

Diel Variation in Detection and Vocalization Rates of King (Rallus elegans) and Clapper (Rallus crepitans) Rails in Intracoastal Waterways

Authors: Stiffler, Lydia L., Anderson, James T., Welsh, Amy B.,

Harding, Sergio R., Costanzo, Gary R., et al.

Source: Waterbirds, 40(3): 263-271

Published By: The Waterbird Society

URL: https://doi.org/10.1675/063.040.0307

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Diel Variation in Detection and Vocalization Rates of King (*Rallus elegans*) and Clapper (*Rallus crepitans*) Rails in Intracoastal Waterways

Lydia L. Stiffler^{1,*}, James T. Anderson¹, Amy B. Welsh¹, Sergio R. Harding², Gary R. Costanzo³ and Todd E. Katzner⁴

¹Division of Forestry and Natural Resources, P.O. Box 6125, West Virginia University, Morgantown, West Virginia, 26506, USA

²Virginia Department of Game and Inland Fisheries, 7870 Villa Park Drive, Suite 400, Henrico, Virginia, 23228, USA

³Virginia Department of Game and Inland Fisheries, 3801 John Tyler Memorial Highway, Charles City, Virginia, 23030, USA

⁴U.S. Geological Survey, Forest & Rangeland Ecosystem Science Center, 970 Lusk Street, Boise, Idaho, 83706, USA

*Corresponding author; E-mail: llstiffler@mix.wvu.edu

Abstract.—Surveys for secretive marsh birds could be improved with refinements to address regional and species-specific variation in detection probabilities and optimal times of day to survey. Diel variation in relation to naive occupancy, detection rates, and vocalization rates of King (*Rallus elegans*) and Clapper (*R. crepitans*) rails were studied in intracoastal waterways in Virginia, USA. Autonomous acoustic devices recorded vocalizations of King and Clapper rails at 75 locations for 48-hr periods within a marsh complex. Naive King and Clapper rail occupancy did not vary hourly at either the marsh or the study area level. Combined King and Clapper rail detections and vocalizations varied across marshes, decreased as the sampling season progressed, and, for detections, was greatest during low rising tides (P < 0.01). Hourly variation in vocalization and detection rates did not show a pattern but occurred between 7.8% of pairwise comparisons for detections and 10.5% of pairwise comparisons for vocalizations (P < 0.01). Higher rates of detections and vocalizations occurred during the hours of 00:00-00:59, 05:00-05:59, 14:00-15:59, and lower rates during the hours of 07:00-09:59. Although statistically significant, because there were no patterns in these hourly differences, they may not be biologically relevant and are of little use to management. In fact, these findings demonstrate that surveys for King and Clapper rails in Virginia intracoastal waterways may be effectively conducted throughout the day. *Received 12 December 2016, accepted 10 May 2017*.

Key words.—Clapper Rail, detection rate, diel, King Rail, *Rallus crepitans, Rallus elegans*, vocalization rate.

Waterbirds 40(3): 263-271, 2017

Secretive marsh birds are challenging to monitor due to the difficulty in locating and trapping them within the dense emergent vegetation they occupy (Zembal and Massey 1983; Perkins et al. 2010). Thus, surveys for these species are usually conducted aurally by human observers who record numbers of vocalizations and estimate numbers of birds (Conway 2011). However, even these surveys can be improved with refinements to address regional, diel, and species-specific variation in detection probabilities (Conway and Gibbs 2011; Wiest and Shriver 2016). In particular, although there may be optimal times of day to survey for given species, these details are poorly understood (Conway and Gibbs 2011).

There are demonstrated temporally driven inconsistencies in detection rates and abundance estimates for birds. This is especially true for members of the Family Rallidae. For example, morning sampling produced higher estimates of relative abundance and detection rate of Clapper Rails (Rallus crepitans) in Maryland, USA (Lehmicke et al. 2013) and California Black Rails (Laterallus jamaicensis coturniculus) in Arizona, USA (Conway et al. 2004). However, in California, USA, Light-footed Rails (R. obsoletus levipes) and California Black Rails were detected more frequently during evening sampling (Zembal and Massey 1987; Conway et al. 2004). In contrast, other studies have found no diel variation in outcomes of surveys conducted for California Black Rails (Spear et al. 1999) and a group of Rallidae species (Harms and Dinsmore 2014).

To better understand patterns in diel variation of King (*R. elegans*) and Clapper rail vocalization behaviors, we studied varia-

tion in detection and vocalization rates of the combined King and Clapper rail complex (Maley and Brumfield 2013) in Virginia, USA, intracoastal waterways. Within Virginia, populations of King and Clapper rails are declining (Wilson et al. 2007; Correll et al. 2016), and both species have been listed as Species of Greatest Conservation Need in the State of Virginia's 2015 Wildlife Action Plan (Virginia Department of Game and Inland Fisheries 2015). We recorded vocalizations of King and Clapper rails using autonomous recording units (ARUs) and evaluated the recordings with survey covariates to determine hourly variation in: 1) the proportion of sites at which individuals in the King and Clapper rail complex were detected, henceforth naive occupancy; 2) estimates of the number of individuals detected; and 3) the frequency of vocalizations.

METHODS

Study Area

We studied King and Clapper rail vocalizations from May through July of 2015 in a marsh complex composed of five tidal marshes along the Pamunkey River near West Point, Virginia, USA. The Pamunkey River is situated within the Chesapeake Bay Watershed and is a tributary of the York River. The five surveyed

marshes were Eltham (288 ha), nearest the confluence with the York River, followed upriver by Lee (579 ha), Hill (508 ha), Sweet Hall (395 ha), and Cousiac (387 ha) (Fig. 1).

These marshes occur along a salinity gradient from mesohaline at Eltham to freshwater at Cousiac (Virginia Institute of Marine Science 2005). Previous avian surveys have shown King and Clapper rail densities to follow the salinity gradient, with the highest densities within Eltham Marsh (S. R. Harding and G. R. Costanzo, unpubl. data) and decreasing densities within Lee and Hill (Paxton and Watts 2002). The marshes themselves are low and inundated twice daily by tidal flow. Vegetation in lower areas is dominated by smooth cordgrass (Spartina alterniflora). The higher, irregularly flooded areas are dominated by saltmeadow cordgrass (S. patens) and big cordgrass (S. cynosuroides). Freshwater and intermediate brackish salt marsh areas are characterized by arrow arum (Peltandra virginica), pickerelweed (Pontederia cordata), and wild rice (Zizania aquatica).

During our study, the average daily temperature was 25.4 °C, with average maximum and minimum temperatures of 30.3 °C and 20.5 °C, respectively. Average daily wind speed was 1.96 m/sec, with maximum wind speeds approaching 5.31 m/sec. Sunrise and sunset occurred at 05:55 hr and 20:12 hr, respectively, on the first day of sampling and at 06:00 hr and 20:27 hr, respectively, on the last day. We obtained daily tidal information from the National Oceanic and Atmospheric Administration predictions for Sewells Point in West Point, Virginia, USA (National Oceanic and Atmospheric Administration 2015) and categorized the information into six tidal stages: high tide, high tide falling, low tide falling, low tide rising, and high tide rising.

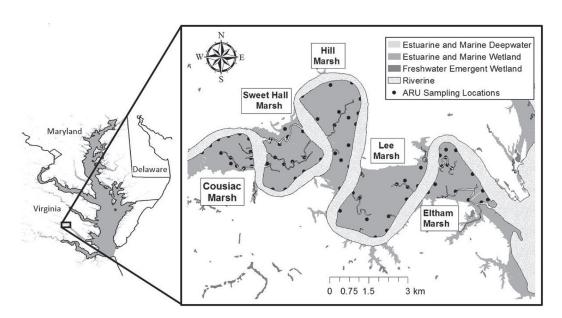


Figure 1. Tidal marshes surveyed for King and Clapper rails, May-July 2015, along the Pamunkey River, Virginia, USA.

Study Species

King and Clapper rails are secretive marsh birds whose ranges overlap along the Atlantic and Gulf coasts of the USA. Although they are challenging to differentiate by physical appearance at a distance, King Rails are slightly larger, heavier, and have chestnut breast coloration, whereas Clapper Rails are more slender and have a grayish-brown coloration (Meanley 1969; Reid et al. 1994). These species coexist along a salinity gradient, with King Rails found in freshwater marshes and Clapper Rails in tidal salt marshes. However, both species can inhabit transitional zones of intermediate brackishsalt marshes (Meanley and Wetherbee 1962; Meanley 1969). King and Clapper rails are genetically similar (Maley and Brumfield 2013) and, in areas of coexistence, hybridization and introgression can occur between the two species (Meanley 1985; Chan et al. 2006).

King and Clapper rails also exhibit acoustic similarities. Both have three main call series, described as "keks", "grunts", and "kek-burrs". Males of both species give a series of sharp "kek" notes, accelerating then slowing at the end (Massey and Zembal 1987). The "grunt" series is given by both species as contact calls. "Grunts" are characterized by fast, sharp notes that gradually decrease in frequency (Massey and Zembal 1987). The "kek-burr" series is used solely by females and is believed to be a way to attract a new mate or to call back a straying mate (Zembal and Massey 1985). This call begins with one or more "kek" notes followed by a "brrr."

Survey Site Selection

We used ArcMap (Environmental Systems Research Institute 2011) to design a simple random sample for survey site selection. We constrained sample site selection so that each location was at least 400 m from every other survey location (Conway 2011), at least 50 m from marsh edge, and easily accessible by boat from the Pamunkey River. In total, we selected 75 locations, with 15 locations in each of the five marshes.

Sampling Protocols

We deployed five Song Meter SM3 (Wildlife Acoustics) ARUs, one per marsh. The ARUs were mounted onto t-posts that were subsequently placed into the ground such that the ARUs were approximately 1.5 m above the marsh substrate. We sampled using one ARU per marsh for a single period of two consecutive days, and we then moved the ARU to a new location within that same marsh and repeated the 2-day protocol. This approach allowed for concurrent sampling across the five marshes. Each sampling period started at midnight and lasted exactly 48 hr. We programmed the ARUs to record 16 bit with a sampling rate at 24 kHz. Recordings were stored hourly onto 128-GB memory cards. In total, we sampled for 30 days in the marsh system along the Pamunkey River.

The order of sampling locations within a marsh at which ARUs were deployed was random. If the water level was too low to access a location, we selected the next sampling location and rescheduled the inaccessible location for the following high tide placement. If upon visiting a location, we determined the location did not meet the original selection constraints, we selected a new randomized replacement site. We delayed sampling for a day during rainy weather or when wind speeds exceeded 20 kmph (Gibbs and Melvin 1993).

Spectrographic Analyses

We placed an ARU for 2 days at each of the 15 sampling locations within the five marshes, resulting in a total of 3,600 hr of acoustic recordings for analysis. We used the interactive sound analysis software Raven Pro (Bioacoustics Research Program 2014) to manually identify vocalizations of King and Clapper rails in the recordings. Since there is no widely accepted acoustic method to definitively differentiate between vocalizations of the two species (Graves 2001; Conway 2011) and hybridization has occurred within the marsh system, we pooled all vocalizations from the King and Clapper rail complex for analysis. We defined a vocalization as a complete series of calling notes. For each vocalization, we identified the start and end points and the duration of calling. As an example, one vocalization could be a single stand alone "kek" note and another, a series of "kek" notes.

Once we identified all vocalizations, we estimated, for each marsh, the total number of individuals detected per hour for each sampling period. Because we could not distinguish between calls of individual King and Clapper rails, we only counted multiple detections when there was overlap in the timing of vocalizations by more than one bird. Finally, within two marshes with high and low apparent densities of King and Clapper rails, we estimated the total number of hourly vocalizations recorded.

Statistical Analyses

To assess hourly variation in naive occupancy at the marsh and study area level, we calculated, by hour, the proportion of sites where at least one King or Clapper rail was detected for all 15 sampling locations in each marsh. We then calculated an average overall hourly proportion of sites where at least one King or Clapper rail was detected across all marshes. We used a χ^2 test (α = 0.05) to assess hourly variation in naive occupancy for: 1) each marsh individually; and 2) the combined study area.

To understand diel fluctuations in number of King and Clapper rails detected, we calculated the number of detections in each hour separately for each marsh. For each hour of the day, we summed data across all 15 sampling points, which was equivalent to 30 sampling days. We removed outliers within the data (Zuur et al. 2010) and, since we detected overdispersion within our count data (R package: Applied Econometrics with R; Kleiber and Zeileis 2008), we developed models using negative binomial distributions (Zuur et al. 2009). We generated univariate and additive linear models (n = 16) with time of day, marsh location, day of the year, and tidal stage as fixed effects to determine which covariates had the greatest effect on our response variable, detection rate per hour (R package: glmmAMDB; Skaug et al. 2016). We used corrected Akaike information criterion (AIC, to compare all combinations of sub-models using log-

likelihoods, and we ranked models based on Δ AIC_c and weights (Burnham and Anderson 2004; R package: AICcmodavg; Mazerolle 2016). We regarded the model with the lowest AIC_c to be the top model and considered models with Δ AIC_c < 2 to have substantial support (Burnham and Anderson 2004). We used parametric bootstrapping to calculate 99% confidence intervals of estimates (n=10,000) for each model parameter of interest to allow for pairwise comparisons between factors while controlling for additional parameters within the model (e.g., the effect of time on detection while controlling for marsh location, day of the year, and tidal stage) (Anderson and Burnham 2002; Hothorn *et al.* 2008; Burnham *et al.* 2011; R package: mnormt; Azzalini and Genz 2016).

To understand variation in the rate of King and Clapper rail vocalizations throughout the day, we calculated the number of vocalizations per hour, summed across all 15 sites and 30 sampling days. For this analysis, we only considered two marshes: Eltham, which had the greatest apparent density of King and Clapper rails, and Hill, which had a low apparent density of King and Clapper rails. We again removed outliers within the data. We used similar model development (n = 16), model selection, and parametric bootstrapping processes as above, building and comparing multiple sub-models with negative binomial distributions. We analyzed data using the statistical program R (R Development Core Team 2013) and RStudio (RStudio, Inc. 2015).

RESULTS

Naive occupancy estimates decreased with decreasing site salinity. The highest

average percentage of ARU sampling sites at which King and Clapper rails were detected occurred at Eltham (86.7% \pm 1.9 SE), followed by Lee (47.0% \pm 2.3 SE), Hill (26.1% \pm 2.6 SE), and Sweet Hall (11.1% \pm 1.6 SE) (Fig. 2). No King and Clapper rails were detected at Cousiac Marsh. Overall, we detected King and Clapper rails at an average of 42.7% \pm 1.6 SE of sites. There was no significant variation in naive occupancy among hourly comparisons within each individual marsh and across the entire study area.

The global model was the single best for estimating frequency of King and Clapper rail detections (Table 1). Detections varied only among a few hours of the day, with significant differences (P < 0.01) among 7.8% (n = 256) of hourly pairwise comparisons of bootstrapped estimates for King and Clapper rail detection (Fig. 3). We found no patterns of increasing or decreasing detection rates at any time throughout the day. Higher rates of detection occurred during the hour of 00:00-00:59 and between the hours of 04:00-06:59 and 13:00-15:59. Lower rates of detection occurred between the hours of 07:00-09:59. The frequency of detections varied significantly amongst all pairwise comparisons of marshes (P < 0.01), with

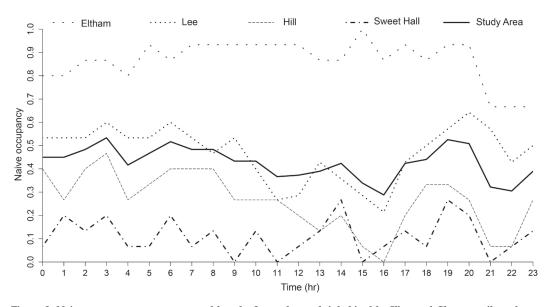


Figure 2. Naive occupancy rates, measured hourly, for each marsh inhabited by King and Clapper rails and surveyed along the Pamunkey River, Virginia, USA. Data were summed across 15 sampling locations.

Table 1. Model selection results for the hourly detection and vocalization rates of King and Clapper rails in intracoastal Virginia, USA, May-July 2015. Models were ranked by difference in corrected Akaike's Information Criterion (Δ AIC $_c$) with the model weight (w_i) and number of parameters (K). Only models with Δ AIC $_c$ < 2 are shown. Parameters included time of day (Time), marsh location (Marsh), day of the year (Date), and tidal stage (Tide).

Model	K	$\Delta {\rm AIC}_{\rm c}$	$w_{\rm i}$
Detection Count ~ Time + Marsh + Date + Tide	34	0	1.000
Vocalization Count ~ Time + Marsh + Date	27	0	0.967

Eltham appearing to have both the highest and most variable detection rate. The number of King and Clapper rails detected varied with tidal stage (P < 0.01), with detection rates lower at low falling tides than at either high tides or low rising tides. Frequency of detections also decreased as the year progressed (P < 0.01).

The best model for estimating frequency of King and Clapper rail vocalizations had fixed additive effects for Time, Marsh, and Date (Table 1). In contrast to the model results for detection frequency, models with Tide were not well supported. Frequency of vocalizations varied with time of day (P < 0.01), with significant differences among 10.5% (n = 256) of hourly pairwise comparisons of bootstrapped estimates for King and Clapper rail vocalizations. As was the case for the previous analysis, we did not detect diel patterns (peaks or valleys) in vocalization rates. Higher rates of vocalizations occurred during the hours of 00:00-00:59, 05:00-05:59, 10:00-11:59, and 14:00-15:59, and lower rates during the hours of 07:00-09:59 and 22:00-23:59. King and Clapper rail vocalizations varied amongst marshes (P < 0.01) and were more frequent and more variable at Eltham than at Hill. Vocalization rates decreased as the season progressed (P < 0.01).

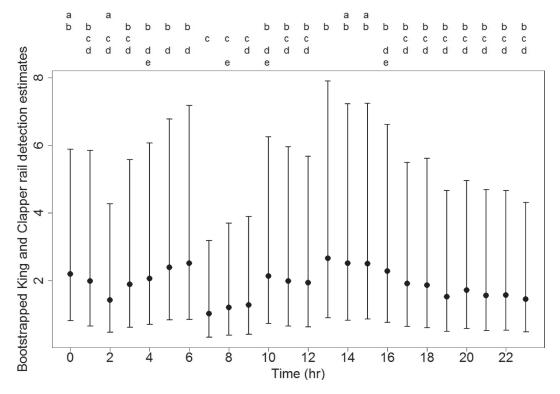


Figure 3. Parametric bootstrapped hourly estimates of King and Clapper rail detection rates from a generalized linear negative binomial model for data collected from tidal marshes along the Pamunkey River, Virginia, USA. Model parameter estimates are shown with a 99% confidence interval estimated by bootstrapping. The letters above each hour represent significance differences indicated by pairwise comparisons between hourly King and Clapper rail estimates.

DISCUSSION

While our findings suggest statistically significant differences in King and Clapper rail vocalization behavior throughout the day, those differences do not represent daily patterns in these rates and are likely only biologically or ecologically significant in a small number of circumstances. For example, although there was diel variation in the rates at which King and Clapper rails vocalized and in the number of birds detected throughout the day, naive occupancy of our sites did not vary hourly. Similarly, although there were differences in hourly detection and vocalization rates, those differences did not appear to be evidence of a biological pattern and provided no clear distinctions between vocalization behavior between the morning and afternoon. While lower detection and vocalization rates occurred during the early morning (07:00-09:59 hr), higher rates occurred at seemingly random times of the day (00:00-00:59 hr, 05:00-06:59 hr, and 14:00-14:59 hr).

As has been observed in other studies, the vocalization and detection frequencies we recorded were greatest early in the season (Conway and Gibbs 2005; Conway and Nadeau 2010; Wiest and Shriver 2016). Tidal stage also had an influence on our data, but only for detection rates and not vocalization rates. Previous studies found reduced detections during high tide (Zembal and Massey 1987; Wiest and Shriver 2016) and greater detection during mid-level tides (Lehmicke *et al.* 2013; Wiest and Shriver 2016).

These findings have important implications both for the King and Clapper rail complex and for design of surveys to detect King and Clapper rails and other secretive marsh birds. There has been little comprehensive study of diel variation of vocalization rates of birds, and our study is the first investigation into 24-hr diel vocalization patterns for secretive marsh birds. The King and Clapper rails we studied vocalized consistently across the day at all study sites where birds were detected, and most hours were similar to each other in vocalization and detection rates. The only differences we detected were small and were between hours during early morning and during late evening following sunset. The higher frequency of vocal activity during sunrise might be influenced by increased social interactions amongst breeders to reinforce territorial mating boundaries following the nocturnal rest period (Massey and Zembal 1987). Decreased nighttime vocal activity may also be a mechanism to decrease nest predation by nocturnal predators (Meanley 1985).

King and Clapper rail density appears to influence the effectiveness and accuracy of acoustic sampling. Apparent high density areas had higher detection and vocalization rates, and King and Clapper rails were detected at a greater proportion of sites in those areas. In contrast, all three metrics were lower at apparently low density areas. This density-dependent response of vocalization probability has been demonstrated for Virginia Rails (Rallus limicola; Glahn 1974; Robertson and Olsen 2014) and Light-footed Rails (Zembal and Massey 1987). This response can be problematic when interpreting sampling data because it increases sampling error and can result in overestimates of abundance (Bart and Schoultz 1984; Conway and Gibbs 2001; Robertson and Olsen 2014).

Our findings have several implications for design of surveys to detect King and Clapper rails and other secretive marsh birds, in particular, the use of ARUs and the timing of surveys. Secretive marsh birds are traditionally sampled via callback surveys to increase detection probability (Conway 2011; Conway and Gibbs 2011). However, since callbacks may change behavior of birds, using callbacks may alter the diel pattern of vocalization for these species. Autonomous devices can provide an alternative method to traditional sampling for long-term, continuous monitoring of secretive marsh birds without introducing bias that playback and human presence may create. The use of autonomous devices can also allow for simultaneous surveying of multiple locations, thereby reducing temporal, spatial, and financial constraints associated with having a person visit each site simultaneously (Tegeler et al.

2012). In addition to having the potential to minimize observer bias, ARUs are also beneficial because they produce a permanent survey record that can be validated by multiple observers and can allow for more frequent detection of rare species (Rempel *et al.* 2005; Acevedo and Villanueva-Rivera 2006; Hutto and Stutzman 2009).

However, ARUs possess drawbacks that impose limitations on their utility. Autonomous devices generate large volumes of acoustic recordings that can be difficult to store and analyze (Rempel et al. 2005). While automated species detectors can be built for spectrographic analysis software, they tend to require large training data sets and they often produce many false positives and false negatives (Waddle et al. 2009; Bardeli et al. 2010; Towsey et al. 2012). Manual analysis of recordings can provide higher accuracy, but is often time and effort consuming (Swiston and Mennill 2009). Autonomous devices may also detect fewer individuals than humans, especially when birds are calling farther away from the recording instrument (Venier et al. 2012; Furnas and Callas 2015).

This study illustrated that in intracoastal Virginia, King and Clapper rail detection and vocalization rates varied minimally with time of day, suggesting that the King and Clapper rail complex can be surveyed there throughout the day. Future vocalization studies may reveal if the lack of diel variation in this study is representative across the entire region or if it is driven by local variability in behaviors.

ACKNOWLEDGMENTS

This publication was completed with funds provided by the Virginia Department of Game and Inland Fisheries through a Federal Aid in Wildlife Restoration grant from the U.S. Fish and Wildlife Service. We thank all landowners and caretakers of each marsh for providing access to conduct this study: Louis Savage, M. C. Lipscomb, Dennis Boswell, the Virginia Institute for Marine Sciences, and Alvin Stitzer. We also thank our field technicians Tyler Woollard and Luke Costilow for assisting with field sampling. We thank two anonymous referees for their helpful comments. All applicable ethical guidelines for the use of birds in research have been followed, including those presented in the Ornithological Council's "Guidelines to the Use

of Wild Birds in Research". This is Scientific Article No. 3312 of the West Virginia Agricultural and Forestry Experiment Station, Morgantown, West Virginia. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

- Acevedo, M. A. and L. J. Villanueva-Rivera. 2006. Using automated digital recording systems as effective tools for the monitoring of birds and amphibians. Wildlife Society Bulletin 34: 211-214.
- Anderson, D. R. and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. Journal of Wildlife Management 66: 912-918.
- Azzalini, A. and A. Genz. 2016. The R package 'mnormt': the multivariate normal and t distributions v. 1.5-5. R Foundation for Statistical Computing, Vienna, Austria. https://cran.r-project.org/package=mnormt, accessed 19 April 2017.
- Bardeli, R., D. Wolff, F. Kurth, N. Koch, K. H. Tauchert and K. H. Frommolt. 2010. Detecting bird sounds in a complex acoustic environment and application to bioacoustics monitoring. Pattern Recognition Letters 31: 1524-1534.
- Bart, J. and J. D. Schoultz. 1984. Reliability of singing bird surveys: changes in observer efficiency with avian density. Auk 101: 307-318.
- Bioacoustics Research Program. 2014. Raven Pro: interactive sound analysis software v. 1.5. Cornell Lab of Ornithology, Ithaca, New York. http://www.birds.cornell.edu/raven, accessed 12 June 2014.
- Burnham, K. P. and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods Research 33: 261-304.
- Burnham, K. P., D. R. Anderson and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65: 23-35.
- Chan, Y. L., C. E. Hill, J. E. Maldonado and R. C. Fleischer. 2006. Evolution and conservation of tidal-marsh vertebrates: molecular approaches. Studies in Avian Biology 32: 54-75.
- Conway, C. 2011. Standardized North American marsh bird monitoring protocol. Waterbirds 34: 319-346.
- Conway, C. J. and J. P. Gibbs. 2001. Factors influencing detection probabilities and the benefits of call broadcast surveys for monitoring marsh birds. Final report, U.S. Department of the Interior, Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland.
- Conway, C. J. and J. P. Gibbs. 2005. Effectiveness of callbroadcast surveys for monitoring marsh birds. Auk 122: 26-35.
- Conway, C. J. and C. P. Nadeau. 2010. Effects of broadcasting conspecific and heterospecific calls on detection of marsh birds in North America. Wetlands 30: 358-368.

- Conway, C. J. and J. P. Gibbs. 2011. Summary of intrinsic and extrinsic factors affecting detection probability of marsh birds. Wetlands 31: 403-411.
- Conway, C. J., C. Sulzman and B. E. Raulston. 2004. Factors affecting detection probability of California Black Rails. Journal of Wildlife Management 68: 360-370.
- Correll, M. D., W. A. Wiest, T. P. Hodgman, W. G. Shriver, C. S. Elphick, B. J. McGill, K. M. O'Brien and B. J. Olsen. 2016. Predictors of specialist avifaunal decline in coastal marshes. Conservation Biology 31: 172-182.
- Environmental Systems Research Institute (ESRI). 2011. ArcGIS v. 10. ESRI, Redlands, California.
- Furnas, B. J. and R. L. Callas. 2015. Using automated recorders and occupancy models to monitor common forest birds across a large geographic region. Journal of Wildlife Management 79: 325-337.
- Gibbs, J. P. and S. M. Melvin. 1993. Call-response surveys for monitoring breeding waterbirds. Journal of Wildlife Management 57: 27-34.
- Glahn, J. F. 1974. Study of breeding birds with recorded calls in north-central Colorado. Wilson Bulletin 86: 206-214
- Graves, C. 2001. Avian use of tidal marshes across a salinity gradient at Savannah National Wildlife Refuge, Georgia-South Carolina. M.S. Thesis, University of Tennessee, Knoxville.
- Harms, T. M. and S. J. Dinsmore. 2014. Influence of season and time of day on marsh bird detections. Wilson Journal of Ornithology 26: 30-38.
- Hothorn, T., F. Bretz and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal 50: 346-363.
- Hutto, R. L. and R. J. Stutzman. 2009. Humans versus autonomous recording units: a comparison of point-count results. Journal of Field Ornithology 80: 387-398
- Kleiber, C. and A. Zeileis. 2008. Applied econometrics with Rv. 1.2-4. Springer-Verlag, New York, New York. https://cran.r-project.org/web/packages/AER, accessed 19 April 2017.
- Lehmicke, A. J. J., J. L. Bowman, A. E. Banning and B. L. Vasilas. 2013. Effect of tide level and time of day on detection rate and abundance of Clapper Rails (*Rallus longirostris*) in a Mid-Atlantic tidal marsh system. Wetlands 36: 364-368.
- Maley, J. and R. Brumfield. 2013. Mitochondrial and Next-Generation sequence data used to infer phylogenetic relationships and species limits in the Clapper/King Rail complex. Condor 115: 316-329.
- Massey, B. W. and R. Zembal. 1987. Vocalizations of Light-Footed Clapper Rail. Journal of Field Ornithology 58: 32-40.
- Mazerolle, M. J. 2016. AICcmodavg: model selection and multimodal inference based on (Q)AIC(c) v. 2.0-4. R Foundation for Statistical Computing, Vienna, Austria. https://cran.r-project.org/package=AICcmodavg, date accessed 19 April 2017.
- Meanley, B. 1969. Natural history of the King Rail. North American Fauna 67: 1-108.

- Meanley, B. 1985. The marsh hen: a natural history of the Clapper Rail of the Atlantic Coast salt marsh. Tidewater Publishers, Centreville, Maryland.
- Meanley, B. and D. K. Wetherbee. 1962. Ecological notes on mixed populations of King Rails and Clapper Rails in Delaware Bay marshes. Auk 79: 453-457.
- National Oceanic and Atmospheric Administration (NOAA). 2015. NOAA tides and currents. U.S. Department of Commerce, NOAA, Silver Spring, Maryland. http://tidesandcurrents.noaa.gov, date accessed 19 April 2017.
- Paxton, B. J. and B. D. Watts. 2002. Bird surveys of Lee and Hill marshes on the Pamunkey River: possible affects of sea-level rise on marsh bird communities. Center for Conservation Biology Technical Report Series CCBTR-03-04, College of William and Mary, Williamsburg, Virginia.
- Perkins, M., S. King and J. Linscombe. 2010. Effectiveness of capture techniques for rails in emergent marsh and agricultural wetlands. Waterbirds 33: 376-380.
- R Development Core Team. 2013. R: a language and environment for statistical computing v. 3.1.3. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org, date accessed 19 April 2017.
- Reid, F. A., B. Meanley and L. H. Fredrickson. 1994. King Rail. Pages 181-191 in Migratory Shore and Upland Game Bird Management in North America (T. C. Tacha and C. E. Braun, Eds.). Allen Press, Lawrence, Kansas.
- Rempel, R. S., K. A. Hobson, G. Holborn, S. L. van Wilgenburg and J. Elliott. 2005. Bioacoustic monitoring of forest songbirds: interpreter variability and effect of configuration and digital processing methods in the laboratory. Journal of Field Ornithology 76:
- Robertson, E. P. and B. J. Olsen. 2014. Density, sex, and nest stage affect rail broadcast survey results. Journal of Wildlife Management 78: 1293-1301.
- RStudio, Inc. 2015. RStudio: integrated development for R v. 0.98.1028. RStudio, Inc., Boston, Massachusetts. http://www.rstudio.com, accessed 19 April 2017.
- Skaug, H., D. Fournier, A. Nielsen, A. Magnusson and B. Bolker. 2016. Generalized linear mixed models using 'AD Model Builder' v. 0.8.3.3. R Foundation for Statistical Computing, Vienna, Austria. http:// glmmadmb.r-forge.r-project.org, accessed 19 April 2017.
- Spear, L. B., S. B. Terrill, C. Lenihan and P Delevoryas. 1999. Effects of temporal and environmental factors on the probability of detecting California Black Rails. Journal of Field Ornithology 70: 465-480.
- Swiston, K. A. and D. J. Mennill. 2009. Comparison of manual and automated cross-correlation methods for identifying target sounds in continuous audio recordings of Pileated, Pale-billed, and putative Ivorybilled woodpeckers. Journal of Field Ornithology 80: 42-50.
- Tegeler, A. K., M. L. Morrison and J. M. Szewczak. 2012. Using extended-duration audio recordings to survey avian species. Wildlife Society Bulletin 36: 21-29.

- Towsey, M., B. Planitzm, A. Nantes, J. Wimmer and P. Roe. 2012. A toolbox for animal call recognition. Bioacoustics 21: 107-125.
- Venier, L. A., S. B. Holmes, G. W. Holborn, K. A. Mc-Ilwrick and G. Brown. 2012. Evaluation of an automated recording device for monitoring forest birds. Wildlife Society Bulletin 36: 30-39.
- Virginia Department of Game and Inland Fisheries. 2015. Virginia's 2015 wildlife action plan. Unpublished report, Virginia Department of Game and Inland Fisheries, Henrico, Virginia.
- Virginia Institute of Marine Science. 2005. Virginia Estuarine and Coastal Observing System (VECOS) Lower Pamunkey Oligohaline dataflow cruise data. Virginia Institute of Marine Science, Gloucester Point, Virginia. http://web2.vims.edu/vecos, accessed 5 March 2017.
- Waddle, J., T. F. Thigpen and B. M. Glorioso. 2009. Efficacy of automatic vocalization recognition software for anuran monitoring. Herpetological Conservation and Biology 4: 384-388.

- Wiest, W. A. and W. G. Shriver. 2016. Survey frequency and timing affect occupancy and abundance estimates for salt marsh birds. Journal of Wildlife Management 80: 48-56.
- Wilson, M. D., B. D. Watts and D. F. Brinker. 2007. Status review of Chesapeake Bay marsh lands and breeding marsh birds. Waterbirds 30: 122-137.
- Zembal, R. and B. W. Massey. 1983. To catch a Clapper Rail-twice. North American Bird Bander 8: 144-148.
- Zembal, R. and B. W. Massey. 1985. Function of a rail "mystery" call. Auk 102: 179-180.
- Zembal, R. and B. W. Massey. 1987. Seasonality of vocalizations by Light-footed Clapper Rails. Journal of Field Ornithology 58: 41-48.
- Zuur, A. F., E. N. Ieno and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1: 3-14.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York.