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Satellite transmitters reveal previously unknown migratory behavior and wintering locations of Yuma Ridgway's Rails

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ABSTRACT. Preventing or reversing population declines of rare species often requires an understanding of their complete annual life cycle, but this information is lacking for many species. Such has been the case for Yuma Ridgway's Rails (*Rallus obsoletus yumanensis*), a federally endangered marsh bird endemic to the Lower Colorado River Basin and Salton Sink in California, Arizona, Nevada, and Mexico. Yuma Ridgway's Rails have been considered non-migratory, but incidental mortalities at solar facilities > 50 km from any rail habitat called this assumption into question. We attached transmitters to 89 Yuma Ridgway's Rails during the summers of 2017 to 2019 and documented the migratory movements of 23 rails, including three adult male Yuma Ridgway's Rails with breeding territories in the United States that wintered in Mexico and returned to the United States the following year. The rails flew > 900 km in the fall to mangrove wetlands along the coast of Sonora and Sinaloa, Mexico, and returned to their breeding areas in the United States the following breeding season. Of the rails in our study, 40.0% (20 of 50) of adults and 21.4% (3 of 14) of juveniles initiated fall migratory movements. Our results invalidate existing paradigms about Yuma Ridgway's Rails by demonstrating that not all individuals remain in their breeding areas throughout the year. Instead, some migrate long distances over inhospitable terrain to reach wintering areas that, in some cases, are in wetland types different from those in their breeding territories. Our results provide actionable data to expand conservation strategies to better account for the annual life cycle of this endangered species and highlight the need for United States-Mexico cooperation, given the regular migration of this rare bird between the two countries.

RESUMEN. **Transmisores satelitales revelan comportamientos migratorios previamente desconocidos y ubicaciones invernales de *Rallus obsoletus yumanensis***

Prevenir o revertir la disminución de la población de especies raras a menudo requiere una comprensión de su ciclo de vida anual completo, pero esta información no existe para muchas especies. Este ha sido el caso para el ralido de Yuma Ridgway's (*Rallus obsoletus yumanensis*), un ave de pantano en peligro de extinción a nivel federal y endémico de la cuenca del río Colorado y la depresión de Salton en California, Arizona, Nevada y México. El ralido de Yuma Ridgway's se han considerado como no migratorio, pero la mortalidad incidental en instalaciones solares > 50 km de cualquier hábitat de los ralidos puso en duda esta suposición. Colocamos transmisores en 89 Ralidos de Yuma Ridgway desde el 2017 al 2019 y documentamos los movimientos migratorios en 23 ralidos, incluidos tres machos adultos de ralidos de Yuma Ridgway con territorios reproductivos en los Estados Unidos que pasaron el invierno en México y regresaron a los Estados Unidos al año siguiente. Los ralidos volaron > 900 km en el otoño a los pantanos de manglares ubicados a lo largo de la costa de Sonora y Sinaloa, México, y regresaron a sus áreas de reproducción en los Estados Unidos la siguiente temporada reproductiva. De los ralidos en nuestro estudio, el 40.0% (20 de 50) de los adultos y el 21.4% (3 de 14) de los juveniles iniciaron movimientos migratorios durante el otoño. Nuestros resultados no respaldan el paradigma existente sobre los ralidos de Yuma Ridgway, al demostrar que no todos los individuos permanecen en sus áreas de reproducción durante todo el año. Por el contrario, algunos migran largas distancias sobre terrenos inhóspitos para llegar a áreas de invernada que en algunos casos se encuentran en humedales de diferentes características a los de sus territorios de reproducción. Nuestros resultados proporcionan datos para tomar rápidas acciones que puedan expandir las estrategias de conservación teniendo en cuenta el ciclo de vida anual de esta especie en peligro de extinción y resaltar la necesidad de la cooperación entre Estados Unidos y México, dada la migración regular de esta rara ave entre los dos países.

Key words: Gulf of California, Lower Colorado River, life cycle conservation, mangrove wetlands, *Rallus obsoletus yumanensis*, secretive marsh birds, Yuma Clapper Rail

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Understanding annual life cycles of imperiled species is imperative for effective conservation. However, most field studies of vertebrate ecology occur during breeding seasons (Marra et al. 2015) and this seasonal bias hinders our ability to develop effective conservation strategies (Faaborg et al. 2010b, Runge et al. 2014). Knowledge of annual life cycles is especially important for managing and conserving migratory or mobile species. For example, the cause of population declines in Swainson's Hawks (*Buteo swainsoni*) measured on their breeding areas in North America puzzled researchers until studies revealed large-scale mortalities in their wintering areas due to an insecticide (Woodbridge et al. 1995, Goldstein et al. 1999). Conservation strategies that fail to address threats across an animal's full annual life cycle may be ineffective and waste valuable resources.

Annual life cycles of some species are well documented, thereby allowing researchers to identify important stressors and allocate resources to pressing conservation issues. For example, the flyway concept was developed to coordinate conservation and management efforts for migratory waterfowl in North America (Boere and Stroud 2006, Faaborg et al. 2010a). The flyway concept is a rare example of using life-history information and movement data to inform management strategies for mobile species and has been replicated for waterfowl globally (Kirby et al. 2008, Catry et al. 2012). However, this approach to management of mobile species is possible only if annual life cycles are well understood. Advances in technology and analytical methods have facilitated studies of the annual movements and behaviors of mobile species (Runge et al. 2014, Marra et al. 2015). Indeed, genetic analyses in conjunction with isotopic assignments revealed the frequency of long-distance dispersal events of California Black Rails (*Laterallus jamaicensis coturniculus*; Hall and Beissinger 2017). Furthermore, miniaturization of tracking technologies has allowed researchers to document annual movements of an increasing diversity of species (e.g., Hewson et al. 2016, Larkin et al. 2017).

Tracking animals throughout their annual life cycle remains difficult (Faaborg et al. 2010b, Runge et al. 2014, Marra et al. 2015). As a result, life cycles of many species remain poorly documented, particularly species that are rare, cryptic, or use less accessible habitats (e.g., Weller et al. 2016, Casale et al. 2018, Soehren et al. 2018). Federally endangered Yuma Ridgway's Rails (*Rallus obsoletus yumanensis*) are an example of a rare bird of high conservation concern (Conway and Eddleman 2000) with a poorly understood annual life cycle. Yuma Ridgway's Rails inhabit emergent wetlands throughout the Lower Colorado River Basin and Salton Sink in California, Arizona, Nevada, and Mexico (Conway and Eddleman 2000, Eddleman and Conway 2020, Stevens and Conway 2020, Harrity et al. 2020). Emergent wetlands within the limited geographic range of this rail are fragmented and embedded in a landscape dominated by desert, human development, and agriculture, i.e., a landscape that is mostly inhospitable to rails. Moreover, Yuma Ridgway's Rails are difficult to study because of their furtive nature and difficult-to-access habitat (Perkins et al. 2010, Conway 2011, Harrity and Conway 2020). As such, basic natural history questions remain unanswered and effective conservation strategies remain elusive (Eddleman and Conway 2020).

Yuma Ridgway's Rails have been considered non-migratory because conventional telemetry studies in the 1980s documented rails that maintained small annual home ranges and rarely, if ever, left the marsh vegetation (Eddleman 1989, Conway 1990, Conway et al. 1993). As such, management and conservation strategies have largely centered on protecting and maintaining early successional emergent marshes where the rails occur (U.S. Fish and Wildlife Service 2010, Conway et al. 2010). Incidental mortalities of Yuma Ridgway's Rails at solar facilities in desert environments far from any emergent wetlands (Kagan et al. 2014) and scattered reports of vagrant rails in unexpected areas (Cooper 2011) have challenged this paradigm and suggest that these rails leave their breeding marshes more than previously thought. However, whether these reports represented erratic dispersal movements or more predictable migratory movements was not known. Regardless of the nature of the movements, the reports highlighted deficiencies in current conservation strategies and identified a need for further research on the annual life cycle of this endangered bird. We equipped

Yuma Ridgway's Rails with solar-powered satellite transmitters to document annual movements. Specifically, we sought to determine the frequency of seasonal movements away from breeding marshes, the nature of those movements (i.e., migration or dispersal), and the phenology and destinations of the movements.

METHODS

We attached satellite transmitters to Yuma Ridgway's Rails at 13 study sites spanning their geographic range and representing all major extant populations. Study sites were located in (1) Imperial County, California, USA, (2) Yuma, Maricopa, La Paz, and Mojave counties, Arizona, USA, (3) Nye and Clark counties, Nevada, USA, and (4) the municipality of Mexicali in Baja California and the municipality of San Luis Río Colorado in Sonora, Mexico (Fig. 1). Study site elevations ranged from −69 m at Sonny Bono Salton Sea National Wildlife Refuge in California to 684 m at Ash Meadows National Wildlife Refuge in Nevada. Southern cattail (*Typha domingensis*) was the dominant emergent plant in most wetlands, but other emergent wetland plants included chairmaker's bulrush (*Schoenoplectus americanus*), California bulrush (*S. californicus*), common reed (*Phragmites australis*), salt cedar (*Tamarix ramosissima*), and alkali bulrush (*Bolboscheonus maritimis*). Wetland condition and management status varied across our study sites, ranging from small managed wetland parcels with tightly regulated water levels (e.g., managed wetlands at Imperial National Wildlife Refuge near Yuma, Arizona) to isolated wetlands located in dense suburban developments (e.g., marshes near Phoenix, Arizona) and expansive wetlands fed with agricultural drainage water (e.g., La Cienega de Santa Clara, Sonora, Mexico, and Salton Sea, California).

We used solar-powered satellite transmitters to document annual movements of Yuma Ridgway's Rails because we did not know either the timing and frequency of movements or their destinations. Hence, we needed transmitters that would transfer data remotely, regardless of when or where the birds moved. We used 6-g solar Argos PinPoint transmitters (Lotek Wireless, Inc., Wareham, UK) and 5-g solar satellite PTTs (Microwave Telemetry, Inc., Colombia, MD, USA). Transmitters made by both manufacturers were solar-powered, collected location data on a user-defined schedule, and transferred data to an online server via the Argos satellite network, thus allowing remote access to location data. We only attached transmitters to rails large enough so that transmitters represented $\leq 3\%$ of total body mass. We used a back-pack harness (Sutherland et al. 2004) and made harnesses with 2.5-mm Spectra ribbon (Bally Ribbon Mills, Bally, PA, USA) and crimp tubes. We captured Yuma Ridgway's Rails with modified drop-door traps (Conway et al. 1993, Bui et al. 2015), mist-nets, and noose carpets (Harrity and Conway 2020).

Solar satellite PTTs generate location data via the Doppler effect and thus achieve a maximum location accuracy of $\pm$ 100 m. Locations are assigned to accuracy classes and we used only PTT locations with < 500-m error in our analyses. We programmed the solar satellite PTTs to transmit data for 10 h followed by a 48-h off period (during which time transmitters recharge). Solar Argos PinPoint transmitters collect GPS locations that are more precise than locations generated from the Doppler effect. We programmed solar Argos PinPoint transmitters to collect one location every 11 to 25 h, depending on season and year. We calculated migration distances by measuring the Euclidean distance between location points (excluding movements within breeding areas and stopover sites). Because 20 km was the maximum distance we observed a rail moving during the summer, we considered any rail that moved > 20 km south of its capture site in the fall to have initiated migration. We defined the duration of migration as the number of days from initial departure to the first day at the minimum latitude location. We estimated migration departure dates as the day before the first location more than 20 km from the breeding (or wintering) areas. We estimated time of day of departure from breeding areas, wintering areas, and stopover sites as diurnal or nocturnal if we had multiple locations within 24 h of departure. Five of 23 (21.7%) transmitters failed to transmit location data for $\geq$ 1 week during migration due to weak batteries and we could not estimate departure dates of those rails. We defined a stopover

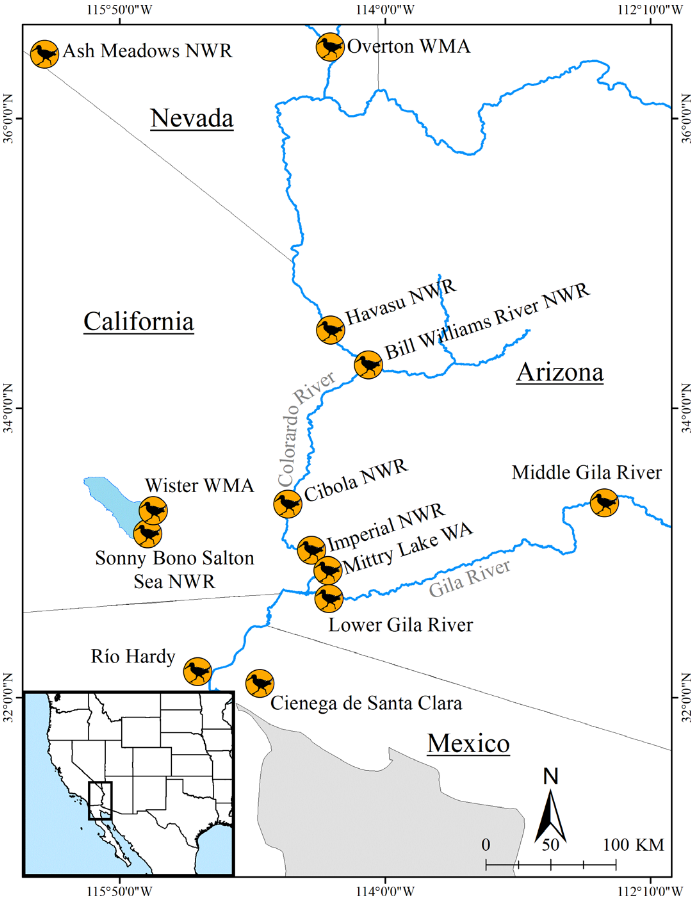

Fig. 1. Location of 13 study sites throughout the breeding range of Yuma Ridgway's Rails. NWR = National Wildlife Refuge, WA = Wildlife Area, and WMA = Wildlife Management Area. [Colour figure can be viewed at wileyonlinelibrary.com]

site as any location where a rail spent ≥ 12 h during migration. We examined high-resolution satellite imagery on Google Earth to determine the dominant vegetation community or land use of each stopover location. We estimated the proportion of rails that migrated from the number of individuals that were alive and transmitting data in October of a given year (4 October was the average date of fall departure in our study). We used Pearson's chi-squared test to determine if the proportion of migrating rails differed by sex or study area, and used *t*-tests to determine if migration parameters differed by sex. We used linear regression to assess the relationship between study site, latitude, and the proportion of rails that migrated. Finally, we grouped the 13 study sites into six geographic areas for analyses, including Nevada, Upper Colorado River, Lower Colorado River, Colorado River Delta, Salton Sea, and Middle Gila River. All analyses were performed in R (R Core Team 2019). Values are presented as means ± SE.

RESULTS

We attached transmitters to 89 Yuma Ridgway's Rails (Table S1) during the summers of 2017–2019. We documented the migratory movements of 23 rails, including 10 that moved to Mexico from breeding areas in the United States, eight that moved south from their breeding areas in the United States, but remained north of the United States-Mexico border, and five that moved south from the Colorado River Delta in Mexico to estuaries further south along the west coast of mainland Mexico (Fig. 2, Table 1). Moreover, we documented complete migrations by three adult male Yuma Ridgway's Rails. These rails flew > 900 km in the fall to mangrove wetlands along the west coast of Sonora and Sinaloa, Mexico, and returned to their breeding areas in freshwater marshes in the United States the following breeding season. One rail returned to within 200 m of its original capture location, whereas two returned to marshes 32 km and 29 km, respectively, from their original capture locations (i.e., breeding dispersal of ≥ 29 km; Fig. S1). The remaining 20 rails that migrated either died during migration ($N = 14$) or their transmitters stopped transmitting data after reaching their wintering areas ($N = 6$).

All 66 rails that did not migrate remained near their original capture sites through the fall. We suspect that 25 of these rails were predated, either based on recovery of transmitters and carcasses or based on transmitter activity (e.g., transmitters that moved abruptly to desert upland adjacent to a marsh area and continued to transmit data without moving were assumed to indicate that rails had been predated). In addition, 35 transmitters stopped transmitting data from four to 12 months after deployment while rails were still active so we could not infer their fate. Six rails have remained active near their original capture locations.

We found that 40.0% (20 of 50) of adult rails and 21.4% (3 of 14) of juvenile rails that were alive in October initiated migratory movements in the fall. We documented no difference between sexes in migratory tendency ($\chi^2_1 < 0.1$, $P = 1$), with 35.0% (7 of 20) of females and 35.9% (14 of 39) of males initiating migration in the fall (numbers include both adults and juveniles of known sex). However, the proportion of Yuma Ridgway's Rails that migrated varied among study areas ($\chi^2_5 = 18.5$, $P = 0.002$). For example, 75.0% of rails that were alive in October at sites on the Upper Colorado River (Havasu and Bill Williams River National Wildlife Refuges) moved south, whereas 50.0% of rails from the Middle Gila River, 38.1% of rails from the Lower Colorado River, 63.0% of rails from the Colorado River Delta, and no rails around the Salton Sea initiated fall migratory movements (Table 1). Study area latitude had no effect on the proportion of rails that migrated ($F_{1,4} = 0.7$, $P = 0.40$). All rails that completed fall migration (regardless of starting location), wintered along the west coast of Mexico in the states of Sonora or Sinaloa. Wintering locations included mangrove wetlands and saltgrass estuaries, and the lowest wintering latitude of a rail was 25.655 (Fig. 2).

On average, rails initiated fall migration on 4 October ± 3.9 d across all three years. Departure date did not differ either between the sexes ($t_{14.2} = 0.4$, $P = 0.67$) or age classes ($t_{2.2} = 0.1$, $P = 0.92$). Average distance of fall migration was 368.3 ± 71.4 km if we include all southward movements > 20 km. However, if we exclude 14 rails that disappeared or died while moving south, average fall migration distance was 619.4 ± 112.6 km. The longest continuous flight without stops by a migrating rail was 390 km and the maximum flight speed achieved by a rail during migration was 73.7 km/h. Average duration of fall migration for those birds that completed fall migration (and for which we have precise estimates of departure dates) was 12.7 ± 4.7 d. Yuma Ridgway's Rails made an average of 2.6 ± 0.5 stopovers during fall migration (Table 2). We tallied 60 stopover events by 18 rails during fall and spring migration from 2017 to 2020. Rails stopped most frequently in sparse desert vegetation (e.g., dry arroyos with scattered creosote (*Larrea tridentata*), mesquite (*Prosopis* spp.), and other desert upland vegetation) during migration, but agricultural fields, coastal wetlands, irrigation canals, and water impoundments were also common stopover locations (Fig. 3, Table 3).

We documented spring migration by three adult male Yuma Ridgway's Rails (two from Middle Gila River and one from Havasu National Wildlife Refuge). Average spring departure was 22 April ± 2.6 d. Two rails completed spring migration in ≤ 5 d, whereas the third rail spent 48 d migrating north (Table 2). Each rail followed similar routes during their respective fall and spring migrations (Fig. 2). For example, one adult rail stopped in agricultural fields < 2.5-km apart in Maricopa, Arizona, during both fall and

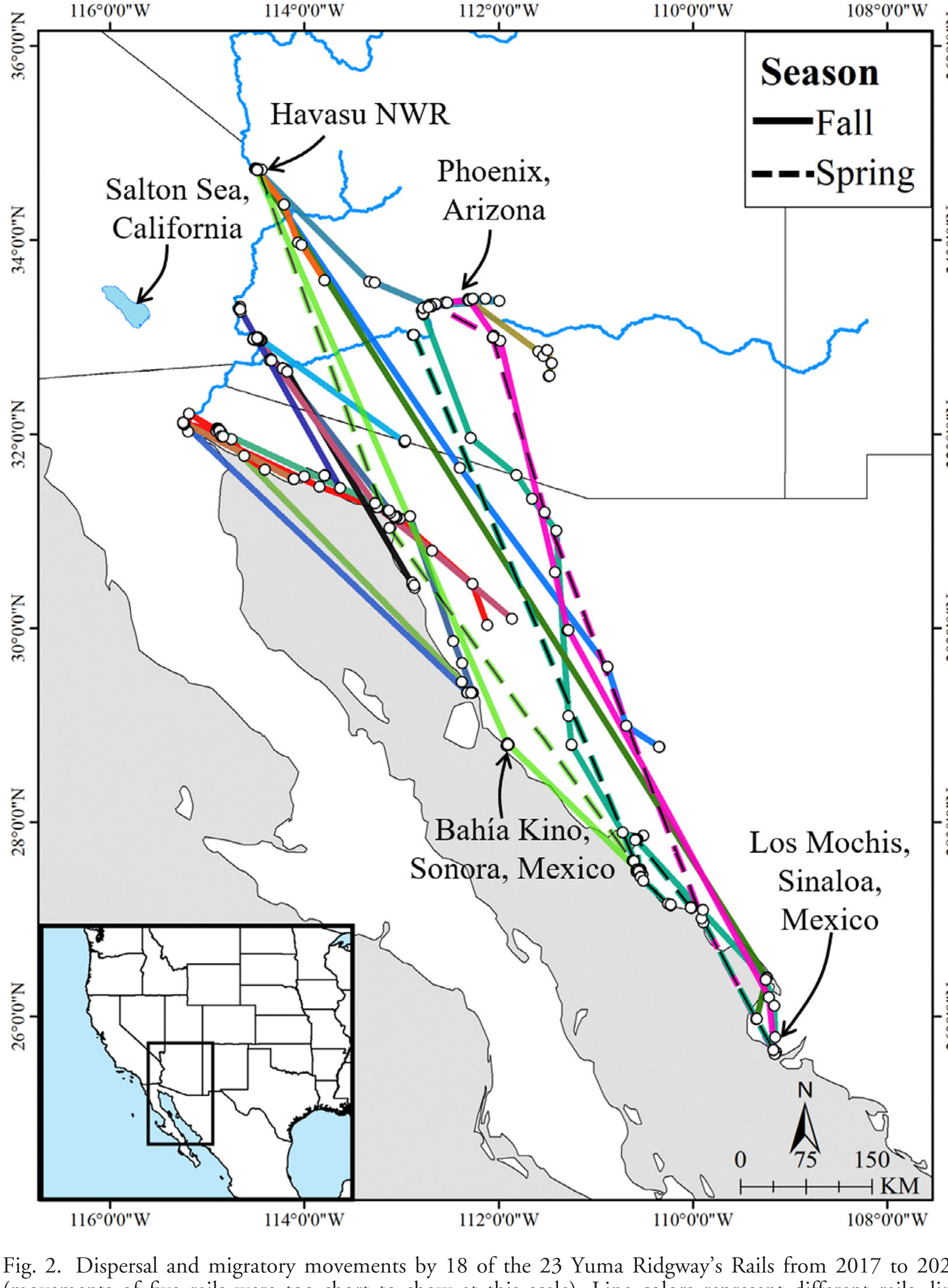

Fig. 2. Dispersal and migratory movements by 18 of the 23 Yuma Ridgway's Rails from 2017 to 2020 (movements of five rails were too short to show at this scale). Line colors represent different rails, line types represent fall and spring movements, and white circles represent locations where transmitters recorded actual coordinates. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1. Minimum proportion of Yuma Ridgway's Rails that initiated fall migration (i.e., rails that were alive in October of any year 2017–2019 and moved at least 20 km during the fall).

			Number active in October		Number moved		Proportion moved		Totals		
Study site	Latitude	Longitude	A[a]	J[a]	A[a]	J[a]	A[a]	J[a]	Number active in October	Number moved	Proportion moved
Nevada[b]	36.475	-115.376	5	–	0	–	0	–	5	0	0
Upper Colorado River[c]	34.641	-114.405	8	–	6	–	0.75	–	8	6	0.75
Lower Colorado River[d]	33.009	-114.509	14	7	6	2	0.43	0.29	21	8	0.38
Colorado River Delta, MX[e]	32.069	-115.003	7	1	4	1	0.57	1.00	8	5	0.63
Middle Gila River, AZ[f]	33.328	-112.588	8	–	4	–	0.50	–	8	4	0.50
Salton Sea, CA[g]	33.181	-114.621	8	6	0	0	0	0	14	0	0
Totals			50	14	20	3	0.40	0.21	64	23	0.36

[a]A = Adult, J = Juvenile, and dash (-) indicates that no rails of that age class were fit with transmitters at the study site.
[b]Includes Ash Meadows National Wildlife Refuge and Overton Wildlife Management Area.
[c]Includes Havasu and Bill Williams River National Wildlife Refuges..
[d]Includes Cibola National Wildlife Refuge, Imperial National Wildlife Refuge, Mittry Lake Wildlife Area, and wetlands along the Lower Gila River near Yuma, Arizona.
[e]Includes Cienega de Santa Clara and Río Hardy.
[f]Includes Base & Meridian Wildlife Area, Arlington Wildlife Area, Tres Rios Overbank Wetlands, and wetlands along the Middle Gila River near Buckeye, Arizona.
[g]Includes Sonny Bono Salton Sea National Wildlife Refuge and Wister Wildlife Management Area.

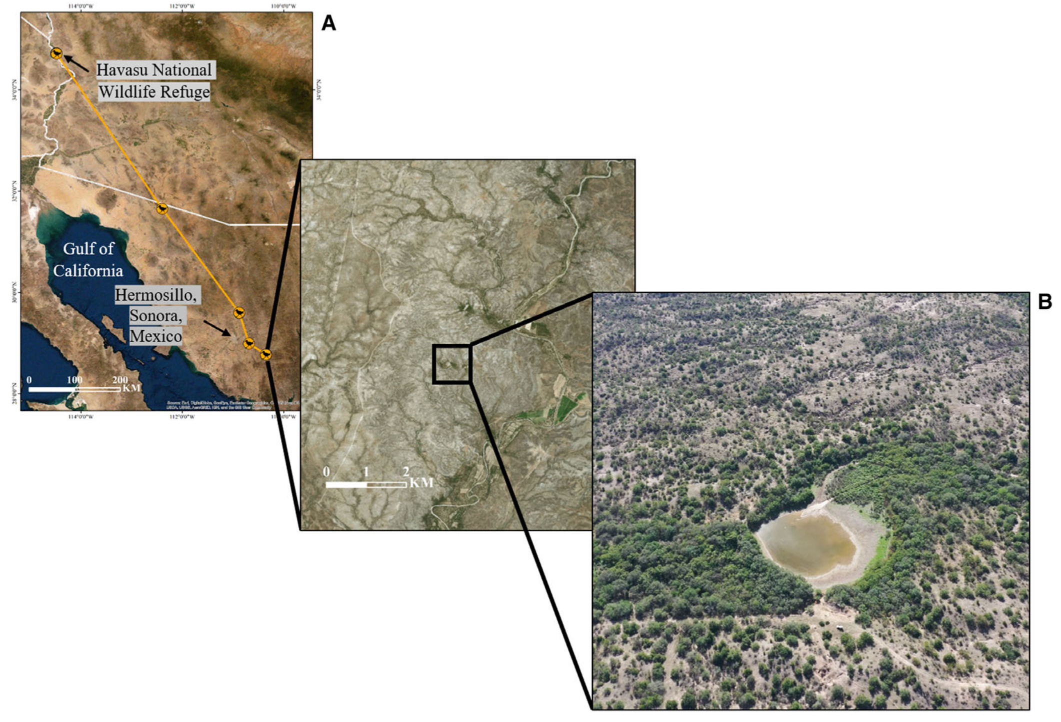

Fig. 3. A Yuma Ridgway's Rail captured at its breeding location at Havasu NWR in the United States migrated > 770 km in October 2019. This rail stopped at several water impoundments (A) before arriving at a small pond near Hermosillo, Sonora, Mexico (B). The rail remained near this pond for nearly two weeks before apparently dying or dropping the transmitter. Aerial photo credit (B): Alberto Macías Duarte. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 2. Migration parameters of Yuma Ridgway's Rails from fall 2017 to spring 2020.

	Fall migration				Spring migration			
Migration parameter	*N*	Mean	SE	Range	*N*	Mean	SE	Range
Departure date	18	4 Oct	3.9 d	6 Sept–3 Nov	3	22 Apr	2.6 d	20–28 Apr
Distance (km)	23	368.3[b]	71.4	37–1050	3	958.3	46.4	900–1050
Duration (days)	9	12.7	4.7	2–26	3	18.7	14.7	3–48
Number of stopovers	18	2.6	0.5	0–11	3	4.3	1.9	2–8

[a]*N* is the number of rails where we had corresponding information and it varied among parameters because we did not have complete information for all fall migratory movements due to transmitter battery failure or rail mortalities during migration.
[b]Average fall migration distance was 619.4 km (range = 155–1050 km) if we exclude 14 rails that died or disappeared during migration.

spring migration (Fig. S1). During both fall and spring migration, 98.0% (50 of 51) of long-distance flights with precise temporal data occurred at night. Finally, all rails that migrated to the west coast of mainland Mexico moved south within 160 km of the Gulf of California.

DISCUSSION

Successful species conservation requires an understanding of an animal's annual life cycle coupled with knowledge of the most pressing conservation issues across all stages of that cycle. We used solar-powered satellite

Table 3. Land-use and vegetation communities of stopover sites used by Yuma Ridgway's Rails during fall and spring migration from 2017 to 2020.

	Land use/vegetation community					
	Desert scrub	Coastal estuary or wetland	Agricultural field	Managed water feature	Emergent marsh	Riparian
Stopovers (*N*)[a]	19	18	10	8	4	1
Percentage	31.7	30.0	16.7	13.3	6.7	1.7

[a]We defined a stopover site as any location where a rail spent > 12 h during migration.

transmitters to track annual movements of endangered Yuma Ridgway's Rails and documented previously undescribed migratory behavior. Moreover, we documented use of novel vegetation communities by Yuma Ridgway's Rails during migration and identified previously unknown wintering areas. Our results change our understanding of the natural history of this species and invalidate existing paradigms of the life cycle of Yuma Ridgway's Rails by demonstrating that these rails are not entirely sedentary. Instead, ~ 40% of the birds in our study migrated long distances over inhospitable terrain to reach wintering territories that were often in dramatically different wetland types compared to their breeding territories. Moreover, rails in some areas of their breeding range were more likely to migrate than those in other areas, with rails being primarily (if not entirely) year-round residents in at the Salton Sea and primarily migratory in the northern portion of their breeding range along the Colorado River and Middle Gila River.

Partial migration is well documented in birds (Berg et al. 2019), but the mechanisms driving partial migration are still debated (Boyle 2008). For example, habitat quality (e.g., winter water levels in marshes or extent of available marshes), prey availability (Bennett and Ohmart 1978), and local population density may influence the decision by rails to migrate. King Rails (*Rallus elegans*) and Clapper Rails (*Rallus crepitans*) also exhibit partial migration. Indeed, King Rails in the Upper Midwest and Clapper Rails along the Atlantic Coast of the United States are migratory, whereas populations of both species along the Gulf of Mexico are year-round residents (Pickens and Meanley 2020, Rush et al. 2018, Kane et al. 2019). Yuma Ridgway's Rails in our study also exhibited leapfrog migration, with those from more northerly populations moving farther south than those from more southerly populations. Rails from Havasu National Wildlife Refuge and the Middle Gila River repeatedly migrated farther south than rails breeding close to the center of their range (i.e., Imperial and Cibola National Wildlife Refuges, Lower Gila River, and the Colorado River Delta, Mexico). A similar pattern of leapfrog migration has been observed in King Rails (Pickens and Meanley 2020).

For many species of migratory birds, the distribution and condition of stopover sites are important, particularly for species that cross large ecological barriers (Faaborg et al. 2010a). We documented Yuma Ridgway's Rails crossing large expanses of desert uplands and stopping indiverse vegetation communities and landcover types during migration, including communities never used during the breeding season. Migrating rails stopped in desert arroyos, windbreaks along highways, agricultural fields, irrigation canals, golf course ponds, and wastewater treatment plants, among others. Stops in desert arroyos and other dry areas tended to be of short duration, often no more than diurnal rest stops. Rails tended to arrive at arid stopover sites in the early morning, remain throughout the day, and depart the following evening. Stopovers in agricultural fields and managed water features frequently lasted longer, presumably because these areas offered foraging opportunities. Managed water features may be particularly important stopover locations for rails traversing the Sonoran Desert in Mexico. Indeed, four migrating rails in our study stopped at water impoundments in northern Mexico during fall migration, including one male that stopped at three different impoundments during the fall of 2019 (Fig. 3). Use of groundwater for livestock, irrigation, and human settlements throughout the Sonoran Desert has depressed water tables and reduced the amount of natural surface water in the region (Custodio 2002, Bogan et al. 2014, Norman et al. 2014). Therefore, managed water features, such as ponds maintained by ranchers for livestock are among the more reliable water sources in the Sonoran Desert and may be important resources for migrating rails. Understanding the stopover ecology of this rare marsh bird will facilitate the creation of more comprehensive conservation strategies.

Yuma Ridgway's Rails are considered the most "freshwater" of all Ridgway's Rail subspecies (Eddleman and Conway 2020) and, indeed, all rails that initiated migration bred in freshwater or brackish marshes. However, these freshwater rails migrate to saltwater environments, i.e., coastal saltgrass estuaries and mangrove wetlands along the west coast of mainland Mexico. Coastal wetlands in northern Mexico face a myriad of conservation threats, including increased human development along the coast, reduced freshwater inflows, and pressures from shrimp farming (Kovacs et al. 2001, Glenn et al. 2006, Ruiz-Luna et al. 2010). Indeed, >95% of mangrove wetlands in northern Mexico have been impacted by shrimp farming (Glenn et al. 2006). Our results demonstrate that geographically distinct populations of Yuma Ridgway's Rail populations–from Havasu National Wildlife Refuge to the Middle Gila River–may be vulnerable to habitat loss and degradation in their wintering areas. Hence, conservation of this endangered rail may depend on international collaboration and additional research to understand the condition of, and major threats to, extant coastal wetlands in northern Mexico.

Our results have implications for other subspecies of Ridgway's Rails. For example, many mangrove wetlands where migrating Yuma Ridgway's Rails have wintered support breeding populations of Ridgway's Rails of a different subspecies (*R. o. rhizophorae;* Eddleman and Conway 2020). This subspecies is considered a year-round resident of the mangrove wetlands in coastal Mexico, but little is known about its annual life cycle. Further study of the life cycle of Ridgway's Rails in coastal Mexico and interactions between resident and migratory rails is warranted. Similarly, California Ridgway's Rails (*R. o. obsoletus*) and Light-footed Ridgway's Rails (*R. o. levipes*) are thought to be year-round residents of tidal marshes in coastal California and Baja California, Mexico (Eddleman and Conway 2020). Although numerous studies have revealed that California Ridgway's Rails rarely leave their local marshes (Overton et al. 2014, Bui et al. 2015, but see Casazza et al. 2008), information about the annual movements of Light-footed Ridgway's Rails is scarce. The results of banding studies have revealed sporadic movements of $\leq$ 160 km by Light-footed Ridgway's Rails (Zembal et al. 2014), but the nature of these movements is largely unknown. Methods used in our study could be expanded to more thoroughly document the annual life cycles and movement behaviors of Ridgway's Rails throughout their range.

Yuma Ridgway's Rails in our study did not follow river corridors during migration, but, rather, crossed vast expanses of desert and open water to reach wintering areas (Fig. 2). Even rails that stopped at multiple coastal wetlands along the Gulf of California during migration moved inland before flying south (Fig. S2). Moreover, Yuma Ridgway's Rails migrated within a relatively narrow movement corridor and during a relatively narrow temporal window (6 September – 3 November for fall migration, and 20 May – 7 June for spring migration). Data on the spatial extent, phenology, and behavior of rail migration may help inform permitting decisions for future solar facilities to minimize risk to rails. For example, we found that most long-distance movements by migrating Yuma Ridgway's Rails occurred at night. As such, solar facilities could alter the arrangement and orientation of solar panels overnight to minimize the "lake effect," thereby reducing risk to migrating rails (Horváth et al. 2010). However, more research is needed to fully document the spatiotemporal extent of Yuma Ridgway's Rail migration so that permitting and land management decisions can better account for potential impacts to this rare bird.

Our results may also affect how agencies monitor populations of Yuma Ridgway's

Rails. Rail surveys are conducted annually throughout the range of the rail following the North American standardized marsh bird survey protocol (Conway 2011). The protocol recommends that three replicate surveys be conducted during an annual survey window beginning on 15 March and concluding by 30 April. In concordance with that recommendation, only 23.8% of marsh bird surveys along the Colorado River and Salton Sea from 2006 to 2018 were completed after 30 April (E. J. Harrity and C. J. Conway, unpubl. data). However, some rails in our study did not return to their breeding areas until after this survey window concludes, so seasonal timing of surveys might need to be adjusted, particularly in areas where rails appear to be most migratory (e.g., Cibola and Havasu National Wildlife Refuges).

Long-distance migration is energetically costly and perilous (Faaborg et al. 2010a, Klaassen et al., 2014, Hewson et al. 2016), and this appears to be true for Yuma Ridgway's Rails. Indeed, 60.9% (14 of 23) of the rails that initiated fall migration died before reaching wintering areas. We confirmed raptor predation for three of the 14 rails that died during migration, but could not confirm the fate of the remaining 11 rails because the satellite transmitters we used were either difficult (solar satellite PTTs) or impossible (solar Argos PinPoints) to track manually. More research is needed to identify the principal causes of rail mortality during migration.

Our study reinforces the importance of research on full annual life cycles to inform effective conservation. Yuma Ridgway's Rails have been considered largely sedentary, year-round residents of freshwater emergent marshes, and conservation strategies have concentrated on protecting and maintaining early successional emergent wetlands within their breeding range. However, we demonstrated that a non-trivial portion of the population is migratory and has much broader habitat requirements (that change seasonally) than previously known. Indeed, migratory rails seem to have three (or more) distinct habitats during the year, including: (1) emergent freshwater marshes during the breeding season, (2) desert arroyos, agricultural fields, coastal marshes, and water impoundments as stopover sites during migration, and (3) coastal wetlands during the winter. Looking beyond breeding habitat to carefully consider land-use decisions on non-marshlands in the migratory pathway of Yuma Ridgway's Rails and seeking international collaboration toprotect wintering areas of this endangered bird may help improve conservation efforts. Further, our results highlight the need for additional study of this rail's migratory behavior and winter distribution. Researchers have increasingly powerful tools to elucidate annual life cycles of mobile species and effective use of these tools can aid in the development of comprehensive conservation strategies to protect such species throughout all stages of their life cycles.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Table S1. Distribution of transmitter deployments on Yuma Ridgway's Rails during the breeding seasons of 2017 to 2019.

Fig. S1. Full annual migration of an adult male Yuma Ridgway's Rail.

Fig. S2. Fall and winter movements of a juvenile female Yuma Ridgway's Rail banded at Imperial National Wildlife Refuge on 12 July 2018.