Estimating Effects of Habitat Characteristics on Abundances of Three Species of Secretive Marsh Birds in Central Florida

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Abstract.—Wetland loss has led to population declines of many species of North American marsh birds. However, due to the secretive nature of many of these species, there is uncertainty about their population status and habitat requirements. Recently developed techniques, such as the Standardized North American Marsh Bird Monitoring Protocol and analytical methods that account for variable detection probabilities, can be used to improve both the quality and quantity of information about secretive marsh birds. In 2009 and 2010, point counts were conducted using the marsh bird monitoring protocol to count Least Bittern (*Ixobrychus exilis*), Purple Gallinule (*Porphyrio martinica*) and Limpkin (*Aramus guarauna*) in the Kissimmee Chain of Lakes, Florida. Habitat factors thought to influence abundance were compared using competing hierarchical mixture models. Abundance of Least Bittern had a positive relationship with amounts of emergent vegetative cover and interspersion (i.e., vegetation to water edge). Purple Gallinule abundance was positively related to percentage of area cover by floating-leaved vegetation, interspersion and diversity of vegetation type. Limpkin abundance was non-linearly related to vegetation cover in both years. In 2009, Limpkin abundance was positively related to vegetation to water edge and vegetation type diversity, and negatively related to vegetation edge in 2010. Results demonstrate that marsh habitats with greater amounts of vegetative cover, interspersion, and vegetation diversity will support the greatest abundance of this suite of marsh birds. *Received 13 November 2013, accepted 11 February 2014.*

Key words.—*Aramus guarauna*, detection probability, Florida, hierarchical mixture models, *Ixobrychus exilis*, lake vegetation, Least Bittern, Limpkin, *Porphyrio martinicus*, Purple Gallinule.

Loss of wetlands has contributed to population declines of many species of secretive marsh birds in the United States (i.e., rails and bitterns; Butcher *et al.* 2007; U.S. Fish and Wildlife Service 2008). Species such as the Least Bittern (*Ixobrychus exilis*), Purple Gallinule (*Porphyrio martinicus*) and Limpkin (*Aramus guarauna*) are listed as State or Federal species of conservation concern due to loss of habitat and apparent population declines (U.S. Fish and Wildlife Service 2008; Florida Fish and Wildlife Conservation Service 2011). These species are secretive and use habitats that are difficult to survey, leading to a lack of reliable population trend and habitat use information (Eddleman *et al.* 1988; Conway and Gibbs 2005). Recent efforts in wetland conservation have helped to slow wetland loss, but there is still an absence of basic species-specific habitat use information for secretive marsh birds, which could improve effectiveness of wetland conservation and restoration projects (Conway 2011; Dahl 2011).

Recent studies have begun to close the information gap on secretive marsh bird habitat use by using methods that control for variable detection rates. The Standardized North American Marsh Bird Monitoring Protocol was developed to improve information about secretive marsh bird populations by using standardized methods to reduce bias in data collection (Conway 2011). Data collected with this protocol can also be used with many recently developed analytical techniques, such as occupancy analysis, to account for potentially biased data arising from variable detection probabilities (Mazerolle *et al.* 2005; Mackenzie *et al.* 2006; Alldredge *et al.* 2007; Conway and Gibbs 2011).

The natural hydrology of the Kissimmee Chain of Lakes in central Florida has been modified by water control structures and increased nutrient inputs from agriculture and development. These changes have altered the littoral vegetation communities in the Kissimmee Chain of Lakes, resulting in large dense stands of emergent vegetation and the formation of floating tussocks that are composed of decaying vegetative material and that facilitate encroachment by woody vegetation (Holcomb and Wegener 1971). These tussocks are troublesome since they limit access for recreation and may increase

access to marsh areas by mammalian predators. Vegetation management efforts, such as herbicide treatments, water level manipulations and mechanical removal of vegetative material, have been implemented to encourage development of more natural vegetation stands. These management efforts largely focus on the structural characteristics of emergent vegetation with goals of decreasing vegetation density of large monotypic stands of vegetation and tussocks, while increasing interspersion of vegetation to water. Many studies during the past decade have found habitat use by secretive marsh birds is related to the structure and arrangement of emergent vegetation (e.g., Rehm and Baldassarre 2007; Macek *et al.* 2009; Darrah and Krementz 2010; Valente *et al.* 2011). However, little information exists on the influence of vegetation structure and arrangement on the abundance of secretive marsh birds.

In this study, we examined relationships between structural habitat characteristics and the abundance of Least Bittern, Purple Gallinule and Limpkin in the Kissimmee Chain of Lakes using the marsh bird monitoring survey protocol and multinomial mixture models (Chandler *et al.* 2011). We predicted that the abundance of these species would be related positively to vegetation characteristics, such as height, density, interspersion, and diversity, altered by vegetation management activities. We also predicted that Purple Gallinule abundance would be positively related to the amount floating-leaved vegetation. We further predicted that abundance of all species would be negatively related to the presence of tussocks.

METHODS

Study Area

The Kissimmee Chain of Lakes is a series of interconnected shallow lakes in central Florida. The five largest of these lakes are Lake Kissimmee (27° 54' 05" N, 81° 15' 47" W; 12,913 ha), Lake Tohopekaliga (28° 12' 37" N, 81° 23' 52" W; 7,615 ha), East Lake Tohopekaliga (28° 17' 33" N, 81° 17' 08" W; 4,470 ha), Lake Hatchineha (28° 01' 15" N, 81° 24' 51" W; 6,629 ha) and Cypress Lake (28° 04' 42" N, 81° 29' 20" W; 1,635 ha). These lakes are highly valued for recreation, and shoreline development varies from undeveloped natural areas to pasture and suburban housing. Littoral vegetation consists primarily of cattail (*Typha* spp.), bulrush (*Scirpus validus*), pickerelweed (*Pontederia cordata*) and spatter-dock (*Nuphar lutea*), but also aquatic grasses (*Panicum repens*, *P. hemitomon*, *Paspalum repens*), club rush (*Eleocharis cellulosa*), white water lily (*Nymphaea odorata*), American lotus (*Nelumbo lutea*), duck potato (*Sagittaria lancifolia*), knotweed (*Polygonum* spp.), alligator weed (*Alternanthera philoxeroides*) and water primrose (*Ludwigia* spp.). Some areas of the lakes are characterized by dense floating tussocks that are composed of decaying organic matter and are dominated by cattail, pickerelweed, water primrose, wax myrtle (*Myrica cerifera*), willow (*Salix* spp.), buttonbush (*Cephalanthus occidentalis*), arrow arum (*Peltandra virginica*) and wild taro (*Colocasia esculenta*).

Marsh Bird Surveys

We established point count locations (*n* = 186) along the interface of open water and littoral vegetation in Lake Kissimmee (*n* = 66), Lake Tohopekaliga (*n* = 46), East Lake Tohopekaliga (*n* = 30), Lake Hatchineha (*n* = 27) and Cypress Lake (*n* = 17). Points were established by randomly selecting points along all possible littoral vegetation stands and placing up to 10 subsequent points 400 m apart to limit double counting of individuals (Conway 2011). Point counts (100-m radius) were conducted following the national marsh bird monitoring protocol (Conway 2011). This protocol consists of a 5-min passive listening period followed by 1-min periods of 30 sec of playback and 30 sec of listening for each focal species. We broadcast calls of Black Rail (*Laterallus jamaicencusis*), Least Bittern, King Rail (*Ralus elegans*), Purple Gallinule and Limpkin as suggested by the Standardized North American Marsh Bird Monitoring Protocol and because these species have been recorded breeding in the area (Bryan 2002; West and Hess 2002; Poole *et al.* 2009). Recordings of calls were obtained from the National Marsh Bird Survey Coordinator (Conway 2011). Order of call-broadcasts was by ascending level of call volume (i.e., Black Rail, Least Bittern, King Rail, Purple Gallinule and Limpkin). However, we detected very few King Rails and no Black Rails so these species were not included in this analysis. We used a double independent observer method with two observers simultaneously recording data for each individual bird detected. Individuals detected were marked as either detected by both observers or by the only observer who detected them. Point counts were conducted three times each year at each location with at least a 2-week period between site visits (2009: Survey 1 = March 5-March 30, Survey 2 = March 31-April 25, Survey 3 = April 26-May 27; 2010: Survey 1 = March 14-April 7, Survey 2 = April 8-May 1, Survey 3 = May 5-May 28). Point counts began 30 min before sunrise and were completed by 3.5 hr after sunrise (Nadeau *et al.* 2008) and were not conducted in periods of high wind (> 15 kmph) or precipitation. Observers were trained to identify focal species by sight and sound and estimate distances to detected birds.

Vegetation Sampling

We quantified vegetation characteristics at each point count location. For 141 points, we sampled vegetation once in either May-June 2009 or May-June 2010. Sampling once at each point was done to limit disturbance to vegetation and resident wildlife. Points ($n = 45$) that were treated with herbicide in fall 2009 were sampled in both years (May-June 2009 and May-June 2010). We sampled vegetation in the 100-m radius (3.14-ha) area surrounding each point count location using systematically located plots (1 m²; $n = 4,725$). Plots were spaced at 25-m intervals along six 100-m transects meeting at the center of each point count location. The first transect ran inland perpendicular to the shore and the others were placed at 45°, 135°, 180°, 225° and 315° in relation to the first transect. In each 1-m² plot, we measured vegetation height (m), percent cover of emergent vegetation and the presence or absence of floating-leaved vegetation and/or tussocks. We used the mean values ($n = 25$) of vegetation height and percent vegetation cover, and the proportion of sampling plots with floating vegetation and tussocks to characterize vegetation at each point count location.

We also used digitized littoral vegetation maps (Avineon, Inc. 2008; Dewberry 2010) to quantify diversity and interspersion of emergent vegetation within 100 m of each point. Diversity of 10 different vegetation types around each point was quantified in Fragstats (McGarigal and Marks 1995) using Simpson's Diversity Index. The vegetation types were classified from the littoral vegetation maps as follows: open water, upland, dead vegetation, floating-leaved vegetation (lilies, spatter-dock, lotus and similar species), medium height emergent vegetation (pickerelweed, duck potato and similar species), tall emergent vegetation (cattail and bulrush), mixture of tall and floating vegetation, mixture of tall and medium height vegetation or tussocks. Simpson's Diversity Index values close to 0 signify monotypic patches, and as patch richness increases and vegetation types are more evenly distributed the index value approaches 1. To quantify interspersion, we measured the length (m) of the vegetation to water interface within 100 m of each point count location; because interspersion increases as edge increases (Rehm and Baldassarre 2007; see Table 1 for summary of covariates).

Probabilities of Detection and Availability

Animal count data may be influenced by the probability that an individual is in the area and produces a detectable cue, and the probability that the observer detects the cue (Chandler *et al.* 2011). To account for this variation, we considered four variables that may influence the probabilities of detection and availability. These included three variables known to influence marsh bird detection probability: time since sunrise, Julian date and point count observer (Conway and Gibbs 2011). We also considered Julian date for availability probability, because birds would be more likely to sing or call depending on the time of the year. We also used the littoral vegetation maps to quantify the amount (ha) of robust emergent vegetation within 1 km of point count locations because individuals may be more likely to temporarily emigrate from the sampled area with increasing amounts of potential surrounding habitat.

Table 1. Mean, standard deviation (SD), minimum (Min) and maximum (Max) values of covariates used in abundance models of marsh birds in the Kissimmee Chain of Lakes, Florida, in 2009 and 2010. All covariates were standardized ($\mu = 0$, $\sigma = 1$) for use in the models. Vegetation was measured within 100 m of point count locations unless otherwise noted. Abundance covariates considered were vegetation height (VegHgt; cm), percent vegetative cover (PerCov), robust emergent vegetation edge (Edge; m), Simpson's Diversity Index (SIMP), and proportion of area covered by floating-leaved vegetation (FltVeg) and/or tussock (Tussock). Availability covariates considered were Julian date of point count (date) and amount of vegetation within 1 km (LandVeg). Detection covariates considered were Julian date of point count (date), hr since sunrise (time) and observer.

Covariate Name	2009				2010			
	Mean	SD	Min	Max.	Mean	SD	Min	Max
Abundance								
VegHgt	144.01	56.38	45.40	323.85	136.29	59.96	30.00	323.85
PerCov	36.40	21.29	3.00	98.23	35.48	21.62	3.00	98.23
Edge	285.28	137.68	18.47	700.64	282.79	138.27	18.47	645.86
SIMP	0.62	0.16	0	0.87	0.63	0.16	0	0.87
Tussock	15.07	16.86	0	65.22	0.15	0.17	0	0.63
FltVeg	20.44	17.87	0	76.00	20.38	17.79	0	76.00
Detection								
Time	1.03	1	-0.57	3.05	0.94	0.95	-0.52	2.98
Date	104.14	24.32	65.00	148.00	111.00	22.34	74.00	149.00
Observer	—	—	—	—	—	—	—	—
Availability								
Date	104.14	24.32	65.00	148.00	111.00	22.34	74.00	149.00
LandVeg	74.31	41.51	5.62	199.13	74.31	41.51	5.62	199.13

Analysis

We used a hierarchical N-mixture model (Chandler *et al.* 2011) developed to estimate abundance (λ), availability (ϕ) and detection probability (p). For this model, availability is defined as the probability that an individual is present and provides a detectable cue, and detection is the probability that an observer detects the provided cue. This model was implemented in the function 'gmultmix' in the 'unmarked' package for R (Fiske and Chandler 2011; R Development Core Team 2012). In our study, this model took the form of:

$$M_i \sim \text{Poisson }(\lambda), N_{it} \sim \text{Binomial }(M_i, \phi), \text{ and}$$
$$y_{it} \sim \text{Multinomial }(N_{it}, \pi_{it})$$

where M_i is the total number of individuals that could be detected at patch i, N_{it} is the number of individuals present in patch i at time t, y_{it} is a vector of counts made in patch i at time t, and π_{it} is a vector of multinomial cell probabilities derived from a detection probability function. Multinomial cell probabilities for a single site visit for the double independent observer technique used would be: 1) probability of observer 1 and not 2 detecting an individual; 2) probability of observer 2 and not 1 detecting an individual; and 3) the probability that both observers detected the individual; or:

$$\pi_1 = p_1(1-p_2), \pi_2 = p_2(1-p_1), \text{ and } \pi_3 = p_1p_2.$$

To facilitate model convergence and improve comparison between covariates, all covariates were standardized ($\mu = 0$, $\sigma = 1$; see Table 1 for values used to standardize covariates). We also checked for correlation between covariates to avoid problems of multicollinearity. We considered each year of the study separately because this temporary emigration model does not account for demographic changes in the population (Chandler *et al.* 2011). We started by comparing detection and availability models to better estimate the influence of observer, time and date, and emergent vegetation within 1 km on detection and availability probabilities. In these models, we held abundance constant and ranked competing models using Akaike's Information Criterion (AIC; Anderson *et al.* 2000). We used the highest ranking of these availability and detection models in our models of Least Bittern, Purple Gallinule and Limpkin abundance. These models included linear and non-linear terms for percent vegetation cover and vegetation cover, and linear terms for vegetation to water edge, Simpson's Diversity Index, and area covered by floating vegetation and/or tussocks. All models were ranked using AIC. Inferences on the relationships between habitat characteristics and abundance were based on model-averaged predictions of models within four ΔAIC units of the highest ranking model. To predict density, this model assumes that availability is not a function of both temporary emigration and other processes such as song rate (Fiske and Chandler 2011). Because we were sampling relatively secretive species, there was a high likelihood that the probability of being available was influenced by low calling rates (Conway and Gibbs 2011). Due to this potentially confounding factor, we limited our estimates to the abundance of the associated super-population (i.e., all the individuals that may use the area through time) at each point count location.

Results

We completed point counts at each location ($n = 186$) on three occasions in each of 2 years ($n = 1,116$ site visits; $n = 2,232$ point counts). We detected more individuals per point in 2009 than in 2010 (all statistics are mean ± SE): 2009: 4.04 ± 0.18, 2010: 3.31 ± 0.15. However, numbers of individuals detected from each species were similar between years; Least Bitterns (2009: 1.48 ± 0.10, 2010: 1.15 ± 0.09), Purple Gallinules (2009: 1.27 ± 0.10, 2010: 0.98 ± 0.09), and Limpkins (2009: 1.28 ± 0.10, 2010: 1.17 ± 0.09) per point sampled.

Detection and Availability Probabilities

Detection models varied by species (Table 2). Least Bittern detection probability was best described as a function of date. However, in 2009 the relationship was positive ($\hat{\beta} = 0.23 ± 0.11$) and in 2010 it was negative (-0.60 ± 0.17). Detection probability of Purple Gallinule was best described by observer differences in 2009 (-0.88 ± 0.23 vs. -0.61 ± 0.24) yet in 2010 there was a positive relationship with date (0.38 ± 0.16). Limpkin detection probability was best described as a function of observer in 2009 (-0.52 ± 0.2 vs. 0.08 ± 0.23), but in 2010 the constant detection probability model was the highest ranking model considered.

Availability model selection favored a relationship with date for most species and years (Table 2). Availability of marsh birds to be detected was positively related to date for Least Bittern in 2009 (0.30 ± 0.06) and 2010 (0.32 ± 0.08) and for Purple Gallinule in 2009 (0.67 ± 0.08) and 2010 (0.73 ± 0.09). Amount of emergent vegetation within 1,000 m was positively related to Limpkin availability in 2009 (0.23 ± 0.09), and in 2010 Limpkin availability was negatively related to Julian date (-0.18 ± 0.06).

Table 2. AIC model selection results for detection and availability models of marsh birds in the Kissimmee Chain of Lakes, Florida, in 2009 and 2010. Models within four ΔAIC of highest ranking model are listed. Parameters estimated were abundance (λ), availability (φ) and detection probability (*p*). Availability covariates considered were Julian date of point count (date) and amount of emergent vegetation within 1 km (LandVeg). Detection covariates considered were Julian date of point count (date), hours since sunrise (time) and observer (obs). ΔAIC = difference in Akaike's Information Criterion relative to the highest ranking model. *w* = AIC weight. K = number of parameters in the model.

Model	ΔAIC	*w*	K
Least Bittern 2009			
λ (.) φ (date) *p* (date)	0.00	0.65	5
λ (.) φ (date) *p* (.)	2.53	0.18	4
λ (.) φ (date) *p* (obs)	3.85	0.10	6
Least Bittern 2010			
λ (.) φ (date) *p* (date)	0.00	1.00	5
Purple Gallinule 2009			
λ (.) φ (date) *p* (obs)	0.00	0.94	6
Purple Gallinule 2010			
λ (.) φ (date) *p* (date)	0.00	0.51	5
λ (.) φ (LandVeg) *p* (date)	1.20	0.28	5
λ (.) φ (date) *p* (.)	3.47	0.09	4
λ (.) φ (date) *p* (obs)	3.89	0.07	6
Limpkin 2009			
λ (.) φ (LandVeg) *p* (obs)	0.00	0.36	6
λ (.) φ (.) *p* (obs)	0.28	0.31	5
λ (.) φ (date) *p* (obs)	1.94	0.13	6
Limpkin 2010			
λ (.) φ (date) *p* (.)	0.00	0.24	4
λ (.) φ (LandVeg) *p* (.)	0.35	0.20	4
λ (.) φ (date) *p* (date)	1.07	0.14	5
λ (.) φ (date) *p* (time)	1.55	0.11	5
λ (.) φ (LandVeg) *p* (time)	1.87	0.10	5
λ (.) φ (LandVeg) *p* (date)	2.35	0.08	5
λ (.) φ (date) *p* (obs)	2.84	0.06	6
λ (.) φ (LandVeg) *p* (obs)	3.13	0.05	6

Abundance

For all species, the top three models were within four ΔAIC units of the highest ranking models; these models made up > 75% of the AIC weight. In addition, for all species and years, the next highest ranking model contained < 5% of AIC weight. Therefore, model-averaged predictions are based on models within four ΔAIC units of the highest ranking model. The variables for vegetation to water edge, percent vegetation cover, Simpson's Diversity Index and proportion

of area covered by floating vegetation were in the highest ranking abundance models (Table 3).

The highest ranking Least Bittern abundance models contained length of vegetation to water edge and percent emergent vegetative cover (Table 3). The highest ranking model predicted an average abundance of 3.02 (CI = 2.30-3.99) and 3.14 (CI = 1.96-5.04) birds per sampling point in 2009 and 2010, respectively. In 2009 and 2010, there was a positive relationship between abundance and length of vegetation to water edge (Table 4; Fig. 1). In 2009 and 2010, Least Bittern abundance also was positively related to percent cover from emergent vegetation (Table 4; Fig. 2).

Purple Gallinule abundance was closely related to proportion of area covered by floating vegetation, length of vegetation to water edge and Simpson's Diversity Index. The highest ranking models predicted Purple Gallinule abundance to average 2.08 (CI = 1.59-2.73) in 2009 and 1.64 (CI = 1.21-2.22) in 2010. Purple Gallinule abundance in both years was related most to proportion of area covered by emergent vegetation (Table 3). The highest ranking models contained proportion of area covered by emergent vegetation and predict a positive relationship with comparatively large beta estimates and small standard errors (Table 4; Fig. 3). Purple Gallinule abundance was more weakly related to Simpson's Diversity Index and length of vegetation to water edge in 2009 and 2010 (Table 4; Fig. 1).

Model selection favored Limpkin abundance models that included percent cover from emergent vegetation, length of vegetation to water edge and Simpson's Diversity Index (Table 4). The highest ranking model predicted abundances of 3.69 (CI = 2.46-5.55) in 2009 and 4.76 (CI = 2.98-7.61) in 2010. There was support for a non-linear relationship between percent cover from emergent vegetation and abundance in both years, but the relationship was stronger in 2010 (Table 4; Fig. 2). Length of vegetation to water edge also occurred in the highest ranking models (Table 3), with a positive relationship predicted in 2009 and a negative

Table 3. AIC model selection results for abundance models of marsh birds in the Kissimmee Chain of Lakes, Florida, in 2009 and 2010. Models within four ΔAIC of highest ranking model are listed. Parameters estimated were abundance (λ), availability (ϕ) and detection probability (p). Abundance covariates considered were percent emergent vegetative cover (PerCov), robust emergent vegetation to water edge (Edge), Simpson's Diversity Index (SIMP), and proportion of area covered by floating-leaved vegetation (FltVeg) and/or tussock (Tussock). Availability covariates considered were Julian date of point count (date) and amount of emergent vegetation within 1 km (LandVeg). Detection covariates considered were Julian date of point count (date), hours since sunrise (time) and observer (obs). ΔAIC = difference in Akaike's Information Criterion relative to the highest ranking model. w = AIC weight. K = number of parameters in the model.

Model Formula	ΔAIC	w	K
Least Bittern 2009			
λ (PerCov + PerCov^2 + Edge) ϕ (date) p (date)	0	0.61	8
λ (PerCov + Edge) ϕ (date) p (date)	1.95	0.23	7
Least Bittern 2010			
λ (PerCov + Edge) ϕ (date) p (date)	0	0.60	7
λ (PerCov + PerCov^2 + Edge) ϕ (date) p (date)	0.84	0.40	8
Purple Gallinule 2009			
λ (SIMP + FltVeg) ϕ (date) p (obs)	0	0.53	8
λ (FltVeg + Edge) ϕ (date) p (obs)	1.11	0.31	8
λ (FltVeg) ϕ (date) p (obs)	2.38	0.16	7
Purple Gallinule 2010			
λ (FltVeg) ϕ (date) p (date)	0	0.39	6
λ (FltVeg + Edge) ϕ (date) p (date)	0.32	0.33	7
λ (SIMP + FltVeg) ϕ (date) p (date)	0.62	0.28	7
Limpkin 2009			
λ (SIMP + Edge) ϕ (LandVeg) p (obs)	0	0.36	8
λ (PerCov + PerCov^2 + Edge) ϕ (LandVeg) p (obs)	0.54	0.28	9
λ (PerCov + PerCov^2 + SIMP) ϕ (LandVeg) p (obs)	1.88	0.14	9
Limpkin 2010			
λ (PerCov + PerCov^2 + Edge) ϕ (date) p (.)	0	0.83	7
λ (PerCov + PerCov^2) ϕ (date) p (.)	3.80	0.12	6

relationship predicted in 2010 (Table 4). In 2009, a positive relationship with Simpson's Diversity Index was found in two of the three highest ranking models (Table 3).

Discussion

We used a hierarchical mixture model to provide more reliable information on the abundance of Least Bitterns, Purple Gallinules and Limpkins by accounting for variation in observed data due to availability and detection probabilities. We found that detection probability varied with date and observer. Bird calling activity has been well documented to increase during the breeding season (Best 1981; Wilson and Bart 1985), and secretive marsh birds seem to follow that trend (Bogner and Baldassarre 2002; Conway and Gibbs 2011). The ob-

served trend of increasing detection probability for Least Bitterns in 2009 and Purple Gallinules in 2010 may reflect this trend. However, models for Least Bittern detection in 2010 predicted a negative relationship with Julian date. While these results may be contrary, they may also reflect what is being estimated in these models. Detection probability in these models is the probability of an observer detecting the species given that the species is present and provides a detection cue (Chandler *et al.* 2011). Individuals that do not provide a detection cue do not factor into the estimation of detection probability. Observed changes in detection rate in similar studies are more likely represented in our estimates of availability, or the probability that a species provides a detection cue. The detection probability estimated in this model may change

Table 4. Parameter estimates ($\hat{\beta} \pm SE$) from models within four ΔAIC of highest ranking models for marsh bird abundance in the Kissimmee Chain of Lakes, Florida, in 2009 and 2010. Parameters estimated were abundance (λ), availability (φ) and detection probability (p). Betas are on the log–scale. Abundance covariates considered were percent emergent vegetative cover (PerCov), robust emergent vegetation to water edge (Edge), Simpson's Diversity Index (SIMP), and proportion of area covered by floating–leaved vegetation (FltVeg) and/or tussock (Tussock). Availability covariates considered were Julian date of point count (date) and amount of emergent vegetation within 1 km (LandVeg). Detection covariates considered were Julian date of point count (date), hours since sunrise (time) and observer (obs).

| Model	Intercept	Percent Vegetation Cover	Percent Vegetation Cover²	Vegetation to Water Edge	Simpson's Diversity Index	Floating Vegetation
Least Bittern 2009						
λ (PerCov + PerCov² + Edge) φ (date) p (date)	1.11 ± 0.14	0.43 ± 0.07	-0.10 ± 0.05	0.16 ± 0.06	—	—
λ (PerCov + Edge) φ (date) p (date)	1.01 ± 0.13	0.36 ± 0.06	—	0.17 ± 0.06	—	—
Least Bittern 2010						
λ (PerCov + Edge) φ (date) p (date)	1.15 ± 0.24	0.29 ± 0.06	—	0.25 ± 0.06	—	—
λ (PerCov + PerCov² + Edge) φ (date) p (date)	1.09 ± 0.25	0.24 ± 0.07	0.06 ± 0.05	0.27 ± 0.06	—	—
Purple Gallinule 2009						
λ (SIMP + FltVeg) φ (date) p (obs)	0.74 ± 0.14	—	—	—	0.14 ± 0.07	0.47 ± 0.05
λ (FltVeg + Edge) φ (date) p (obs)	0.74 ± 0.14	—	—	—	—	0.48 ± 0.05
λ (FltVeg) φ (date) p (obs)	0.74 ± 0.14	—	—	—	—	0.47 ± 0.05
Purple Gallinule 2010						
λ (FltVeg) φ (date) p (date)	0.50 ± 0.15	—	—	—	—	0.49 ± 0.06
λ (FltVeg + Edge) φ (date) p (date)	0.50 ± 0.16	—	—	0.09 ± 0.07	—	0.49 ± 0.06
λ (SIMP + FltVeg) φ (date) p (date)	0.49 ± 0.16	—	—	—	0.09 ± 0.08	0.48 ± 0.06
Limpkin 2009						
λ (SIMP + Edge) φ (date) p (LandVeg) p (obs)	1.31 ± 0.21	—	—	0.16 ± 0.06	0.23 ± 0.07	—
λ (PerCov + PerCov² + Edge) φ (LandVeg) p (obs)	1.47 ± 0.21	0.16 ± 0.08	-0.19 ± 0.06	0.17 ± 0.06	—	—
λ (PerCov + PerCov² + SIMP) φ (LandVeg) p (obs)	1.45 ± 0.22	0.13 ± 0.08	-0.15 ± 0.07	—	0.19 ± 0.08	—
Limpkin 2010						
λ (PerCov + PerCov² + Edge) φ (date) p (.)	1.56 ± 0.24	0.28 ± 0.08	-0.36 ± 0.07	-0.16 ± 0.07	—	—
λ (PerCov2) φ (date) p (.)	1.51 ± 0.23	0.28 ± 0.08	-0.34 ± 0.07	—	—	—
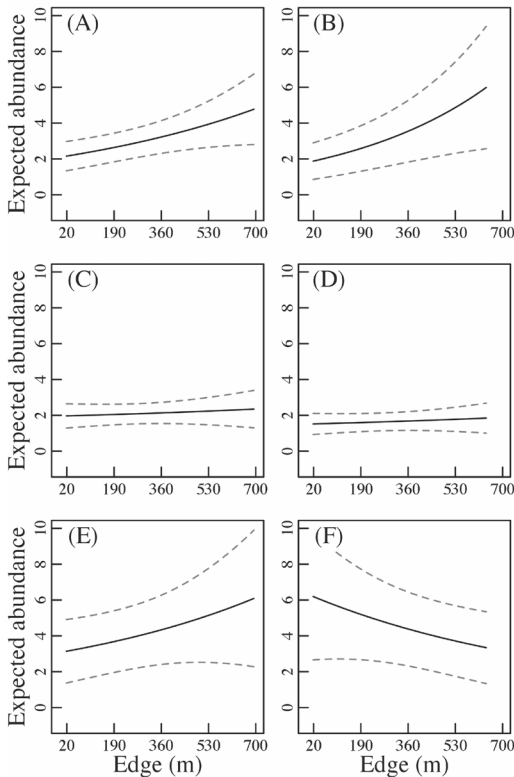
Figure 1. Predicted relationships (solid lines) between length of vegetation edge and abundance (± 95% confidence intervals; dashed lines) of Least Bitterns in 2009 (A) and 2010 (B), Purple Gallinules in 2009 (C) and 2010 (D), and Limpkins in 2009 (E) and 2010 (F) in the Kissimmee Chain of Lakes, Florida. Predictions are based on Akaike's Information Criterion ranked hierarchical mixture models of abundance.

with time due to observer ability, or even waning attentiveness as the study progresses. We also found support for models that estimate differences in observer ability for Purple Gallinules and Limpkins in 2009. Differences in the ability of observers to detect species are well known (Rosenstock *et al.* 2002), and observer effectiveness can change during a study (Norvell *et al.* 2003). Differences in observers also have been shown in studies of secretive marsh birds (e.g., Nadeau *et al.* 2008; Rush *et al.* 2009). Our study supports the idea that there may be differences in count data that arise from observation date and count observers, and these variables should be considered when accounting for detection probability.

Availability of Least Bitterns and Purple Gallinules in both years and Limpkins in 2010 was found to be closely related to Julian date. In 2009, however, availability of Limpkins was influenced mostly by the amount of littoral vegetation surrounding the point count location. Bird calling activity has been shown to increase during breeding periods. Dates of observed breeding activity in Florida tend to agree with our estimates. Least Bitterns in Florida start breeding in mid-March and continue through June, Purple Gallinules start later and continue breeding into mid-summer, and Limpkins are nearly year around breeders (Stevenson and Anderson 1994). Our estimates of increasing availability of Least Bitterns and Purple Gallinules from March through May coincide with these breeding dates. The weaker relationship of date with Limpkin availability may reflect a less concentrated breeding season. Availability is influenced not only by calling behavior but also by movement of individuals (Chandler *et al.* 2011). We hypothesized that individuals would be more likely to move out of the sampling area with increasing amounts of potential habitat surrounding the point. However, in 2010 we found the opposite with a positive relationship between Limpkin availability and potential habitat. However, other studies have found that birds may call more as the density of neighbors increases (McShea and Rappole 1997; Penteriani *et al.* 2002). These results may reflect the potential for increased territorial behavior due to more neighbors occupying surrounding habitat. To better account for differences in count data arising from individuals not producing detectable cues, researchers should account for differences in activity arising from seasonal activity patterns and habitat differences.

The amount of vegetation to water edge and percent vegetation cover had the greatest effect on Least Bittern abundance in both years of our study. Abundance was predicted to increase 1.33 and 1.51 times in 2009 and 2010, respectively, with every 100-m increase in vegetation to water edge and by 2.97 and 2.10 times with every 25% increase in vegetation cover. For many water bird species, an
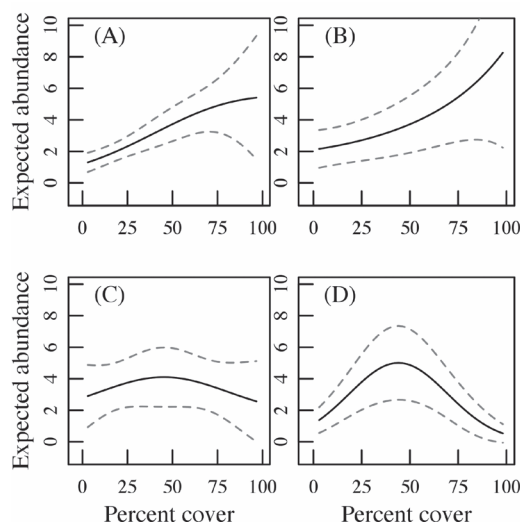
Figure 2. Predicted relationships (solid lines) between percent cover of emergent vegetation and abundance (± 95% confidence intervals; dashed lines) of Least Bitterns in 2009 (A) and 2010 (B) and Limpkins in 2009 (C) and 2010 (D) in the Kissimmee Chain of Lakes, Florida. Predictions are based on Akaike's Information Criterion ranked hierarchical mixture models of abundance.

ideal marsh is considered to have an equal mix between vegetation and water, and the distance of vegetation to water edge will increase as vegetation and water become more interspersed (Rehm and Baldassarre 2007). Recent studies also have shown positive relationships between interspersion and occupancy and relative abundance of Least Bitterns (Winstead and King 2006; Rehm and Baldassarre 2007; Valente *et al.* 2011). Cover from robust emergent vegetation also has been found to be positively related to occupancy probability and nesting success in Least Bitterns (Lor and Malecki 2006; Budd and Krementz 2010; Valente *et al.* 2011). There was some evidence for a non-linear relationship between percent vegetation cover and Least Bittern abundance, but this relationship varied between years. Models predicted that abundance would decrease past some threshold of vegetation cover in 2009 but increase past a threshold of vegetation cover in 2010. However, this parameter may not be informative since it had high standard errors, was not the highest ranking

model in 2010 and was within two AIC of the next highest ranking model in 2009 (Arnold 2010). Both emergent vegetative cover and interspersion between emergent vegetation and open water were found to be important structural characteristics.

Model selection for Purple Gallinules favored models with floating vegetation, length of vegetation to water edge, and vegetation diversity in both years. Abundance was predicted to increase 2.81 and 2.95 fold in 2009 and 2010, respectively, with every 25% increase in area covered by floating vegetation. Relationships between abundance and length of vegetation to water edge or vegetation diversity were minimal. Purple Gallinule abundance could be expected to increase by 1.36 and 1.25 times with a 25% increase in vegetation diversity scores and 1.18 and 1.19 times with every 100-m increase in vegetation to water edge in 2009 and 2010, respectively. In addition, models with floating vegetation and either vegetation to water edge or vegetation diversity had similar AIC scores to a model with only floating vegetation, suggesting that these parameters were uninformative (Arnold 2010). At our study site, much of the floating-leaved vegetation was comprised of spatter-dock, which is a fairly robust floating-leaved plant often growing 20-40 cm above the water. This type of vegetation may provide adequate cover and feeding areas without being interspersed with open areas and tall robust emergent vegetation. While we found little support for models with interspersion and vegetation diversity, other studies have found similar parameters to be important (Valente *et al.* 2011). Although our results may not be as applicable to habitats with less robust floating-leaved vegetation, our study does support the hypothesis that habitats with greater amounts of floating-leaved vegetation are needed by Purple Gallinules.

Vegetation cover, vegetation to water edge and vegetation diversity were included in the highest ranking models of Limpkin abundance in 2009. Only vegetation cover and vegetation to water edge were favored in 2010. Results also suggest that Limpkin abundance was greatest in areas with mod-
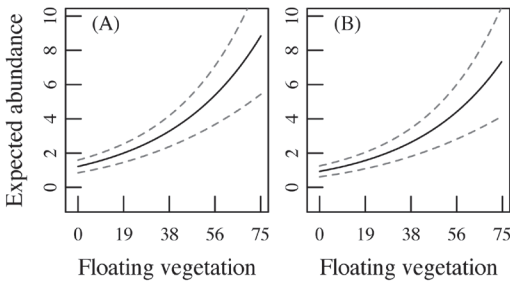
Figure 3. Predicted relationship (solid lines) between proportion of area with floating-leaved vegetation and abundance (± 95% confidence intervals; dashed lines) of Purple Gallinules in 2009 (A) and 2010 (B) in the Kissimmee Chain of Lakes, Florida. Predictions are based on Akaike's Information Criterion ranked hierarchical mixture models of abundance.

erate vegetation cover. The non-linear term was in two of the three highest ranking models in 2009 and in both models with a combined 95% of the AIC weight in 2010. This relationship was weaker in 2009, with abundance expected to increase by a greater amount in 2010. In addition, the ratio of standard error to beta estimate was larger in 2009 compared to 2010, revealing more uncertainty in those estimates. There was also a positive relationship between Limpkin abundance and vegetation to water edge in 2009; however, this trend was reversed in 2010. Abundance was predicted to change by a factor of 1.19 and -1.28 with every 100-m increase in the length of vegetation to water edge in 2009 and 2010, respectively (Fig. 1). In both years, there was some uncertainty in our estimates, leading us to believe this relationship may not be very strong or non-existent. In either case, annual variation in observations could lead to estimates of a positive or negative relationship. A positive relationship between vegetation diversity and Limpkin abundance was also found in the highest ranking models in 2009, with abundance expected to increase by a factor of 1.47 with a 25% increase in Simpson's Diversity Index score. While few studies have been conducted on habitat use of Limpkins, there is evidence that they are more likely to use patchy and moderately dense emergent vegetation (Bryan 2002; Macek *et al.* 2009). In addition, apple snails, the Limpkin's pri-

mary food source, require emergent vegetation for egg laying and aerial respiration, preferring vegetation that provides some cover, but not so dense as to impede adult movement (Karunaratne *et al.* 2006). Our observations of a non-linear relationship between vegetation cover and Limpkin abundance likely reflects use of habitats that meet requirements for apple snails. Limpkins are also larger, and thus less agile, when moving though thicker emergent wetlands than other species in this study. As a result, they may use moderate density vegetation to provide cover but still allow easier movement.

It is difficult to estimate abundance and habitat use of marsh birds because of variable detection rates (Conway and Gibbs 2011). Thus, researchers need to generate more precise estimates of detection rates to improve management decisions and conservation efforts. We used hierarchical mixture models to partition the various sources of variation in detection rates and availability of individuals to better estimate abundance and habitat use in three marsh bird species. Our data indicate the amount of vegetation to water edge, percent cover of emergent and floating-leaved vegetation, and vegetation diversity had the greatest influence on marsh bird abundance, regardless of species. Management actions that encourage a diversity of vegetation stands with these characteristics will likely harbor greater abundance of marsh birds. Unfortunately, managing for these habitat characteristics may conflict with sport fishing and recreational access in the Kissimmee Chain of Lakes (Moyer *et al.* 1994; Allen *et al.* 2003); therefore, robust planning of aquatic plant management activities should include input from all stakeholders before management activities are implemented.

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