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MOVEMENTS OF THE MANGROVE WARBLER IN BAJA CALIFORNIA SUR

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ABSTRACT: Mangrove forests are one of the most productive ecosystems in the world. Despite this, over half of the world's mangroves have been lost through human activities. As suitable habitat declines, mangrove birds are forced into small isolated patches, exposing them to the dynamics of small populations. Our primary objective was to quantify local movement of Mangrove Warblers of the apparently sedentary subspecies *Setophaga petechia castaneiceps,* endemic to mangroves of Baja California Sur. In 2010, we captured and color-banded 108 breeding adult Mangrove Warblers at 16 sites, then surveyed all surrounding mangroves during the following winter and breeding seasons. We found no movement from one stand of mangroves to another, but we did find territory switching within a stand from winter to the breeding season. The rate of replacement of birds in a territory was high, suggesting that the proportion of floaters is high. We found no significant changes in population density by season or sex.

The underlying framework for the conservation of fragmented populations is founded on the principles of island biogeography (MacArthur and Wilson 1967), that the probability of a species' occurrence in a patch of habitat varies as a function of the patch's size and isolation (Prugh et al. 2008). Simberloff (1974) stated, "any patch of habitat isolated from similar habitat by different, relatively inhospitable terrain traversed only with difficulty by organisms of the habitat patch may be considered an island." The wildlife of habitat islands risks extirpation through random variation in demographic rates and environmental conditions, loss in genetic heterozygosity, edge effects, cultural erosion, and human disturbance (Burkey 1995, Ludwig 1996). Small populations inhabiting habitat islands are especially vulnerable to these pressures (Smith et al. 2006). Rates of habitat fragmentation are so high that virtually all natural (continuous) terrestrial habitats and protected areas (such as nature preserves and parks) are certain to become habitat islands (Groombridge and Jenkins 2002).

Worldwide, over 50% of mangroves have been destroyed (Holguin et al. 2006). The mangrove forest of Baja California Sur, Mexico, is a mosaic of small islands as a result of habitat fragmentation due to human activity. Within 20 years (1972–1992), 65% of mangrove forests in Mexico were destroyed (Herrera-Silveira and Ceballos-Cambranis 2000), and a further 70,000 ha were lost from 1993 to 2000 (SEMARNAT 2003). In northwestern Mexico, 2300 ha were lost from the early 1970s to 2005 (Ruiz-Luna et al. 2010), Furthermore, this region is affected by seasonal hurricanes, which damage mangroves by reducing their stem density and basal area and by uprooting trees (Kovac et al. 2001). Not only are tropical depressions common, 78% of Mexico's national total of hurricanes occur here (Flores-Verdugo et al. 1992). Some stands of mangroves in this area are weakened, being homogeneous in tree structure and diversity, broken by gaps, or in poor health from lack of benthic microbes, heightening the need for these unique habitats to be studied and their biodiversity preserved.

In 2003, mangrove management in Mexico was regulated by Norma Oficial Mexicana NOM-022-SEMARNAT-2003, which "established the specifications for preservation, conservation, sustainable use and restoration of the coastal wetlands in mangrove areas" (SEMARNAT 2003). This law allowed for the enforcement of mangrove protection, until the agreement in 2004 to add Article 4.43, which states, "the prohibition of work and activities set out in paragraphs 4.4 and 4.22 and the limits set out in paragraphs 4.14 and 4.16 may be excluded if there is a preventative report of environmental impact statement, or if the case establishes compensation arrangements for the benefit of wetlands and it obtains corresponding authorization for change of land use" (Diario Oficial de la Federación, 3 May 2004). This addition drew immediate attention from many environmental organizations calling for revision of the article. In 2007 another article was added (Article 60 TER of the Wildlife General Law), in which "it is forbidden to remove, fill, transplant, prune, or conduct any work or activity which directly or indirectly affects mangroves" (Diario Oficial de la Federación, 1 February 2007). Under this addition, Mexico prohibited nearly all urban development harmful to mangrove ecosystems.

Few birds specialize in mangrove forests, and detailed research on the ecology of these specialists is sparse (Hogarth 1999, Luther and Greenberg 2009). One of the many subspecies of the Yellow Warbler (Browning 1994), *Setophaga petechia castaneiceps* is endemic to the mangroves of Baja California Sur. It is an apparently sedentary (although no published data have confirmed this) habitat specialist confined to mangroves year round (Curson et al. 1994). Although Baja California Sur has dry and rainy seasons, Cox (1968) considered the lack of extreme seasonality to be a major factor in tropical birds' ability to maintain territories and often monogamous pair bonds year round.

As the Mangrove Warbler specializes on a unique yet declining habitat, more research on its patterns of movement is needed. Rates of immigration and emigration into and out of mangrove stands in part determine the subspecies' susceptibility to the risks run by isolated, small populations. Presumably the number of birds living in one patch is limited by space and competition for resources such as nesting sites and food (e. g., Holmes 2010). Low numbers, coupled with isolation and a sedentary lifestyle (possibly no immigration and emigration), may be depressing genetic variation (Harrison and Hastings 1996, Callens et al. 2011). Inbreeding may be making the populations more susceptible to environmental changes. Five named hurricanes crossed Baja California Sur between 2001 and 2009 (NOAA 2011), displacing birds, destroying habitat, and possibly adding to genetic complications. Also, increasing fragmentation of mangroves may be increasing edge effects. Because these factors may threaten the viability of *S. p. castaneiceps*, we attempted to quantify its local movement.

STUDY AREA

The study area included the known range of *S. p. castaneiceps,* which inhabits patches of mangroves on both coasts of Baja California Sur north to San Ignacio Lagoon and Estero el Coyote (Pond Lagoon) on the Pacific coast and to Ejido San Lucas (27.23° N) on the Gulf of California (Browning 1994, Dunn and Garrett 1997) (Figure 1). On the basis of locations reported by Whitmore et al. (2000), we established within this range 16 study sites in five general areas: La Paz, Mulegé, and Ejido San Lucas, comprising 13 sites along the Sea of Cortez, and Magdalena Bay and Puerto Adolfo López Mateos, comprising 3 sites along the Pacific coast (Figure 1). Each study site was a discrete mangrove stand separated by desert from the next closest stand.

The stands of mangrove at all study sites on the Sea of Cortez were less than 1.8 km (straight line distance) in maximum length or width. Their area ranged from 2.4 to 6 ha, except for site LP6, which covered 25.1 ha. On the Pacific coast, Magdalena Bay supports a large continuous mangrove stand stretching (straight-line distance) approximately 115 km along the coast. Our largest site (67.8 ha) was at Magdalena Bay. The entire study area spanned a total straight-line distance of 390 km and total area of 127.5 ha. The distance between neighboring study sites averaged 6.6 km but ranged from 0.9 to 31.8 km.

Arid Baja California Sur has an annual precipitation <300 mm and mean temperatures of 20–22°C (Ruiz-Luna et al. 2010). Its mangroves are of three species, *Avicennia germinans* (black mangrove), *Rhizophora mangle* (red mangrove), and *Laguncularia racemosa* (white mangrove) (Hogarth 1999, Flores-Verdugo et al. 1992, Ruiz-Luna et al. 2010). Unlike those elsewhere, in Baja California Sur mangrove trees seldom exceed 5 m in height (Felger et al. 2001). Our study areas were dominated by red mangrove (pers. obs.).

METHODS

Data Recording

At each study site, we captured and banded Mangrove Warblers during the breeding season (May 2010) by using recordings of their songs to lure them into mist nets. When broadcasting the songs, we assessed the birds' territoriality by their behavior, considering them to be defending a territory if they fluttered their wings, flew at the speaker or observer, chirped, chased other birds, or countersang to the recording.

We banded each bird with a U.S. Geological Survey aluminum band and unique combination of color bands for identification of individuals. We recorded locations of capture via a GPS unit with a minimum accuracy of 10 m. After being banded, birds were released at the point of capture.

All birds captured were adult by plumage and skull pneumatization. We observed no juveniles or fledglings; apparently nestlings had not yet fledged by the time of our banding, and the broadcasting of song targeted territorial adults. When possible, we sexed the birds by coloration and presence of brood patch or cloacal protuberance (Howell and Webb 1995, Pyle 1997).

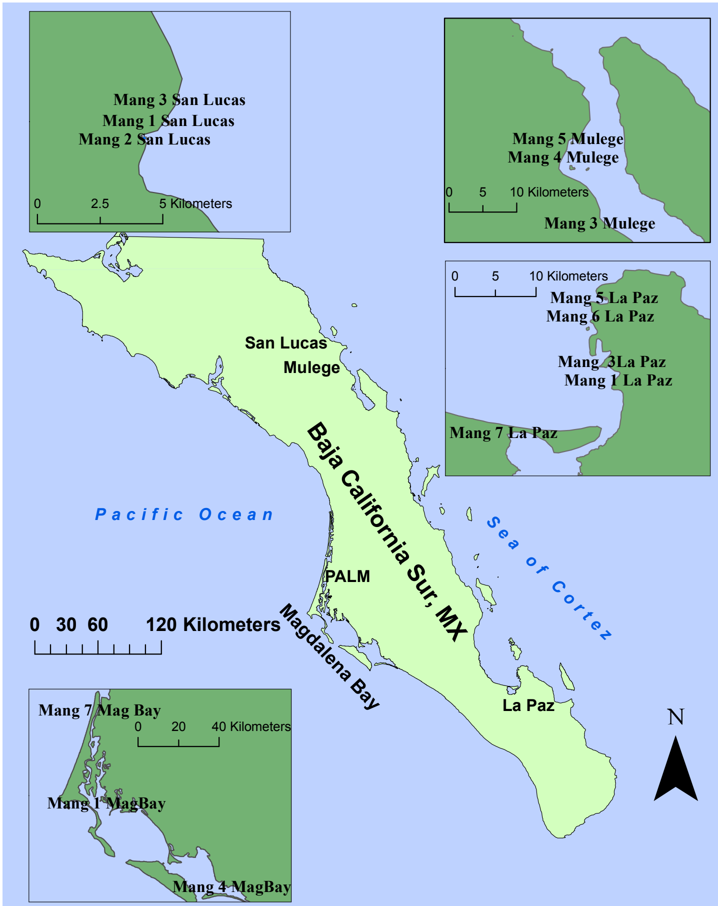

Figure 1. Five major study areas (San Lucas, Mulegé, Puerto Adolfo López Mateos (PALM), Magdalena Bay, and La Paz) and specific sites of study of movements of the Mangrove Warbler in Baja California Sur, Mexico.

We recorded a pair if both a female and male were captured at the same location and defended the territory together.

As reported by Salgado-Ortiz et al. (2008), at Celestún, Yucatán, subspecies *bryanti* defends territories and maintains permanent pair bonds and a stable population density year round. Since we were interested in movements year round, we searched for banded birds in November 2010 as well as in the following breeding season (April 2011).

We revisited each point of original capture (net location) at least once in November and April. At each location, we broadcasted Mangrove Warbler vocalizations for 15 minutes or until we detected a bird (banded or unbanded). We recorded all individuals detected during the 15 minutes within 10 m of the point (Hutto et al. 1986) and noted their behavior. We chose a small radius because of the density of the vegetation and to ensure 100% detection within that radius. We spent more than 15 minutes at the location if needed to confirm if a bird was banded, but we recorded no individuals after the 15-minute survey.

To standardize our effort at resighting, we recorded net hours and observation hours to keep effort as equal as possible (Winker et al. 1997) per location of original capture. We attempted to resight the birds at the same times of the day as the original capture and under desirable field conditions, with slight differences due to seasonal changes in the times of sunrise and sunset. By standardizing effort at resighting by location of original capture (regardless of how many birds were captured there) we attempted to keep the distance the broadcasts could be heard equal, reducing the chance the birds would be drawn in to the area of broadcast.

Data Analyses

We excluded from our analyses the six individuals we could not sex. Individuals that were detected multiple times during a resighting survey were only counted once. If a Mangrove Warbler followed the observers from one survey point to a neighboring point (which was obvious), we counted it only once at the point where it first actively defended a territory.

We defined resighting success as the percent of banded birds resighted during each survey. Because we visited some study sites more often than others during the follow-up surveys, we needed to express the percent of birds resighted by a measure of effort. To this end, we divided the total number of individuals resighted by number of individuals we attempted to resight. We calculated population density by dividing the number of individuals detected during the 15-minute surveys by the area of the site.

Using a repeated-measures analysis of variance (ANOVA) in SAS (version 9.2), we tested for significant differences in densities by sex category (male, female, and pair) and survey season We used ArcMap 9.3.1 to measure the distances banded birds moved from their location of original capture. We confirmed birds' switching territories and replacing others in a territory by comparing their locations to their previous locations by GPS.

RESULTS

Capture, Territoriality, and Resighting Success

During the breeding season of 2010, we captured and banded 74 adult males and 34 adult females (28 pairs, Figure 2) at 57 locations within the 16 study sites. Every individual captured was actively defending its territory. Chipping was the main territorial cue Mangrove Warblers used both in winter and the breeding season; song was secondary. Even in the morning during the breeding season, song was infrequent and the birds communicated more consistently with their chip notes. Playing song and chip notes during both follow-up surveys led to aggression by both the male and female territory holders in which they chased off intruders (including migrant Yellow Warblers). Adult males' responses involved more flying and chasing, whereas females' aggression was harsh chipping accompanied by hopping through the mangrove trees looking for the unrecognized individual.

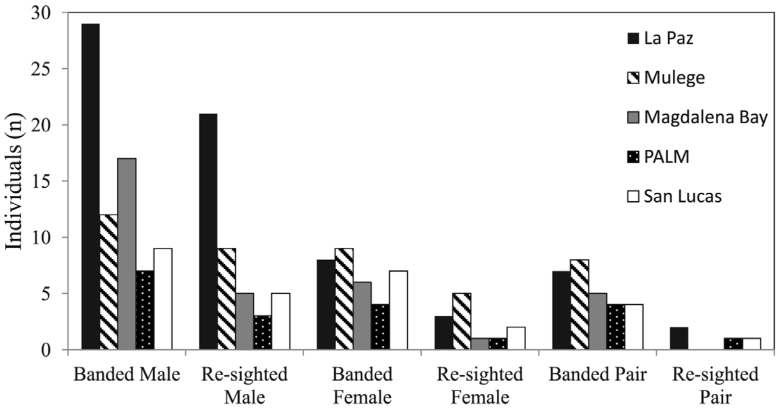

Figure 2. Number of Mangrove Warblers banded (May 2010) and resighted (November 2010, April 2011) in Baja California Sur by site. PALM, Puerto Adolfo López Mateos.

We resighted 43 marked males and 13 marked females, representing 52% of all birds banded. Nine marked males and two marked females were resighted in both November and April, as were four pairs that remained together through the year of this study. The highest number of resighted banded birds (25) was in the La Paz study area; the lowest (6) was at Magdalena Bay (Figure 2). The percentage of resighted banded birds, both males (75%) and females (56%), was greatest at Mulegé (Table 1). The percentage of banded males resighted was 58%, that of females 38% (Table 1). The percentages of males (37%, n = 22) and females 20%, n = 5) resighted during November were greater than those during the following April (30% and 14%, respectively, Table 1).

Population Density

The density of adult males, adult females, and pairs was greatest in the San Lucas study area in the breeding season of 2010 (2.2/ha, 1.7/ha, and 1.7/ha, respectively) and in November 2010 (1.5/ha, 1.0/ha, and 1.0/ha, respectively) (Table 2). In April 2011, these densities were highest at Mulegé (1.1/ha, Table 2). All sites and seasons combined, the average density of adult males was 1.3/ha, that of adult females 0.9/ha, and that of pairs 0.9/ha. The density of males was significantly higher than that of females and pairs during all three seasons surveyed (P = 0.02). There was no significant change in overall density from season to season.

Territory Switching

We detected no movements from one patch of mangroves to another. From November 2010 to April 2011, however, eight banded males moved their territories within a patch, by an average distance of 0.59 km. We observed movement of only one female, to the closest neighboring territory with a male.

Table 1 Percentages of Banded Mangrove Warblers Resighted by Study Period, Area, and Sex

Study area and site	November 2010				April 2011				Total	
	% Resighted by effort		% Resighted of number banded		% Resighted by effort		% Resighted of number banded		% Resighted of numberbanded	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
La Paz	58.30	33.3	48.3	25.0	48.3	12.5	48.3	12.5	66.7	37.5
LP1	0	0	0	0	0	0	0	0	0	0
LP3	100		100		50		50		100	
LP4	100	50	100	50	100	0	100	0	100	50
LP6	63.6	100	58.3	33.3	50	0	50	0	83.3	33.3
LP7	16.7	0	10	0	30	50	30	50	40	50
Magdalena Bay	11.8	0	11.1	0	27.8	28.6	27.8	28.6	27.8	28.6
MB1	15.4	0	15.4	0	23.1	0	23.1	0	23.1	0
MB3	0	0	0	0	40	66.7	40	66.7	40	66.7
Puerto Adolfo López Mateos					42.9	25	42.9	25	42.9	25
Mulegé	40	12.5	33.3	11.1	50	55.6	50	55.6	75	55.6
MU2	60	0	60	0	40	100	40	100	80	100
MU3	0	50	0	50	100	50	100	50	100	50
MU4	100	0	33.3	0	33.3	50	33.3	50	66.7	50
MU5	0	0	0	0	50	0	50	0	50	0
MU6	0	0	0	0	100	0	100	0	100	0
San Lucas	11.1	16.7	11.1	14.3	33.3	28.6	33.3	28.6	44.4	28.6
SL1	0	0	0	0	0	0	0	0	0	0
SL2	33.3	50	33.3	50	33.3	100	33.3	100	66.7	100
SL3	0	0	0	0	40	0	40	0	40	0
Total	37.3	20	29.7	14.7	43.2	32.4	43.2	32.4	58.1	38.2

Territory Replacement

Forty-seven males and 21 females vacated their territory during the study. Vacancies of males were filled by another male in 32 cases (68%). An opening for a female was filled 14 times (67%). Unbanded males and females were more likely to fill vacant territories (n = 25) than were banded males (n = 7) and females (n = 1). Of the 28 pairs of which we banded both the male and the female, we resighted 4. Of the remaining 24 pairs, 11 were not observed again, while of the 13 of which one of the pair was resighted, 11 individuals were resighted with a new mate and 2 males remained in their territories but we did not see a mate with them.The majority of the territory replacements took place between November 2010 and April 2011; only four took place between May and November 2010.

DISCUSSION

Our results confirm that *S. p. castaneiceps* is a year-round resident. Territorial birds, both males and females, moved minimally and defended the territory year round, much like other tropical passerines (Greenberg and Gradwohl 1986, 1997, Lefebvre et al. 1992, Morton et al. 2000, Salgado-Ortiz et al. 2008). Although not all banded individuals were resighted, and we observed new unbanded adult Mangrove Warblers during both follow-up

Table 2 Population Density[a] of the Mangrove Warbler in Baja California Sur

Study area and site	March–July 2010			November 2010			April 2011		
	Male	Female	Pairs	Male	Female	Pairs	Male	Female	Pairs
La Paz	0.72	0.22	0.22	0.72	0.37	0.35	0.47	0.32	0.42
LP1	0.42	0.42	0.42	1.27	0.84	0.84	0.42	0	0
LP3	0.54	0	0	0.54	0.27	0.27	0.27	0.54	0.27
LP4	1.11	0.55	0.55	2.77	1.39	1.39	1.94	0.83	0.83
LP6	0.48	0.16	0.16	0.36	0.24	0.20	0.40	0.32	0.32
LP7	1.70	0.34	0.34	0.85	0.17	0.17	1.02	0.85	0.85
Magdalena Bay	0.27	0.10	0.10	0.15	0.10	0.10	0.13	0.13	0.13
MB1	0.50	0.15	0.15	0.35	0.23	0.23	0.23	0.19	0.19
MB3	0.12	0.07	0.07	0.02	0.02	0.02	0.07	0.10	0.10
Puerto Adolfo López Mateos	1.08	0.62	0.62	—	—	—	0.77	0.77	0.77
Mulegé	1.37	1.03	0.91	0.91	0.23	0.23	1.14	1.14	1.14
MU2	3.55	2.13	2.13	2.13	0	0	2.13	2.84	2.84
MU3	2.86	5.71	2.86	2.86	2.86	2.86	2.86	2.86	2.86
MU4	0.93	0.62	0.62	0.62	0	0	0.93	0.93	0.93
MU5	0.68	0.34	0.34	0.34	0	0	0.68	0.34	0.34
MU6	1.14	1.14	1.14	1.14	1.14	1.14	1.14	1.14	1.14
San Lucas	2.23	1.73	1.73	1.49	0.99	0.99	0.99	0.99	0.99
SL1	5.88	5.88	5.88	5.88	0	0	0	0	0
SL2	1.72	1.15	1.15	1.72	1.72	1.72	1.15	1.15	1.15
SL3	2.36	1.89	1.89	0.94	0.47	0.47	0.94	0.94	0.94

[a]Number of individuals per hectare.

surveys, we infer that adults of *S. p. castaneiceps* are sedentary, only juveniles dispersing. Failure to resight could be due to mortality, loss of bands, or missed detections. On the east coast of Baja California Sur, failure to resight banded birds cannot be due to their emigration from study sites because we surveyed all mangrove stands in that region. During the initial surveys in the breeding season of 2010, the unbanded adults may have been present as floaters, missed because of their nonterritorial behavior. The density of mangrove stands makes Mangrove Warblers difficult to detect.

Despite the high rate of replacement of individuals, territory occupancy and density of *S. p. castaneiceps* remained fairly stable through the year, much like those of *S. p. bryanti* (Salgado-Ortiz et al. 2008). This pattern is consistent with other sedentary tropical birds (Cox 1985, Greenberg and Gradwohl 1986, 1997, Gorrell et al. 2005). We observed only one addition of a territorial pair to a mangrove patch. The density of males appearing greater than that of females and pairs may be due males' more assertive defense of their territories, leading to a higher detection rate.

Of the 43 banded males we resighted, all adults, 8 (19%) moved to another territory. In all of these cases, the male was seen with a new female. One male switched his territory to a neighboring territory (abandoning his female), paired with the female already in that territory, and recruited an additional female from a neighboring territory from which the male had disappeared.

Territory switching by tropical birds that are territorial year round is common; for example, Greenberg and Gradwohl (1997) reported that 37.5%

of Checker-throated Antwrens (*Epinecrophylla fulviventris*) of known age switched territories. Vacant territories are filled within a day (Levin 1996, Morton et al. 2000). Mangrove Warblers maintain type A territories within which courtship, mating, nesting, and foraging all occur. Territory switching may be due to vacancy of a territory with more resources or an available mate (Morton et al. 2000, Fedy and Stutchbury 2004). Whether the original territorial males were displaced or died and subsequently replaced by another individual is unknown.

Experiments with the sedentary White-bellied Antbird (*Myrmeciza longipes*) found that when adult males were temporarily removed from their territories, some neighboring territorial males switched to the new open territories (Fedy and Stuchbury 2004). Switching to territories where more food (Gorrell et al. 2005) or foraging substrate (Morton et al. 2000) is available has also been recorded in other species of resident territorial birds, presumably helping the birds increase their survivorship or fitness.

We observed a high rate of replacement of individuals (53% of males, 62% of females). In habitats where birds maintain a stable population density and are territorial year round, it is common that vacant territories are filled within a matter of hours (Greenberg and Gradwohl 1997, Morton et al. 2000, Fedy and Stutchbury 2004). In November, we observed many Yellow Warblers throughout the mangrove sites but we could not confirm whether these were migrant Yellow Warblers from farther north, immature Mangrove Warblers, or floaters. We do not know where or when these individuals moved to the vacant territories, but it is plausible they were floaters. A high incidence of floaters could be due to lack of dispersal of young, the limited extent of habitat suitable for territory establishment, or possibly a response to an increase in the density of males (Smith et al. 2006). Other studies, however, report that floaters are uncommon among sedentary territorial birds (Levin 1996, Morton et al. 2000, Fedy and Stuchbury 2004).

It is possible that the individuals that gained access to the territories were the young from the previous year (as a function of density dependence; Woolfenden and Fitzpatrick 1984). We do not know whether the young disperse out of their natal mangrove stand, as we captured no juveniles. Salgado Ortiz et al. (2008) found that fledglings of *S. p. bryanti* remained in natal territories for an average of 27.4 days but did not investigate their movements or dispersal after this time.

In a resident island population of the Song Sparrow (*Melospiza melodia*), Smith et al. (2006) found that 35% of territory replacements were by first-year floaters. They also reported that about 25% of the displaced territory holders became floaters in their previously held territory. These territory replacements differed by the male's age, males 2 and 3 years old being more likely to take over territories than those 1 or ≥4 years old.

Given the rate of destruction and fragmentation of mangroves worldwide, continued research on mangrove specialists is crucial. Information on dispersal of young Mangrove Warblers is needed for a better understanding of site fidelity, floaters, and possibly founding of new populations as a result of tropical storms. Furthermore, estimates of the population size and a better understanding of basic life history would aid any efforts toward the conservation of both the Mangrove Warbler and mangrove ecosystems.

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