



Research Article

Density, Sex, and Nest Stage Affect Rail Broadcast Survey Results

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ABSTRACT The National Marsh Bird Monitoring Program is being initiated to document population trends with call-broadcast surveys. We examined effects of site-estimated vocalization density (birds calling per ha), breeding stage, call type, and sex differences on marsh bird response probability to improve marsh bird surveys. We conducted 335 broadcast surveys 10 m from 113 known Virginia rail (*Rallus limicola*) and sora (*Porzana carolina*) nests in 10 wetlands over 2 breeding seasons (2010–2011) to determine important variables for predicting response probability. The odds of both species responding to broadcast increased as vocalization density increased. Recent nest predation decreased the odds of both species responding and increasing nest age additionally decreased sora response. Both species responded similarly to broadcast during egg laying, incubation, and hatching. In addition, we present methods to confirm nesting stage during broadcast surveys using vocalization type. Both species possess 1) calls that we detected exclusively during the pre-nesting phase but not prior to replacement clutches, which may indicate unpaired birds; and 2) calls detected exclusively during the late incubation through brooding stages, which may be useful for inferring nest success from broadcast surveys. Spectrogram analysis of recorded vocalizations showed that male Virginia rails responded to broadcast calls with louder (possibly related to approach distance), longer, and faster calls (hence higher detectability) than females. We recommend that marsh bird population estimates account for detectability biases in density, stage, and sex and use call type to infer nonbreeding status and nest fate. © 2014 The Wildlife Society.

KEY WORDS broadcast surveys, density, Maine, marsh bird, *Porzana carolina*, *Rallus limicola*, reproduction, sora, Virginia rail, vocalizations.

Virginia rail (*Rallus limicola*) and soras (*Porzana carolina*) rarely flush or fly during the breeding season, vocalize infrequently, and are cryptic in dense, emergent, wetland habitat (Gibbs and Melvin 1993). Most density estimates of marsh bird populations are from broadcast surveys using digital recordings of territorial calls (Spear et al. 1999, Rehm and Baldassarre 2007, Conway 2009). The National Marsh Bird Monitoring Program provides guidance for conducting marsh bird surveys (Conway 2011). It recognizes that more information on detectability is needed (Conway 2011) and it does not yet adequately control for detectability related to bird density, breeding stage, call type, or sex differences. Broadcast survey responses often correlate with nest abundance (Mangold 1974, Zembal and Massey 1981, Brackney and Bookhout 1982), spot-mapped territory abundance (Griese et al. 1980), and numbers of captures (Tacha 1975, Kwartin 1995). The effects of vocalization densities (birds calling per ha) on response probability, however, are unknown.

The effects of breeding stage on the vocalizations of marsh birds have been examined in some species for small numbers of radio-tagged individuals (Conway et al. 1993, Legare et al.

1999, Bogner and Baldassarre 2002), although never within a specified radius of known nest sites. As a result, distance effects on response probability remained uncontrolled. Black rail (*Laterallus jamaicensis*) responses were documented at nesting and non-nesting phases using radiotelemetry, with birds in non-nesting phases having higher responsiveness, but the birds were not further distinguished by breeding stages (Legare et al. 1999). Bogner and Baldassarre (2002) studied radio-tagged least bitterns (*Ixobrychus exilis*) during different breeding stages, and found them to be more responsive after nest initiation compared to during incubation and hatching, although the sample size was very limited ($n = 9$).

Sex differences in detection probabilities also have been reported in many species with broadcast surveys (Bibby et al. 1992, Buckland et al. 1993, Reid et al. 1999, Gregory et al. 2003). Sex differences in vocalization probability have been estimated in black rails and common gallinule (*Gallinula galeata*; Brackney and Bookhout 1982, Legare et al. 1999) but not for other marsh bird species. Determining detection differences by sex during broadcast surveys may improve marsh bird population estimates (Newson et al. 2005) by providing sex-specific detectability rates. However, sex-specific differences in detection of species, such as the Virginia rail, are hampered by an inability to differentiate the sexes in the field (Tacha and Braun 1994).

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The types of calls used by marsh birds vary throughout the season (Conway et al. 2004) and with nesting status (Bogner and Baldassarre 2002). Survey estimates likely vary with call type (Conway and Nadeau 2006); however, call type detectability differences during the breeding season have not been examined for Virginia rails and soras (Kaufmann 1983, Zembal and Massey 1987).

Estimates from marsh bird surveys are being used, perhaps inaccurately, to estimate population sizes and trends (e.g., Erwin et al. 2002, Allen et al. 2004, Conway et al. 2004, Rehm and Baldassarre 2007, Nadeau et al. 2008). Our objectives were to improve survey methodology for marsh bird surveys by 1) testing for differences in call type by breeding stage and by passive or broadcast survey methods, 2) quantifying the influence of breeding stage, nest age, vocalization density, calendar date, and year on response to broadcast, and 3) examining differences in Virginia rail detectability by sex.

STUDY AREA

We randomly selected 65 freshwater wetlands that were within a 200-mile radius of Orono, Maine to survey for Virginia rail and sora presence. We used 10 sites with responsive pairs in this study. These sites ranged in size from 40 ha to 272 ha ($\bar{x} = 98$, $SD = 155$): 5 in Penobscot County (Penobscot River watershed) and 5 within Washington County (Eastern Coastal Plain watershed) in Moosehorn National Wildlife Refuge (322 km east). All sites were within the Eastern Coastal Plain biophysical region (Krohn et al. 1999). Common plant species at our sites included *Typha latifolia*, *T. angustifolia*, *Myrica gale*, *Carex* spp., *Calamagrostis canadensis*, *Spirea alba*, *Spirea tomentosa*, *Salix* spp., *Alnus* spp., *Sagittaria latifolia*, *Dulichium arundinaceum*, *Pontedaria cordata*, *Lemna minor*, *Lysimachia terrestris*, *Galium palustre*, *Equisetum* spp., *Vaccinium macrocarpon*, *Scirpus* spp., *Calla palustris*, *Polygonum* spp., *Sparganium americanum*, *Chamaedaphne calyculata*, *Juncus* spp., *Triadenum virginicum*, and *Potentilla palustris*.

METHODS

From 1 April through 15 August in 2010 and 2011, we searched for Virginia rail and sora nests at 10 sites found during a pilot field season (2009) that had responsive pairs during broadcast surveys. We played broadcasts of calls and randomly searched areas for nests where we heard the duetting descending call of the Virginia rail or the paired whinny of the sora (Kaufmann 1983) using our hands or a stick to sift through thick clumps of vegetation. We visited nests every 3–5 days to determine breeding stages (egg laying, incubation, hatching, hatched, and failed) and to conduct broadcast surveys. We conducted broadcast surveys 10 m from each nest to minimize observer detectability issues (Conway et al. 2004, Sauer et al. 2008), to maximize the probability of recording the nesting pair's responses rather than birds from neighboring territories, and to control for different responses at different distances from nests. We used a portable speaker (Altec, New York, NY) with an mp3 player (SanDisk, Milpitas, CA) for broadcast surveys at

80–90 dB (measured 1 m away) with 5 minutes of silence (the passive period), followed by 30 seconds of sora calls, 30 seconds of silence, 30 seconds of Virginia rail calls, and 30 seconds of silence (the active period) using an audio track ordered from the National Marsh Bird Monitoring Program (Conway 2011). We played first the sora and then the Virginia rail calls with the least intrusive call first as recommended by Ribic et al. (1999). Sora calls, in order, included the whinny ($n = 2$), per-weep ($n = 3$), and the peep ($n = 3$). Virginia rail calls, in order, included the descending call ($n = 1$), kadic-kadic ($n = 2$), and the kicker ($n = 2$). We followed guidelines in the North American Marsh Bird Monitoring Program (Conway 2011) for time of day, weather, and wind speed. We conducted surveys 30 minutes before to 3 hours after sunrise or 3 hours before sunset (Gibbs and Melvin 1993, Conway et al. 2004). We surveyed only when wind speed was < 20 km/hr (or < 3 on the Beaufort scale) and not during periods of rain or heavy fog. We used 8 observers that were trained in recognizing call types prior to sampling. They recorded whether birds responded to each survey and, if so, whether it was during the passive or active period. For birds that responded, we recorded date, time until first response, call type, estimated distance of the responding individual from the nest, estimated distance of the responding individual from broadcast speaker, nest stage (egg laying, incubation, hatching, hatched, and failed), and estimated nest age, which was derived by back-dating from the hatch date and assuming mean incubation lengths. We conducted surveys at least 5 days apart to maximize independence between them and to reduce vocal habituation (Legare et al. 1999). We trained all observers in estimating distances (0–200 m) using laser finders at the beginning of the season. During all of the broadcast surveys, we recorded the call type of individual responses during both the passive and active broadcast periods.

Rehm and Baldassarre (2007) suggested the possibility of using call type to distinguish breeding and migrating (pre-breeding) marsh birds during point-count surveys. To test this possibility for Virginia rails and soras, we did an initial pre-nesting (after calling began but prior to finding nests and prior to back-dated initiation dates of all found nests) point-count survey at our site with the highest breeding density to compare with call types of birds with known active nests. We surveyed 1 transect that contained 12 survey points each separated by 200 m at the site on 1 May 2009 and recorded responses, distances, and call types at each point.

To obtain site-scale density estimates of vocalizations, we conducted broadcast surveys along a single transect of each wetland with 4 survey points per transect and each point separated by 200 m to determine relative vocalization densities for Virginia rails and soras combined (hereafter density) for 7 of our nest-searching sites (3 sites that were nest-searched were not surveyed for density estimates because of time constraints). We conducted broadcast surveys twice at the 7 sites, once in mid-May and once in mid-June. We combined the species for vocalization density estimates because previous studies have found Virginia rails and soras to be equally responsive to each other's calls as to

their own (Glahn 1974, Allen et al. 2004). We followed the National Marsh Bird Monitoring Protocol where we broadcast both species' calls at each survey. We used the *distsamp* package in R (R Core Development Team 2011) to obtain density estimates at each call survey site accounting for distance-biased detectabilities.

We examined response probabilities of each species during the broadcast survey. We used logistic regression to model the response (yes/no) of each species to the broadcast using the Laplace approximation with random intercepts for individual nests to account for repeated measurements during the different breeding stages. We used literature searches and field observations to select a priori models and evaluated models for support using an information-theoretic approach (Burnham and Anderson 2002). Sora responses in the field seemed to get quieter as the nest got older. Virginia rails did not show this pattern but both species usually became quiet or left the nest area following predation events. Not expecting a linear decline in responsiveness with nest age for Virginia rails, we included 5 categorical breeding stages (egg laying, incubation, hatching, hatched, and depredated) in the Virginia rail model and both nest age (because of a suspected linear decline for soras) and a binomial variable for predation status in the sora model. We also noticed during fieldwork that both species were more vocal early in the season and in wetlands with greater densities of calling Virginia rails and soras so we included Julian date and density in both models. We controlled for variation due to time of day by conducting our surveys within time windows defined above permitted by the National Marsh Bird Monitoring Program protocols (Conway 2011). We preliminarily looked at responsiveness each year by examining numbers of responses per number of surveys. We did not see yearly differences in sora responses so we did not include year in our final model set but there were differences in Virginia rail yearly response probabilities so we included year in the Virginia rail model set. The Virginia rail model set included breeding stage, Julian date, density, and year. Sora explanatory variables included nest age, Julian date, density, and predation status. We evaluated 16 candidate models for each species that included the 4, single-component models, all 6, 2-component models, all 4, 3-component models, the full 4-component model, and the constant-intercept model. We evaluated the global-model with a Hosmer and Lemeshow (2000) goodness-of-fit test. We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) for model selection and categorized top models as those that had the lowest AIC_c and a $\Delta AIC_c < 2$. We model averaged all models with cumulative Akaike $w_i < 0.9$ and evaluated the importance of each variable by examining whether the odds ratio confidence intervals overlapped with 1 and also by summing the Akaike weights across all models containing the parameter (Burnham and Anderson 2002).

We captured Virginia rails with a cast net on the nest during incubation to obtain genetic samples for sex identification. Once we caught 1 bird of the pair, its mate typically began incubation within minutes. While holding the first bird at least 20 m from the nest and after waiting

5 minutes, we played a broadcast call (the Virginia rail descending call only) to the newly incubating bird and recorded the descending call response with an mp3 recorder (Edirol-R-09; Roland, Hamamatsu, Japan) and a microphone (SM57; Shure, Niles, IL). We then caught the second incubating bird with the cast net and, afterwards, released the first individual. After waiting 5 minutes, we played a broadcast call to the first individual (while holding its mate) and recorded any descending call responses.

We obtained blood samples from the cutaneous ulnar vein of both birds. We genetically ascertained sex via the sex-specific CHD1 gene by P2/P8 (Griffiths et al. 1998) and 2550F and 2718R (Fridolfsson and Ellegren 1999) primer pairs. We used multiple primer sets as recommended by Casey et al. (2009). We analyzed recorded calls from the captured birds with Raven version 1.3 (Charif et al. 2006). We created figures of spectrograms with Fourier transform (FFT) and a sampling rate of 44.1 kHz to digitize signals (McCracken and Forstner 2006). Variables examined included song average power (loudness), song length, and interval length (time between each call note), which we noticed in the field as distinctive call type differences within paired duet descending calls.

We applied linear discriminant analysis with jackknifed prediction in Program R to vocal measurements (song and interval length) of 9, known-sex Virginia rails (5 male, 4 female). We did not include power (loudness) in this analysis because we wanted results that were independent of bird distance from the microphone. We assessed effectiveness of the discriminant function in 2 ways. First by determining the correct classification of known-sex birds using all 9 individuals in the analysis. Second, using a jackknifing procedure, which repeats the analyses leaving a single bird out each time and then classifies that individual using the function derived from the remaining birds (Sokal and Rohlf 1981, van Franeker and ter Braak 1993, Counsilman et al. 1994). We also tested for differences in loudness (power) for males and females using a Student's *t*-test.

RESULTS

Call Type

Virginia rails responded during 175 of 255 (68.6%) surveys at known nest sites including within 1 week post-failure or within 1 week post-hatching. Birds first responded during the passive period in 24.3% of surveys and first during the active period in 43.1% of surveys. Broadcasting increased detection probability in comparison with the passive period by 1.78 times ($n = 255$).

Virginia rail calls during nesting included the descending, duet descending, kiu, kadic-kadic, and peep calls (Table 1). The kiu call is a distress call (Kaufmann 1983) and we heard it at all breeding stages other than depredated and pre-nesting (Table 1). We heard the peep call only during incubation and hatched stages and it is thought to be a contact call among family members (Kaufmann 1983; Table 1). Virginia rails primarily used the descending call during depredation and hatched stages (Table 1). We heard

Table 1. Virginia rail and sora call types in Maine (2010 and 2011) during breeding stages (lay = egg-laying, inc = incubation, hatching, hatched, depredated, pre-nest = pre-nesting) in response to independent broadcast surveys.

Species	Call type	Stages						Total
		Lay	Inc	Hatching	Hatched	Depredated	Pre-nest	
Virginia rail	kiu	2	4	6	7	0	0	19
	peep	0	4	0	3	0	0	7
	duet descending call	6	8	0	5	5	0	24
	descending call	27	60	11	15	12	6	131
	kadic-kadic	0	0	0	0	0	1	1
Sora	kiu	0	1	2	1	0	0	4
	peep	0	1	0	2	0	0	3
	paired whinny	1	0	0	0	0	0	1
	per-weep	0	0	0	0	0	10	10
	whinny	8	10	8	5	1	4	36

the 1 kadic-kadic call early in the season when birds were searching for mates and we did not hear the call from any of our nesting birds. During the pre-nesting survey, we detected 7 Virginia rails that replied with either the descending call or the kadic-kadic call (Table 1). During non-survey times (not included in Table 1), we heard the kadic-kadic call frequently before nesting began.

Soras responded to the broadcast calls 40 of 80 times (50.0%) during nest surveys, which included 1 week post-failure and 1 week post-hatching. The first response of a bird occurred during the passive period in 13 of the 80 surveys (16.3%), and in the active period in 27 of the surveys (33.8%). Broadcasting calls during the active period increased the detection probability of a bird in comparison with the passive period by 2.08 times ($n = 80$).

Sora calls during nesting included the whinny, paired whinny, kiu, per-weep, and peep calls. We heard the paired whinny during the egg-laying stage (Table 1). Birds used the per-weep call at the start of the breeding season and we did not hear any known-nesting birds use it. The kiu call is a distress call (Kaufmann 1983) and we heard it at all breeding stages post-egg-laying aside from post-predation (Table 1).

We heard the peep call only during late incubation through hatched stages and it is thought to be a contact call among family members (Kaufmann 1983; Table 1). We had only 1 sora respond out of 16 post-failure surveys (Table 1). Soras in the hatched stage, however, continued to use the whinny, followed by the peep, and the kiu call (Table 1). During the pre-nesting survey on 1 May 2009, we detected 14 soras at Pond Farm that replied with either per-weep calls or whinny calls (Table 1).

Virginia Rail Response Model

We conducted 255 broadcast surveys to 63 unique Virginia rail nests with an average of 4 surveys per nest. The global model fit the observed values ($\chi^2_8 = 12.04$, $P = 0.15$). Our final model set based on a cumulative Akaike $w_i > 0.9$ included 6 models (Table 2), which we model averaged in an effort to incorporate model selection uncertainty into parameter estimates and their standard errors. The top 3 models had $\Delta AIC_c < 2$ and included stage, Julian date, and density (Table 2). Akaike weights for these 3 top models were 0.30, 0.20, and 0.20 (Table 2). The probabilities of a bird responding during all nest stages (incubation, hatching,

Table 2. Model selection results for Virginia rail response probability to broadcast surveys in Maine (2010 and 2011). The first 6 models listed are the $\geq 90\%$ confidence set of the original 16 considered. $\text{Log}_e(L)$ is the value of the maximized log-likelihood function, K is the number of parameters, AIC_c is Akaike's Information Criterion for small sample sizes, and w_i is the Akaike weight.

Model ^a	K	AIC_c	ΔAIC_c	w_i	Cumulative w_i	$\text{Log}_e(L)$
Density + stage	8	79.34	0.00	0.3	0.29	-30.29
Density	3	80.05	0.71	0.2	0.49	-36.82
Density + Julian date	4	80.52	1.18	0.2	0.66	-35.90
Year + stage + density	9	81.48	2.14	0.1	0.76	-29.98
Density + Julian date + stage	9	81.68	2.33	0.1	0.85	-30.07
Density + year	4	82.36	3.01	0.1	0.91	-36.82
Density + Julian date + year	5	82.71	3.36	0.1	0.96	-35.81
Julian date + year + stage + density	10	84.20	4.86	<0.1	0.99	-29.90
Stage	7	88.18	8.84	<0.1	0.99	-36.09
Julian date	3	89.39	10.05	<0.1	1.00	-41.50
Null (constant-intercept)	2	90.37	11.02	<0.1	1.00	-43.08
Stage + Julian date	8	90.80	11.46	<0.1	1.00	-36.09
Stage + year	8	90.80	11.46	<0.1	1.00	-36.09
Julian date + year	4	91.54	12.2	<0.1	1.00	-41.43
Year	3	91.69	12.35	<0.1	1.00	-42.65
Julian date + year + stage	9	93.51	14.16	<0.1	1.00	-36.09

^a Variable descriptions: density is Virginia rail and sora density per site, Julian date is the numerical calendar date of the survey, stage is the breeding stage of the nest (including egg laying, incubation, hatching, hatched, or depredated), and year is the year we conducted the survey.

Table 3. Summed Akaike weights (w_i) from the original 16 models, model-averaged parameter estimates with unconditional standard errors (SE), and odds ratios with unconditional 95% confidence intervals for variables in the top 6 models for Virginia rail response probability to broadcast surveys in Maine (2010 and 2011). The parameter estimates and odds ratios of the separate breeding stages (failed, hatched, incubation, and hatching) are relative to the reference egg-laying stage.

Variable ^a	Summed (w_i)	Estimate	SE	Odds ratio (95% CI)
Density	0.99	0.45	0.18	1.57 (1.11, 2.20)
Breeding stage	0.52			
Failed		-4.94	0.18	0.01 (0.00, 0.25)
Hatched		-1.99	1.35	0.14 (0.01, 1.92)
Incubation		-1.04	1.12	0.35 (0.04, 3.16)
Hatching		-1.81	1.25	0.16 (0.01, 1.90)
Year	0.24	0.46	1.16	1.58 (0.31, 15.49)
Julian date	0.34	-0.03	0.06	0.97 (0.88, 1.08)

^a Variable descriptions: density is Virginia rail and sora vocalization density per site, Julian date is the numerical calendar date of the survey, stage is the breeding stage of the nest (including egg laying [reference], incubation, hatching, hatched, or depredated [failed]), and year is the year we conducted the survey.

and hatched stage) were not different from the egg-laying (reference) stage (Table 3). The failed stage had a lower probability of response than the egg-laying stage and the odds ratio confidence interval for the failed stage did not overlap 1 (Table 3, Fig. 1). The odds of parents of a failed nest responding was 99% less (CI: 0.00, 0.25) than the odds of birds from an egg-laying nest responding (Table 3). Probability of response was positively related to density, whereas we did not find support for the effects of Julian date or year on bird response when we controlled for breeding

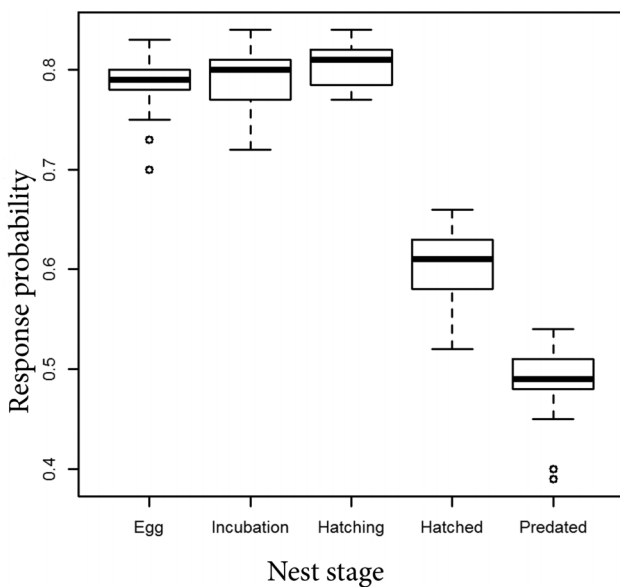


Figure 1. Virginia rail response probability to broadcast surveys at different breeding stages in Maine (2010 and 2011). We derived model-averaged estimates from our top 6 models that included combined site-scale Virginia rail and sora vocalization density, Julian date, breeding stage, and year. The top and bottom of the box represent the first and third quartiles, the heavy line in the box represents the median, the whiskers represent the maximum and minimum values excluding outliers, and the circles are outliers.

stage and density (Table 3). A 1-unit increase in density (Virginia rails and soras calling/ha) increased the odds of response by 1.57 times (CI: 1.11, 2.20; Table 3). Densities at our sites ranged from 0.96 to 8.70 birds calling/ha ($\bar{x} = 3.17$, $SD = 2.56$, $n = 7$).

The probability of a Virginia rail responding to a broadcast call was 0.73 ($SE = 0.08$) as determined from the model-averaged estimates. Breeding stage and density had the greatest effects on the probability of a Virginia rail responding (Table 3). The density covariate was in all of the 6 top models and the 95% confidence intervals of the odds ratio from the model-averaged estimate did not overlap 1 (Tables 2 and 3). Breeding stage was in 3 of the top models and the model-averaged estimate for the failed stage was lower than the egg-laying reference stage (Tables 2 and 3). Density summed Akaike weights were greater than breeding stage (0.99 vs. 0.52; Table 3). Two of the top 6 models included year and Julian date, but the 95% confidence interval of the odds ratios included 1.0 for both variables indicating no effect (Tables 2 and 3). Summed Akaike weights were 0.34 for Julian date and 0.24 for year (Table 3).

Sora Response Model

We conducted 80 broadcast surveys at 18 sora nests (average of 4.4 surveys per nest). The global model fit the observed values using the Hosmer and Lemeshow (2000) goodness-of-fit test ($\chi^2_8 = 9.46$, $P = 0.30$). Overall mean probability of a sora responding to broadcast surveys was 0.51 ($SE = 0.15$, $n = 80$) determined from the model-averaged estimates. Our final model set included 5 models with a cumulative Akaike $w_i > 0.9$ (Table 4), and these were used for model averaging. The top 2 models had $\Delta AIC_c < 2$ and included combinations of all 4 explanatory variables (Table 4). Akaike weights for the top 2 models were 46% and 32% (Table 4). Predation status and nest age were in all 5 and 3 of the top 5 models, respectively. Odds ratio confidence intervals of predation status and nest age did not overlap 1 and indicated a negative effect on the probability of a sora responding (Figs. 2 and 3). Birds from recently depredated nests had 97% less odds of responding than birds on nests that were not depredated (Table 5). A 1-day increase in nest age decreased the odds of response by 12% (Table 5). Density was in 4 of the top 5 models and the odds ratio 95% confidence interval did not overlap 1. A 1-unit increase in density (Virginia rails and soras calling/ha) increased the odds of sora response by 48% (Table 5). Predation status had the highest summed Akaike weights followed by density and age (Table 5). We did not find support for an effect of Julian date (2 of the top 5 models) when controlling for the other parameters in these models (Table 5).

Sex

Male and female Virginia rails were correctly classified in 100% of the known-sex jackknifed-procedure samples using interval and song length variables (Fig. 4). Males ($\bar{x} = 3.7$ sec, $SD = 0.6$, $n = 5$) had longer songs than females ($\bar{x} = 2.7$ sec, $SD = 0.5$, $n = 4$; $t_7 = -1.27$, $P = 0.25$) and shorter intervals between descending call syllables (males: $\bar{x} = 1.3$ sec, $SD = 0.01$, $n = 5$; females: $\bar{x} = 1.4$ sec, $SD = 0.02$, $n = 4$; $t_6 = 1.21$,

Table 4. Model selection results for sora response probability to broadcast surveys in Maine (2010 and 2011). The first 5 models listed are the $\geq 90\%$ confidence set of the original 16 considered. $\text{Log}_e(L)$ is the value of the maximized log-likelihood function, K is the number of parameters, AIC_c is Akaike's Information Criterion for small sample sizes, and w_i is the Akaike weight.

Model ^a	K	AIC_c	ΔAIC_c	w_i	Cumulative w_i	$\text{Log}_e(L)$
Age + predation status + density	5	65.96	0	0.46	0.46	-27.37
Julian date + age + predation status + density	6	66.69	0.72	0.32	0.79	-26.47
Density + predation status	4	70.55	4.59	0.05	0.83	-30.88
Predation status + age	4	70.65	4.68	0.04	0.88	-30.92
Density + Julian date + predation status	5	70.94	4.97	0.04	0.92	-29.86
Density + age	4	72.23	6.26	0.02	0.94	-31.71
Predation status + Julian date	4	72.47	6.51	0.02	0.95	-31.84
Julian date + age + predation status	5	73.03	7.06	0.01	0.97	-30.90
Density + Julian date + age	5	73.53	7.57	0.01	0.98	-31.15
Age	3	73.87	7.9	0.01	0.99	-33.70
Predation status	3	74.86	8.89	0.01	0.99	-34.19
Julian date + age	4	76.19	10.23	0	1	-33.70
Julian date	3	76.73	10.76	0	1	-35.13
Density + Julian date	4	77.67	11.71	0	1	-34.44
Density	3	78.82	12.86	0	1	-36.18
Null (constant-intercept)	2	79.97	14.01	0	1	-37.87

^a Variable descriptions: density is Virginia rail and sora vocalization density per site, Julian date is the numerical calendar date of the survey, predation status is whether or not the nest was depredated, and age is nest age.

$P=0.27$) within the jackknife procedure. Males ($\bar{x}=71.98$ dB, $SD=4.8$, $n=5$) also had louder (higher average power) songs than females ($\bar{x}=54.95$ dB, $SD=3.2$, $n=4$; $t_6=-2.93$, $P=0.021$).

DISCUSSION

Vocalization and Call Type Variability

Estimates of Virginia rail detection probability during broadcast surveys were within the range of previous estimates

of 20–100% (Glahn 1974) and 64–82% (Gibbs and Melvin 1993). Detection probability quantified in this study differed by being conducted at known nest sites, and accounted for density, stage, year, and Julian date. Sora detectability estimates were also within the range of previous estimates of 20–100% (Glahn 1974) and slightly lower than the 59–84% reported by Gibbs and Melvin (1993). Similar to previous studies (Gibbs and Melvin 1993, Allen et al. 2004, Conway and Gibbs 2005), we found that compared to the passive period, broadcasting increased detection probability by 1.78 times for Virginia rails and 2.08 times for soras. Our results were slightly lower, however, than Conway and Gibbs

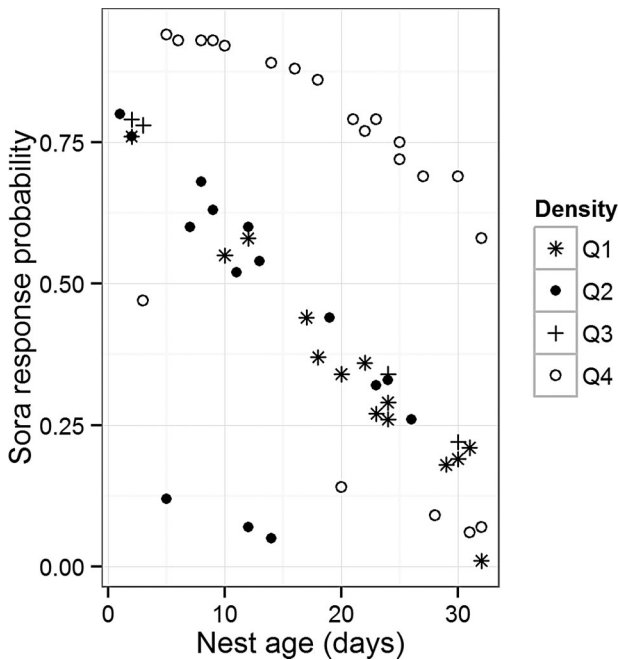


Figure 2. Sora broadcast survey response probability as a function of nest age (days) in Maine (2010 and 2011). We derived model-averaged estimates from our top 5 models that included breeding stage (post-predation or not), site-scale Virginia rail and sora vocalization density, Julian date, and nest age. Density quartiles (Q1–Q4) were 0.97–1.90, 1.91–2.43, 2.44–3.14, and 3.15–8.70 birds/ha and are represented by symbols.

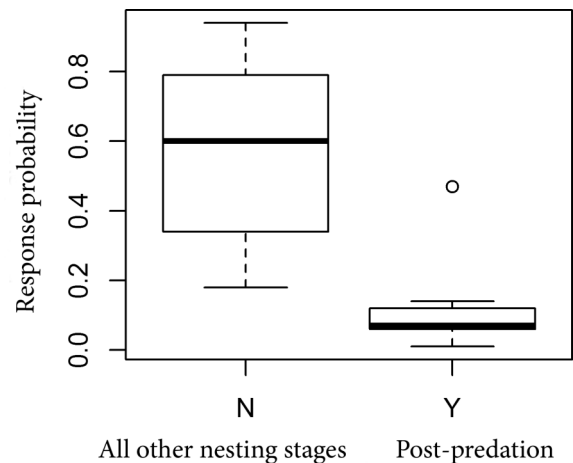


Figure 3. Sora broadcast survey response probability for post-predation versus all other nesting stages (egg-laying, incubation, hatching, hatched) in Maine (2010 and 2011). We derived model-averaged estimates from our top 5 models that included breeding stage (post-predation or not), combined site-scale Virginia rail and sora vocalization density, Julian date, and nest age. The top and bottom of the box represent the first and third quartiles, the heavy line in the box represents the median, the whiskers represent the maximum and minimum values excluding outliers, and the circles are outliers.

Table 5. Summed Akaike weights (w_i) from the original 16 models, model-averaged parameter estimates with unconditional standard errors (SE), and odds ratios with unconditional 95% confidence intervals for variables in the top 5 models for sora response probability to broadcast surveys in Maine (2010 and 2011).

Variable ^a	Summed (w_i)	Estimate	SE	Odds ratio (95% CI)
Predation status	0.95	-3.57	1.52	0.03 (0.00, 0.46)
Density	0.90	0.39	0.17	1.48 (1.07, 2.05)
Age	0.88	-0.13	0.06	0.88 (0.77, 0.99)
Julian date	0.41	0.05	0.08	1.05 (0.91, 1.22)

^a Variable descriptions: density is Virginia rail and sora vocalization density per site, Julian date is the numerical calendar date of the survey, predation status is whether or not the nest was depredated, and age is nest age.

(2005), who found that broadcast increased detection of Virginia rails by 7.35 times and soras by 2.63 times and Rehm and Baldassarre's (2007) findings that 76% of Virginia rail and 90% of sora responses were during or after the broadcast. These differences are likely due to our method of standardizing survey distance from nests, which give a more accurate estimate of the benefits of using broadcast rather than passive listening surveys during the breeding season.

Similar to Kaufmann (1983), we found that the sora per-weep call is used mostly pre-nesting, which indicates a role in pair formation. This is a call that could be used to distinguish pre-breeding from breeding individuals during broadcast

surveys, which could be helpful in determining ratios of breeders to nonbreeders in a population without requiring nest monitoring. The kadic-kadic call has similar function for the Virginia rail but is quieter and would be slightly more difficult to detect, unlike the sora per-weep call, which is loud and persistently used. The Virginia rail descending call is the most common call of the species, but it is used across all measured breeding stages. The peep call of both species is used only in late incubation, hatching, and post-hatching by paired birds (often in a duet of peeping back and forth), and it may be useful to index nest success (recognizing that some of these nests with peep calls may be in late incubation and may fail before hatching). This call is fairly quiet but can be heard within approximately 50 m.

Factors Affecting Detectability

During broadcast surveys at Virginia rail nests, the stage (specifically post-failure) and the density of Virginia rails and soras at the site strongly influenced response probability. Individuals whose nests failed were less likely to vocalize, possibly because they no longer had offspring to defend. Surveys following predation events may be misinterpreted as having a lower abundance of individuals. Virginia rails responded similarly to broadcast during their egg-laying, incubation, and hatching stages and we did not find support for an effect of Julian date. These results contrasted with Rehm and Baldassarre (2007) who found that Virginia rail responses increased by 0.22 birds/week in New York from 11 April to 8 July. This may be due to differences in survey methodologies. We conducted broadcast surveys 10 m from known nests, whereas they broadcast along transects with unknown numbers of nests near their survey points. Our results give a more accurate reflection of how nesting individuals respond to broadcast surveys during the breeding season. They also suggest that there may be a wider time window available for Virginia rails to be surveyed than Rehm and Baldassarre's (2007) results suggest.

During broadcast surveys at sora nests, we found that the age of the nest, density, and predation status had the greatest impact on response probability. A post-predation broadcast survey decreased the odds of response compared with all other stages of breeding. This is likely due to decreased parental defense with no remaining offspring and, similar to Virginia rails, could lead to misinterpreting surveys following predation events as having a lower abundance of individuals. The odds of a sora responding to surveys decreased as the age of the nest increased. This quieting over the nesting cycle may be a nest hiding mechanism that progresses with increasing time investment in offspring. Other studies found similar trends in soras. Rehm and Baldassarre (2007) found that sora responses decrease slowly (0.01 birds/week) during point count surveys over the breeding season, and Johnson and Dinsmore (1986) found that soras peak in early May and then responses decrease until early June when there are only a few birds responding. Both their results and ours emphasize the importance of surveying soras early in the nesting season.

The odds that either Virginia rails or soras responded to broadcast increased as density of both species increased

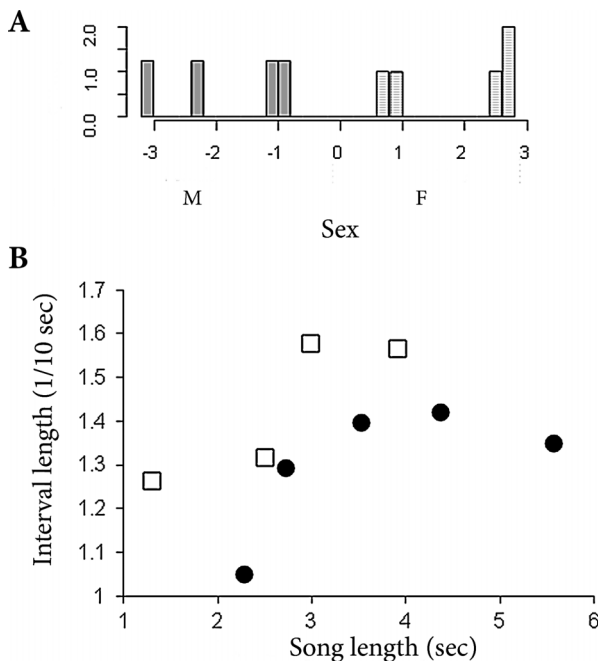


Figure 4. (A) Complete separation of male (gray bars) and female (striped bars) Virginia rail descending calls using linear discriminant analysis with jackknifed prediction in R and variables song length and interval length from broadcast survey responses in Maine (2010 and 2011). The metrics on the x-axis are the standardized jackknife influence values. (B) Virginia rail descending call song length (sec) versus interval length (0.1 sec) between descending calls as measured in RAVEN in response to broadcast recording in Maine (2010 and 2011). Males are indicated in filled circles and females in open squares.

within the site. Dow (1970) mentioned the possibility that birds might have increased responsiveness with high densities, and Glahn (1974) qualitatively noticed increased responses of Virginia rails and soras in wetlands with greater densities. Our study found that site-scale vocalization density greatly influenced detectability. Densities of soras and Virginia rails (\bar{x} = 3.17, SD = 2.56, n = 7) at our sites were similar to those reported in other studies (Pospichal and Marshall 1954, Tanner and Hendrickson 1954, Tacha 1975) although 1 site had a density of 8.70 birds that was more than double the maximum density reported elsewhere. These results suggest that broadcast surveys may be overexaggerating abundance differences amongst sites. High density sites have louder vocalizations, higher detectability, and will overestimate abundance, whereas low density sites have quieter vocalizations, lower detectability, and will underestimate abundance. Accounting for these density-based detectability differences would more accurately elucidate abundance differences amongst sites.

An assumption of our study was that the nesting pair was responding to our broadcasts 10 m from their nests and it was not neighboring individuals. We could not be completely certain of the nest owner's identity and this would be possible only with radio-tagged individuals, which would limit sample size or greatly increase costs.

Sex Influences on Detection

Male Virginia rails responded to broadcast surveys with faster descending calls (shorter intervals between individual call notes) that continued for a longer time. This may be a graded signal of enthusiasm and suggests greater territorial behavior in males, which is common in avian species (Falls 1963, Arcese 1987). We also detected significant differences in the volume of male versus female calls (not used in our sex determination tests to prevent confounding song attributes with distance), which is likely due to either endogenous increases in volume or more closely approaching the microphone following broadcast. Either of these mechanisms also supports increased male response to playback. Longer and louder songs are heard more easily during surveys, which results in higher detectability for males. Detection probability of male black rails is also higher than females during broadcast surveys (Legare 1999). Sex biased detection probabilities that are not accounted for will alter abundance estimates.

MANAGEMENT IMPLICATIONS

We recommend that marsh bird abundance estimates account for density and sex-biased detectability differences. Detectability differences due to density can be calculated fairly easily using broadcast survey data and distance sampling programs. Sex-based detectability can be calculated if the sexes are dimorphic and are visible during surveys. Because visibility is usually not possible with marsh birds, and some species are monomorphic, more studies are needed to determine sex-specific detectability differences for each marsh bird species. We suggest training observers in recording data on call types and frequency of call types.

Calls such as the per-weep and kadic-kadic could assist in determining numbers of unpaired individuals throughout the breeding season. Calls such as the peep could also help delineate when breeding begins and ends and the rate at which it does so, which could be used to generally infer nesting success.

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