforested areas	1.58	1.85	1.94
AG1KM	Agriculture	All active and fallow agricultural fields	0.70	-2.08	2.08

^a Values highlighted in bold indicate variables which substantially improved the reduced model ($\Delta AIC_C \leq 2$). An asterisk indicates that the variable was not included in the global model for the species due to high correlation with another variable that was included.

^b Reduced model includes variables accounting for detection probability, and the effects of year and local wetland area on occupancy.

Finally, we modeled ψ for each species as a function of all possible combinations of the retained habitat variables; again, each model included covariates to account for the effects of year and wetland size within our survey area. To determine the magnitude and direction of each variable effect, we calculated the weighted natural average of the parameter estimates from all candidate models (Burnham and Anderson 2002:152). Standard errors for these parameter estimates were calculated as the square root of an unconditional estimate of variance (Burnham and Anderson 2002:162). We also compared the relative importance of each habitat variable by summing the AIC_C weights of all models containing those variables. Lastly, we assessed the

fit of global models and tested them for overdispersion (\hat{c}) by comparing its Pearson's χ^2 test statistic to a χ^2 distribution generated from 10,000 bootstrapped data sets (MacKenzie and Bailey 2004).

Results

We conducted 499 bird surveys during the breeding season at 114 sites (4.38 surveys/site) from 29 April 2007 through 25 June 2007, and 457 surveys at 82 sites (5.57 surveys/site) from 28 April 2008 through 17 June 2008. We encountered one American Bittern and two Soras during

the 2007 breeding season and two American Bitterns and one Sora during the 2008 season. Neither species was detected after 10 May in any year (Fig. 2a) nor did we see any indications of breeding behavior (i.e., courtship

displays, nests, nest building, or hatch year birds). American Coots were the most abundant SMB species in early spring, yet we only had 43 detections during the 2007 breeding season and 21 during the 2008 breeding season. Detections decreased drastically by mid-May (Fig. 2b) and we observed no American Coot breeding behavior during the study. In 2007 we encountered two King Rails with the latest detection occurring on 30 March 2007. In 2008 we encountered 14 King Rails; eight detections occurred during the breeding season, and paired individuals were noted at three sites.

Common Moorhens, Least Bitterns and Purple Gallinules were encountered continually during the breeding seasons of both years (Fig. 2c). We encountered one or more of these species at >35% of surveyed sites in each year and regularly recorded signs of breeding (e.g., courtship behavior, copulation, nests and hatch year birds). These were the only species for which we had sufficient data to build breeding habitat models.

We detected Common Moorhens within 100 m of 23 of the 105 survey points (22%) used for habitat modeling in 2007, and 28 of the 73 points (38%) used in 2008. Least Bitterns and Purple Gallinules were respectively detected within 100 m of 12 (11%) and 15 (14%) of these points in 2007, and 15 (21%) and 16 (22%) points in 2008. Model averaged parameter estimates indicated that ψ for all species was positively influenced by local wetland area, and was greater in 2008 than 2007. Specific results for these variables are not presented because we were merely interested in accounting for their effects rather than quantifying them.

The best detection probability model for Common Moorhens included only a time of day effect, indicating that p was reduced from 0.65 in the morning (SE=0.04) to 0.51 (SE=0.05) in the evening. The top detection probability model for Least Bitterns indicated that p ranged from 0.11 (SE=0.07) to 0.58 (SE=0.08) depending on observer. For Purple Gallinules p estimates ranged from 0.26 (SE=0.10) to 0.75 (SE=0.09). The top detection probability model indicated that in the mornings p decreased with time since sunrise, and similarly, increased in the evenings as sunset approached. Detection probabilities for this species also decreased with date, indicating more reticent behavior later in the summer.

Six models containing individual habitat variables showed substantial improvement over the reduced model for both Least Bitterns and Purple Gallinules, while only two did for Common Moorhens (Table 1). TALLHERB was eliminated from further consideration in the Least Bittern models due to high correlation ($r=0.85$) with ROBUST and NR_SHORTHERB was eliminated due to correlation with NR_HERB ($r=0.93$). Similarly, TALLWOODY was eliminated from consider-

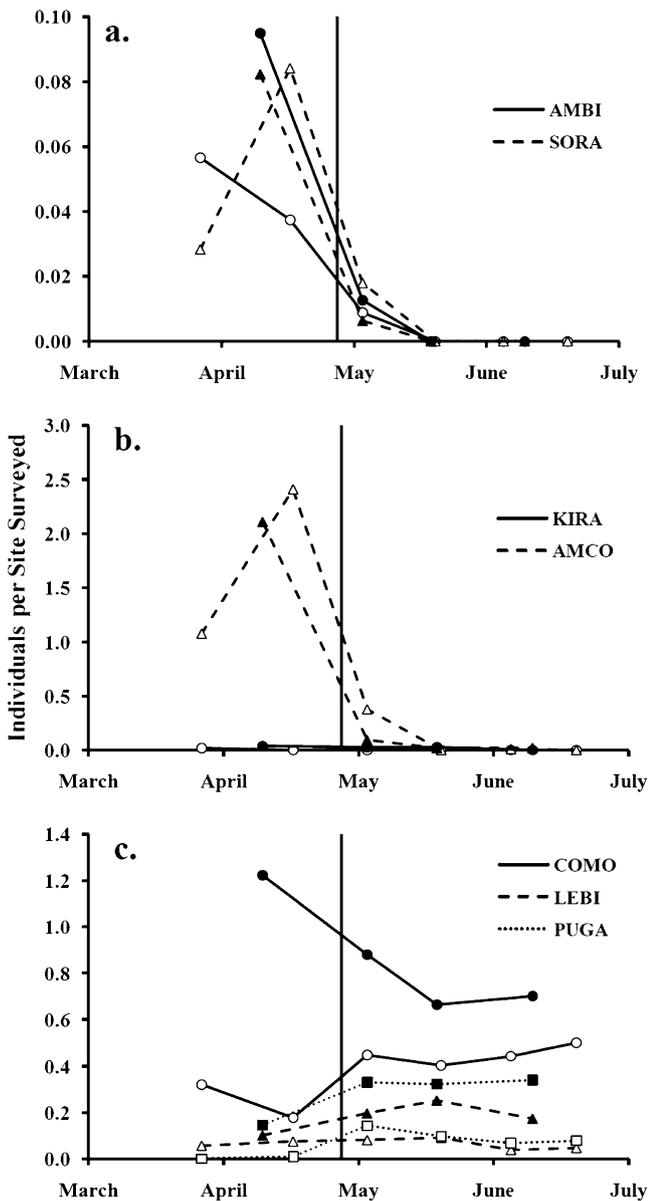


Fig. 2 Secretive marsh birds detected at 118 wetlands sites in northeastern Louisiana during the spring and summer of 2007 and 2008. All surveys conducted during a single sampling period (10–14 days) were combined into 1 data point, and that point is plotted as the median date of the period. Lines with open symbols represent trends from 2007 and those with closed symbols represent trends from 2008. We could not determine whether birds detected prior to 28 April (marked by vertical line) were migrants or breeders, so these detections were excluded from breeding habitat analyses. Results indicate that **a** no American Bitterns (AMBI) or Soras (SORA) breed in the region, **b** very few King Rails (KIRA) and American Coots (AMCO) breed and **c** Common Moorhens (COMO), Least Bitterns (LEBI) and Purple Gallinules (PUGA) breed regularly. Note the different scales on each graph

ation for Purple Gallinules due to high correlation ($r=0.91$) with WOODY. None of the global models showed evidence of lack of fit or overdispersion (Table 2). Model averaged parameter estimates indicated that ROBUST had a positive influence on ψ for all three species, and was the most important variable in explaining site occupancy in each case as well (Fig. 3).

Discussion

The results of this study indicate that at least three SMB species (Common Moorhens, Least Bitterns, and Purple Gallinules) breed commonly in MAV wetlands. Additionally, we detected low densities of King Rails, a species of widespread conservation concern (Cooper 2008), and thus the MAV could play a critical role in supporting this species as well. Our results also suggest that the habitat characteristics preferred by breeding SMBs differ substantially from those used by migrating shorebirds and wintering waterfowl and management and restoration objectives for these species may be inadequate for enhancing SMB habitat.

King Rails are known to breed throughout the eastern United States, and occupancy estimates for coastal Louisiana rice fields range as high as 0.5 (Pierluissi and King 2008). Interestingly, we detected numerous individuals in early spring and many of our sampled wetlands had attributes which would presumably be attractive to these breeding birds (Reid 1989; Meanley 1992; Darrah and Krementz 2009). Budd (2007) also found very low numbers of breeding King Rails in the MAV of Arkansas and our combined results seem to indicate that this species breeds very infrequently in the region. There could be several plausible explanations for this. First, Pierluissi (2006) found a negative correlation between King Rail nest densities and local cover by tall trees around rice fields, so it is possible that these birds have never been abundant in this historically forested region. It is also possible that, because King Rail populations are depressed throughout most of its range, adequate habitat in the MAV may simply be underutilized.

Lastly, our knowledge of breeding King Rail habitat requirements is limited, and it is possible that the quality of the wetlands in our study area is simply not sufficient to support successful breeding birds.

Local habitat variables consistently played a more important role in predicting ψ for SMBs than landscape habitat variables. In fact, a positive association with the proportion of a wetland dominated by robust emergent vegetation was the most important factor in predicting ψ for all three SMB species examined. Numerous researchers have documented the partiality of Least Bitterns for wetlands dominated by cattail (*Typha* spp.; Mancini and Rusch 1988; Gibbs and Melvin 1990; Frederick et al. 1990) and cutgrass (*Zizaniopsis miliacea*; Winstead and King 2006). Similarly, Common Moorhens (Brackney 1979; Post and Seals 2000; Bannor and Kiviat 2002) and Purple Gallinules (Helm et al. 1987; West and Hess 2002) also seem to prefer these plant species. Robust emergent plants provide excellent structure for these birds which bend and weave the broad leaves to build a nesting platform over standing water (Gibbs et al. 1992; Bannor and Kiviat 2002; West and Hess 2002). Robust emergent vegetation cover appears to be limiting in the lower MAV; of our randomly selected wetland sites, 84% and 73% in 2007 and 2008 respectively had <10% cover by robust emergent vegetation. However, when we pooled the data across both years we found that approximately 82% of flooded robust emergent patches ≥ 0.04 ha were utilized by at least one breeding SMB species, indicating these birds may not require large tracts of habitat for nesting.

For Purple Gallinules, ψ was also positively associated with the proportion of the wetland dominated by floating vegetation. This relationship was likely driven by the species' apparent affinity for floating water hyacinth (*Eichornia crassipes*). These sturdy, broad-leaved plants often create dense mats on the water surface, and we regularly observed both Purple Gallinules and Common Moorhens exhibiting courtship behavior and foraging with broods in such areas. Thus we were surprised that FLOAT was not included in the global Common Moorhen occupancy

Table 2 Fit statistics calculated for global habitat models of breeding secretive marsh birds detected at wetlands in northeast Louisiana in 2007 and 2008

Species	Global Model ^a	χ^2	<i>p</i>	\hat{c}
Common Moorhen	P(TOD) Ψ (YR, WETLAND, ROBUST, TALLWOODY)	216.7	0.39	0.87
Least Bittern	P(OB) Ψ (YR, WETLAND, ROBUST, WATER1KM, NR_HERB, AG1KM)	245.2	0.42	0.98
Purple Gallinule	P(DATE, TIME) Ψ (YR, WETLAND, ROBUST, FLOAT, WOODY, TREES100M, NR_TALLHERB)	235.2	0.37	0.94

^a Survey-specific covariates represent whether the survey was conducted in the morning or evening (TOD), observer identity (OB), Julian date (DATE), and the number of minutes before or after sunrise or sunset (TIME). Site-specific covariates are defined in Table 1.

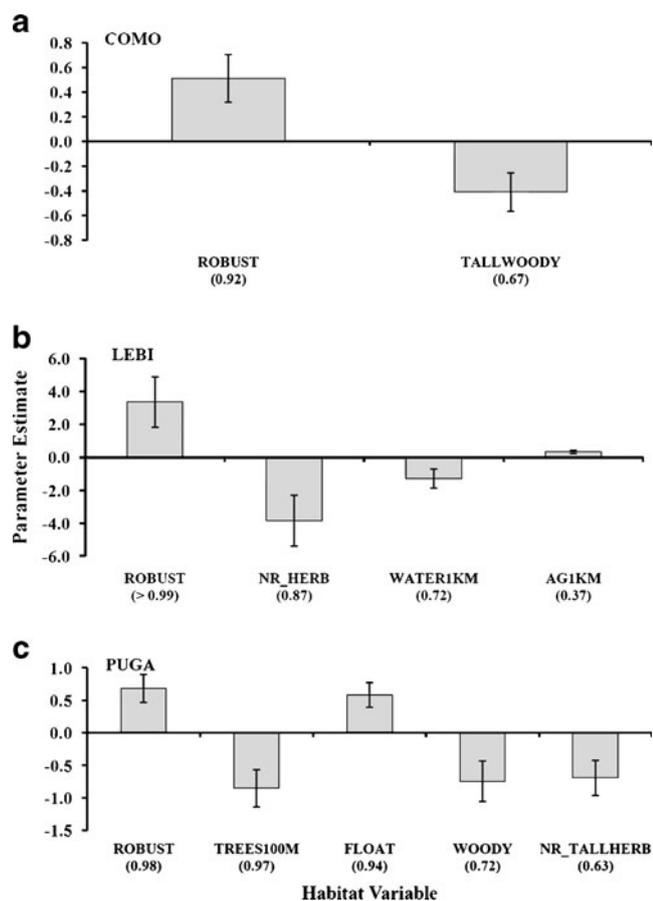


Fig. 3 Model averaged estimates (\pm SE) of the magnitude of habitat variable effects on wetland site occupancy for breeding **a** Common Moorhens, **b** Least Bitterns and **c** Purple Gallinules in northeastern Louisiana in 2007 and 2008. The relative importance of each variable is indicated in parentheses

model, but it is possible that the observed association may have been statistically diluted in the analyses by some of the other plant species included in the floating vegetation category (e.g., pondweed [*Potamogeton* spp.] and American lotus [*Nelumbo lutea*]).

Purple Gallinules were deterred by woody vegetation in the wetland and Common Moorhens showed a similar response to tall woody vegetation. Purple Gallinules also showed a negative association with the proportion of the wetland supporting tall, non-robust herbaceous vegetation, and Least Bitterns apparently avoided wetlands dominated by all non-robust herbaceous emergent vegetation. These other wetland vegetation types may not provide the solid foundation SMBs require for nesting, preening, foraging, courting, and copulating, and possibly provide low quality cover, rendering adults, eggs, and chicks vulnerable to predation.

Other researchers have found evidence to suggest that some SMB species tend to avoid wetlands surrounded by forest (Pierluissi 2006; Winstead and King 2006; Budd

2007; Pierluissi and King 2008). Pierluissi and King (2008) hypothesized that this may be indicative of a predator avoidance strategy, as forests can provide habitat for avian and mammalian predators. In our study the proportion of the local upland dominated by trees negatively influenced ψ for Purple Gallinules, and it was the second most important variable in predicting occurrence for that species. However, the TREES100M and TALLTREES100M variables did not appear to have much influence on ψ for either of the other two species examined. In the MAV, tall bottomland hardwood forest is still one of the dominant land cover types, and presence of tall trees was recorded within our local survey area at >75% of sites in both years. In this region, then, wetlands with quality nesting structure in areas with low forest cover may be rare.

No landscape variables showed any indication of improving occupancy models for either Common Moorhens or Purple Gallinules, and while the global model for Least Bitterns did include two landscape-scale variables, they had lower relative importance in explaining ψ than either of the local variables. Interestingly, Least Bitterns were negatively associated with the proportion of the landscape dominated by water, and positively associated with the proportion dominated by agriculture, results that were both contrary to their hypothesized outcomes. It is important to note that the WATER1KM variable was not indicative of emergent wetland habitat, but rather included all lakes, rivers, and streams which tend to be dominated by open water. Additionally, in light of the fact that Least Bitterns have been shown to avoid forested areas in previous studies (Pierluissi 2006; Winstead and King 2006; Budd 2007), it is feasible that these birds are exhibiting some affinity for more open landscapes, and that open landscapes in this region happen to be dominated by agriculture. However, these perplexing results could be at least partially influenced by the fact that landscape scale habitat information was based on aerial photographs taken in 2007, and that the MAV was subjected to substantially more flooding in the spring of 2008 than in 2007. The Mississippi River was above flood stage for 20 days in Baton Rouge during the course of the breeding season in 2008, while it never exceeded flood stage in the breeding season of 2007. Consequently, the landscape may have looked different to breeding SMBs in the second season than it did in the first, and our landscape scale data may not be indicative of the way habitat was actually perceived. Alternatively, this outcome may simply be further evidence that broad scale habitat variables are unlikely predictors of breeding site selection for SMBs.

Although occupancy models are a valuable tool for characterizing resource use (Mackenzie 2006), habitat selection is not necessarily indicative of habitat quality. Resource selection functions are only one measure of habitat

quality, but even more important are survival, reproduction, and dispersal characteristics (Van Horne 1983). Our study did not quantify food availability or predator concentrations and we did not measure any variables indicative of breeding or dispersal success. Rather, we focused on structural characteristics of the wetlands and surrounding landscapes that attract breeding birds. Future research should address whether SMB species are breeding successfully in the MAV and verify that regional wetlands are not ecological traps.

Management Implications

In the MAV the availability of robust emergent vegetation may be the single most important factor in attracting breeding SMBs, yet our study indicates that availability of such structure is limited. This may be indicative of the fact that regional wetland management is often focused on providing food and habitat for migrating and wintering waterfowl (Strader and Stinson 2005), a process that encourages frequently resetting succession and eliminating robust emergent plants (Kross et al. 2007). Management for breeding SMBs may be incorporated into an overall wetland management strategy by allowing ditches, deeper water bodies, moist soil units, or parts of units already dominated by robust emergent plants to remain flooded during the spring and summer. Both cattail and cutgrass initially germinate on moist mudflats, so designing wetlands with gradual slopes would help promote establishment of these species. Additionally, managing wetlands on longer cycles (i.e., >3 years between disturbances) would give the plants time to mature, although it may also create challenges with woody encroachment by willows (*Salix* spp.). Lastly, there has been a great deal of interest recently in creating habitat for the purpose of augmenting King Rail populations, and the lower MAV has been identified as a potentially important ecoregion for such restoration (Cooper 2008). Additional research is necessary to determine whether King Rails will utilize this region given appropriate habitat.

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