

Research Article

Auriel M.V. Fournier*, Doreen C. Mengel, David G. Krementz

Virginia and Yellow Rail autumn migration ecology: synthesis using multiple data sets

<https://doi.org/10.1515/ami-2017-0003>

Received April 15, 2017; accepted August 3, 2017

Abstract: Virginia and Yellow Rails are among the least studied birds in North America, and there is a specific lack of information about their autumn migration ecology and migratory habitat use. We conducted nocturnal surveys across 11 public wetlands in Missouri, USA from 2012–2016, and compared the timing of autumn migration from our surveys with three opportunistic datasets: 1) eBird records, 2) building strikes, and 3) state ornithological records. The observed timing (start and end date and duration) of Virginia Rail autumn migration varied between the opportunistic data and our surveys. Virginia Rail opportunistic data were bimodal, while our surveys had a single peak the second week in October. Yellow Rail autumn migration through Missouri peaked earlier in our surveys than opportunistic datasets which peaked during the second week in October. Both rails were found in moist soil habitats, however Virginia Rails selected perennial vegetation more than was available, while Yellow Rails selected annual plant species. Both species showed no selection for water depth and used shallow flooded wetlands. Understanding the autumn migration period and habitat requirements will allow wetland managers to better manage lands for autumn migrating Virginia and Yellow Rails.

Keywords: Virginia Rail, Yellow Rail, Autumn Migration, eBird, Building Strikes, Phenology, Wetlands, Habitat Use

1 Introduction

Migration is a critical period of the annual cycle for many avian species, yet it is often overlooked because it is difficult to study, and frequently only represents a small portion of the year [1–2]. To conserve migratory species, threats and pressures that operate in all parts of their annual cycle must be studied, including those that may limit the habitats the species use during migration, and consequently affect survival [3–4]. Studying species that have low detection rates, such as rails, which are among the least studied birds in North America, can be especially difficult [5–6]. While the migration ecology of some rails in North America, such as the Sora (*Porzana carolina*) has been studied [5], the Virginia Rail (*Rallus limicola*) and Yellow Rail (*Coturnicops noveboracensis*) (Figure 1) are among the least abundant, and consequently are two of the most poorly known [6–7]. An understanding of rails' habitat selection during migration, including when they use those habitats, is needed before conservation and management efforts can be successful. However, rails' secretive behavior, including cryptic coloration, time spent in dense vegetation, rare daytime flight and infrequent vocalizations, makes them challenging to survey [8–9]. As a result, combining multiple data sources could provide us with a better assessment of the migratory phenology of rails [10].

Opportunistic accounts, rather than formal surveys, provide most of the information on the phenology of rail autumn migration [6,11]. Virginia Rail migration has been described as variable, occurring between late-August and late-October, peaking around 1 October [6,12]. Similarly, Yellow Rails have been recorded from the last week of August through the first week of November with the peak in late September [7]. Opportunistic observations are important sources of information but not sufficient for informing conservation decisions, especially for cryptic species where specific methods (such as call broadcast surveys) are needed to increase odds of detecting an individual when it is present.

*Corresponding author: Auriel M.V. Fournier, Arkansas Cooperative Fish and Wildlife Research Unit, Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701 USA, E-mail: aurielfournier@gmail.com

Auriel M.V. Fournier, Current Address: Mississippi State University, Biloxi, Mississippi 39532 USA

Doreen C. Mengel, Resource Science Division, Missouri Department of Conservation, Columbia, Missouri 65201 USA

David G. Krementz, U.S. Geological Survey, Arkansas Cooperative Fish and Wildlife Research Unit, Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701 USA



Fig. 1. Virginia Rail (*Rallus limicola*, left, photo credit [Auriel Fournier]) and Yellow Rail (*Coturnicops noveboracensis*, right, photo credit [Nick Seeger]) in the hand.

Virginia and Yellow Rails use managed wetlands as autumn migration stopover habitat, but our knowledge of the specific habitat preferences of both species is incomplete. Much of the wetland habitat available as stopover habitat for both species on public land is managed under a moist soil system [13], where soil disturbance and manipulation of water levels are used to set back succession and promote desired plant communities at certain times of year. Current management practices are targeted at migratory waterfowl, and may not meet the needs of migratory waterbirds. Virginia Rail stopover habitat includes dense perennial moist soil plant cover, flooded with 5-10 cm of water [6,11,14-15]. Yellow Rail habitat is less well understood. Previous observations of Yellow Rail habitat found them using sites dominated by perennial wetland cover [16], wet prairie and pastures [17], and shallow flooded emergent wetlands [14]. In the current study our objectives were to more thoroughly document the migratory timing and habitat use of Virginia and Yellow Rails through the central portion of the Mississippi Flyway using a synthesis of our surveys and opportunistic migratory records.

2 Methods

2.1 Migratory phenology

We surveyed managed moist soil wetlands [13] in Missouri, USA from August-October in 2012-2016 with ATV-based

nocturnal spotlight flushing surveys under a distance sampling framework [18]. At each property, we surveyed moist soil wetland impoundments (a wetland surrounded by a levee, with manual water level manipulation; 4.5-300 ha in size; mean = 26.5 ha; Supplementary Table 1). We chose this method because methods developed to increase detection of rails during the breeding season (call broadcast surveys) are not effective during autumn migration since the call rate drops [18]. ATVs were driven along transects, as described in [18] and whenever a rail was observed, either flushing out of the vegetation or on the ground, a point was taken where the bird was first detected. While this method detected thousands of Sora over the five-year project [4], we detected far fewer Virginia and Yellow Rails.

We combined three additional datasets with our own to characterize Virginia and Yellow Rail migration phenology. These additional datasets included observations collected by the Audubon Society of Missouri (Fournier, A.M.V. 2016. The Bluebird Rail Dataset. figshare. doi:10.6084/m9.figshare.2760913.v2), eBird citizen science observations [19], and published data from building strikes [20]. We used observations from these datasets from 1 August through 30 November, and within latitudes 36.5 - 40.5°N in the Mississippi Flyway because these areas represent primarily migratory habitat for both species [5-6] (Figure 2, Table 1). These additional datasets will be referred to as “opportunistic” datasets hereafter. Similar datasets have been used in combination with other data sources to infer migration phenology of other

Table 1. Sample sizes from data sources used to characterize Virginia Rail (*Rallus limicola*) and Yellow Rail (*Coturnicops noveboracensis*) autumn migration in Missouri, USA. The Bluebird is the journal of the Audubon Society of Missouri (Fournier, A.M.V. 2016. The Bluebird Rail Dataset. figshare. doi:10.6084/m9.figshare.2760913.v2). eBird is a citizen science database of birding checklists [19]. Building Strikes are records of either species from building strike monitoring programs [20].

Data Source	Sample Size Yellow Rail	Sample Size Virginia Rail	Years Represented	Median Migration Date Yellow Rail	Median Migration Date Virginia Rail
Audubon Society of Missouri	20	20	1963-2016	Oct 11	Sept 30
eBird	53	261	2000-2015	Oct 12	Sept 13
Building Strikes	1	3	1973-2010	Oct 24	Oct 15
Our Study (total)	64	97	2012-2016	Sept 30	Oct 1
Our Study (2012)	34	33	2012	Sept 25	Sept 23
Our Study (2013)	4	26	2013	Oct 11	Oct 9
Our Study (2014)	1	14	2014	Sept 30	Oct 5
Our Study (2015)	12	7	2015	Oct 9	Oct 17
Our Study (2016)	13	17	2016	Oct 10	Oct 2

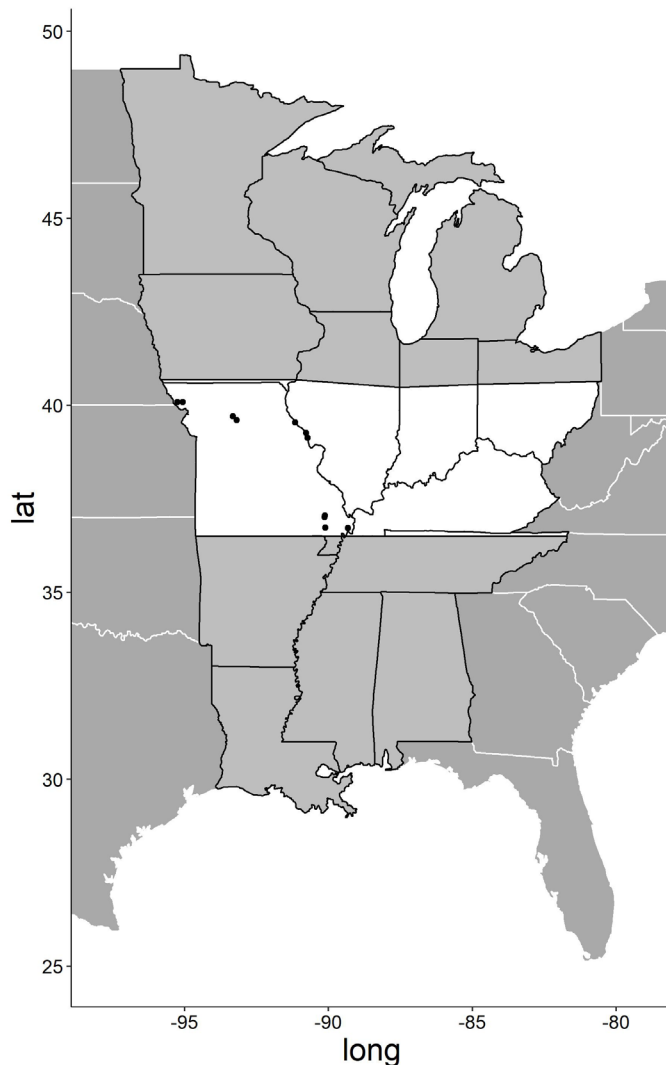


Fig. 2. Area of the Mississippi Flyway (light grey, black outline) where opportunistic observations of Yellow Rail (*Coturnicops noveboracensis*) and Virginia Rail (*Rallus limicola*) during autumn migration were collected (white with black outline). Black points in the state of Missouri represent the study sites our data were collected on.

bird species [10]. Each data set used has inherent biases; for example, the Audubon Society of Missouri and eBird data represent ‘presence only’ information collected by birders, who are not evenly spread over space or time. The building strike dataset could also be biased if cities attract or repel rails during migration, but whether either is the case is unknown. While we recognize these biases, these opportunistic datasets are our only source of comparisons for our data. Our results should be less biased because our data were collected under a statistically-based protocol on the same sites over several years. We compiled records into one data set, which we refer to hereafter as opportunistic observations. We compared median date of migration among our surveys and the opportunistic observations with a Mann-Whitney test. We compared the distribution of observations using a Kolmogorov-Smirnoff non-parametric test.

2.2 Habitat selection

We collected habitat data, the day after surveys, at 5 random plots for every one plot where a Virginia or Yellow Rail was detected during our standardized surveys. The random plots were within the same impoundment where the Virginia or Yellow Rail was detected. We used a ratio of 5 to 1 available-to-used points because this is considered adequate to reduce bias and ensure convergence of parameter estimates [21]. In each 25 m-diameter plot, we recorded the mean of five water depths (cm) measured at the center of each plot and 5 m from the center in each cardinal direction. We visually estimated the percent cover (to 1%) of annual moist soil plants, perennial moist soil plants, and upland vegetation in the plot [22-23]. Annual moist soil plants include species that fall below the water surface at the end of the growing season such as annual smartweeds (*Polygonum* spp.) and millets [24] (*Echinochloa* spp.). Perennial moist soil plant species persist above the water surface at the end of the growing season, and include perennial smartweeds (*Polygonum* spp.), bulrush (*Schoenoplectus* spp.) and cattails (*Typha* spp.) [24]. We measured these variables because they have been found to be important to migrating rails [6, 7, 11, 14-16].

We had too few detections for distance sampling or occupancy modelling to be effective for Virginia and Yellow Rails, so we used counts of individuals in our analyses of habitat preferences. While this approach does not take into account detection probability, we did not have sufficient data to do so. We analyzed the differences in habitat variables between used and available points for each species separately using resource selection

functions in the R package ‘ResourceSelection’ [25-26] (package version 0.2-6, R version 3.3.1), which followed the functions described in [25-26]. For Virginia Rails, we included annual moist soil vegetation, perennial moist soil vegetation and average water depth in our model. For Yellow Rails, we included the same covariates as Virginia Rail as well as upland vegetation because Yellow Rails are often characterized as a wet prairie species [17]. We assessed model fit using the Hosmer and Lemeshow goodness of fit test [28].

3 Results

3.1 Migratory phenology

We detected 97 Virginia Rails during 1049 hours of surveying during autumn 2012-2016 (range: 16 August-23 October). Opportunistic observations of Virginia Rails occurred between 1 August-26 November ($n=284$, Table 1, Supplementary Figure 1, Supplementary Table 2). Our observations overlapped with the Birds of North America account but have a slightly wider window of migration [6]. The distribution of Virginia Rail detections clearly differed between our surveys and opportunistic data (Kolmogorov-Smirnoff Test, $D = 0.37$, $p < 0.001$), with a single peak in our surveys compared to two peaks in the opportunistic data. The median date from survey data also was later than that of opportunistic data (median date vs. median date, respectively) (Mann Whitney, $U = 12692$, $p < 0.001$).

We detected 64 Yellow Rails during 1049 hours of surveying during autumn 2012-2016 (range: 22 August-23 October). Yellow Rails were reported in opportunistic observations between 27 August and 6 November ($n=74$, Table 1, Supplementary Figure 1, Supplementary Table 2). Our surveys and the opportunistic observations were coincident with the Birds of North America account range of migration ([7], Figure 3). The median date of Yellow Rails was 12 days earlier (Mann Whitney, $U = 3808.5$, $p < 0.001$) than that of opportunistic data, which contributed to the difference in distribution of detections (Kolmogorov-Smirnoff Test, $D = 0.35$, $p < 0.001$).

3.2 Habitat selection

Virginia Rails selected sites with greater perennial moist soil vegetation cover than were available and did not select sites with water depths or percent annual moist soil vegetation cover different than available (Table 2, Figure 4, Supplementary Data I and II). Yellow Rails

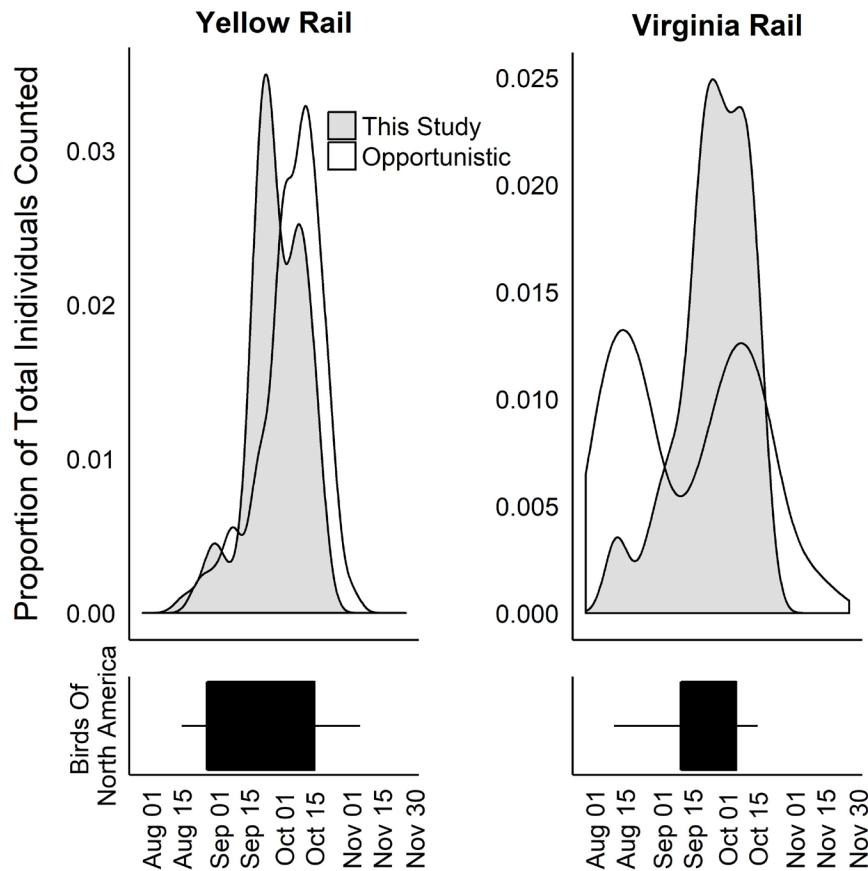


Fig. 3. Distribution of observations of Yellow Rail (*Coturnicops noveboracensis*) and Virginia Rail (*Rallus limicola*) during autumn migration comparing our data, opportunistic data points and the range reported in Birds of North America.

Table 2. Beta estimates and p-values from resource selection functions to explain habitat selection of Virginia Rail (*Rallus limicola*) and Yellow Rail (*Coturnicops noveboracensis*) during migration in Missouri, USA.

Species	Variable	β Estimate	Standard Error	P-value
Virginia Rail	Annual Moist Soil Vegetation	0.008	0.004	0.080
	Perennial Moist Soil Vegetation	0.011	0.006	<0.001
	Mean Water Depth	0.008	0.011	0.442
Yellow Rail	Annual Moist Soil Vegetation	0.023	0.005	<0.001
	Perennial Moist Soil Vegetation	0.006	0.012	0.652
	Mean Water Depth	-0.023	0.011	0.083
	Upland Vegetation	0.012	0.007	0.062

selected sites with greater annual moist soil vegetation than what was available and did not select sites with water depths different or percent cover of upland or perennial moist soil vegetation than were available (Table 2, Figure 4, Supplementary Data I and III). The Virginia Rail model fit the data ($\chi^2 = 7.336$, $df = 8$, $p = 0.50$) as did the Yellow Rail model ($\chi^2 = 11.2$, $df = 8$, $p = 0.19$).

4 Discussion

Our survey results for Virginia Rail showed its migration contained a single later peak when compared to the two peaked wider distribution of opportunistic records (Figure 3). Meanwhile, the entire migration period for Virginia Rail was shorter than that of the Sora (11 August

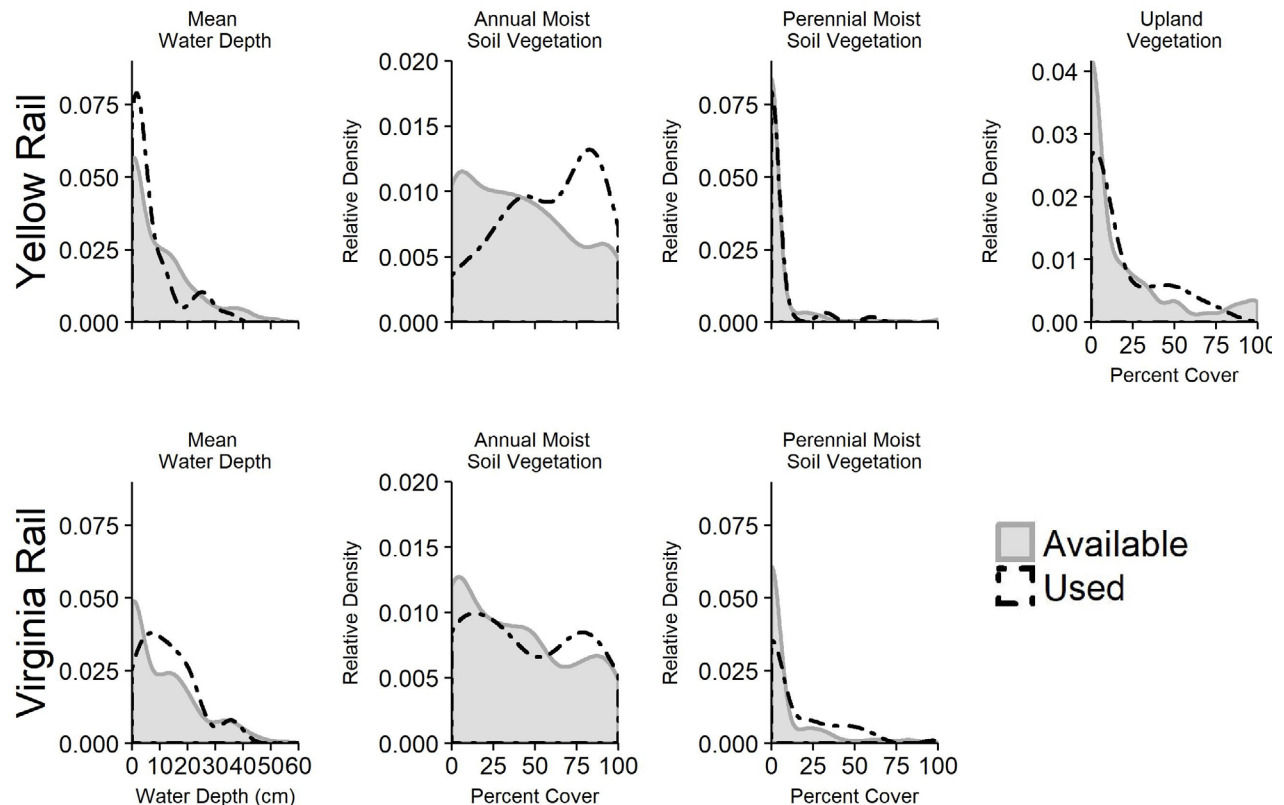


Fig. 4. Distribution of used vs available habitat variables for Yellow Rail (*Coturnicops noveboracensis*) and Virginia Rail (*Rallus limicola*) during autumn migration in Missouri, USA

to 27 October, median September 23 [4]), and Virginia Rails were less abundant during concurrent surveys (~8000 Sora and 97 Virginia Rails; [4]). These differences in abundance led us to speculate as to the effectiveness of our survey method at detecting Virginia Rails. Previous researchers [12] found walk-in traps captured ~10% as many Virginia Rails as Sora, and hypothesized their traps were positioned where the mean water level was too deep for Virginia Rails. We surveyed wetlands that spanned from dry to 50 cm water depth, so we doubt water depth influenced our ability to detect Virginia Rails. We assessed this concern using radio-tagged Sora, and found that marked Sora did not run away from the approaching ATV [18] but future study is needed to understand the behavioral reaction of Virginia Rails to approaching ATVs at night using radio-marked birds. Because there are no formal population estimates for Virginia Rails and Sora we are unable to further infer differences between species abundances in our counts.

Our survey results for Yellow Rails showed an earlier peak in migration than that seen in opportunistic records, though the range of both was in line with the published literature [7]. Yellow Rails have a broad migratory period,

which is shorter than Sora [4]. We observed many fewer individual Yellow Rails than Sora, though again the lack of formal population estimates limits our comparisons of these counts. Further, additional work is needed to understand how Yellow Rails react to our survey method. More importantly, Yellow and Virginia Rails are migrating earlier than most waterfowl, suggesting traditional waterfowl management may not meet the needs of rails because waterfowl habitat management is timed for later in the fall.

We found Virginia Rails selected for perennial moist soil plant habitat, including perennial *Polygonum* and *Eleocharis* spp., which is in line with previous work [14]. Virginia Rail water depth selection has varied in previous research findings with median values ranging from 2.4 to 19 cm [11, 14-15]. We did not find that Virginia Rails selected for water depths different than were available, but we note that available water depths in our study wetlands were similar to the range of values reported in other studies.

We found Yellow Rails in shallow flooded stands of annual moist soil plants, which may differ from previous work since perennial moist soil plants were less abundant within the wetlands we surveyed (which were dominated

by annual moist soil vegetation). Previous work described the area where Yellow Rails were found as shallow flooded (~4cm, range 0-11cm) wetlands with high percent cover of perennial moist soil plants such as *Panicum* and *Cyperus* spp. [14,16]. Overall, our results are similar to previous work which characterized Yellow Rail habitat as shallow flooded, densely vegetated, wetlands and wet prairies; the results differ in the plant community making up the dense vegetation [17, 29-30]. Previous researchers [11] suggested “rails probably selected habitat because of water conditions and vegetation structure rather than species composition” which supports our findings as well.

Understanding species' habitat selection during autumn migration is vital to understanding how migration impacts demography [4,31]. Future work in this area should consider the landscape around each wetland, and the degree of wetland isolation on the landscape, as these have been found to be important during the breeding season for rails and during migration for shorebirds [32-33]. Our study provides missing information that can be used to implement direct conservation and management actions, namely the active flooding of wetlands, in a way that maximizes the benefit to migratory waterbirds, including rails. While closely related species are often described as having similar characteristics, we show here that these two rails have different habitat needs than each other and different migratory timing than each other and Sora [18]. Understanding these differences is vital to the conservation and management of all rails as well as their wetland communities.

Acknowledgements: Our research was funded by the U.S. Fish and Wildlife Service, the Missouri Department of Conservation, the U.S. Geological Survey Arkansas Cooperative Fish and Wildlife Research Unit, and the University of Arkansas. We would like to thank K. Ackley, C. Alger, R. Bell, M. Bowyer, K. Brunke, G. Calvert, C. Chambers, K. Cordell, C. Crisler, C. Freeman, M. Flaspohler, R. Kelly, L. Landowski, J. Hager, M. Hanan, M. Marks, F. Nelson, B. Pendley, A. Raedeke, D. Welchert, S. Whitson, and J. Wilson for help in coordinating field work and site access. Special thanks to M. Boone, L. Brinkman, D. Datlof, J. Fournier, J. Lehman, H. Pavisich and N. Seeger for their diligent work in the field collecting data. Research completed under University of Arkansas IACUC #15049 and #15023 and state and federal property special use permits. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

- [1] Webster M.S., and Marra P.P., The Importance of Understanding Migratory Connectivity and Seasonal Interactions, Pages 199–209 in R. Greenberg and Marra, editors. *Birds in Two Worlds: The Ecology and Evolution of Migration*, The Johns Hopkins University Press, Baltimore, Maryland, USA, 2005.
- [2] Webster M.S., Marra P.P., Haig S.M., Bensch S., and Holmes R.T. Links Between Worlds: Unraveling Migratory Connectivity, *Trends Ecol Evol*, 2002, 17, 76–83.
- [3] Hostetler J.A., Sillett T.S., and Marra P.P. Full-Annual-Cycle Population Models for Migratory Birds, *Auk*, 2015, 132, 433–449.
- [4] Marra P.P., Cohen E.B., Loss S.R., Rutter J.E., and Tonra C.M. A Call for Full Annual Cycle Research in Animal Ecology, *Biol Lett*, 2015, 11, 2015.0552.
- [5] Fournier A.M.V., Mengel D.C., Gbur E.E., and Krementz D.G. 2017. The Timing of Autumn Sora (*Porzana carolina*) Migration, *Wilson J Ornith*. 129
- [6] Conway C. J. Virginia Rail, Page 173 in. *The Birds of North America*. Ithaca: Cornell Laboratory of Ornithology, 1995.
- [7] Bookhout T. A. Yellow Rail, Page 139 in. *The Birds of North America*. Ithaca: Cornell Laboratory of Ornithology, 2015.
- [8] Nadeau C.P., Conway C.J., Smith B.S., Lewis T.E. Maximizing Detection Probability of Wetland-Dependent Birds During Point-Count Surveys in Northwestern Florida, *Wilson J Ornithol*, 2008, 120, 513-518.
- [9] Conway C.J., and Nadeau C.P. Effects of Broadcasting Conspecific and Heterospecific Calls on Detection of Marsh Birds in North America, *Wetlands*, 2010, 30, 358–368.
- [10] Bond A.L., and Lavers J.A. Flesh-footed Shearwaters (*Puffinus carneipes*) in the Northeastern Pacific Ocean: Summary and Synthesis of Records from Canada and Alaska, *Can Field Natur*, 2015, 129, 263–267.
- [11] Rundle W.D., and Fredrickson L.H. Managing Seasonally Flooded Impoundments for Migrant Rails and Shorebirds, *Wildl Soc Bull*, 1981, 9, 80–87.
- [12] Haramis G.M., and Kearns G.D. Soras in Tidal Marsh: Banding and Telemetry Studies on the Patuxent River, Maryland, *Waterbirds*, 2007, 30 Special Issue, 105–121.
- [13] Strader R.W., and Stinson P.H. 2005. Moist-Soil Management Guidelines for The U.S. Fish and Wildlife Service Southeast Region. U.S. Fish and Wildlife Service Southeast Region, Jackson, Mississippi, USA.
- [14] Reid F.A. Differential Habitat Use by Waterbirds In a Managed Wetland Complex, PhD Thesis, University of Missouri-Columbia, Missouri, USA, 1989.
- [15] Sayre M.W., and Rundle W.D. Comparison of Habitat Use by Migrant Soras and Virginia Rails, *J Wildl Manage*, 1984, 48, 599–605.
- [16] Butler C. J., Pham L.H., Stinedurf J.N., Roy C.L., Judd E.L., Burgess N.J., and Caddell G.M. Yellow Rails Wintering in Oklahoma, *Wilson J Ornith*, 2010, 122, 385–387.
- [17] Jacobs B. Birds of Missouri, Jefferson City, MO. 2001.
- [18] Fournier A.M.V., and Krementz D.G. Nocturnal Distance Sampling All-Terrain Vehicle Surveys for Non-Breeding Rails, *Wildl Soc Bull*, 2017, 41, 151-156

- [19] Sullivan B.L., Wood C.L., Iliff M.J., Bonney R.E, Fink D., and Kelling S. eBird: A Citizen-based Bird Observation Network in the Biological Sciences, *Bio Cons*, 2009, 142, 2282–2292.
- [20] Loss S.R., Will T, Marra P.P., Loss S.S., and Marra P.P. Bird–Building Collisions in the United States: Estimates of Annual Mortality and Species Vulnerability, *Condor*, 2014, 116, 8–23.
- [21] Northrup J.M., Hooten M.B., Anderson C.R. Wittenmyer, G. 2013 Practical Guidance on Characterizing Availability in Resource Selection Functions Under a Use–Availability Design, *Ecology*, 2013, 94, 1456–1463.
- [22] Darrah A. J., and Kremenz D.G. Occupancy and Habitat Use of The Least Bittern and Pied- Billed Grebe in The Illinois And Upper Mississippi River Valleys, *Waterbirds*, 2010, 33, 367–375.
- [23] Darrah A. J., and Kremenz D.G. Habitat Use of Nesting and Brood-rearing King Rails in the Illinois and Upper Mississippi River Valleys, *Waterbirds*, 2011, 34, 160–167.
- [24] Cowardin L. M., Carter V., Golet F.C., and Laroe E.T. Classification of Wetlands and Deepwater Habitats of the United States, Biological Services Program, 1979.
- [25] Lele S.R., Keim J.L., and Solymos P. ResourceSelection: Resource Selection (Probability) Functions for Use-Availability Data, 2016.
- [26] Lele S.R. A New Method for Estimation of Resource Selection Probability Function, *J Wildl Manage*, 2009, 73, 122–127.
- [27] R Core Team, R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. 2016.
- [28] Lele S.R., and Keim J.L. Weighted Distributions and Estimation of Resources Selection Probability Functions, *Ecology*, 2006, 87, 3021–3028.
- [29] Robert M., Cloutier L., and Laporte P. The Summer Diet of the Yellow Rail in Southern Quebec, *Wilson Bull*, 1997, 109, 702–710.
- [30] Robert M., Jobin B., Shaffer F., Robillard L., Gagnon B., Obert M.I.R., Obin B.E.J., and Haffer F.R.S. Yellow Rail Distribution and Numbers in Southern James Bay, Quebec, Canada, *Waterbirds*, 2004, 27, 282–288.
- [31] Sheehy J., Taylor C.M., and Norris D.R. The Importance of Stopover Habitat for Developing Effective Conservation Strategies for Migratory Animals, *J Ornith*, 2011, 152, 161–168.
- [32] Brown M., and Dinsmore J.J. Implications of Marsh Size and Isolation for Marsh Bird Management, *J Wildl Manage*, 1986, 50, 392–397.
- [33] Albanese G., and Davis C.A. Characteristics Within and Around Stopover Wetlands Used by Migratory Shorebirds: Is the Neighborhood Important? *Condor*, 2015, 117, 328–340.

Supplemental Material: The online version of this article

(DOI: 10.1515/ami-2017-0003) offers supplementary material.

Files for Supplemental Tables 1 and 2, plus Supplemental Data files 1, 2, and 3 are online at <https://doi.org/10.6084/m9.figshare.c.3849274.v1>