

**RESPONSES OF RAIL PRODUCTIVITY TO WATER LEVEL VARIABILITY AND
FACTORS AFFECTING RAIL BROADCAST SURVEY RESULTS**

By

Ellen Padgett Robertson

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Advisory Committee:

Brian J. Olsen, Assistant Professor of Biology and Ecology, Co-Advisor

William E. Glanz, Associate Professor of Zoology and Cooperating Associate
Professor of Wildlife, Co-Advisor

Cynthia S. Loftin, Unit Leader, Maine Cooperative Fish and Wildlife Research Unit and
Associate Professor of Wildlife Ecology

Danielle E. D'Auria, Wildlife Biologist, Maine Department of Inland Fisheries and
Wildlife

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Thesis advisors: Dr. Brian J. Olsen and Dr. William E. Glanz

An Abstract of the Thesis Presented
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Virginia rail (*Rallus limicola*) and sora (*Porzana carolina*) (hereafter “rails”) populations are thought to be declining and we examined habitat variables potentially affecting productivity of 75 Virginia rail and 22 sora nests in Maine during 2010-2011. We identified the mechanisms for nest failure (nest scale) and characteristics of wetlands (wetland scale) that predict reproductive success with logistic-exposure models and an information-theoretic approach. Our results suggest that water-level variation is a positive predictor of rail nest success and rail density in Maine wetlands. Hydrologic variation creates low-sloped wetland edges where emergent plants thrive. Wetlands with large areas of shallow depths and abundant emergent vegetation improve habitat condition for nesting rails. The presence of a waterfowl impoundment did not affect water-level variability, nest survival, or clutch size in our models.

The National Marsh Bird Monitoring Program is being initiated to document marsh bird population trends with call-broadcast surveys. We examined effects of site-estimated rail density, breeding stage, call type, and sex differences on marsh-bird response probability to improve marsh bird surveys. We conducted 335 surveys on 113 rail nests in ten wetlands during 2010 and 2011. We determined important variables for predicting response probability of

Virginia rails and soras to broadcast surveys 10 m from known nests with generalized linear models. The odds of both rail species responding to broadcast increased as rail density increased. Nest age and recent nest failure owing to predation significantly decreased the odds of sora response. For Virginia rails, the post-predation stage decreased the odds of response to broadcast calls and rail response was marginally less, although not significantly so during the post-hatch stage. Rails responded similarly to broadcast during egg laying, incubation, and hatching. Virginia rails and soras both used “peep” call late in late nesting/post-hatching stages, and this call could be used during surveys later in the breeding season as an index of nest success. The “kadic-kadic” (Virginia rail) and the “per-weep” (sora) calls are used primarily during the pre-nesting phase (and not prior to replacement clutches) and may be indicators of unpaired birds. These vocalization differences could be used to strengthen population estimates by differentiating between presence and active breeding throughout the season. 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 large-scale marsh-bird population trend estimates take density and sex detectability issues into account and recognize that wetlands with low response rates may underestimate population estimates more than those with high response rates owing to lower bird densities and differences in sex ratios and breeding stage.

THESIS ACCEPTANCE STATEMENT

On behalf of the Graduate Committee for Ellen Padgett Robertson I affirm that this manuscript is the final and accepted thesis. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine.

Brian J. Olsen

February 12, 2012

Assistant Professor of Biology and Ecology

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CHAPTER 1

RESPONSES OF RAIL PRODUCTIVITY TO WATER LEVEL VARIABILITY

1.1. Introduction

Wetland habitat loss is a significant threat to marsh-bird populations (Tacha and Braun 1994). Declines in Virginia rails (*Rallus limicola*) (2.2% annually from 1982 to 1991) and soras (*Porzana carolina*) (3.3% annually from 1966 to 1991) are proportional to wetland habitat loss during the same period (Conway et al. 1994). Virginia rails and soras (hereafter “rails”) selectively use moist-soil wetlands with shallow water, emergent vegetation, and substrate with abundant invertebrates (Frederickson and Reid 1986, Gibbs and Melvin 1990, Tacha and Braun 1994, Conway 1995, Poole 2007). Rails forage in these shallow muddy areas and eat a variety of invertebrates, aquatic plants, and emergent plant seeds (Pospichal and Marshall 1954, Irish 1974, Tacha and Braun 1994). Emergent plants are also used by rails as nesting material.

Hydrologic variability increases emergent vegetation abundance (Euliss et al. 2008, Galat et al. 1998) and small scale topographic diversity (Galat et al. 1998) important for rail food and nesting habitat (Lor and Malecki 2007). It also increases habitat diversity (Melvin and Gibbs 1996, Galat et al. 1998, Rehm and Baldassarre 2007, Euliss et al. 2008) and macroinvertebrate diversity important as a rail food source (Tacha and Braun 1994). Rails are sensitive to water variability, however, as it can also decrease nesting success by increasing nest loss, changing optimal foraging sites, and increasing rail movements (Baird 1974, Tacha 1975, Griese et al. 1980). Nests may be raised with additional nesting material to keep eggs above floodwater (Walkinshaw 1940, Pospichal and Marshall 1954) such as along the Connecticut River where soras survived flood conditions by building up nests 43-48 cm tall (Billard 1948) but flooding

can also increase nest failure in Virginia rails and soras (Conway 1995, Melvin and Gibbs 1996) such as a Colorado study where 13 of 15 sora nests flooded water levels rose greater than 20 cm (Griese et al. 1980). The relative risk of flooding is negatively correlated with the risk of nest predation in many wetland birds (Greenberg et al. 2006) and drought may increase nest accessibility by terrestrial predators (Weller 1961, Post 1998), such as snakes, muskrat, weasels, and raccoons (Tacha and Braun 1994).

A common management technique to offset wetland habitat loss is the impoundment of aquatic areas to lengthen the duration of wetland flooding for waterfowl use (Frederickson and Taylor 1982, Greer et al. 2007). Impoundment management generally increases inundation duration during the summer or varies water levels in early spring or late fall to increase seed production for waterfowl consumption (Frederickson and Taylor 1982). Water control structures in most managed wetlands are designed to maintain water at a greater depth with less fluctuation than is hydrologically natural (Euliss et al. 2008, Smith et al. 2008). Flooding periodicity and intensity in these wetlands are decreased and, over time, can encourage plant monocultures (Galat et al. 1998, Euliss and Mushet 2004, Euliss et al. 2008), a decrease in emergent vegetation abundance (Weller et al. 1991), and decreases in macroinvertebrate diversity and ecosystem productivity (Galat et al. 1998, Euliss and Mushet 2004). Periodic, shallow flooding or partial drawdowns through impoundment management can be used, however, to concentrate invertebrate prey (Nelson and Kadlec 1984, Frederickson and Reid 1986, Eddleman et al. 1988) and promote seed germination, plant diversity and productivity (Weller and Fredrickson 1974, Weller 1981, Frederickson and Reid 1984), emergent plant growth, and restrict weed succession (Andrews 1973, Johnson 1984, Frederickson and Reid 1986).

We identified the mechanisms of nest failure (nest-scale), reproductive success (wetland-scale), and rail density (wetland-scale) and also compared hydrologic variation and rail productivity on wetlands with and without waterfowl-management impoundments.

1.2. Study Area

Our nest-scale sites included five wetlands (2 impounded) in Penobscot county (near Bangor Maine) and five wetlands (3 impounded) within Moosehorn National Wildlife Refuge (200 miles east near Calais, Maine) ranging 40 to 272 ha ($\bar{x} = 98$, $SD = 155$). The impoundments are a levee equipped with a floodgate to manually regulate water levels, however, there has been minimal manipulation of floodgates since construction. Impoundments at Moosehorn were created during 1950-1974 in historical beaver dam locations and have remained flooded other than occasional drawdowns (Hierl et al. 2006). All sites were within the Eastern Coastal Plain biophysical region (Krohn and Boone 1999) and dominant species included *Typha latifolia*, *Typha angustifolia*, *Myrica gale*, *Carex* sp., *Calamagrostis canadensis*, *Spirea alba*, *Spirea tomentosa*, *Salix* sp., *Alnus* sp., *Sagittaria latifolia*, *Dulichium arundinaceum*, *Pontedaria cordata*, *Lemna minor*, *Lysimachia terrestris*, *Galium palustre*, *Equisetum* sp., *Vaccinium macrocarpon*, *Scirpus* sp., *Calla palustris*, *Polygonum* sp., *Sparganium americanum*, *Chamaedaphne calyculata*, *Juncus* sp., *Triadenum virginicum*, and *Potentilla palustris*. Nests were found in vegetation including *Myrica gale*, *Typha latifolia*, *Calamagrostis canadensis*, *Juncus* sp., *Carex* sp., and *Leersia oryzoides*. Earliest nest initiation date at our sites was 24 April and the latest nest initiation date was 1 July. Sites included Pond Farm Wildlife Management Area (Howland, ME), Sedgunkedunk Stream of Field's Pond (Orrington, ME), Penjajawoc Marsh (Bangor, ME), Wheeler Brook Stream (Hermon, ME), Pleasant Lake

(Stetson, ME), Cranberry Lake (Moosehorn Wildlife Refuge, ME), West Dudley Flowage (Moosehorn Wildlife Refuge, ME), Dudley Swamp (Moosehorn Wildlife Refuge, ME), Magurrewock (Moosehorn Wildlife Refuge, ME), and Barn Meadow (Moosehorn Wildlife Refuge, ME).

1.3. Methods

1.3.1. Measurements at Nest Scale

We searched for Virginia rail and sora nests in areas where we heard paired birds responding to broadcast rail calls during mid-April to early August 2010-2011. Observers recorded the date, nest contents (eggs, chicks, or evidence of predation or flooding), and measurements of water depth and nest height (nest base to nest lip), and we revisited nests every 3-5 days until hatching or failure. A successful nest hatched at least one young, whereas, a depredated nest lost all eggs before the anticipated time of hatching or had obvious signs of predation such as nest damage or egg albumin. Institutional Animal Care and Use approval was obtained (protocol number A2009-04-05).

We estimated nest initiation dates for incomplete clutches by counting backwards from the last egg laid, and assumed females laid 1 egg/day. We estimated nest initiation date for complete clutches by counting backwards from hatch date, and assumed an average nest period of 28 days for both species. If the exact hatch date was not known, we estimated it as the midpoint between the last nest visit with eggs and the following visit with chicks. For nests found in incubation that failed before eggs hatched we assumed that nests were found in the middle of incubation.

We modeled nest survival as a function of explanatory variables with a logistic exposure model (Shaffer 2004) using the “nestsurvival” package (Herzog 2011) in R (R Core Development Team 2011). This is a generalized linear model with a binomial response distribution and a logit link function that takes into account varying nest-visitation interval lengths (Shaffer 2004). We chose *a priori* models with the information-theoretic approach (Burnham and Anderson 2002) that made biological sense based on field observations, literature searches, and exploratory data analysis. We chose to examine change in water depth at the nest because we noticed that rails tended to forage and nest in areas of shallow water with high water-level variation and because of previous studies showing a positive relationships between rail habitat use and habitat parameters associated with water variability such as emergent vegetation and invertebrate and seed diversity (Tacha and Braun 1994, Melvin and Gibbs 1996, Lor and Malecki 2007). We chose change in nest height between visits (and its interaction with water depth change) because we commonly saw rails building their nest in response to water level variation. We added age of nest (hereafter “age”) into the model because previous studies have found time-specific patterns to be important additions to nest-survival models (Grant et al. 2005). Our study was designed to look at the effects of impoundments on rail nesting success so we also included this as a variable in our final model set. We tested 16 candidate models 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. Variables included nest age, nest height, water depth, change in nest height, change in water depth, and impoundment presence or absence. We evaluated the importance of each variable by summing the Akaike weights across all models (Burnham and Anderson 2002). We examined global-model goodness-of-fit with a Hosmer and Lemeshow (2000) goodness of fit test and assessed overdispersion using the

Pearson χ^2 statistic (Burnham and Anderson 2002). We used effective sample size (Rotella et al. 2004) ($n = \text{failed} + \text{successful intervals}$) for model selection with Akaike's information criterion for small sample size (AIC_c). Model averaging was used for the group of models with a combined $w_i \geq 90\%$ to account for model selection uncertainty on parameter estimates (Burnham and Anderson 2002) using the "nestSurvival" package in R (Herzog 2011). We tested for multicollinearity by calculating the variance inflation factors for each predictor variable.

We examined whether the presence of an impoundment had a significant effect on change in water depth, change in nest height, water depth, clutch size, and daily survival rate using a Welch Two-Sample t -test or a Wilcoxon Signed-Rank Test.

1.3.2. Measurements at Wetland Scale

We surveyed our seven wetland sites for rail densities with survey points 200-m apart and a 5 minute passive period followed by broadcasting 30 seconds sora calls, 30 seconds silence, 30 seconds Virginia rail calls, 30 seconds using a CD from the National Marsh Bird Monitoring Program.

We placed Onset HOBO water-level data loggers (U-20 freshwater 13-foot-depth) in perforated PVC pipes (5' length and 1.5" diameter) in each monitored wetland downstream from all nests. Water depths were taken every 30 minutes to obtain a detailed graph of water level changes over the nesting season. Logger accuracy was verified with hand measurements and logger data was calibrated for barometric pressure variation with barometric pressure loggers.

We processed water logger data using Indicators of Hydrologic Alteration (IHA) Version 7.1 (The Nature Conservancy, 2009). IHA parameters provide information on ecologically

significant features of wetland-scale water regimes. We used the non-parametric statistic option and limited “analysis days” to the rail nesting season.

We were interested in relative water depth changes rather than absolute measurements, so for each of the seven wetlands we subtracted the site-specific mean water depth from all parameters. Wetland-scale parameters included the minimum water-depth mean over the season at three time scales (1, 3, and 7-day moving averages), the maximum water-depth mean over the season at three time scales (1, 3, and 7-day moving averages), Julian date of the deepest, one-day mean water level, Julian date of shallowest one-day mean, the number and duration of low pulses, number and duration of high pulses, the median rate of increase and decrease for the season, the number of reversals (“rising” versus “falling” water depths), mean June low flow, extreme low flow duration, timing, and frequency, and small flood duration, timing, and rise rate. Pulse, flow, and flood limits were defined by IHA’s default setting.

We took vegetation measurements at all nests within a two-week time period at the end of the nesting season (early July). Measurements included width and height measurements of nest vegetation; percent nest concealment in four cardinal directions at a distance of 1 m; percent shrubs, forbs, water, duckweed, and mud at a 2-m radius from the nest center; and vegetation density in four cardinal directions at a 1-m radius from the nest.

ArcGIS (ESRI 2011) was used to determine wetland size, distance of each nest from the nearest upland border, and 14-digit HUC subdrainage size. Wetland sites were digitized on the National Agriculture Imagery Program (2009, 1-m digital orthoimagery layer) using the National Wetlands Inventory layer as a guideline. The 14-digit HUC (Hydrologic Unit Code) was used to determine drainage sub-watershed area for each of the wetland sites. Hydrologic units are drainage areas that obtain surface water directly from upstream areas and indirectly from

associated surface areas. The 14-digit HUC is a drainage sub-watershed that has a typical size of 10,000-40,000 acres and is completely contained within one 11-digit HUC. Our sites ranged from a 14-digit HUC of 6,800 to 69,600 acres ($\bar{x} = 48,200$, $SD = 3,700$).

We used Principle Components Analysis (PCA) to identify the major axes of variation in our vegetation, hydrology, and GIS wetland-scale data. We used model-averaged Daily Survival Rates (DSR) from the 97 rail nests in our Nest-Scale model to obtain DSR per site. Logit-transformed, site DSR ($n = 7$) were used as the response variable and all seven principle components and highly loaded variables ($>|0.2|$) from PCA were tested individually (to avoid overfitting) as potential predictor variables.

We used the “distsamp” package in R to obtain rail density estimates at each site accounting for distance-based detection variability. Rail responses and distances from our wetland broadcast surveys were input into “distsamp”. Site density from “distamp” results was used as the response variable and principle components and highly loaded variables from the PCA were tested individually as potential predictor variables.

We tested all Regression and ANOVA models in R. AIC_c was used for model selection and models with $\Delta AIC_c < 2.0$ were considered equivalent. We used a Welch Two Sample t -test (if normal and equal variances) or a Wilcoxon Signed Rank Test to examine whether the presence of an impoundment had a significant effect on number of reversals, high pulse count, low pulse count, fall rate, rise rate, high pulse duration, and rail density.

1.4. Results

1.4.1. Nest-Scale Results

We monitored 75 Virginia rail and 22 sora rail nests with an effective sample size of 986 monitored nest days. The overall daily survival rate from our logistic exposure model was 97.60 % (CI, 93.70, 99.02) and overall nesting-period survival rate was 50.52 % (CI, 16.18 to 75.86 %). Apparent nesting success was 31/85 nests or 63.5%. Most of our rail nest failures (90.3%, $n = 31$) were from predation. Only 6.4% of failures ($n = 2$) were due to flooding and 3.2% from nest abandonment ($n = 1$).

Our final model set included eight models with a cumulative Akaike weight of 0.9 (Table 1). The global model fit the observed values (Hosmer and Lemeshow goodness-of-fit test; $\chi^2 = 10.05$, $P = 0.26$). The Pearson χ^2 test also indicated there was good model fit without overdispersion ($\phi = 1.08$, $P = 0.16$). Variance-inflation factors for all predictor variables were less than 2.2.

The top two models had $\Delta AIC_c = 1.6$ and included variables that were all significantly (+) related to nest success including age (Figure 1), water depth change (Figure 2), and the interaction between change in water depth and nest height change (Figure 3) (Table 1,2). Akaike weights for the top two models were 40% and 18% of all weights for the 16-candidate-model set (Table 1). The effect of nest height change was not significantly related to nest success, although the parameter was included in both the top-ranked models (Table 1, 2). The second-best fitting model ($\Delta AIC_c = 1.6$) included the effect of impoundment, however, the effect was not statistically significant (Table 1, 2).

Water depth change and age had the greatest effects on nest survival. Both were found in six of the top eight models and the model-averaged estimates were statistically significant (Table 1, 2, 3). Water depth change was slightly more important than age (summed Akaike weights = 0.83 vs. 0.82) (Table 2). The interaction of water depth change and nest height change

significantly affected nest survival and was included in four of the top eight models (Table 1, 2). The Akaike weights for the interaction of water depth change and nest height change summed to 0.71 (Table 2). Four of the top eight models also included impoundment and nest height change but the 95% CI of the odds ratios included 1.0, making it difficult to assess their strengths (Table 1, 2). Summed Akaike weights were 0.76 for nest height change and 0.31 for impoundment (Table 2).

Nests in wetlands with impoundments versus those without did not differ for water depth change ($t = -0.16$, $P = 0.87$), nest height change ($t = 0.03$, $P = 0.98$), Virginia rail clutch size ($T = 581.5$, $P = 0.41$), sora clutch size ($T = 1627.5$, $P = 0.08$), or daily survival rate ($T = 6531$, $P = 0.1357$) (Figure 4). Impounded wetlands had a trend ($t = -1.8$, $P = 0.07$) of deeper mean water depths ($\bar{x} = 24.69$ cm, $SD = 19.99$, $n = 191$) than non-impounded wetlands ($\bar{x} = 21.72$, $SD = 10.34$, $n = 77$).

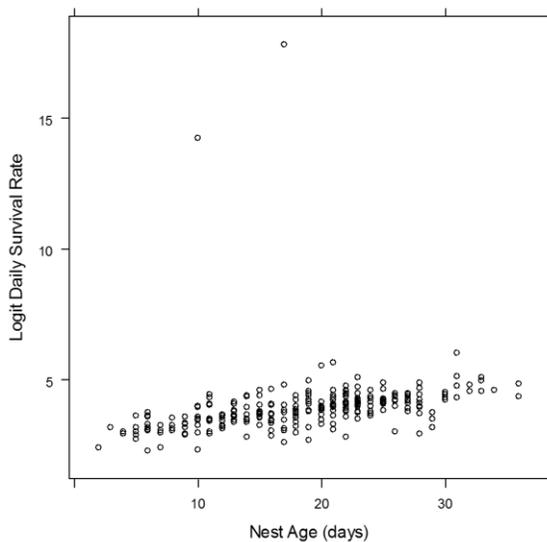


Figure 1. Age and Daily Survival Rate: Logit-transformed daily survival probability increased as nest age (days) increased for Virginia Rails and soras in Maine (2010 & 2011).

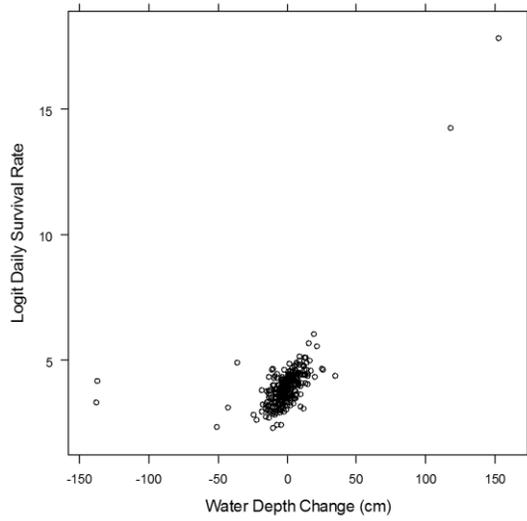
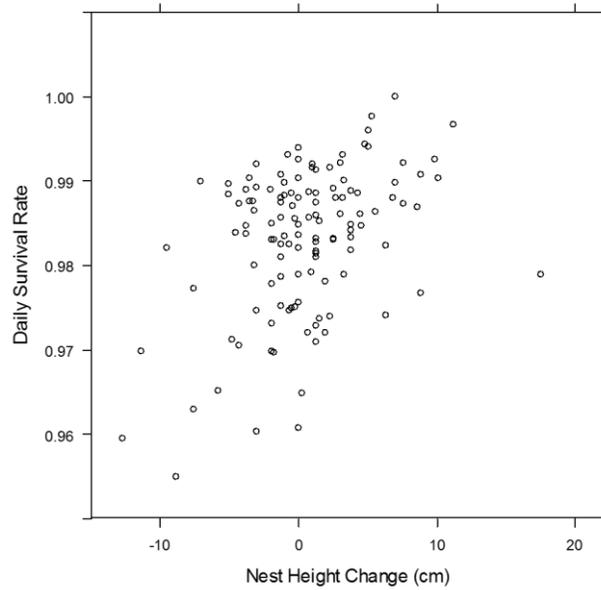
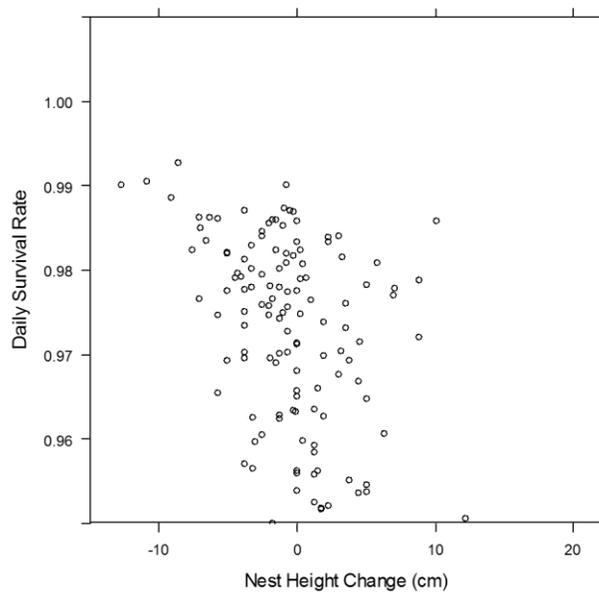


Figure 2. Water Depth Change and Daily Survival Rate: Logit-transformed daily survival probability versus Water Depth Changes (cm) at nests for Virginia Rails and soras in Maine (2010 & 2011).



A.



B.

Figure 3. Nest Height Change With Changing Water Depths: A) For nests with increasing water depths, daily survival probability increased as the nest was built up. B) For nests with decreasing water depths, daily survival probability was highest for nests that compressed the most (had experienced higher water levels in the past).

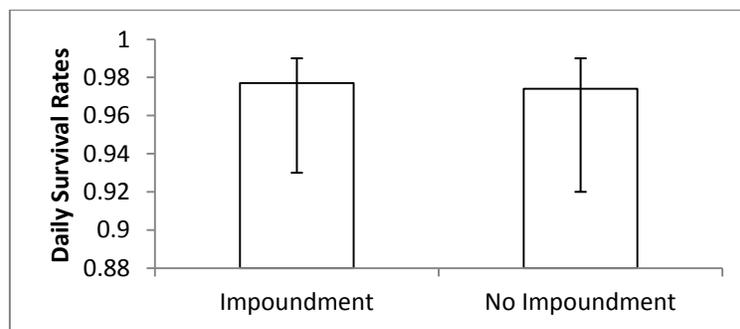


Figure 4. Impoundment and Daily Survival Rate: Daily survival probabilities (\pm 95% CI) for wetlands with and without waterfowl-management impoundments in Maine 2010 & 2011.

Table 1. Rail Nest Survival Models: Results of model selection examining factors affecting rail nest survival in Maine (2010 & 2011). The first eight 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, AIC_c is the Akaike's information criterion for small sample sizes, and w_i is the Akaike weight. A smaller AIC_c and a larger Akaike weight represent more support for the model.

Model	AIC _c	ΔAIC _c	w _i	Log _e (L)
water depth change*nest height change+water depth change+nest height change+age	160.4	0	0.40	1.00
impoundment + water depth change*nest height change+water depth change+nest height change+age	162.0	1.6	0.18	0.46
water depth change*nest height change+water depth change+nest height change	163.3	2.9	0.09	0.23
age+water depth change	164.0	3.5	0.07	0.17
age	164.0	3.6	0.07	0.17
impoundment+water depth change*nest height change+water depth change+nest height change	165.2	4.7	0.04	0.09
impoundment+age+water depth change	165.4	5.0	0.03	0.08
impoundment+age	165.6	5.2	0.03	0.08
age+nest height change	165.9	5.5	0.03	0.06
null (constant intercept)	166.8	6.4	0.02	0.04
water depth change	166.8	6.4	0.02	0.04
impoundment+age+nest height change	167.5	7.1	0.01	0.03
impoundment+water depth change	168.5	8.1	0.007	0.02
impoundment	168.6	8.1	0.007	0.02
nest height change	168.7	8.3	0.006	0.02
impoundment+ nest height change	170.4	10.0	0.003	0.007

Table 2. Rail Nest Survival Model-Averaged Parameter Estimates: Model-averaged parameter estimates with unconditional standard errors (SE) and odds ratios with unconditional 95% confidence intervals, p values, and summed Akaike weights (w_i) for variables in the top eight models for nest survival of Virginia rails and soras in Maine, 2010 & 2011. Note that the odds ratio is difficult to interpret for variables included in the interaction.

Parameter	Estimate ± SE	Odds ratio (95% CI)	Summed (w_i)
intercept	2.53 ± 0.61		
age	0.06 ± 0.03	1.07 (1.01, 1.13)	0.81
water depth change	0.15 ± 0.05	1.17 (1.05, 1.30)	0.83
nest height change	-0.04 ± 0.13	0.96 (0.75, 1.23)	0.76
impounded	0.30 ± 0.44	1.34 (0.57, 3.19)	0.31
water depth change * nest height change	0.06 ± 0.03	1.06 (1.01, 1.12)	0.71

Table 3. Rail Nest Measurements Descriptive Statistics: Descriptive statistics for covariates measured at rail nests (nest height, water depth, water depth change, nest height change, water to nest lip difference) and also clutch sizes of Virginia rail and sora in Maine 2010 & 2011.

Measurement (cm)	Min	Max	Mean	SD
nest height	3.8	28.0	13.0	4.1
water depth	0.0	163.2	23.9	17.8
water depth change	-50.8	34.54	-0.7	19.3
nest height change	-12.7	19.6	0.2	4.3
water to nest lip distance	0.0	50.8	12.5	6.1
sora clutch size (# eggs)	8.0	18.0	11.6	2.6
Virginia rail clutch size (# eggs)	5.0	13.0	8.4	1.5

1.4.2. Wetland-Scale Results

Principle Component 3 (PC3), reflecting water level variation from falling to rising or vice versa, was the best wetland-scale predictor of daily survival rates (Figure 5) ($F_{1,5} = 31.83$, $P = 0.002$)(Adj. $R^2 = 0.84$). PC3 characterizes wetlands with water levels that often rise and fall (with faster rates of falling than rising) that possess more shrub coverage with dense, leafed branches above and open, water-covered ground below with high loadings (>0.2) including positive relationships with low pulse count, high pulse count, fall rate, width of nest vegetation clump, the percentage of nest concealment from above, percentage of water cover in a 2-m radius, vegetation stem density, and negative relationships with percentage of nest concealment from the sides, percentage of ground cover by forbs within a 2-m radius, and rise rate

The number of reversals ($t = -1.15$, $P = 0.324$), high pulse counts ($t = -1.46$, $P = 0.20$), low pulse counts ($t = -0.45$, $P = 0.67$), fall rates ($t = -0.98$, $P = 0.40$), rise rates ($t = -0.415$, $P = 0.70$), high-pulse durations ($t = 0.87$, $P = 0.47$), or rail densities ($T = 3$, $P = 0.40$) did not differ with impoundment presence.

Number of hydrologic reversals was the best predictor of rail density at the wetland-scale (Figure 6) ($F_{1,5} = 12.21$, $P = 0.02$)(Adj. $R^2 = 0.65$). Wetland sites with greater water level variability, that frequently shifted between rising and falling water levels, had higher densities of

rails. The data point representing the densest wetland had very high leverage and we would need to include a greater range of rail densities to determine whether this was a spurious result.

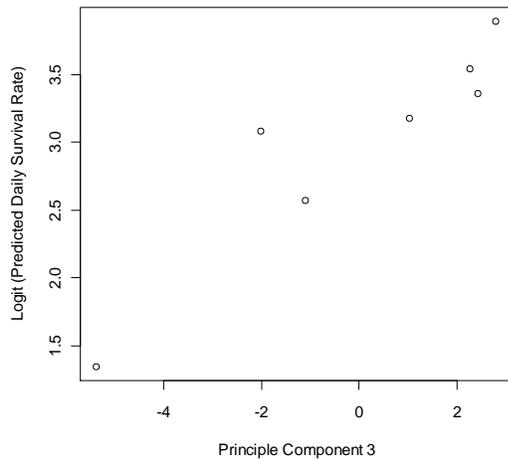


Figure 5. Wetland Daily Survival Rate and PC3: Logit-transformed Daily Survival probability versus Principle Component 3 (which was tightly linked to water-level variability) for rail nests in Maine (2010 & 2011).

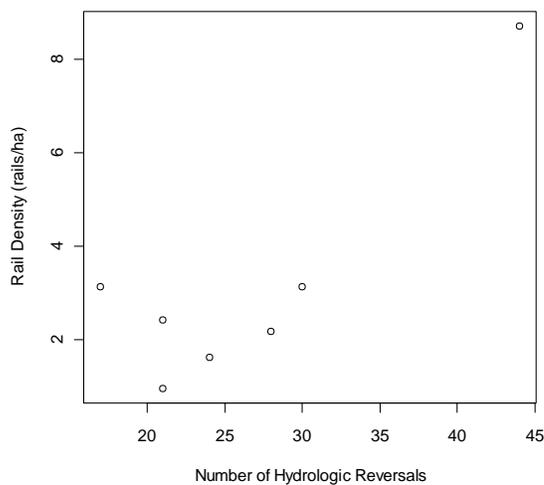


Figure 6. Rail Density and Hydrologic Reversals: Rail density (rails/ha) versus Number of Hydrologic Reversals (number of times the water levels changed between rising and falling) for rail nests in Maine (2010 & 2011).

1.5. Discussion

Our estimates of overall nest survival are within the range of estimates reported in previous studies (Billard 1948, Pospichal and Marshall 1954, Tanner and Hendrickson 1954, Conway et al. 1994, Lor and Malecki 2006) and our data was collected over two fairly dry seasons (4-5 cm less rainfall during May-July than average: NOAA 2011). During a pilot season (2009), rainfall was greater than normal (19.4 cm more rainfall during May-July than average: NOAA 2011) and of 10 monitored nests, one Virginia rail nest was completely flooded and two sora nests were partially flooded (with a few eggs hatching pre-flood).

Nest survival was greater with increased water-level variation at both nest and wetland scales, and rail density was greater in wetlands with more variable water levels. Wetlands with greater water level variation are also associated with increased emergent vegetation (Weller et al. 1991), increased macroinvertebrate diversity, and greater ecosystem productivity (Galat et al. 1998, Euliss and Mushet 2004). Rails use areas of dynamic water depths to forage on emergent plant seeds and invertebrates, and their nesting strategies respond to frequent water-level change. We witnessed rails building their nests up 18 cm higher in a few days as water levels increased. They experienced relatively few nest flooding events despite water levels that fluctuated at the nest by as much as 30.54 cm over a three day period. Rail density did not reflect daily survival rate although both responded to water-level variability.

Predation caused significant nest failure in our study, and nests that were in deepening water had greater survival than those that were in unchanging water or water that was becoming shallower (Figure 2) possibly due to changes in predator accessibility (Weller 1961). The linear relationship between nest survival and water depth change could be due to the relatively dry nesting seasons during our study, and we assume that some degree of water level increase, beyond the range we observed, would lead to increases in nest loss.

The interaction between nest height change height and water depth change can be explained by separating data into rising and falling water depths (Figure 3). For nests experiencing increasing water levels, greater increases in nest height were associated with higher nest success. For nests with decreasing water levels, however, nests that lost the most height (settle) fared the best. Nest height change is a good indicator of water variation at the nest over the entire nest period, as very tall nests must have experienced deep water at some point and very short nests cannot have. A highly exposed nest (with significant nest build-up above the current water level) has experienced a high water-level change at some point in the past. Moreover, higher nests compress more when water depths fall as the heavier nesting material settles. Nests that are shorter (and have experienced less water variation in the past) do not compress as much with the same degree of water recession. As a result, during water level increases rails that build up their nests more (larger nest height change) are found in the most variable areas within the wetland (greatest increases in water depth), and experience the lowest predation risk (Figure 3). During water level decreases, on the other hand, rail nests that are collapsing more are the nests in the most variable areas within the wetland (due to being taller from experiencing higher variation in the past) (Figure 3). In both cases, indicators of water variation at the nest site are associated with increases in nest success. The interaction of nest height change with water depth change is important in our top models in addition to water level change by itself, because nest height change adds additional information about water variation experienced by nests outside of our period of observation.

Nest survival increasing with older nest age potentially reflects increasing parental aggressiveness (Kozma and Kroll 2010), early nest loss due to placement in poor locations (Klett and Johnson 1982), or environmental changes with time that increase predation (Schaub et al

1992). We documented nest predation by marsh wrens at our study but other likely predators include snakes, blackbirds, crows, muskrats, and other mammals.

The impoundment single-variable model was better than the null model, and the impoundment variable also was included in our second best model, however, it did not have a significant effect on nest survival and there were no significant hydrologic differences with wetland impoundment. Inference of results is limited to passively managed wetlands. Active management may show values of hydrologic change outside the range considered in this study. Water management regimes that actively attempt to limit water level variation during the breeding season, however, have the potential to limit the wetland area that experiences periodic flooding and thereby limit the wetland area that is suitable for rail nesting and foraging.

1.6. Management Implications

Water-level variation enhances nesting success in Maine and conservation and management efforts that preserve this variation will result in gently sloped wetland edges with large shallow areas and abundant emergent vegetation that benefits rails. This “maximum area between moist soil and marsh” creates optimal rail nesting habitat and potentially enhances rail foraging (Eddleman et al. 1988). Passively operated waterfowl-management impoundments did not negatively impact rail productivity. Further research into active water-level manipulation is needed to assess timing and durations of drawdowns and flooding and their impacts on rail populations.

CHAPTER 2

FACTORS AFFECTING RAIL BROADCAST SURVEY RESULTS

2.1. Introduction

Virginia rail (*Rallus limicola*) and soras (*Porzana carolina*) (hereafter “rails”) rarely flush or fly during the breeding season, vocalize infrequently, and are cryptic in dense, emergent, wetland habitat (Gibbs and Melvin 1993). Most estimates of rail population densities 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 does not yet adequately control for detectability issues related to bird density, breeding stage, call type, or sex differences.

There have been no studies of site density effects on marsh bird response probability, although breeding densities appear to affect Virginia rail and sora response (Kaufman 1971, Glahn 1974). 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); however, no studies have examined direct effects of estimated bird densities on nesting bird vocalization probability.

Breeding stage effects on the vocalizations of marsh birds have been examined for radio-tagged birds (Conway et al. 1993, Legare et al. 1999, Bogner and Baldassarre 2002), however, not directly from individual birds responding at known nest sites. Black rail (*Laterallus jamaicensis*) responses were documented at nesting/non-nesting phases using radiotelemetry but were not further subdivided by breeding stages (Legare et al. 1999). Radio-tagged least bitterns

were examined during different breeding stages, however, this was only one species and a very limited sample size (n=9) (Bogner and Baldassarre 2002).

Marsh bird call types vary throughout the season (Conway et al. 2004), with nesting status (Bogner and Baldassarre 2002), or with breeding stage. It is likely that survey estimates vary with call type (Conway and Nadeau 2006); however, call type detectability differences during the breeding season have not been examined for rails (Kaufman 1983, Zembal and Massey 1987).

Sex differences in vocalization probability have been estimated in black rails and common moorhens (*Gallinula chloropus*) (Brackney and Bookhout 1982, Legare 1999) but not for other marsh bird species. Sex variation in detection probabilities have been reported in many species with broadcast surveys (Bibby et al. 1992, Buckland et al. 1993, Reid et al. 1999, Gregory 2003). Determining sex detection probability differences during broadcast surveys would improve marsh bird population estimates (Newson et al. 2005); however, their use for Virginia rails has been hampered by an inability to differentiate the sexes in the field (Tacha and Braun 1975).

Estimates from marsh bird surveys are being used, perhaps inaccurately, to estimate densities, population sizes, and trends at a management unit scale (e.g. Johnson and Dinsmore 1986, Gibbs and Melvin 1993, Spear et al. 1999, Benoit and Askins 2002, Erwin et al. 2002, Allen et al. 2004, Conway et al 2004, Rehm and Baldassare 2007, Nadeau et al. 2008). Our objectives were to improve survey methodology for marsh bird surveys by 1) identifying rail call types to test for differences in call type by breeding stage and passive/broadcast surveys; 2) quantifying rail response rates to broadcasts and determining factors that influence response rates

including breeding stage, nest age, adult density, calendar date, and year; and, 3) examining Virginia rail sex differences in detectability.

2.2. Study Area

Sites included ten freshwater wetlands in Maine: five in Penobscot county (Penobscot watershed) and five within Washington county (Eastern Coastal Plain watershed) at Moosehorn National Wildlife Refuge (200 miles east) ranging from 40 to 272 ha ($\bar{x} = 98$, $SD = 155$). All sites were within the Eastern Coastal Plain biophysical region (Krohn and Boone 1999). Five sites had water control structures that were passively managed. Dominant species at our sites included *Typha latifolia*, *Typha angustifolia*, *Myrica gale*, *Carex* sp., *Calamagrostis canadensis*, *Spirea alba*, *Spirea tomentosa*, *Salix* sp., *Alnus* sp., *Sagittaria latifolia*, *Dulichium arundinaceum*, *Pontedaria cordata*, *Lemna minor*, *Lysimachia terrestris*, *Galium palustre*, *Equisetum* sp., *Vaccinium macrocarpon*, *Scirpus* sp., *Calla palustris*, *Polygonum* sp., *Sparganium americanum*, *Chamaedaphne calyculata*, *Juncus* sp., *Triadenum virginicum*, and *Potentilla palustris*. Sites included Pond Farm Wildlife Management Area (Howland, ME), Sedgunkedunk Stream of Field's Pond (Orrington, ME), Penjajawoc Marsh (Bangor, ME), Wheeler Brook Stream (Hermon, ME), Pleasant Lake (Stetson, ME), Cranberry Lake (Moosehorn Wildlife Refuge, ME), West Dudley Flowage (Moosehorn, ME), Dudley Swamp (Moosehorn Wildlife Refuge, ME), Magurrewock (Moosehorn Wildlife Refuge, ME), and Barn Meadow (Moosehorn Wildlife Refuge, ME).

2.3. Methods

2.3.1. Broadcast Surveys

During 2010 - 2011, we searched for Virginia rail and sora nests from mid-April to early August (greatest nest activity was during early May to mid-July). We played broadcasts of rail calls and randomly searched areas where we heard paired birds responding (the duetting “descending call”, sensu Kaufman 1983, of the Virginia rail or the paired “whinny”, sensu Kaufman 1983, of the sora). We visited nests every 3-5 days to determine nesting, hatching, or failure stages.

We conducted surveys at each nest during five, potential breeding stages (egg laying, incubation, hatching, post-hatching, post-predation) for each territorial pair that exhibited those stages during observation. Surveys were conducted at least 5 days apart to reduce vocal habituation and to maximize independence between trials (Legare et al. 1999). We placed our broadcast survey location 10m from each nest to compromise between observer detectability issues (Conway et al. 2004, Sauer et. al 2008) and our probability of recording the nesting pair’s responses rather than birds from neighboring territories. We used an Altec Lansing Orbit-MP3 portable speaker with a Sansa SanDisk mp3 player for broadcast surveys at 80-90 dB (measured 1m away) with 5 minutes of silence, 30 seconds sora calls, 30 seconds of silence, 30 seconds Virginia rail calls, and 30 seconds silence using a CD ordered from the National Marsh Bird Monitoring Program (Conway 2011). We played first the sora and then the Virginia rail calls 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 grunt (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. Surveys were conducted 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 sustained drizzle, rain, or heavy fog. Observers recorded whether birds responded to each survey and, if so, whether it was during the passive or post-broadcast period. For birds that responded, we recorded time until first response, call type, distance from the nest, distance from broadcast speaker, nest stage/age, and date. All observers were trained in estimating distances (0-200 m) using laser finders at the beginning of the season.

2.3.2. Density

We surveyed points with the broadcast methods described above along a single transect of the wetland area with 4 survey points per wetland each separated by 200 m to determine rail densities for each of seven wetland sites (three sites that were nest-searched were not surveyed for density estimates owing to time constraints). We used the “distsamp” package in R (R Core Development Team 2011) to obtain rail density estimates at each wetland site (hereafter “wetland density”) accounting for distance-biased detectability differences.

2.3.3. Call Type

During all of the surveys described above, we recorded the call type of individual responses during both the passive and 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” (prior to finding nests and prior to back-dated initiation dates of found nests) point-count survey at our site with the highest breeding density of rails, Pond Farm

(Howland, Maine), to compare with our known-nesting bird response call types. We surveyed 12 points at Pond Farm (200m apart) on 1 May 2009 and recorded responses, distances, and call types at each point.

2.3.4. Broadcast Response Models

We examined response probabilities of each species during the passive period, post-broadcast period, and during the entire survey (passive and broadcast combined). Of birds that were estimated as calling from the nest (nest distance = 0), we determined the percent of birds responding to broadcast and breeding stage. We constructed two logistic regression models for Virginia rail and sora response to broadcast (yes or no) fit by the Laplace approximation with random intercepts for individual nests to account for repeated measurements during the different breeding stages in. We used the information-theoretic approach with knowledge gained in the field (Burnham and Anderson 2002) to select *a priori* models. During exploratory analysis we noticed that sora response probability was linearly affected by age. Virginia rails did not have a linear pattern to their response probability but did show differences by stage, especially the post-predation stage. For this reason we included breeding stage in the Virginia rail model and both nest age and a binomial variable for breeding stage (post-predation or not) in the sora model. We also noticed during fieldwork that both species were more vocal early in the season and in wetlands with higher rail densities so we included these variables. Other studies have found temporal components to vocalization probability so we included year as a fourth variable for Virginia rail because we were already controlling for time of day and seasonal variation in detection probability by conducting our surveys within time windows permitted by National Marsh Bird Monitoring Program protocols (Conway 2011). We did not see year effects on sora

response probability in exploratory analysis so we did not include it in final models. Virginia rail explanatory variables included breeding stage, Julian date, wetland density, and year. Sora explanatory variables included nest age, Julian date, wetland density, and breeding stage (post-predation). We tested 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 used Akaike's Information Criterion corrected for small sample sizes (AIC_c) for model selection, and we evaluated the importance of each variable by summing the Akaike weights across all models (Burnham and Anderson 2002). We examined global-model goodness-of-fit with a Hosmer and Lemeshow (2000) goodness of fit test.

2.3.5. Sex Vocalizations

Virginia rails were captured on the nest while incubating with a cast net. Once we caught one bird, the second bird usually rushed to the nest to takeover incubation. While holding the first bird at least 20m from the nest, we played a broadcast call to the newly incubating bird and recorded the "descending call" response with an Edirol-R-09 wave/mp3 recorder and a Shure SM57 microphone. We then caught the second rail with the cast net and, afterwards, released the first rail. We played a broadcast call to the first rail and recorded any "descending call" responses.

We also obtained blood samples from the cutaneous ulnar vein of both birds while captured. We genetically ascertained sex via the sex-specific CHD1 gene by P2-P8 primer pairs (Griffiths 1998, Baker et al. 1999, Cerit and Avanus 2007). Multiple primer sets were used as recommended by Casey et al. (2009).

Recorded calls from the captured birds were analyzed with Raven version 1.3 (Charif et al. 2006). Figures of spectrograms were created with Fourier transform (FFT) and a sampling rate of 44.1 kHz to digitize signals (McCracken 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 in male and females.

Linear Discriminant Analysis with “Jackknifed Prediction” in Program R was applied 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. Discriminant function effectiveness was assessed first in terms of the correct classification of known-sex birds using all individuals in the analysis. Secondly it was tested by a jackknifing procedure which repeats the analyses leaving out a single bird each time and then classifies that individual using the function derived from the remaining birds (Rohlf and Sokal 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.

2.4. Results

2.4.1. Call Type

At least one Virginia rail responded during 172 of 255 (67.5 %) surveys at known nest-sites (including inactive nests). Birds first responded during the passive period of the survey in 62 out of 255 (24.3 %) trials and first during the post-broadcast period in 110 of 255 (43.1 %) trials. The responding bird was estimated as calling from the nest 44/255 (17.3 %) times. These nest calls occurred 63.6 % (n = 28) of the time during incubation, 20.5 % (n = 9) of the time

during hatching or within 12 days of hatching, 13.6 % (n = 6) of the time during egg laying, and 2.3 % (n = 1) after 1 day following a nest predation event.

Soras responded 40/80 times (50.0 %) during nest surveys. The passive section had 13/80 (16.3 %) responses and the post-broadcast section had 27/80 (33.8 %) responses. The responding bird was estimated as calling from the nest 8/80 times (10.0 %) during nest surveys. These nest calls were comprised of 6/8 (75.0 %) incubation stage, 1/8 (12.5 %) egg laying, and 1/8 (12.5 %) post-hatched.

Sora calls during nesting (n= 40 vocalizations) included the whinny, paired whinny, kiu, and peep calls (Kaufman 1983) (Table 4). The whinny was the dominant call during the nesting season (n=32) (Table 4). The paired whinny (two birds doing the whiny call at same time) (n=4), was used especially during the egg-laying stage but was also heard throughout the nesting season (Table 4). The per-weep call was most common at the start of the breeding season and we did not hear any known-nesting birds use it, suggesting that it is associated with pair formation. The kiu call (n=4), was the primary distress call and was often heard while we were at the nest (Table 4). The peep call (n=3) was only heard during late incubation, hatching, and after hatching and seemed to be used as contact calls between family members (Table 4). We only had one sora out of 16 post-failure surveys that responded and it used the whinny call (Table 4). Post-hatching soras (n=8), however, continued to use the whinny (n=5), followed by the peep (n=2), and the kiu call (n=1) (Table 4). The per-weep calls were heard mostly early in the season (when birds were searching for mates) and we did not hear them from any of our nesting birds. During the pre-nesting survey at Pond Farm (1 May 2009) we detected 14 soras that replied with per-weep calls (n=10) and whinny calls (n=4) (Table 4).

Virginia rail calls during nesting (n = 176 vocalizations) included the descending call, duet descending call, kiu, and peep (Kaufman 1983) (Table 4). The descending call (n = 125) was the dominant call during the nesting season followed by the duet descending call (n = 24) (Table 4). The kiu call (n = 19) was the primary distress call and was often heard while we were at the nest (Table 4). The peep call (n=7) was heard only during late incubation and post-hatching and seemed to be used as contact calls between family members (Table 4). Post-failure Virginia rails still primarily used the descending call (n = 12) followed by the duet descending call (n = 5) (Table 4). Post-hatching Virginia rails (n = 30) also primarily used the descending call (n = 15) followed by the duet descending call (n = 5), peep (n = 3), and the kiu (n = 7) (Table 4). The kadic-kadic calls were heard mostly early in the season (when birds were searching for mates) and we did not hear them from any of our nesting birds. During the pre-nesting survey at Pond Farm (1 May 2009) we detected 7 Virginia rails that replied with descending calls (n=6) and kadic-kadic calls (n=1) (Table 4).

Table 4. Rail Call Types During Breeding Season: Virginia rail and sora response call types at different breeding stages (LAY= Laying, INC= Incubation, HING= Hatching, HD= Hatched, DEP= Depredated, PRE= Pre-nesting) following broadcast surveys conducted 10 m from nests in Maine, 2010 & 2011.

		LAY	INC	HING	HD	DEP	PRE
Virginia							
Rail	kiu	2	4	6	7	0	0
	peep	0	4	0	3	0	0
	duet descending call	6	8	0	5	5	0
	descending call	27	60	11	15	12	6
	kadic-kadic	0	0	0	0	0	1
Sora							
	kiu	0	1	2	1	0	0
	peep	0	1	0	2	0	0
	paired whinny	1	0	0	0	0	0
	per-weep	0	0	0	0	0	10
	whinny	8	10	8	5	1	4

2.4.2. Virginia Rail Response Model

We conducted 194 broadcast surveys to 63 unique Virginia rail nests (average of 3.1 surveys per nest). Virginia rails responded on 72.7 % of surveys (141 responses for 194 surveys). The global model fit the observed values using the Hosmer and Lemeshow (2000) goodness-of-fit test ($\chi^2_8 = 12.04$, $P = 0.15$). Our final model set included six models with a cumulative Akaike $w_i > 0.9$ (Table 5). The top four models had $\Delta AIC_c > 2$ and included combinations of all four explanatory variables (Table 5). Akaike weights for the top four models were 30%, 20%, 20%, and 10% of all weights for the 16-candidate-model set (Table 5). All nest stages (incubation, hatching, post-hatching, and post-predation) were negatively related to response probability in comparison to the egg-laying stage reference level (Table 6). The model-averaged estimates for the predation stage were significant but the other stages were not (Table 6) (Figure 7). Density was positively related to response probability, while there was no significant effect of Julian date or year controlling for breeding stage and density (Table 6). Densities of rails (Virginia rails and soras combined) at our wetland sites ranged from 0.96-8.70 birds/ha ($\bar{x} = 3.17$, $SD = 2.56$, $n=7$).

We used model averaging on the top six models in an effort to include model selection uncertainty into parameter estimates and their standard errors (Table 6). Overall Virginia rail response probability from broadcast surveys from the model-averaged estimates was 0.73 (SE=0.08%, $n = 194$). Stage and density had the greatest effects on Virginia rail response probability. Density was found in all six top models and the model-averaged estimates were statistically significant (Table 5, 6). Stage was found in three of the top six models and the model-averaged estimate for the predation stage was statistically significant (Table 5, 6).

Density was also more important than breeding stage when looking at the summed Akaike weights (0.99 vs. 0.52) (Table 6). Two of the top six models included year and Julian date but the 95% CI of the odds ratios included 1.0, making it difficult to assess their strengths (Table 5, 6). Summed Akaike weights were 0.34 for Julian date and 0.24 for year (Table 6). Overall Virginia rail response probability from broadcast surveys from the model-averaged estimates was 0.73 (SE=0.08%, n = 194).

Table 5. Virginia Rail Response Probability Models: Model selection results for Virginia rail response probability to broadcast surveys in Maine (2010 & 2011). The first six 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, AIC_c is the Akaike’s information criterion for small sample sizes, and w_i is the Akaike weight. A smaller AIC_c and a larger Akaike weight represent more support for the model. Parameters considered include rail density within the wetland (“density”), the numerical calendar date of the survey (“Julian date”), breeding stage (including egg laying, incubation, hatching, hatched, or failed), and year.

Model	K	AIC _c	ΔAIC _c	w _i	Cumulative	
					w _i	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	-35.9
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	-29.9
stage	7	88.18	8.84	<0.1	0.99	-36.09
Julian date	3	89.39	10.05	<0.1	1.00	-41.5
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

Table 6. Virginia Rail Model-Averaged Parameter Estimates: Summed Akaike weights (w_i) from original 16 models and model averaged parameter estimates with unconditional standard errors (SE) and odds ratios with unconditional 95% confidence intervals for variables in the top six models for Virginia rail response probability to broadcast surveys in Maine, 2010 & 2011. Parameters considered include rail density within the wetland (“density”), the numerical calendar date of the survey (“Julian date”), breeding stage (including egg laying, incubation, hatching, hatched, or failed), and year. The parameter estimates and odd ratios of the separate breeding stages (failed, hatched, incubation, and hatching) are relative to the reference egg-laying stage.

Variable	Summed (w_i)	Estimate \pm SE	Odds Ratio (95% CI)
density	0.99	0.45 \pm 0.18	1.57 (1.11 , 2.20)
breeding stage	0.52		
failed stage		-4.94 \pm 1.82	0.01 (0.00 , 0.25)
hatched stage		-1.99 \pm 1.35	0.14 (0.01 , 1.92)
incubation stage		-1.04 \pm 1.12	0.35 (0.04 , 3.16)
hatching stage		-1.18 \pm 1.25	0.31 (0.01 , 1.90)
year	0.24	0.46 \pm 1.16	1.58 (0.31 , 15.49)
Julian date	0.34	-0.03 \pm 0.06	0.97 (0.88 , 1.08)

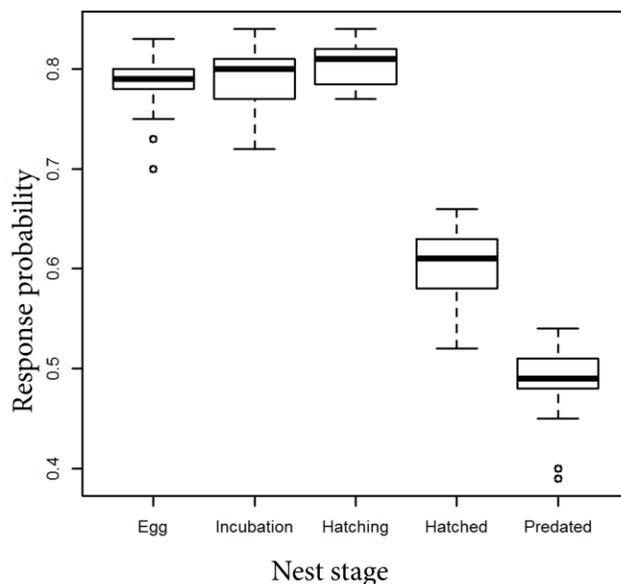


Figure 7. Virginia Rail Breeding Stage and Daily Survival Rate: Virginia rail response probability to broadcast surveys was significantly smaller for post-predation nests and had a smaller trend for post-hatched nests in Maine (2010 & 2011).

2.4.3. Sora Response Model

We conducted 54 broadcast surveys to 18 unique sora nests (average of 3.0 surveys per nest). Soras responded on 51.9 % of surveys (28 responses for 54 surveys). The global model fit the observed values using the Hosmer and Lemeshow (2000) goodness-of-fit test ($\chi_8^2 = 9.46$, $P = 0.30$).

Our final model set included five models with a cumulative Akaike $w_i > 0.9$ (Table 7). The top three models had $\Delta AIC_c > 2$ and included combinations of all four explanatory variables (Table 8). Akaike weights for the top four models were 46%, 32%, 5% of all weights for the 16-candidate-model set (Table 7). Breeding stage (post-predation) and nest age both had significant, negative effects on sora response probability (Table 8) (Figure 8, 9). Wetland density was significantly positively related to response probability (Table 8). There was no effect of Julian date controlling for the other parameters in these models (Table 8).

We used model averaging on the top five models to include model selection uncertainty into parameter estimates and their standard errors (Table 7). Breeding stage (post-predation), rail density, and nest age had the greatest effects on sora response probability (Table 7, 8). Breeding stage was found in all five, top models and the model-averaged estimate was statistically significant (Table 7, 8). Density was found in four of the top five models and the model-averaged estimate was statistically significant (Table 7, 8). Age was found in three of the top five models and the model-averaged estimate was statistically significant (Table 7, 8). Breeding stage (post-predation) had the highest summed Akaike weights (0.95) followed by density (0.90) and age (0.88) (Table 8). Two of the top five models included Julian date but the 95% CI of the odds ratio included 1.0, making it difficult to assess its strength (Table 7, 8). Summed Akaike weights were 0.41 for Julian date (Table 8). Overall sora response probability from broadcast surveys from the model-averaged estimates was 0.51 (SE = 0.15, n = 54).

Table 7. Sora Response Probability Models: Model selection results for sora response probability to broadcast surveys in Maine (2010 & 2011). The first five 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, AIC_c is the Akaike’s information criterion for small sample sizes, and w_i is the Akaike weight. A smaller AIC_c and a larger Akaike weight represent more support for the model. Parameters considered include rail density within the wetland (“density”), the numerical calendar date of the survey (“Julian date”), breeding stage (post-predation)(“predation”), and nest age (“age”).

Model	K	AIC _c	ΔAIC _c	w _i	Cumulative	
					w _i	Log _e (L)
age+predation+density	5	65.96	0	0.46	0.46	-27.37
Julian date+age+predation+density	6	66.69	0.72	0.32	0.79	-26.47
density+predation	4	70.55	4.59	0.05	0.83	-30.88
predation+age	4	70.65	4.68	0.04	0.88	-30.92
density+Julian date+predation	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+Julian date	4	72.47	6.51	0.02	0.95	-31.84

Julian date+age+predation	5	73.03	7.06	0.01	0.97	-30.9
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	-33.7
predation	3	74.86	8.89	0.01	0.99	-34.19
Julian date+age	4	76.19	10.23	0	1	-33.7
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

Table 8. Sora Model-Averaged Parameter Estimates: Summed Akaike weights (w_i) from original 16 models and model-averaged parameter estimates with unconditional standard errors (SE) and odds ratios with unconditional 95% confidence intervals for variables in the top five models for sora response probability to broadcast surveys in Maine, 2010 & 2011. Parameters considered include rail density within the wetland (“density”), the numerical calendar date of the survey (“Julian date”), predation (whether nest was depredated or not), and year.

Variable	Summed (w_i)	Estimate \pm SE	Odds Ratio (95% CI)
predation	0.95	-3.57 \pm 1.52	0.03 (0.56 , 0.00)
density	0.90	0.39 \pm 0.17	1.48 (1.07 , 2.05)
age	0.88	-0.13 \pm 0.06	0.88 (0.77 , 0.99)
Julian date	0.41	0.05 \pm 0.08	1.05 (0.91 , 1.22)

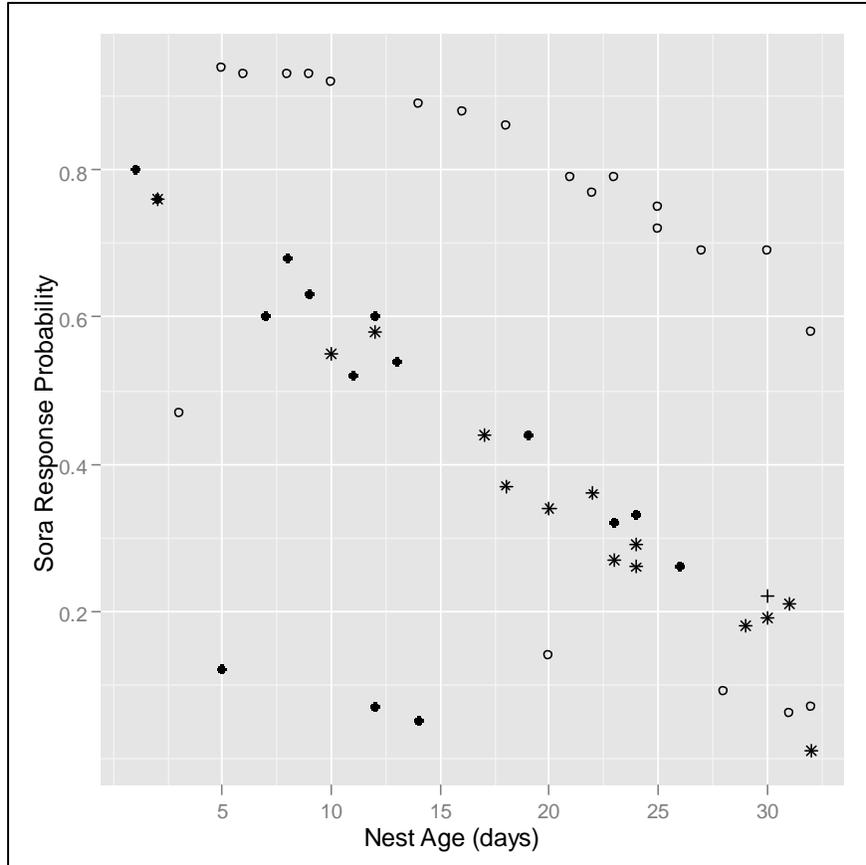


Figure 8. Sora Nest Age and Daily Survival Rate: Response probability to broadcast surveys decreased as nest age (days) increased for soras in Maine (2010 & 2011). Density quartiles are represented by symbols (Q1=star, Q2=black dot, Q3=cross Q4= white dot).

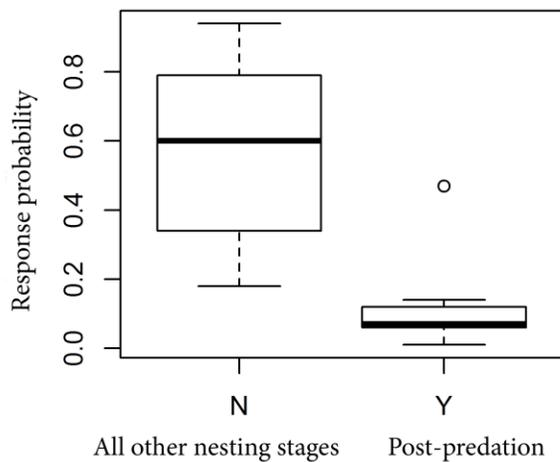


Figure 9. Sora Breeding Stage and Daily Survival Rate: Response probability to broadcast surveys was lower for post-predation sora nests in Maine (2010 & 2011).

2.4.4. Sex Vocalizations

Male and female Virginia rails were correctly classified 100% in both known-sex samples and jackknifed-procedure samples using interval and song length variables (Figure 10). Males (3.7 ± 0.6 secs) have longer songs than females (2.7 ± 0.5 secs) and shorter intervals between “descending calls” (males: 1.3 ± 0.07 secs; females: 1.4 ± 0.08 secs). Males (71.98 ± 4.8 dB) also had louder (higher average power) songs than females (54.95 ± 3.2) ($t_{6,6} = -2.93$, $P = 0.02$).

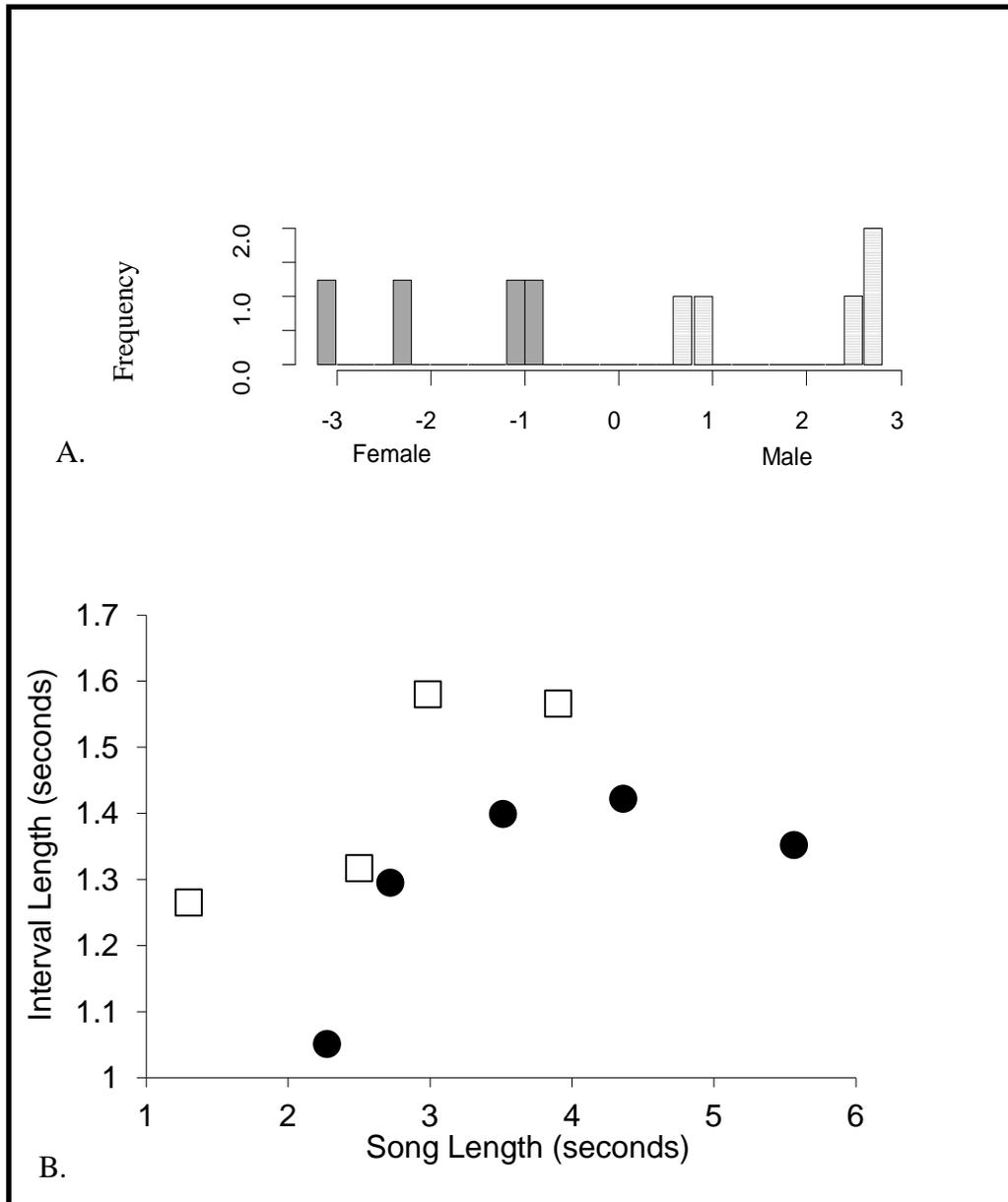


Figure 10. Linear Discriminant Analysis Virginia Rail Vocalizations By Sex: A) Complete separation of male and female Virginia Rails using Linear Discriminant Analysis with Jackknifed Prediction in R and variables song length and interval length as measured in RAVEN in response to broadcast recording in Maine, 2010 & 2011. B) Virginia rail “descending call” song length vs. interval length (seconds) between descending calls) as measured in RAVEN in response to broadcast recording in Maine, 2010 & 2011. Males (genetic sexing) are indicated in filled circles and females in open squares.

2.5. Discussion

2.5.1. Vocalization and Call Type Variability

Virginia rail detectability estimates from our study (67.45% broadcast response and 72.70% from model-averaged estimates) were within the range of previous estimates of 20-100% by Glahn (1974) and 64-82% by Gibbs and Melvin (1993). Our detectability estimates are likely more accurate as they were conducted at known nest sites and the model-averaged estimates took density, stage, year, and Julian date differences into account. Sora detectability estimates (50% broadcast response and 51.31% from model-averaged estimates) were also within the range of previous estimates of 20-100% from Glahn (1974) and slightly lower than the 59-84% estimate by Gibbs and Melvin (1993). Similar to previous studies (Melvin and Gibbs 1993, Allen et al. 2004, Conway and Gibbs 2005), we found that broadcasting increased detection probability in comparison with the passive period by 1.78 times for Virginia rails (n=255) and 2.08 times for soras (n=80). Our results were slightly lower, however, than Conway and Gibbs (2005) who found that broadcast increased Virginia rails 7.35 times and soras 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 could be due to the proximity of our surveys to nests (Legare 1999).

Similarly to Kaufman (1983) we found that the sora "per-weep" call is mostly used pre-breeding, which may suggest a role in pair formation. This is a call that could be used to distinguish pre-breeding from breeding males during broadcast surveys. The kadic-kadic call has similar uses for the Virginia rail but is quieter and would be slightly more difficult to detect unlike the per-weep call which is loud and persistently used by soras. The descending call is the most common call (and loudest, excluding the kiu) of the Virginia rail but it is used

independently to breeding stage. The “peep” call of both species is only used in late incubation, hatching, and post-hatching by pairs of birds (often in a duet of peeping back and forth), and it could be used to index nest success and family groups during the late breeding season.

2.5.2. Factors Affecting Rail Detectability

During broadcast surveys at nests the stage of Virginia rail nests (specifically post-predation) and the density of rails at the site both strongly impacted response probability. Rails whose nests had recently been depredated were significantly less likely to vocalize than those who had not. Virginia rails responded similarly to broadcast during their egg-laying, incubation, and hatching stages. Response rate after hatching (successful nest) was lower, but not significantly, from these other stages. Qualitatively we notice that both Virginia rails and soras were more responsive in the pre-nesting stage, which confirms trends in other marsh bird species (Conway et al. 1993, Legare 1999, Bogner and Baldassarre 2002).

During broadcast surveys at sora nests, we found that the age of the nest, density of rails at the site, and whether or not the nest had been recently depredated had the greatest impact on response probability. A post-predation broadcast survey significantly decreased the odds of response compared with all other stages of breeding. The odds of a sora responding to surveys decreased as the age of the nest increased. 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 and then get quiet with few responding after early June. Our results suggest these phonological patterns are due to changes in the average breeding stage of the individuals involved rather than other processes correlated with date. Rehm and Baldassarre (2007) also found, however, that Virginia rail responses

increased by 0.22 birds/week in New York, which disagrees with our more behaviorally mechanistic results (Rehm and Baldassarre 2007).

The odds that either Virginia rails or soras responded to a broadcast increased as rail density increased 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 higher rail densities. Other studies have found correlations between number of rails heard and numbers of nests found (Mangold 1974, Zembal and Massey 1981, Brackney and Bookhout 1982, Pierluissi and King 2008), number of territories spot mapped (Griese et al 1980), and number of rails captured (Tacha 1975, Kwartin 1995), but our study is the first to quantify the effects of site-level density and its influence on rail detectability. Densities of 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). One site (Pond Farm, Howland, Maine) however, had a density of 8.70 birds that was more than double the maximum density reported in other studies.

2.5.3. Sex Influences on Rail Detection

Male Virginia rails respond to broadcast surveys with faster “descending calls” (shorter intervals between individual call notes) that continue for a longer time. This may be a graded signal of enthusiasm and suggests greater territorial behavior in males. 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 a closer approach distance to the microphone following broadcast. Either of these mechanisms also support increased male response to

playback. Longer and louder songs are heard more easily during surveys, which would result in higher detectability for male rails. Qualitatively, we had a pair of nesting Virginia rails and a pair of soras that each had an extremely aggressive male that would run up to the nest and peck our hands, call loudly, and flap their wings while we were examining the nest. The females usually remained hidden and silent, suggesting that male rails may possess a “boldness” or “aggressiveness” syndrome, relative to females (Wilson et al. 1994, Réale et al. 2007), which extends into both territorial and nest defense behaviors. Other studies have found that other male marsh birds that share in incubation duties are more responsive than females to broadcast surveys, including least bittern (*Ixobrychus exilis*) (Bogner and Baldessarre 2002), black rail (Legare 1999), and common moorhen (*Gallinula chloropus*) (Brackney and Bookhout 1982). Male and female rails certainly both respond to broadcasts, however, as evidenced by our numerous observed “duets” and our vocalization recordings of 7 genetically sex-determined female Virginia rails (whose calls were slower, shorter and, qualitatively, quieter, than male responses).

2.6. Management Implications

We recommend that large-scale marsh bird population trend estimates take density-based detectability issues into account. Wetlands with low responses may underestimate populations more than wetlands with higher densities. Suboptimal wetlands with higher proportions of unpaired males may also result in more detections than wetlands with mostly paired birds due to unpaired males vocalizing loudly and persistently for mates. We suggest training observers and

recording data on the “peep”, “kadic-kadic”, and “per-weep” calls. The per-weep and kadic-kadic calls could assist in determining numbers of unpaired, surplus rails throughout the breeding season (which could possibly help mediate the density issue). They could also help delineate when rail breeding begins and ends and the rate at which it does so, which could be used to generally infer nesting success. The “peep” call toward the end of the season could give further insight into the numbers of successful nests/family groups found in a wetland. This call is fairly quiet but can be heard within approximately 50m and it could strengthen population estimates by including family groups with males, females, and young. Further information is needed to quantify response probability of female Virginia rails and soras. We agree with the Conway (2011) protocol for using both passive and active broadcast survey methods and that multiple surveys should be conducted surrounding the time of peak breeding due to nest age and stage variation during the nesting season. This is especially important for soras which have decreasing detectability with increasing nest age.

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BIOGRAPHY OF THE AUTHOR

Ellen Padgett Robertson was born in Asheville, N.C on March 24, 1982. She graduated from Carolina Day School (Asheville) in 2000. She attended Furman University (Greenville, S.C.) and earned a B.S. in Biology in 2003 after also doing semesters at the Biosphere (Columbia University: Oracle, Arizona), “Semester at Sea” (University of Pittsburgh), and Otago University (Dunedin, New Zealand). Ellen worked as a biological science technician in the Frank Church Wilderness of No Return (Idaho), Glacier National Park (Montana), Yellowstone National Park (Wyoming), North Carolina, and Maine from 2003-2009 studying both botany and wildlife. She is a candidate for the Master of Science degree in Ecology and Environmental Science from the University of Maine in May, 2012.