

Avian Behavior, Ecology, and Evolution

# Larger male Yellow Warbler (*Setophaga petechia*) occupy smaller home ranges over winter in natural and agricultural sites in western Mexico

Los machos más grandes de la Reinita de Manglar (*Setophaga petechia*) ocupan áreas de actividad más pequeñas durante el invierno en sitios naturales y agrícolas del oeste de México

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ABSTRACT. Agroecosystems are becoming increasingly important bird habitats as natural Neotropical habitats are converted to agriculture at a rate of 3.5 million ha annually. We still know little about how some of the most common herbaceous crops (e.g., maize, sorghum) are used by wintering birds and the consequences of wintering in these agroecosystems. We used radio-tracking to estimate home ranges of 49 wintering Yellow Warblers (*Setophaga petechia*) across agriculture and two natural habitats of known quality for Yellow Warblers (high-quality riparian forest and poor-quality coastal vegetation) in Mexico. We assessed whether traits related to competitiveness (sex, age, body size, and migratory origin) interacted with land cover to influence home range size and if home range size influenced annual (apparent) return probability. We found that home range size of wintering Yellow Warblers is highly variable (range = 0.02-3.99 ha) and influenced by land cover, sex, and body size. Home ranges in high-quality riparian forest were smaller than those in coastal vegetation and agriculture. Across all land covers, males tended to have smaller home ranges than females (males: mean = 0.56 ha, 84% CI = 0.36-0.77 ha, females: mean = 0.90 ha, 84% = 0.65-1.16 ha). Body size did not influence home range size for females, but larger males had smaller, presumably better-quality territories than smaller males. In agricultural sites, this meant larger birds (predominantly males) had small, exclusive territories in the hedgerow, while smaller males and females had large, non-exclusive home ranges in the crops. Our work shows that the different components of low-intensity agriculture provide foraging opportunities for different population segments. Because agriculture intensification is expected to increase in Latin America, retaining hedgerows, small field sizes, and crop heterogenicity is important to ensure co-benefits for people and birds.

RESUMEN. Los agroecosistemas se están volviendo hábitats cada vez más importantes para las aves, ya que los hábitats neotropicales naturales son convertidos en hábitats agrícolas a una tasa de 3,5 millones de ha por año. Aún sabemos poco acerca de cómo los cultivos herbáceos más comunes (e.g., maíz, sorgo) son usados por las aves invernantes y las consecuencias de invernar en estos agroecosistemas. Utilizamos radiotelemetría para estimar las áreas de actividad de 49 Reinitas de Manglar invernantes (Setophaga petechia) a través de un hábitat agrícola y dos hábitats naturales de calidad conocida para las Reinitas de Manglar (bosque ribereño de alta calidad y vegetación costera de mala calidad) en México. Evaluamos si caracteres relacionados con la competitividad (sexo, edad, tamaño corporal y origen migratorio) interactuaron con la cobertura terrestre para influenciar el tamaño de las áreas de actividad y si el tamaño de las áreas de actividad influyó en la probabilidad anual (aparente) de retorno. Hallamos que el tamaño del área de actividad de las Reinitas de Manglar invernantes es altamente variable (rango = 0,02-3,99 ha) y es influenciado por la cobertura terrestre, sexo y tamaño corporal. Las áreas de actividad en el bosque ribereño de alta calidad fueron más pequeñas que aquellas en el hábitat de vegetación costera y el hábitat agrícola. En todas las coberturas terrestres, los machos tendieron a tener áreas de actividad más pequeñas que las hembras (machos: promedio = 0,56 ha, IC 84% = 0,36–0,77 ha, hembras: promedio = 0,90 ha, IC 84% = 0,65–1,16 ha). El tamaño corporal no influyó en el tamaño del área de actividad para las hembras, pero los machos más grandes tuvieron territorios más pequeños, presumiblemente de mejor calidad, que los machos más pequeños. En los sitios agrícolas, esto significó que las aves más grandes (predominantemente machos) tuvieron territorios pequeños y exclusivos en el seto, mientras que los machos más pequeños y las hembras tuvieron áreas de actividad grandes y no exclusivas en los cultivos. Nuestro trabajo muestra que los diferentes componentes de la agricultura de baja intensidad proveen oportunidades de alimentación para diferentes segmentos de la población. Dado que se espera que la intensificación de la agricultura aumente en América Latina, es importante conservar los setos, tamaños de campo pequeños y una heterogeneidad de cultivos para garantizar beneficios colaterales para las personas y las aves.

Key Words: agroecosystem; body size; home range; land birds; Neotropical migrant; warblers; wintering range

# INTRODUCTION

Of the 448 landbird species that breed in North America, 241 species migrate to the Neotropics (Webster and Marra 2005). The wintering range for most of these species extends from Mexico to Panama (Wilson et al. 2019), an area encompassing 2.7 million km<sup>2</sup>. This is roughly 1/6 of the 18.6 million km<sup>2</sup> of the breeding range in North America (Newton 2010). High population

densities in the wintering season may increase competition for resources and for high-quality territories (Brown et al. 2000, Smith et al. 2011). Competitive interactions among conspecifics can lead to bigger individuals (Smith et al. 2011), older individuals (Wunderle 1995, Marra and Holmes 2001), or early arriving individuals occupying higher quality sites (Kresnik and Stutchbury 2014). Birds excluded from higher quality habitats may roam and occupy large, non-exclusive home ranges (Winker 1998). Indeed, some insectivorous Wood Warblers exhibit different rates of persistence and flexible space-use strategies during the wintering season. In these species, some individuals may exhibit site-faithful territoriality, whereas others might be site-faithful but not defend a territory, and still others might roam large home ranges without being attached to a specific location and join intraspecific flocks (Latta and Wunderle 1996, Brown and Long 2007, Faaborg et al. 2010). The optimal strategy used by a non-breeding individual can depend on competitive ability and resource availability (Brown and Long 2007). Territoriality will be favored when resources are both predictable and defendable (Milinski and Parker 1991). Conversely, large-non-exclusive home ranges will be favored if resources are unpredictable or scattered (Brown et al. 2000, Brown and Sherry 2008).

Space-use strategies employed during the wintering season have consequences for Neotropical migrants throughout the annual cycle. They can directly affect overwinter survival (Rappole et al. 1989, Studds and Marra 2005), body condition (Johnson et al. 2006), mortality during migration (Bearhop et al. 2004), as well as migration timing and thus arrival date to the breeding grounds and in turn reproductive success (Marra et al. 1998, Marra and Holmes 2001). Individual consequences of space use strategies, if widespread, can affect population demography (Brown and Long 2007). Given that migratory species often spend more time in the wintering grounds than in their breeding grounds (Bächler et al. 2010, Ryder et al. 2011), habitat-use strategies during the wintering season can have a large effect on migratory bird populations.

Agricultural habitats are an ever-increasing proportion of total habitats available to wintering Neotropical migrants because of the high rate of natural habitat conversion to agriculture in Neotropics (~3.5 million ha / year lost; FAO 2015). The majority of the converted habitat is turned into seasonally harvested herbaceous crops (Johnson et al. 2011). Given the increasing importance of agricultural habitat, it is critical to understand how competition, space-use strategies, and survival varies within these land cover types.

In this study, we assess how individual traits influence space-use strategies of Yellow Warblers (Setophaga petechia) occupying natural and anthropogenic land cover during the wintering period. We radio-tracked Yellow Warblers in western Mexico across two natural habitats (high-quality riparian forest and lowquality coastal vegetation) and agricultural land cover. Previous work showed that density and monthly survival rates of Yellow Warblers are highest in riparian forest and agriculture, and lowest in coastal vegetation (a mix of scrub and mangrove) indicating that both riparian forest and agriculture provide relatively highquality wintering sites for Yellow Warblers, whereas coastal vegetation is poorer (Valdez-Juarez et al. 2018, 2019). In this study, we predicted the following: (1) If wintering site quality influences space-use strategies in Yellow Warblers, birds in riparian forest and agriculture (high-quality sites) would have smaller home ranges than those in coastal vegetation (low-quality sites). (2) Assuming early arrival on the wintering grounds is advantageous for winter site acquisition, Yellow Warblers with a northern natal

or migratory origin that arrive first at the wintering grounds during fall migration (Kelly 2006) would be more likely to settle in high-quality habitat and have smaller home ranges than those with a more southern migratory origin. (3) If competitive asymmetries determine space-use strategies, large, adult males would tend to be territorial and thus have smaller home ranges, whereas smaller, female, or juvenile birds would tend to have larger home ranges. (4) Last, if large, non-exclusive home ranges are disadvantageous, we predicted that birds with large home ranges would be less likely to remain in the home range or to survive, and therefore would be less likely to be re-sighted in a subsequent year.

# **METHODS**

# Study species and study site

Yellow Warblers are 7- to 11-g long-distance migrants that breed throughout most of the Nearctic realm between May and July and spend approximately seven months, between September and May, in wintering habitat in the Neotropics from Mexico to northern Peru (Lowther et al. 1999). Yellow Warblers are territorial (Greenberg and Salgado-Ortiz 1994) and occupy sites with both natural (e.g., riparian forest and mangrove) and anthropogenic land cover (e.g., cattle pasture and agriculture: Hutto 1980, Greenberg et al. 1996, Valdez-Juárez et al. 2018). We studied behavior of wintering Yellow Warblers from late January to the end of April in 2012, 2013, and 2014. Our study sites were located on the Pacific Coast of Mexico near the Chamela-Cuixmala Biosphere Reserve (19°30'N, 105°03'W), in the municipality of La Huerta, in the state of Jalisco. Yellow Warblers in this region of Mexico originate mainly from Canada and Alaska (Boulet et al. 2006, Valdez-Juárez et al. 2018).

We established two study plots of 2.5 ha each within each of three land cover types: agriculture, riparian forest, and coastal vegetation. Agriculture occurs in the vicinity of the towns of Punta Pérula and Zapata and consists of small (< 4 ha) fields bordered by 1-2 m wide hedgerows. Our field sites had a mixture of crops; most were seasonally harvested herbaceous crops such as sorghum (Sorghum bicolor), corn (Zea mays), jalapeño peppers (Capsicum annum), tomatoes (Solanum lycopersicum), and cucumbers (Cucumis sativus), but a few fields had perennial plantations such as papayas (Carica papaya) and mangos (Mangifera indica). Our riparian forest plots were located in margins and riverbeds of the Chamela and the Cuixmala rivers. The main tree species there include Astronium graveolens, Brosimum alicastrum, Bursera arborea, Couepia polyandra, and Cynometra oaxacana (Lott 1993). Finally, coastal vegetation surrounds lagoons on undeveloped private land, where canopy grades from mangrove (Rhizophora mangle) at the shoreline to tropical dry forest in dryland land areas. The main tree species include Avicennia germinans, Conocarpus erectus, and Laguncularia racemosa (Lott 1993).

We attempted to capture all Yellow Warblers in each plot using both passive mist-netting and mist-netting combined with playbacks of a conspecific "chip" call. A previous study (Neudorf and Tarof 1998) and our own observations show that it is unlikely that playback use led to a male bias in our sample. Mist-netting began at sunrise and ended at sunset, with a 3-hour break at noon. We aged (second year / after second year birds) and sexed all captured Yellow Warblers based on their plumage and mandible color (Pyle 1997). Interannual recapture and resighting data suggest that 95% of birds were assigned to the correct sex and age at banding (Valdez-Juárez et al. 2018). We fitted all captured birds with a unique combination of color bands, and measured maximum wing chord to the nearest 1 mm with a wing ruler (Pyle 1997). We used wing chord as a proxy for body size because it is the best predictor and the most reproducible single metric for measuring general body size (Gosler et al. 1998). We calculated scaled sex-specific wing chord so that sex and wing chord could both be included as terms in our statistical models (see below). We did not use a principal component analysis (PCA) as a measure of size because of its low informative value in our sample (see Jackson 1993). A PCA that included tail, head-bill length, wing chord, and tarsus explained only 42.6 and 46.2% of male and female body size, respectively.

# Yellow Warbler radio-tracking

We fitted Lotek Picopip radio transmitters (Lotek Wireless, Ontario) to 89 Yellow Warblers. All radio transmitters weighed less than 5% (mean 3.9%, range: 3.5-4.4%) of a bird's mass (mean bird mass = 8.2, range = 6.9-9.5 g). Birds that weighed 8.5 g or less (n = 68) were fitted with an AG337 (0.30 g) radio transmitter and birds that weighed 8.6 g or more (n = 21) were fitted with an AG317 (0.38 g) radio transmitter. In 2012, we used cyanoacrylate glue to attach radio transmitter and glued both on the intrascapular region after clipping back feathers (Johnson et al. 1991). In subsequent years we attached radio transmitters using a leg-loop harness made of stretch cord (Rappole and Tipton 1991) to reduce the probability of radio transmitters falling off prematurely (see Results).

We used two Lotek Biotracker radio receivers (Lotek Wireless, Ontario) attached to a 3-element hand-held Yagi antenna to locate each radio-tagged bird (detection range ~80 m) once a day during the radio transmitter's lifespan (up to 34 days). Pairs of observers used stealth homing (White and Garrott 1990) to get as close as possible to each tracked bird (~10 m). If we directly observed the bird, we recorded the exact GPS location (~20% of the locations). Alternatively, two observers recorded their GPS location and simultaneously recorded a compass bearing toward the bird. We estimated bird location with a user defined trigonometry function in R 4.3.2 statistical computing environment (R Core Team 2023) to determine where the two bearings intersected. We recorded individual locations ensuring that we obtained at least one location for each daylight hour. We excluded locations one half hour after sunrise and one half hour before sunset, when many birds are commuting from their roosting locations (Smith et al. 2008).

## Spatial analysis

We estimated Kernel Utilization Distributions (UDs) that provide a probabilistic distribution of an individual's location (Worton 1989). We used the "kde" function from the "ks" package (Duong 2024) in the R 4.3.2 statistical computing environment (R Core Team 2023). We estimated core area as the 50% UD and home range area as the 90% UD (Börger et al. 2006, Townsend et al. 2010). We calculated all UDs with a code derived from the Manual of Applied Spatial Ecology (Walter and Fischer 2016). We used the plug-in smoothing parameter that is considered to be more appropriate than the Least Square Cross Validation (LSCV) smoothing parameter in human-modified landscapes (Adams 2001).

We used a subsample of 21 birds with  $\geq$  25 locations to determine the minimum number of locations required to robustly estimate home range size. To do this, we estimated mean home range size and variance for location sample sizes of 10, the minimum locations recommended (Börger et al. 2006), to 24 using 100 bootstrapped draws of each sample size from each individual's full location data. We considered the accuracy of estimated home ranges to be 100% if the estimate distribution centered on 1.0 relative to the estimate obtained from each bird's full data set. We estimated precision using the bootstrapped variance. The area estimation for home ranges with 14 random locations increased to 82% relative to those calculated with all locations and had a 14% variance. Each additional location after 14 increased the accuracy by < 2% and decreased the variance by < 1%. We therefore set the minimum number of locations required for an individual to be included in the analyses as 14 and excluded data from all other birds. Home range size was independent of the number of locations used to calculate the home range of birds located between 14 and 34 times ( $F_{1,39} = 1.3$ , P = 0.25).

We estimated the core area (50% UD) and home range size (90% UD) for a total of 49 wintering Yellow Warblers. Yellow Warbler's core (50% UD) and home range (90% UD) areas were strongly correlated (r = 0.93, P < 0.001). Because models predicting core and home range area produced identical conclusions, we only report results from analyses examining variation in home range (90% UD) below but present the complete results for the home range and the core area models in Table 1.

# Feather isotope analysis

We used stable hydrogen isotope ratios ( $\delta^2$ H) of flight feathers (P1) grown on the breeding grounds to infer the latitude of the natal or migratory origin for radio-tracked individuals. We describe our stable isotope methods in more detail in Valdez-Juarez et al. (2018). Briefly, we washed feathers in a 2:1 chloroform: methanol solution for 24 hr, then drained and airdried them in a fume hood for an additional 24 hr to remove excess solvent. We placed  $0.700 \pm 0.004$  (SE) mg of each bird's feathers into a 9  $\times$  35 mm smooth-walled silver capsule (Elemental Microanalysis, Okehampton, Devon, UK). All samples were analyzed in a zero-blank carousel (Hekatech HT Elemental Analyzer, 1350 °C) in line with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon, Crewe, Cheshire, UK) at the University of California Davis Stable Isotope Facility (Davis, California, USA). The non-exchangeable hydrogen isotope ratios  $(\delta^2 H)$  are expressed in per mil units relative to the Vienna Standard Mean Ocean Water standard (V-SMOW). The estimated precision of each measurement precision is 2‰, based on withinrun replicates of keratin standards (see Valdez-Juarez et al. 2018 for further details).

## Statistical analysis

We used a generalized linear model to assess if the UDs varied with land cover or individual traits (sex, age, body size, and migratory origin). The model included all the main effects listed above plus sex\*size, habitat\*size, sex\*age, and age\*size interactions to allow evaluation of whether size effects varied **Table 1.** Results for the general linear model analyses testing the influence that land cover and individual traits have on home range and core area for Yellow Warblers (*Setophaga petechia*) wintering in Mexico. Home range was estimated as the 90% Kernel Utilization Distribution (UD) and core range as the 50% UD. Bird size was estimated with a scaled sex-specific wing chord. The asterisk indicates statistical significance (P < 0.05).

	F	Р
Home range (90% UD)		
Overall model for home range: $n = 45$ , $df = 32$ , $r^2 = 0.2$	5, $P = 0.04*$	
Land cover	5.31	0.01*
Sex	4.74	0.04*
Age	2.15	0.15
Size	2.33	0.14
No. of locations	2.20	0.15
$\delta^2 H$	0.50	0.48
Age*Size	0.003	0.96
Land cover*Size	0.65	0.53
Sex*Size	11.59	0.007*
Sex*Age	0.34	0.56
Core Range (50% UD)		
Overall model for home range: $n = 45$ , $df = 32$ , $r^2 = 0.2$	1, P = 0.06	
Land cover	5.15	0.01*
Sex	3.79	0.06
Age	1.13	0.30
Size	1.09	0.30
No. of locations	2.41	0.13
$\delta^2 H$	0.40	0.53
Age*Size	0.07	0.79
Land cover*Size	0.74	0.48
Sex*Size	7.72	0.006*
Sex*Age	0.003	0.96

depending on the sex or age of the bird. We did not include year or interactions between land cover type and age and land cover type and sex because of the small sample size. We used the "lm" function in the built-in package "stats" (R Core Team 2023) to create the models and then used the "Anova" function from the "car" package (Fox and Weisberg 2019) to assess the significance of the relationships.

Last, we used the "glm" function in the base "stats" package to build 2 models that assessed the factors that influenced apparent return rates of wintering Yellow Warblers. The dataset for the first model included color-banded birds and radio-tracked birds that were observed at least once after first capture to minimize inclusion of vagrant or commuting birds. We excluded four colorbanded birds from the dataset because of incomplete data. This model included sex, age, land cover type, and all first-order interactions as predictor variables. The second model evaluated the influence of home range size and land cover type on apparent return rates, using data exclusively from radio-tracked birds. We were only able to do this analysis for males because of insufficient return data for females (see Results). Prior to all analyses, we used diagnostic model plots to check for homoscedasticity, and influential outliers, and to evaluate data distribution. We report apparent return rates as we are unable to distinguish between bird dispersal and mortality. We report all confidence intervals at 84% to better approximate an  $\alpha = 0.05$  (Payton et al. 2003). We performed all analyses in the R 4.3.2 statistical computing environment (R Core Team 2023).

# RESULTS

### Fate of radio-tracked Yellow Warblers

We relocated 54 of 106 (51%) Yellow Warblers fitted only with color-bands and 83 (95%) of the 87 birds fitted with both color bands and radio-trackers. Of those with radio-tracker, 54 (64%) were relocated only in the same year they were banded. We obtained 14 or more relocations for 49 of the 87 birds fitted with a radio transmitter; of the 38 birds that did not get 14 or more locations, 28 were because the radio transmitter fell off prematurely. Radio transmitters were more likely to fall off if they had been attached with glue rather than with a leg-loop harness (glue: 24 of 37; leg-loop harness: 4 of 50; 1,  $\chi^2$  = 30.9, 1 df; *P* < 0.001). Of the four fallen leg loop harnesses, three were deliberately damaged and removed by the birds themselves. Depredation prevented us from obtaining 14 or more locations for two birds in riparian forest (a juvenile female and a juvenile male). In both cases, we found the radio transmitters in clumps of Yellow Warbler feathers. We observed a Collared-forest Falcon (Micrastur semitorquatus) and a Sharp-shinned Hawk (Accipiter striatus) in the vicinity. We found the intact carcass of a juvenile female within a jalapeño pepper field where this bird had previously foraged for five days. This field had been heavily sprayed with a toxic chlorpyrifos pesticide to curb an infestation of beet armyworm (Spodoptera exigua) 24 hr prior. We found the intact carcass of the fourth bird, an adult female, in the hedgerow between two agricultural fields. We did not observe any sign of injury on either of the two intact carcasses.

## Yellow Warbler space-use

The number of relocations per bird ranged from 1 to 38 (median number location = 16, interquartile range = 7–24). Our home range sample included birds of both sex and age classes across all three land cover types (Table 2). We found considerable variation in Yellow Warblers home range estimates (90% isopleth: range = 0.02-3.99 ha, median = 0.29 ha, interquartile range = 0.11-0.97 ha). We found 11 of the 49 birds had home ranges < 0.1 ha, often consisting of a single tree or shrub that was defended from conspecifics. By contrast, 11 birds had ranges larger than 1 ha, the largest being almost 4 ha. We found that birds with large non-exclusive home ranges in agriculture actively foraged in standing crops such as jalapeño peppers, maize, and sorghum (Fig. 1). We documented 5 instances where birds foraging in crops moved between fields that had different crops (Fig. 1).

#### Feather isotope analysis

We determined the hydrogen isotope signature for feather samples for 45 of the 49 birds with estimated home ranges. The  $\delta^2$ H signatures for this sample ranged from -175.0 to -102.3 (mean -138.2 ± 2.5 %<sub>0</sub>) suggesting that most of the birds in our sample

**Table 2.** Sex and age distribution of the 49 radio-tracked wintering Yellow Warblers (*Setophaga petechia*) for which home range estimates were obtained.

	Riparian forest		Coastal vegetation		Agriculture	
	Male	Female	Male	Female	Male	Female
Adult	6	2	2	-	9	2
Juvenile	4	3	6	1	4	10
Total	10	5	8	1	13	12

**Fig. 1.** Home ranges of 11 Yellow Warblers (*Setophaga petechia*) wintering in agricultural fields in Jalisco, Mexico in 2014. (A) Near the township of Zapata (map center at 19°36'N, 105°7'W) and (B) near the township of Punta Pérula (map center at 19°23'N, 104°58'W). Home ranges are defined by the 90% Kernel Utilization Distribution, with a minimum of 14 locations. Agricultural fields at the study sites are relatively small (200 x 200 m), surrounded by hedgerows where larger Yellow Warblers established exclusive territories defended from conspecifics. Smaller Yellow Warblers actively foraged in various crops within larger, non-exclusive home ranges. Bird ID6937 switched from maize to a jalapeño pepper field when the plants in the latter reached ~50 cm. Bird ID6933 switched from a jalapeño pepper field to a fallow field when the jalapeño pepper field was cleared.



originated from Alaska or the western Canadian provinces rather than from the contiguous USA (Valdez-Juárez et al. 2018). The model that included all previously described main effects and interactions showed that migratory origin ( $\delta^2$ H signatures) was not correlated with home range size (Table 1).

## Factors influencing home range size

Yellow Warbler home range size was associated with land cover type, sex, and by body size (Table 1). Home ranges in riparian forest were smaller than those in either coastal vegetation or agriculture (Table 1, Fig. 2). Males had smaller home ranges than females (males: mean = 0.56 ha, 84% CI = 0.36–0.77 ha, females: mean = 0.90 ha, 84% = 0.65–1.16 ha). Male home range size decreased with body size (Fig. 3), while females, regardless of their size, had a home range size similar to that of small males. We found no evidence that home range size varied with age in male or female Yellow Warblers (Table 1: age, age\*sex). This conclusion was not altered if age effects were examined in an a posteriori model that excluded body size, sex, and their interactions (P = 0.72,  $F_{39.5} = 0.6$ ).

## Interannual apparent return rates to wintering sites

Of the 81 color-banded males, 40 (49%) were seen in a subsequent year, whereas only 13 (25%) of the 52 color-banded females were seen in a subsequent year. Apparent return rate difference between sexes was supported by the model (n = 133,  $\chi^2 = 3.8$ , 1 df; P =0.05). We found no evidence that apparent return rate of color banded birds was influenced by age (n = 133,  $\chi^2 = 2.3$ , 1 df; P =0.13), land cover type (n = 133,  $\chi^2 = 4.4$ , 2 df; P = 0.12) or any of the interactions (all P > 0.26). Of the 53 individuals relocated between years, only 2 (4%) changed their home range location and size between years. Both of these individuals, an adult male and a juvenile female, relocated from non-exclusive, large home

**Fig. 2.** Means and 84% confidence intervals for 49 Yellow Warbler (*Setophaga petechia*) winter home range areas (90% Kernel Utilization Distribution) across three land cover types in western Mexico. Home ranges in riparian forest were smaller. We found no evidence of differences in home range variance among land cover types despite agriculture having both the smallest and the largest home ranges in our sample. A secondyear (SY) male with a home range of 3.99 ha in agriculture was excluded from the figure for clarity but included in all analyses. ASY = after second year.



**Fig. 3.** Relationship between body size and home range size in 49 wintering Yellow Warblers (*Setophaga petechia*). Larger males had smaller home ranges compared to smaller males, while we found no association between female body size and female home range size. Body size was estimated with a scaled sex-specific wing chord. Home range was defined by the 90% Kernel Utilization Distribution. Grey areas represent the 84% confidence interval. SY = second year; ASY = after second year.



ranges within crops to smaller territories in hedgerow. We observed similar inter-annual apparent return rates for both color-banded only and for color-banded and radio tracked birds  $(n = 133, \chi^2 = 0.03, 1 \text{ df}; P = 0.86)$ . Apparent return rate of radio-tracked males was not influenced by home range size  $(n = 32, \chi^2 = 0.6, 1 \text{ df}; P = 0.45)$ , land cover type  $(n = 32, \chi^2 = 2.5, 2 \text{ df}; P = 0.29)$ , or their interaction  $(n = 32, \chi^2 = 0.3, 2 \text{ df}; P = 0.87)$ . Within our known territory size group, only two females returned, precluding a formal test. Anecdotally these females' territories were well below the mean for the sex (0.9 ha) with home ranges of 0.15 and 0.55 ha.

# DISCUSSION

Like other Neotropical migrants (e.g., Wunderle 1995, Brown et al. 2000, Faaborg et al. 2010, Townsend et al. 2010, Oliviera et al. 2022), Yellow Warblers exhibited considerable intraspecific variation in the space-use strategies they employed during the wintering season. In this study, Yellow Warbler space-use ranged from occupying small, exclusive territories (often consisting of a single tree) to foraging within > 1 ha, non-exclusive territories. As we predicted, Yellow Warblers in riparian forest (high-quality sites) had smaller home ranges than those in coastal vegetation (low-quality sites), but contrary to our prediction, home ranges in agriculture were similar to home ranges in coastal vegetation. Across habitats, females had larger home ranges than males, and body size was inversely related to home range size in males. We found Yellow Warblers to be predominately site-faithful: 96% of returning birds (51 individuals) settled within their previous home ranges.

## Factors influencing home range size and their consequences

Our work shows differential space use-patterns between males and females, with large males having the smallest home ranges. This differential pattern extends to agricultural landscapes, where there was a tendency for females to have large home ranges in the crops and males to have small home ranges in the hedgerow. Our previous work shows that, across all land cover types, females have lower apparent monthly survival rates than males (juvenile females = 0.908, SE = 0.045, adult females = 0.934, SE = 0.032, juvenile males = 0.957, SE = 0.023, adult males = 0.969, SE = 0.016: Valdez-Juarez et al. 2019). The relationship between body size and home range together with lower female within-season survival, suggest space use patterns of wintering Yellow Warblers were at least partially driven by despotic segregation, as is the case with other wintering warblers (Marra and Holmes 2001, Smith et al. 2011, 2012). Female exclusion from high-quality wintering sites can lead to higher female mortality because of increased predation risk (Cuadrado 1997) or lower food availability in lower-quality home ranges (Marra et al. 1993). The differences in home range size by sex, as found in our study, can negatively influence population structure and dynamics if large home ranges are associated with lower survival (Adams 2001) and in turn, this can limit Neotropical migratory warbler populations (Sherry and Holmes 1996).

We found no evidence that age, another trait linked to competitive ability (Brown and Sherry 2008, Kresnik and Stutchbury 2014), influences home range size. These results with (sexually dimorphic) Yellow Warblers are in alignment with previous studies where sexually dimorphic species exhibited sex-based differences in space use patterns (Marra and Holmes 2001, Wunderle et al. 2014), whereas sexually monomorphic species had age-based differences in space-use patterns (Brown and Sherry 2008, Kresnik and Stutchbury 2014). We also found no evidence that migratory origin influenced home range size. This may be because migratory origin did not influence where an individual settled, or it may be because it did not influence an individual's ability to acquire and retain a territory. Regardless of the cause, our results match work with Ovenbirds (Seiurus aurocapilla), where migratory origin did not influence wintering home range size (Kresnik and Stutchbury 2014).

Our finding that Yellow Warbler home ranges were smaller in riparian forest than in coastal vegetation is consistent with survival data (Valdez-Juárez et al. 2019) that indicates coastal habitat is lowest quality land cover for wintering Yellow Warblers in our study system. It also aligns with previous studies that found Black-throated Blue Warblers (Setophaga caerulescens), Wilson's Warblers (Cardellina pusilla), and Kirtland's Warblers (Setophaga kirtlandii) had smaller home ranges in higher-quality natural habitats (Wunderle 1995, Ruiz-Sánchez et al. 2017, Wunderle et al. 2024). Our results for birds in agriculture relative to riparian habitat are more complex. Our previous work showed that birds in agriculture and riparian forest had similar survival rates. Our present work showed that birds in agriculture had, on average, larger home ranges than birds in riparian forest. Similar survival rates between riparian forest and agriculture, despite the larger home ranges in agriculture, could be because large home ranges in agriculture do not have a negative effect on Yellow Warbler survival. Alternatively, large home ranges in agriculture could have a negative effect on survival, but this effect is offset by high survival rates of Yellow Warblers with smaller territories. Our data do not have the resolution to distinguish between these two alternatives. Regardless of the cause, the high density of birds in agriculture (Valdez-Juárez et al. 2018), their similar survival rates with birds in riparian forest (Valdez-Juárez et al. 2019), and our present results, suggest that some features in agriculture (see below) provide suitable wintering sites for Yellow Warblers.

We found lower apparent return rates for females than males. This matches other warbler species (e.g., Latta and Faaborg 2002). Although the 49% male return rate found in our study is similar to other male wintering warblers return rates, the 25% female return rate in our study is lower than those found for Prairie Warblers (Setophaga discolor), Cape May Warblers (Setophaga tigrina), and American Redstarts (Setophaga ruticilla), at 45, 50%, and 51%, respectively (Marra and Holmes 2001, Latta and Faaborg 2001, 2002). Lower female return rates in our study could be due to higher female mortality in the breeding grounds as a result of the high costs associated with reproduction and greater predation pressure for nesting females (Thomson et al. 1998), or alternatively, it could be due to lower site-fidelity/higher female dispersal into more suitable wintering sites (Faaborg et al. 2010). Given that female interannual return rates at our wintering site are lower than the 30% female return rate observed at a western breeding location (Pavlik 2023), we believe lower winter site fidelity is a component. We observed one female switching home range between years; it is likely that many more were not observed. Our future work will model year-round survival for Yellow Warblers.

## Yellow warbler space-use patterns in agriculture

To our knowledge, this study presents the first quantification of space-use of a Neotropical migrant within seasonal agriculture. Our study shows that features present at our agriculture sites, such as diverse crop plantings, irrigation, and small fields divided by hedgerows and trees, provide foraging opportunities for Yellow Warblers. Small field size and non-crop vegetation likely increase habitat connectivity and foraging opportunities by increasing insect abundance and diversity (Hass et al. 2018). The asynchronous growth of the many crops at our site provides opportunities for habitat generalists that can track and exploit increased insect diversity in sites with heterogeneous crops (Hass et al. 2018, Sirami et al. 2019). This type of tracking produced some of the largest home ranges in our sample as birds foraged across different fields. These features may partially explain our previous findings that females in agriculture and riparian forest have similar survival rates (Valdez-Juarez et al. 2019).

# CONCLUSION

Our work has important implications for Neotropical migratory bird conservation in Latin America, where agricultural intensification is expected over the next three decades (Wilson et al. 2019). Practices associated with industrialized agriculture such as hedgerow removal, large field size, and monoculture, will reduce available wintering habitat for already declining migratory bird populations (Wilson et al. 2019). Industrialized agriculture and increased pesticide use may disproportionally impact females that are excluded from high-quality sites and forage in crops more frequently than males. Higher female mortality could potentially limit and reduce breeding populations (Faaborg et al. 2010). Further industrialization of agriculture in western Mexico will likely lead to declines in western populations, not only of Yellow Warblers but of many of the Neotropical migratory birds present at our field sites (Valdez-Juarez 2020). There is an opportunity to identify the key components of low-intensity cultivation that allow this form of agriculture to provide bird habitat. Retaining these components could ensure that there are co-benefits for people and birds in the future.

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# **Data Availability:**

*The data used for this analysis are available in Zenodo (<u>https://doi.org/10.5281/zenodo.13975037</u>). Please contact the lead author for access.* 

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