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RESEARCH ARTICLE

Behavioral plasticity in nest building increases fecundity in marsh birds

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ABSTRACT

Many bird species nest in precarious, unpredictable locations to decrease the risk of predation. Although it is likely that many species have adapted behaviors to deal with stochastic habitats, there is currently limited evidence of plastic behavior increasing avian fecundity in the wild. Virginia Rails (*Rallus limicola*) and Soras (*Porzana carolina*) live in the littoral zones of wetlands that experience high hydrologic variability. During the summers of 2010 and 2011, we tested for the effects of hydrology and behavioral plasticity on the survival of Virginia Rail ($n = 75$) and Sora ($n = 22$) nests across 10 wetlands in Maine, USA. We identified the best predictors of both (1) nesting success at individual nests and (2) mean nesting success at the site level, using logistic-exposure models and an information-theoretic approach. Daily nesting survival was 98% for both species, and apparent nest survival was 31 of 85 nests, or 63.5%. Ninety percent of all nesting failures was from predation. Hydrology had a positive effect on nesting survival, and deeper, more variable water levels increased both individual nesting survival and mean site-level nest survival. Both species added material to their nests throughout the season in response to water-level increases, and we found that this behavioral plasticity had a positive effect on nesting survival. We caution that more variable water depths than those observed during our 2 yr of study could lead to increases in flood-related nest loss, because these birds require a delicate balance: the water must be deep enough to deter predators, yet shallow enough that they can build up their nests to prevent flooding during rain events. More information is needed on the extent of this behavior across marsh birds and other bird species.

Keywords: hydrology, marsh bird, nest building, nest survival, plasticity, Sora, Virginia Rail, wetland

La plasticidad comportamental en la construcción del nido aumenta la fecundidad en las aves de marisma

RESUMEN

Muchas especies de aves anidan en lugares precarios e impredecibles para disminuir el riesgo de depredación. Aunque es probable que muchas especies hayan adaptado sus comportamientos para adecuarse a los hábitats estocásticos, hay poca evidencia de que el comportamiento plástico aumente la fecundidad de las aves en los ambientes silvestres. *Rallus limicola* y *Porzana carolina* viven en zonas litorales de humedales que experimentan una alta variabilidad hidrológica. Durante los veranos de 2010 y 2011, evaluamos los efectos de la hidrología y de la plasticidad comportamental sobre la supervivencia de los nidos de *R. limicola* ($n = 75$) y *P. carolina* ($n = 22$) a lo largo de 10 humedales en Maine, EEUU. Identificamos los mejores predictores del (1) éxito de nidificación en nidos individuales y (2) éxito de nidificación promedio a escala de sitio, usando modelos de exposición logísticos y un enfoque teórico de la información. La supervivencia diaria del nido fue 98% para ambas especies, y la supervivencia aparente del nido fue de 31 de 85 nidos, o 63.5%. Noventa por ciento de todos los fracasos de nidificación fueron debidos a depredación. La hidrología tuvo un efecto positivo sobre la supervivencia del nido, y los niveles de agua más profundos y variables aumentaron la supervivencia individual del nido y la supervivencia media del nido a escala de sitio. Ambas especies agregaron materiales a sus nidos a lo largo de la estación en respuesta a los incrementos en el nivel de agua, y encontramos que esta plasticidad comportamental tuvo un efecto positivo sobre la supervivencia del nido. Advertimos que profundidades más variables de agua que las observadas durante nuestro estudio de dos años pueden llevar a un aumento en las pérdidas de nidos causadas por inundaciones, debido a que estas aves requieren un balance delicado: el agua debe ser lo suficientemente profunda como para desalentar a los depredadores, pero lo suficientemente baja como para que puedan construir sus nidos para evitar que se inunden durante los eventos de lluvia. Se necesita más información sobre el alcance de este comportamiento en las aves de marisma y en otras especies de aves.

Palabras clave: aves de marisma, construcción del nido, hidrología, humedal, plasticidad, *Porzana carolina*, *Rallus limicola*, supervivencia del nido

INTRODUCTION

Behavioral plasticity is the ability of an organism to adapt behaviorally in response to changing environmental conditions. In birds, behavioral plasticity has been observed in breeding timing (Svensson 1997), nest placement (Peluc et al. 2008), development (Hegyí and Török 2007), parental care and clutch-size reduction under increased predation risk (Ghalambor and Martin 2002, Doligez and Clobert 2003), and the hormonal initiation of seasonal songs (Brenowitz 2004). The effects of these plastic traits on demography in the wild are few, and there have been only a couple of studies, to our knowledge, on avian nest-building plasticity. The results of these studies were limited, in that the experimenters (1) induced changes to environmental conditions rather than observing natural environmental variation and (2) did not document effects of nest-building plasticity on avian fecundity. One such study found that Chinstrap Penguins (*Pygoscelis antarcticus*) added stones to their nests, presumably to prevent flooding, when snow was artificially added surrounding their nests (Fargallo et al. 2001). Kentish Plovers (*Charadrius alexandrinus*) also demonstrated experimentally induced plasticity by adjusting nesting material when nesting material was experimentally taken away or added to regulate nest temperature (Szentirmai and Székely 2002). Nest-building plasticity may be a widespread behavior for avian species that breed in stochastic habitats, including wetlands, where they must weigh the risks of nesting in shallower water with higher predation (Picman et al. 1993) or in deeper habitat with higher hydrologic stochasticity. Virginia Rails (*Rallus limicola*) and Soras (*Porzana carolina*) (hereafter referred to collectively as “rails”) are found in the littoral zones of wetlands, in areas where water cover is shallow enough for walking and foraging (approximately 1–20 cm), and is interspersed with pockets of emergent vegetation for nesting (Pospichal and Marshall 1954, Irish 1974, Fredrickson and Reid 1986, Gibbs and Melvin 1990, Tacha and Braun 1994, Conway 1995; Figure 1). Hydrologic variability creates and maintains this habitat by increasing emergent vegetation abundance (Galat et al. 1998, Euliss et al. 2008) and the topographic diversity (Galat et al. 1998), which are important for rail food and nesting habitat (Lor and Malecki 2006). It also increases habitat diversity (Melvin and Gibbs 1996, Galat et al. 1998, Rehm and Baldassarre 2007, Euliss et al. 2008) and the diversity of macroinvertebrates, an important rail food source (Tacha and Braun 1994). High hydrologic variability is associated with deeper water, which can protect wetland nests by decreasing their accessibility to terrestrial predators (Weller 1961, Picman et al. 1993, Post 1998). Rails can be sensitive to too much hydrologic variability, however: Rapidly changing water levels can flood nests, change the availability of optimal



FIGURE 1. A Sora in typical habitat, searching for food. Photo credit: Jonathan D. Mays

foraging sites, and force rail movements (Baird 1974, Tacha 1975, Griese et al. 1980). Flooding can dramatically increase nesting failure rates in the 2 study species (Conway 1995, Melvin and Gibbs 1996) with rapid water-level increases of only 20 cm (Griese et al. 1980). Rails are adapted to moderate levels of water variability by a nest-building behavior whereby they insert additional nesting material to raise both the nest and eggs during storm events. Some individuals are able to raise nests by as much as 25 cm in a 3-day period (personal observation) during storm events. Following a heavy rain, Billard (1948) witnessed nests that were 48 cm above the water. This nest-building behavior allows them to nest in areas of constantly changing water depths, areas that also provide decreased accessibility of nests to terrestrial predators (Weller 1961, Tacha and Braun 1994, Post 1998).

We examined rail nesting survival across 10 wetlands with varying hydrology (5 wetlands had wildlife management impoundments and 5 wetlands did not). We looked for hydrologic and behavioral predictors of nesting failure at each nest site (nest level), and also for predictors of mean nesting success within each wetland (site level). Our main objectives were to determine (1) whether hydrology affected nesting survival in marsh birds and (2) whether behavioral plasticity for building up nests in response to hydrology increased nesting survival. We predicted that increased water levels would increase nest survival and that nest-building plasticity in response to rising water would also increase nest survival.

Study Area

Our sites were all in Maine, USA, including 5 wetlands (2 impounded) in Penobscot County and 5 wetlands (3 impounded) within Moosehorn National Wildlife Refuge in Washington County. The sites ranged in size from 40 to 272 ha (mean \pm SD = 98 \pm 155; n = 10). Impoundments

at Moosehorn were created during 1950–1974 in historical beaver-dam locations and have remained unmanipulated since construction except for a limited number of occasional drawdowns (Hierl et al. 2007). The history of the Penobscot County impoundments is less documented, but water levels at these wetlands are not currently manipulated by the Maine Department of Inland Fisheries and Wildlife, the state agency that manages them.

All of the wetlands are within the Eastern Coastal Plain biophysical region (Krohn et al. 1999). Dominant plant species included *Typha latifolia*, *T. angustifolia*, *Myrica gale*, *Carex* sp., *Calamagrostis canadensis*, *Spirea alba*, *S. 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 *M. gale*, *T. latifolia*, *C. canadensis*, *Juncus* sp., *Carex* sp., and *Leersia oryzoides*. The earliest nest initiation date detected at our sites was April 24, and the latest nest initiation date was July 1.

METHODS

Nest-level Measurements

We searched for rail nests from mid-April to early August in 2010 and 2011, in areas where paired birds responded to broadcast calls. Observers revisited all nests every 3–5 days until hatching or failure and 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) at the nest. We defined “nesting success” as a nest that hatched at least 1 egg, and “nesting failure” as a nest with obvious signs of predation (e.g., nest damage or egg albumin and no eggs remaining) or a nest that lost all of its eggs prior to the expected hatching date without any observed flooding. Nesting success is an important component of fecundity, although future studies on breeding propensity, clutch size, fledgling survival, renesting, and multiple broods could improve estimates of this parameter.

We estimated nest initiation dates for incomplete clutches by counting backward from the last egg laid and assumed that females laid 1 egg day⁻¹ (Tacha and Braun 1994). We estimated nest initiation date for complete clutches by counting backward from the date of hatch, assuming an average nest incubation period of 18 days for both species (Tacha and Braun 1994). If the exact hatch date was not observed, we estimated it as the midpoint between the last nest visit with eggs and the following visit with chicks. For nests where neither laying nor hatching was observed, we assumed that nests were found on day 9 (the middle) of incubation.

We modeled nest survival with a logistic exposure model (Shaffer 2004) using the “nestSurvival” package (Herzog 2011) in R (R Development Core 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). The relative performance of all models was assessed with the information-theoretic approach (Burnham and Anderson 2002). Our 5 variables included hydrology (a principal component for water depth and hydrologic variation described below), the change in nest height over the observation interval (measured from base to lip of nest), species, and nuisance variables to control for wetland type (impounded or not) and year. An interaction term between water depth and nest-height change was included in all models containing both variables to represent behavioral plasticity. Principal component analysis (PCA) was used to make a hydrology variable because water depth and water-level variation (the change in water depth at the nest from 1 visit to the next) were positively correlated but were both of interest. The principal component had high positive loadings (>0.70) for water depth and hydrologic variation at the nest.

We investigated the effects of hydrology because previous studies have shown a positive relationship between rail habitat use and habitat characteristics associated with water depth and variability, such as emergent vegetation and invertebrate and seed diversity (Tacha and Braun 1994, Melvin and Gibbs 1996, Lor and Malecki 2006). We also knew that predation was a common cause of nest failure for avian species and that wetland predation could be higher with shallower or decreasing water depths as a result of greater predator accessibility (Weller 1961). Rails in our study were anecdotally observed adding material to nests following heavy rain on a few occasions. They did so by adding pieces of nesting material (such as 2.5-cm pieces of dead *Typha* sp.) into the middle or bottom of the nest. They continued nest building even with eggs in the nest and occasionally mistakenly buried eggs during the process. On a few occasions, entire eggs were found buried in the middle of nests (E. P. Robertson and B. J. Olsen personal observation). We included an interaction between the nest-building and hydrology variables to represent this behavioral plasticity in which nest-building occurred during rainfall events and not when water levels were receding. We added year and impoundment as nuisance variables to control for any effects the passive impoundments and yearly environmental conditions may have had on nest survival at our sites. We also included a variable to account for any differences between the 2 species. We tested all subsets of these variables because we had no a priori biological reasons to think that any of the variable combinations were not plausible.

We evaluated the importance of each variable by summing the Akaike weights across all models (Burnham and Anderson 2002), examined global-model goodness-of-fit with a Hosmer and Lemeshow (2000) goodness-of-fit test, and assessed overdispersion using the Pearson chi-square statistic (Burnham and Anderson 2002). We used effective sample size (*sensu* Rotella et al. 2004) for model selection with Akaike's Information Criterion corrected for small sample sizes (AIC_c). Model averaging was used for the group of models with a combined model weight (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.

Site-level Measurements

We monitored site hydrology with an Onset HOBO water-level data logger (U-20 freshwater 13-foot-depth) placed in a perforated PVC pipe (5 feet in length and 1.5 inches in diameter) at each wetland downstream from all monitored rail nests. Water depths were taken every 30 min to obtain a detailed graph of water-level change at each site over the nesting season. Logger accuracy was verified with hand measurements, and logger data were calibrated for barometric-pressure variation with local barometric-pressure loggers (1 for Penobscot County and 1 for Washington County). We processed water-logger data using Indicators of Hydrologic Alteration (IHA) version 7.1 (Nature Conservancy 2009). This program produces composite hydrological variables that provide information on ecologically significant features of wetland-scale water regimes. We used the nonparametric statistic option and limited our analysis days to the rail nesting season.

Hydrologic variables included the minimum water-depth mean over the season at 3 time scales (1-, 3-, and 7-day moving averages); the maximum water-depth mean over the season at the same 3 time scales; the Julian date of the deepest 1-day mean water level; the Julian date of the shallowest 1-day mean water level; the number and duration of low pulses; the number and duration of high pulses; the median rate of increase and decrease for the season; the number of reversals ("rising" verses "falling" water depths); mean June low flow; the duration, timing, and frequency of extreme low flow; and small-flood duration, timing, and rise rate. We were interested in relative water-depth changes, so for each of the 7 wetlands, we subtracted the site-specific mean water depth from all variables. Pulse, flow, and flood limits were defined by IHA's default settings.

We took vegetation measurements at all nests within a single 2-wk period at the end of the nesting season (early July). Measurements included the width and

height of the nest vegetation (the homogeneous patch of vegetation within which the nest was placed); the percentage of the nest visible from the 4 cardinal directions at a distance of 1 m ("horizontal nest concealment") and vertically above the nest at a distance of 1 m ("vertical nest concealment"); the percentage of ground cover by shrubs, forbs, water, duckweed, and mud at a 2-m radius from the nest center; and vegetation density along four 1-m transects from the nest center in the 4 cardinal directions.

ArcGIS (ESRI 2011) was used to determine wetland size, distance of each nest from the nearest upland border, and 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 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. Our subdrainages ranged from 275 to 4,500 ha. We used PCA to identify the major axes of variation in our combined vegetative, hydrologic, and landscape data.

We used model-averaged daily survival rates (DSR) from the 97 rail nests in our nest-scale model to obtain DSR per site. Generalized linear models were used to examine site-level effects on nest survival with logit-transformed site DSR ($n = 7$) as the response variable. All 7 principal components and highly loaded variables ($>|0.2|$) from PCA were tested individually (to avoid overfitting) as potential predictor variables. AIC_c was used for model selection, and models with $\Delta AIC_c < 2.0$ were considered equivalent.

RESULTS

Nest-level Results

We monitored 75 Virginia Rail and 22 Sora nests, with an effective sample size of 1,035 monitored nest days. Daily survival rates were similar for Virginia Rail (98.3%; 95% CI: 95.7–99.3) and Sora (98.5%; 95% CI: 96.5–99.4). The overall daily survival rate from our logistic exposure model was 98.4% (95% CI: 95.8–99.31), and the overall nesting-period survival probability (assuming a mean incubation length of 28 days) was 50.5%. Apparent nesting success was 31 of 85 nests, or 63.5%. Most of the nesting failures (90.3%; $n = 31$) were due to predation. We documented nest predation by Marsh Wrens (*Cistothorus palustris*) at our study area, but other likely predators included snakes (Serpentes), Red-winged Blackbirds (*Agelaius phoeniceus*), American Crows (*Corvus brachyrhynchos*), muskrats (*Ondatra zibethicus*), and other mammals. Only 6.4% of failures ($n = 2$) were due to flooding, and 3.2% to nest abandonment ($n = 1$).

TABLE 1. Results of model selection to examine factors affecting Virginia Rail and Sora nesting survival in Maine, USA (2010 and 2011), for models within 4 ΔAIC_c of the top model. $\text{Log}_e(L)$ is the value of the maximized log-likelihood function, AIC_c is Akaike's Information Criterion corrected for small sample sizes, and w_i is the Akaike weight. A smaller AIC_c and a larger w_i represent more support for the model.

| Model ^a | df | ΔAIC_c | w_i | $\text{Log}_e(L)$ |
|--|----|----------------|-------|-------------------|
| Nest + Hydro + Plasticity | 4 | 0.00 | 0.42 | -53.26 |
| Nest + Hydro + Species + Plasticity | 5 | 1.89 | 0.16 | -53.16 |
| Nest + Imp + Hydro + Plasticity | 5 | 2.08 | 0.15 | -53.25 |
| Nest + Hydro + Year + Plasticity | 5 | 2.08 | 0.15 | -53.25 |
| Nest + Hydro + Species + Year + Plasticity | 6 | 3.98 | 0.06 | -53.15 |
| Nest + Hydro + Imp + Species + Plasticity | 6 | 3.98 | 0.06 | -53.16 |

^a Variable descriptions: "Nest" is the change in nest height, "Hydro" is a principal component of water depth and hydrologic variation, "Plasticity" is the interaction between "Nest" and "Hydro," "Species" is binary for Virginia Rail or Sora, "Imp" is binary for whether the wetland site has an impoundment or not, and "Year" is the year the nest was present.

Our final nesting-survival model set included 6 models with $\Delta AIC < 4$ (Table 1). The global model fits the observed values (Hosmer and Lemeshow goodness-of-fit test; $\chi^2 = 10.91$, $P = 0.21$). The Pearson chi-square test also indicated good model fit without overdispersion ($\phi = 1.08$, $P = 0.16$). Variance-inflation factors for all predictor variables were < 2.2 . The top 2 models had $< 2\Delta AIC_c = 1.89$. The top model included hydrology, nest building, and the interaction of hydrology and nest building ("plasticity"); the second-best model additionally included species. Akaike weights for the top 2 models were 42% and 16% among the final model set (Table 1). Nest daily survival rates increased with deeper and more variable water levels (Figure 2C) and also with nest-building behavior in response to deepening water (Figure 2A, 2B). Nest-building was a response to hydrology at the nest and fluctuated, along with water depth, over the breeding season (Figure 3). We witnessed rails increasing their nest height by as much as 18 cm in only 2 days after a heavy

rain (E. P. Robertson and B. J. Olsen personal observation). Hydrology (summed Akaike weight = 1) and plasticity (summed Akaike weight = 1) had the greatest effect on nest survival. Both were found in all of the top 6 models, and the model-averaged parameter estimates had statistically significant confidence intervals (Tables 1 and 2). Impoundment, year, and species were not significant predictors of daily nest survival rates (Table 2).

Site-level Results

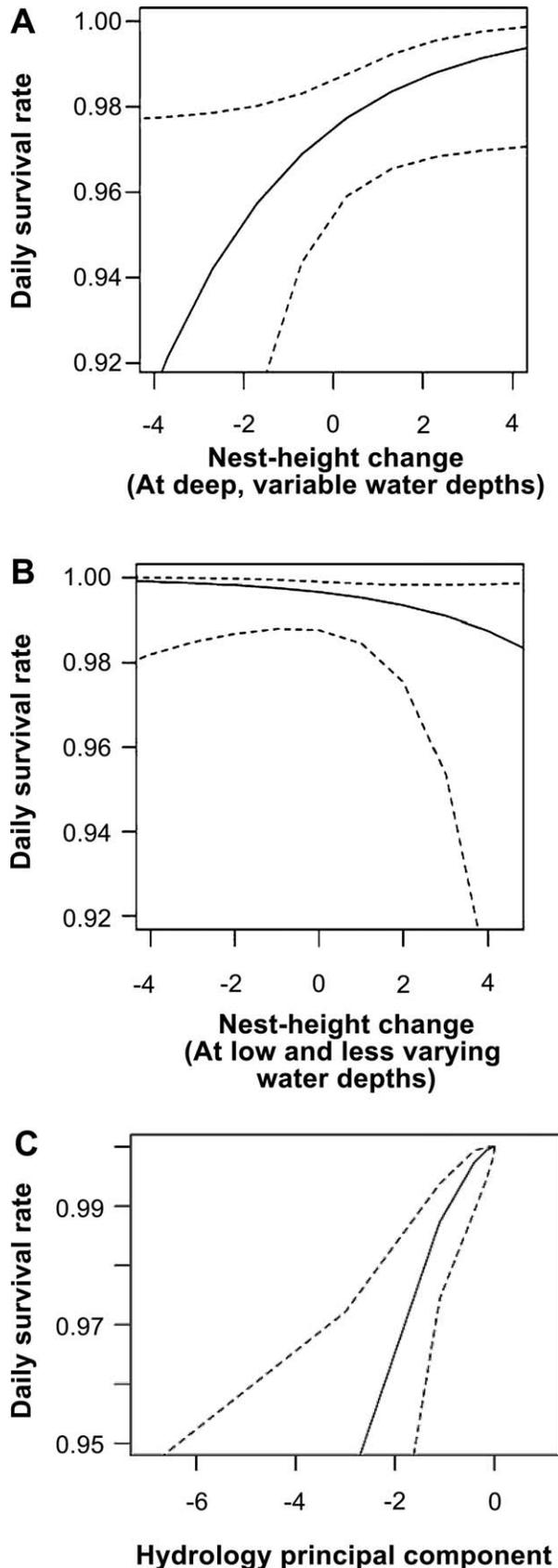
Principal component 3 (PC3) was the best site-level predictor of daily nest survival rates ($F_{1,5} = 31.83$, $P = 0.002$, $R^2 = 0.84$; Figure 4). PC3 described hydrology and nest concealment at sites, and high PC3 values were associated with increased hydrologic variability, extensive water cover, and thick vegetation clumps for hiding nests. Variables with high positive loadings (> 0.20) included those describing hydrologic variability (low pulse count, high pulse count, and fall rate), vegetative density above

TABLE 2. Model-averaged parameter estimates with unconditional standard errors (SE) and odds ratios with unconditional 95% confidence intervals, and summed Akaike weights (w_i) for variables in the top 6 models (Table 1) for nesting survival of Virginia Rails and Soras in Maine, USA (2010 and 2011).

| Variable ^a | Estimate | SE | Odds ratio and 95% CI ^b | Summed (w_i) |
|-------------------------|----------|------|------------------------------------|------------------|
| Intercept | 4.44 | 0.50 | | |
| Nest | -0.05 | 0.18 | 0.67 ≤ 0.95 ≤ 1.35 | 1 |
| Hydro | 1.56 | 0.45 | 1.09 ≤ 1.21 ≤ 1.51 | 1 |
| Plasticity | 0.51 | 0.20 | 1.40 ≤ 1.60 ≤ 1.90 | 1 |
| Species (Virginia Rail) | 0.31 | 0.67 | 0.36 ≤ 1.36 ≤ 5.11 | 0.28 |
| Imp | -0.04 | 0.54 | 0.33 ≤ 0.96 ≤ 2.76 | 0.21 |
| Year | 0.03 | 0.52 | 0.37 ≤ 1.03 ≤ 2.87 | 0.21 |

^a Variable descriptions: "Nest" is the change in nest height, "Hydro" is a principal component of water depth and hydrologic variation, "Plasticity" is the interaction between "Nest" and "Hydro," "Species" is binary for Virginia Rail or Sora, "Imp" is binary for whether the wetland site has an impoundment or not, and "Year" is the year the nest was present.

^b Odds ratio and associated 95% confidence interval [CI] of Hydro, Nest, and Plasticity are not interpretable because of the interaction of 2 continuous variables.



the nest (width of the nest vegetation clump, shrub cover viewed from above, and stem density), and water cover surrounding nests (percentage of ground covered by water in a 2-m radius). Variables with high negative loadings (less than -0.20) included water levels that rose rapidly (rise rate), poor nest concealment (percentage of ground covered by forbs within 1 m of the nest), or too much horizontal nest concealment (percentage of nest concealment horizontally).

DISCUSSION

Nesting survival of rails was greater in areas with increased water-level variation at both the nest and wetland scales (Figure 2C). Wetlands with greater water-level variation are 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 these areas of dynamic water depths to forage on emergent plant seeds and invertebrates, and they have behavioral plasticity to deal with nesting in these areas of high hydrologic variability by building up their nests during water-level increases (E. P. Robertson and B. J. Olsen personal observation). They experienced relatively few nest-flooding events, despite water levels that fluctuated at the nest by as much as 30.5 cm over a 3-day period, because of their ability to rapidly increase nest height. Behavioral plasticity can be visualized by examining the relationships between nest height change and nest survival over periods of rising versus falling water depths (Figure 2A, 2B). Among nests that experienced increasing water levels, individuals that built up their nests had higher nesting success. Among those that experienced decreasing water levels, nests that stayed at the same height or lost a little height (because of settling) fared the best (Figure 2A, 2B).

Behavioral plasticity is a useful indicator of the hydrologic variability of the nest site in rails. During

FIGURE 2. (A, B) Behavioral plasticity of Virginia Rails and Soras in Maine (2010 and 2011), demonstrated by daily nest survival probability as a function of nest-height change for time intervals that experienced (A) increasing water depths and (B) decreasing water depths. Model-averaged estimates were derived from our top 6 models (Table 1), which included water-depth change, nest-height change, water-depth change \times nest-height change ("plasticity"), species, year, and impoundment. (C) Daily nest survival probability (logit-transformed) as a function of a hydrology principal component (representing water depth and water-level variation) at Virginia Rail and Sora nests in Maine (2010 and 2011). Model-averaged estimates were derived from our top 6 models (Table 1), which included water-depth change, nest-height change, water-depth change \times nest-height change ("plasticity"), species, year, and impoundment.

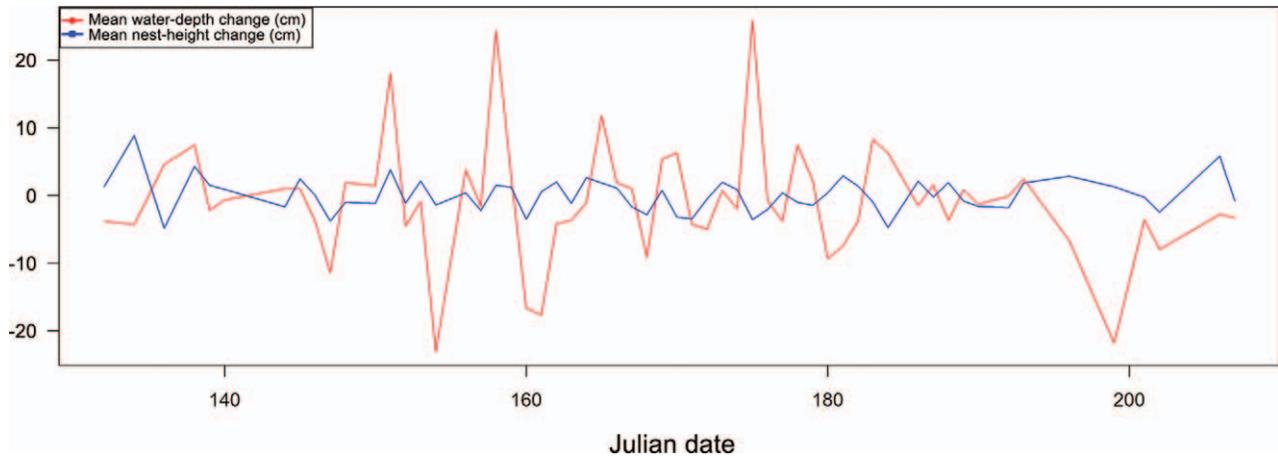


FIGURE 3. Mean nest-height change (blue) compared with mean water-depth change (red) at all nests throughout the breeding season. Virginia Rails and Soras built up their nests with additional nesting material to adapt to water-depth fluctuations.

water-level increases, individuals that *increased* their nest height the most (larger nest-height change) were located in the deepest and most variable hydrologic areas within the wetland, and they experienced the lowest predation rates, most likely because of reduced predator accessibility (Weller 1961; Figure 2A, 2B). During water-level decreases, on the other hand, nests that were *decreasing* in height were located in the most variable hydrologic areas, because they had the greatest ability to settle, being higher as a result of past high water levels (Figure 2A, 2B).

High hydrologic variability, extensive water cover, and thick vegetation clumps increased site-level nesting survival of rails, whereas rapidly rising water, poor vertical nest concealment, and too much horizontal nest concealment decreased it. The importance of hydrologic variability and water cover, and the dangers of water that rises too rapidly, correspond with what we saw at the nest level. We suspect that clumps of nesting vegetation are important for hiding nests from predators, because the majority of our nesting failures were due to predation and because most nests we found were in thicker clumps of vegetation surrounded by more open areas that are preferred for foraging. Of the predation events that we could identify, the majority were from Marsh Wrens, which may explain why vertical concealment had positive effects on nesting survival (concealing nests from aerial predators), whereas too much horizontal concealment had negative effects (possibly indicating habitat that is too thick for efficient movement or foraging by rails).

Our estimates of overall nest survival are within the range of estimates reported in previous studies (Billard 1948, Pospichal and Marshall 1954, Tanner and Hen-

drickson 1954, Conway et al. 1994, Lor and Malecki 2006). It should be noted, however, that our data were collected over 2 fairly dry seasons (4–5 cm less rainfall during May–July than average: National Oceanic and Atmospheric Administration [NOAA] 2011). The positive, linear relationship between nest survival and water-depth change that we report here could be a result of the limited range of precipitation observed during our study, and we assume that some degree of water-level increase beyond

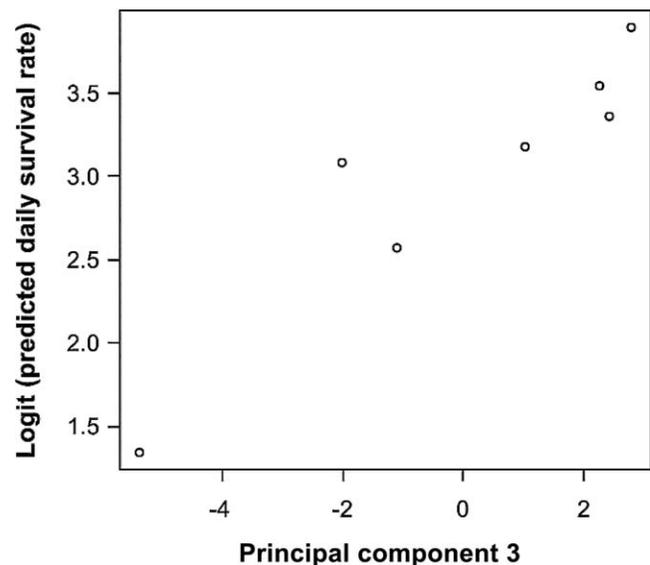


FIGURE 4. Site-level nest survival probabilities (logit transformed) versus principal component 3 (tightly linked to water-level variability, extent of water cover, and adequate nest concealment) from principal component analysis of vegetation, hydrology, and landscape data for Virginia Rail and Sora nests in Maine, USA (2010 and 2011).

this range would lead to increases in nest loss. Indeed, 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, 6 lost eggs to flooding.

In summary, we found in these two marsh species that deeper, more variable water levels and behavioral plasticity for nest building in response to an unpredictable environment increased fecundity. Few other avian studies have linked plasticity to demographic responses, and none has looked at the effects of adding nesting material to increase nest height during rainfall events in a stochastic wetland environment. Our results illustrate the sensitivity of marsh birds to hydrology and the careful balance they must maintain between losing their nests to predators or to floods. We suspect that this behavior may be widespread throughout marsh birds, and possibly other species, though more studies are needed to confirm this.

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