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RESEARCH ARTICLE

Use of natural and anthropogenic land cover by wintering Yellow Warblers: The influence of sex and breeding origin

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ABSTRACT

Sex, age, body size, and breeding origin can influence the nonbreeding distribution of long-distance migratory birds. At continental scales, differential migration can lead to segregation of various classes or populations among different regions. At local scales, class segregation can occur among habitats of differing qualities, often due to dominance interactions related to sex, age, and body size. Conversion of natural habitats to agriculture in the Neotropics is leading to more birds wintering in modified landscapes. We examined how sex, age, size, and breeding origin influenced the use of 3 land cover types (riparian gallery forest, coastal lagoon vegetation, and agriculture) by wintering migratory Yellow Warblers (*Setophaga petechia*) in western Mexico. Between 2012 and 2014, we used point counts in 6 study sites to estimate Yellow Warbler densities, and we captured, sexed, and aged 205 birds to characterize individuals using each land cover type. Breeding origin was inferred using stable hydrogen isotope ratios (δ^2H) in feathers. Contrary to our expectations, Yellow Warbler densities were highest in agricultural sites (5.6 ± 0.7 SE birds ha^{-1}) and lower in sites with natural land cover (riparian gallery forest: 3.6 ± 0.5 birds ha^{-1}; scrub mangrove: 2.0 ± 0.4 birds ha^{-1}). The Yellow Warbler population wintering in our study sites was male-biased (64%), and the use of sites with natural vs. agricultural land cover was not influenced by sex, age, or size of individuals, suggesting that competitive interactions are not limiting access to sites with different land cover. We found that females from more northerly breeding or natal origins were more likely to winter in sites with natural land cover, while females from more southerly origins were more likely to use agricultural sites. Our results suggest that localized population declines could occur via survival differences or carryover effects if condition or subsequent reproductive success differs between birds wintering in sites with natural vs. agricultural land cover.

Keywords: Nearctic–Neotropical migrant, wintering ecology, agriculture, stable isotopes, deuterium, Yellow Warbler, *Setophaga petechia*

Uso de coberturas del suelo naturales y antropogénicas por individuos invernantes de *Setophaga petechia*: Influencia del sexo y el origen de cría

RESUMEN

El sexo, la edad, el tamaño corporal y el origen de cría pueden influenciar la distribución no-reproductiva de las aves migratorias de larga distancia. A escala continental, la migración diferencial puede llevar a la segregación de varias clases o poblaciones entre diferentes regiones. A escalas locales, la segregación de clases puede darse entre hábitats de diferentes calidades, usualmente debido a interacciones de dominancia relacionadas al sexo, la edad y el tamaño corporal. La conversión de los hábitats naturales a agricultura en el Neotrópico está llevando a que más aves invernen en paisajes modificados. Examinamos cómo el sexo, la edad, el tamaño y el origen de cría influenciaron el uso de 3 tipos de coberturas de suelo (bosque ripario de galería, vegetación aledaña a lagunas costeras y agricultura) por parte de individuos migratorios de *Setophaga petechia* en el oeste de México. Del 2012 al 2014 llevamos a cabo puntos de conteo en 6 sitios de estudio para estimar densidades de *S. petechia* y determinamos el sexo y la edad de 205 aves capturadas con el fin de caracterizar a los individuos que usan cada tipo de cobertura de suelo. El origen de cría se infirió usando cocientes de isótopos estables de hidrógeno (δ^2H) en las plumas. Contrario a nuestras expectativas, las densidades de *S. petechia* fueron más altas en los sitios con agricultura (5.6 ± 0.7 EE aves ha^{-1}) y más bajas en los sitios con cobertura de suelo natural (bosque ripario de galería = 3.6 ± 0.5 aves ha^{-1}; vegetación aledaña a lagunas costeras

= 2.0 ± 0.4 aves ha^{-1}). La población de *S. petechia* invernando en nuestros sitios de estudio esta conformada en su mayoría por machos (64%) y el uso de sitios con cobertura del suelo natural o agrícola no estuvo influenciado por el sexo, la edad o el tamaño de los individuos, sugiriendo que las interacciones competitivas no limitan el acceso a los sitios con diferente cobertura de suelo. Encontramos que las hembras provenientes de orígenes de cría o nacimiento más al norte tuvieron mayor probabilidad de invernar en sitios con cobertura del suelo natural, mientras que las hembras de orígenes más al sur tuvieron mayor probabilidad de usar sitios con agricultura. Nuestros resultados sugieren que las disminuciones poblacionales localizadas podrían ocurrir debido a diferencias en la supervivencia o si la condición o si el éxito reproductivo subsecuente difiere entre aves invernando en sitios con cobertura de suelo natural o agrícola.

Palabras clave: agricultura, deuterio, ecología de invernada, isótopos estables, migrante neártico-neotropical, *Setophaga petechia*

INTRODUCTION

Population declines of many long-distance migratory songbirds over the last 4 decades (Sanderson et al. 2006, Holmes 2007, Rosenberg et al. 2016) have prompted a call for ecologists to move away from studies that focus only on breeding season ecology and toward studies that take a comprehensive approach that integrates all stages of the annual cycle (Faaborg et al. 2010, Marra et al. 2015, Rushing et al. 2016). Study of the full annual cycle requires an understanding of multiregional connectivity patterns between breeding grounds, stopover sites, and wintering grounds (Hobson et al. 2014a, 2014b), as well as factors that influence fine-scale winter habitat use (La Sorte et al. 2015, 2017). Stable isotope analyses of feathers grown at different periods of the annual cycle have been useful for establishing basic multiregional connectivity patterns for small songbirds in Europe and the Americas (Hobson 2008, Hobson et al. 2014a, 2014b). However, relatively few studies have examined how breeding origin influences the fine-scale habitat use of migrants in their wintering areas (but see de la Hera et al. 2012).

Migratory songbirds occupy a variety of habitats on their wintering grounds (Hutto 1980, Lynch 1989). For several species, condition, survival, and the ability to initiate migration earlier in the spring is linked to the type of habitat in which an individual spends the winter (Marra and Holmes 2001, Latta and Faaborg 2002, Smith et al. 2010). Further, competitive ability can influence whether an individual is able to overwinter in high-quality habitat. Thus, competitive asymmetries among classes of individuals can lead to uneven distributions of these classes across wintering habitats (Webster and Marra 2005). Indeed, numerous studies have reported that age (Latta and Faaborg 2002, Catry et al. 2004), size, and sex (Lopez Ornat and Greenberg 1990, Wunderle 1995, Marra 2000) can influence winter habitat use by songbirds, with younger, smaller, and female birds experiencing a competitive disadvantage. Alternatively, gender differences in winter habitat use might be a product of innate habitat preferences between males and females; however, support for this hypothesis is limited (but see Morton 1990).

Winter habitat use could additionally be influenced by breeding origin via timing of arrival at wintering sites. On the breeding grounds, timing of arrival has been shown to affect the quality of the breeding territory that a bird is able to acquire (Smith and Moore 2005, McKellar et al. 2013), with potential consequences for offspring condition and survival (Vitz and Rodewald 2011). Breeding or natal origin can also influence the timing of arrival of songbirds at stopover sites during fall migration (Dunn et al. 2006, Kelly 2006, González-Prieto et al. 2011) or arrival at wintering grounds (Bueno 1998, Martell et al. 2001). If arrival time at the wintering grounds influences an individual's ability to obtain a high-quality winter territory, breeding origin could influence the habitat use of species that are territorial in winter. However, there is currently little evidence to suggest that breeding origin influences winter habitat use of migratory songbirds (de la Hera et al. 2012, Catry et al. 2016).

Segregation of winter habitat use by sex, age, or breeding origin has the potential to explain spatial patterns of population declines on the breeding grounds (Marra et al. 2015, Rushing et al. 2016). Widespread declines are predicted to occur if a region-wide loss of high-quality habitat differentially forces a particular class of birds into poor-quality habitat on the wintering grounds, thus reducing their survival or productivity (Marra and Holmes 2001, Diggs et al. 2011). Localized population declines on the breeding grounds are predicted to occur if there is a high degree of migratory connectivity between a given breeding location and a wintering location experiencing high rates of habitat loss (Rubenstein et al. 2002).

Clearing of native vegetation and conversion of natural habitat to agriculture has resulted in extensive loss of natural land cover in Mexican lowlands (Bonilla-Moheno et al. 2012). From 1993 to 2011, tropical dry forest and riparian gallery forest cover shrank by 8% and 14%, respectively (FAO 2015). The current rate of deforestation has diminished but continues at an annual rate of 0.14% (FAO 2015). Mexican lowlands have the highest diversity of wintering migrants in the Neotropics (Hutto 1980, Rich et al. 2004). Consequently, many wintering migrant species now use both floristically diverse natural cover and simpler

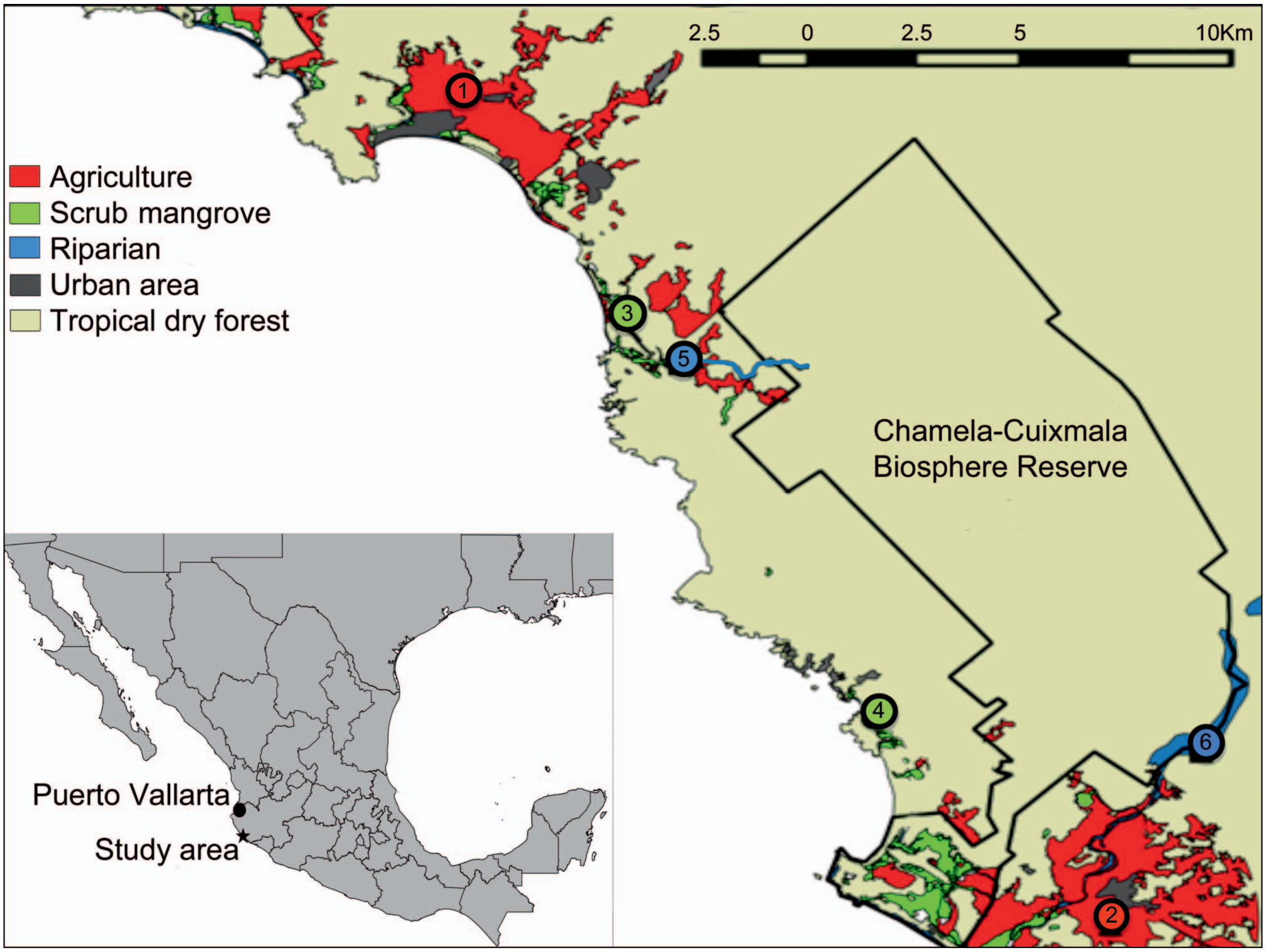

FIGURE 1. Locations of study sites near the Chamela-Cuixmala Biosphere Reserve in Jalisco, Mexico, where we examined how age, sex, size, and breeding origin influenced the use of 3 land cover types by wintering Yellow Warblers. The locations of nearby towns (1,2), beaches (3,4), and rivers (5,6) are indicated by circles, and coordinates are as follows: (1) Punta Pérula, 19.6019°N, 105.1197°W; (2) Zapata, 19.3797°N, 104.9722°W; (3) Xametla Beach, 19.5382°N, 105.0806°W; (4) Careyitos Beach, 19.4339°N, 105.0238°W; (5) Chamela River, 19.5274°N, 105.0717°W; and (6) Cuixmala River, 19.4421°N, 104.9358°W. Land use data are modified from CONABIO (2015).

agricultural land cover. Despite the potential implications of land use changes for wintering migratory songbird populations, we know little about which individual attributes (i.e. sex, age, breeding origin) might influence the use of natural and anthropogenic land cover in Mexico.

We investigated the winter use of 3 different land cover types by migratory Yellow Warblers (*Setophaga petechia*) in Jalisco, western Mexico (Figure 1). We used stable hydrogen isotope analysis of primary feathers (δ^2H_f) to determine the likely breeding origins of individuals in this wintering population. We then examined how sex, age, body size, and breeding origin influenced the use of 2 types of natural land cover (riparian gallery forest and coastal lagoon vegetation, hereafter 'scrub mangrove') and agriculture. The quality of winter habitat for some migratory passerines increases with moisture (Sherry and Holmes 1996, Latta and Faaborg 2002). At our study site, we thus predicted that more mesic riparian gallery forest would provide the highest quality land cover, irrigated agriculture intermediate quality land cover, and drier coastal scrub mangrove the lowest quality land cover. If competitive asymmetries between age and sex classes drive the use of different land cover types, we would predict that older, larger, male birds would be more abundant in the riparian gallery forest, while younger, smaller, and female birds would predominate in the drier scrub mangrove. Further, if the timing of arrival influences settlement patterns, we would predict that northern-origin birds (which pass through stopover sites earlier than southern-origin populations during fall migration; Kelly 2006, González-Prieto et al. 2011) would be more likely to occupy riparian gallery forest than southern-origin birds.

METHODS

Study Species

Migratory Yellow Warblers include 3 lineages distinguishable by their mitochondrial DNA (Boulet et al. 2006). All 3 lineages are Nearctic–Neotropical migrants; however, each lineage has a distinct pattern of migratory connectivity. The western lineage breeds west of Manitoba (Canada) and winters mainly in western Mexico and Central America. The southern lineage breeds in the southwestern U.S. and winters mainly in northwestern Mexico. Lastly, the eastern lineage breeds east of Manitoba and winters predominantly in Yucatan (Mexico), Central America, and northern South America (Boulet et al. 2006). Yellow Warblers spend the winter in the Neotropics in a variety of natural (e.g., riparian gallery forest, mangroves, evergreen forest) and human-modified land cover types (e.g., coffee and palm plantations, cattle pasture, and cropland), typically at elevations <500 m above sea level (Hutto 1980, Greenberg et al. 1996, Curson 2010, S. O. Valdez-Juárez personal observation).

Adult Yellow Warblers replace all of their flight feathers during a prebasic molt on the breeding grounds before fall migration (Pyle 1997, Quinlan and Green 2011). Therefore, wintering birds can be assigned to breeding origin using δ^2H analyses of feathers replaced during the prebasic molt (Quinlan and Green 2011) and an established North American feather δ^2H isoscape (Hobson et al. 2012).

Study Area

We studied Yellow Warblers adjacent to the Chamela-Cuixmala Biosphere Reserve, ~160 km southeast of Puerto Vallarta in Jalisco, Mexico (19.4789°N, 105.0439°W; Figure 1). Average annual precipitation in this region is 788 mm, with 80% falling between June and November and only 5% from January to May (IBUNAM 2007). Vegetation within the reserve is predominantly tropical dry forest. Land cover in the surrounding area is a mixture of natural vegetation on undeveloped private properties and agriculture (Figure 1). Exploratory surveys found that Yellow Warblers were abundant in riparian gallery forest, scrub mangrove, and agriculture, but were not present in tropical dry forest. We did not observe any resident male Mangrove Yellow Warblers with their diagnostic red heads. Our observations are consistent with previous surveys that have not recorded resident Mangrove Yellow Warblers in Jalisco (Hutto 1980, eBird 2012).

Riparian gallery forest in our study area is found primarily along the Chamela and Cuixmala rivers, which border the Biosphere Reserve, and this forest is relatively undisturbed by human activity. The dominant tree species along these rivers are *Astronium graveolens*, *Brosimum alicastrum*, *Bursera arborea*, *Couepia polyandra*, and *Cynometra oaxacana* (Lott 1993). Scrub mangrove surrounds coastal lagoons on undeveloped private land and is a mixture of mangrove trees at the shoreline grading to tropical dry forest. The dominant tree species are *Rhizophora mangle*, *Avicennia germinans*, *Conocarpus erectus*, and *Laguncularia racemosa* (Lott 1993). Agriculture is found in the vicinity of the towns of Punta Pérula and Zapata (populations <1,000; INEGI 2010) and consists of small (4 ha) irrigated fields bordered by 1–2 m wide hedgerows containing a mixture of small shrubs and larger trees. The main crops of the region include papayas and mangoes (grown in plantations) and seasonally harvested herbaceous crops (sorghum, corn, chili peppers, tomatoes, cucumbers, and watermelons).

Field Protocols

We established 2 study sites of ~4.5 ha each in each of the 3 land cover types. Sites with the same type of land cover were at least 10 km apart (Figure 1). We estimated Yellow Warbler density within land cover types using 10-min point counts during February and March of 2013 and 2015. We placed point count locations within the same study site 250 m apart along nonoverlapping transects. In agricultural sites, transects followed the lanes separating fields. The length of each transect and consequently the number of point counts that we were able to conduct varied in relation to the availability of each land cover type (riparian forest: $n = 169$ point counts; scrub mangrove: $n = 86$ point counts; agriculture: $n = 194$ point counts). Point counts began at sunrise (~0700 hours) and were continued until 1100 hours. An observer recorded all Yellow Warblers detected by sight and sound without attempting to determine age or sex. A total of 3 trained observers conducted all point counts. We estimated the distance from the observer to each bird within 10 m intervals. We selected a narrow distance interval to minimize the tendency to overestimate bird density using distance-based sampling with wide distance intervals (Quesada et al. 2010).

Bird banding took place from January to April in 2012, 2013, and 2014; however, only birds captured in January–March were included in analyses as transients start arriving in the area in early April (S. O. Valdez-Juárez personal observation). We attempted to capture all birds within each site using both passive mist-netting and mist-netting with playback of conspecific calls. Although the use of playback can potentially bias capture rates if males respond more frequently to conspecific calls than females (Lecoq and Catry 2003), a more frequent male response is not universal across species (Chin et al. 2014, Wojczulanis-Jakubas et al. 2016). We found that female Yellow Warblers were as likely as males to respond to the "chip" calls used during playback. Neudorf and Tarof (1998) also found that both sexes were equally likely to respond to "chip" call playback. We therefore do not believe that using call playback biased the sex ratio of our sample. Mist-netting took place from sunrise to sunset, with a break during the hottest part of the day (1200–1500 hours). We fitted each captured bird with a U.S. Geological Survey (USGS) aluminum band and 3 color bands in a unique combination. We recorded all birds resighted in each study site during visits on every second day from January to April. Banding and resighting efforts were evenly distributed across habitats in 2012 and 2013. In 2014, we were not able to band birds in scrub mangrove, but we still resighted birds across all 3 habitats; in scrub mangrove we looked for birds banded in previous years.

We determined the sex and age (juvenile [second-year] or adult [after-second-year]) of each captured bird using plumage coloration, molt limits, and the presence of tapered feathers and pale lower mandibles (Pyle 1997). The sexing of wintering adult males is reliable, but there is some uncertainty around the sexing and aging of females and juveniles caught between September and March (Pyle 1997). However, resighting and recapture data across years suggested that we correctly aged and sexed the majority of birds (see Results). We measured tarsus to the nearest 0.1 mm and unflattened wing chord to the nearest 1 mm with calipers and a wing rule, respectively. Before release, we also collected a summer-grown outermost primary covert (PC9) from each wing to determine the Nearctic breeding origin of each individual. Collected feathers were placed in individually labeled paper envelopes and stored in a cardboard box at room temperature.

Stable Isotope Analysis and Assignment to Breeding Origin

We washed all feathers in a 2:1 chloroform:methanol solution for 24 hr, then drained and air-dried them in a fume hood for an additional 24 hr to remove excess solvent. We placed 0.700 ± 0.004 (SE) mg of each bird's feathers into a 9 × 5 mm smooth-walled silver capsule (Elemental Microanalysis, Okehampton, Devon, UK). Samples were analyzed at the University of California Davis Stable Isotope Facility (Davis, California, USA) using a zero blank carousel Hekatech HT Elemental Analyzer (1,350°C) in line with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon, Crewe, Cheshire, UK). We corrected for the uncontrolled isotopic exchange between feathers and ambient water vapor with comparative equilibration using 3 calibrated keratin standards (CBS [caribou hoof standard]: –197.0‰, BWB [bowhead whale baleen]: –108.0‰, and KHS [kudu horn standard]: –54.1‰; Wassenaar and Hobson 2003). The nonexchangeable hydrogen isotope ratios (δ^2H) are expressed in per mil units relative to the international standard V-SMOW (Vienna Standard Mean Ocean Water), with an estimated measurement precision of <2‰ based on within-run replicates of keratin standards.

We determined probable breeding (adult) or natal (juvenile) origins of wintering Yellow Warblers using a spatially explicit assignment model following Hobson et al. (2014a). We restricted the potential breeding origin to the portion of the range in which $>50\%$ of Yellow Warblers from the western and southern lineages occur, given that Yellow Warblers wintering in western Mexico belong exclusively to these lineages (Boulet et al. 2006). We then clipped a GIS-based model (Terzer et al. 2013, IAEA 2017) of expected amount-weighted growing-season average δ^2H in precipitation ($\delta^2\text{H}_\text{p}$) to the modified breeding range using the functions in the raster package (Hijmans 2016) in the R 3.3.3 statistical computing environment (R Core Team 2014). We transformed the clipped $\delta^2\text{H}_\text{p}$ isoscape into a feather δ^2H ($\delta^2\text{H}_\text{f}$) isoscape using the calibration equation for nonground-foraging Nearctic–Neotropical migrants: $\delta^2\text{H}_\text{f}$ isoscape $= -27.09 + 0.95 * \delta^2\text{H}_\text{p}$ (Hobson et al. 2012). Each raster cell (18.8 km^2) in the resulting surface therefore contained the expected local $\delta^2\text{H}_\text{f}$ value. We used the following equation to determine the likelihood of a bird originating from a given cell in the $\delta^2\text{H}_\text{f}$ isoscape:

$$f(y^*|\mu_c,\sigma_c)=\left(\frac{1}{\sqrt{\pi\sigma_c}}\right)exp\left[-\frac{1}{2\sigma_c^2}(y^*-\mu_c)^2\right],$$

where $f(y^* \mid \mu_c, \sigma_c)$ is the probability that a given cell in the $\delta^2\text{H}_\text{f}$ isoscape represents the origin for an individual (origin y^*), given the expected mean $\delta^2\text{H}_\text{f}$ for that cell (μ_c) and the expected standard deviation (σ_c) of $\delta^2\text{H}_\text{f}$ between individuals growing their feathers in the same locality. We used a value of $\sigma_c = 14.4$‰, based on the estimate for nonground-foraging Neotropical migrants reported by Hobson et al. (2012).

We used the likelihood ratios obtained from the above equation to obtain a set of spatially explicit probability densities for individual birds. We reclassified the probability densities for each cell into likely vs. unlikely origins by specifying a 2:1 odds ratio. We coded cells that defined the upper 67% of estimated probabilities of origin as 1 (likely) and all others as 0 (unlikely). We then stacked the resulting maps for individual birds to provide depictions of probable origins for each age and sex class separately.

Statistical Analysis

We estimated the density of Yellow Warblers in each land cover type using point count survey data and program Distance 7.0 (Thomas et al. 2010). The initial detection probability models included observer, time of day, and year as covariates. We selected the best detection function for each land cover type and a final model based on the lowest Akaike's information criterion (AIC) value. The best detection function was half-normal in riparian gallery forest and agriculture, and uniform in scrub mangrove. The best model included time of day and observer as covariates. The radius of detection was truncated to 60 m to improve the fit of the detection function. Our analysis therefore included 94% of all the birds detected. Significant differences in bird density between land cover types were assessed by the extent of overlap of the 84% CI, rather than the 95% CI, to minimize type I error (MacGregor-Fors and Payton 2013). All values are reported as means ± SE.

We used chi-square tests ($P < 0.05$) in the built-in package stats in R 3.3.3 (R Core Team 2014) to compare the proportion of males and females and the proportion of juveniles and adults banded across years and in the 3 land cover types. We then compared the δ^2H_f of males vs. females and juveniles vs. adults using 2-way ANOVA ($P < 0.05$). We used diagnostic model plots to evaluate the distribution of the data, to verify that the residuals showed no trends and were homoscedastic, and to check for overly influential outliers.

We then used a series of multinomial logistic regression analyses to examine whether the sex, age, size, or breeding origin of warblers influenced their use of the 3 land cover types. We again used diagnostic model plots to confirm normality, homoscedasticity, absence of overly influential outliers, and lack of trends in the residuals. Breeding origin was inferred using the δ^2H_f of the PC9 primary covert feathers. We estimated skeletal body size using the first principal component (PCA1) of a principal components analysis that combined unflattened wing chord and tarsus length (Marra 2000). We selected the minimal adequate model by starting with a full model that included all 4 main effects and all 2-way interaction terms and sequentially eliminating nonsignificant ($P > 0.1$) interaction terms and main effects until only significant terms remained. Significance was assessed using likelihood ratio tests that compared models with and without the term of interest. To further investigate weak evidence for differences between the sexes in the factors influencing the use of different land cover types (see Results), we repeated this analysis separately for females and males. We used packages nnet (Venables and Ripley 2002) and car (Fox and Weisberg 2011) in R for the multinomial logistic regression analyses.

RESULTS

Overwintering Yellow Warbler density varied with land cover (Figure 2). Agriculture had the highest density of Yellow Warblers (5.6 ± 0.7 birds ha^{-1}). Yellow Warbler density was intermediate in riparian gallery forest (3.6 ± 0.5 birds ha^{-1}) and lowest in scrub mangrove (2.0 ± 0.4 birds ha^{-1}). We captured a total of 205 birds: 94 in agriculture, 66 in riparian gallery forest, and 45 in scrub mangrove. The sex ratio of birds captured for the first time was significantly male-biased (60%, $n = 205$; $\chi^2 = 9.11$, $P = 0.003$). Although there was no detectable year effect on the percentage of males captured (2012 = 65%, 2013 = 58%, 2014 = 52%; year effect, $\chi^2_2 = 2.09$, $P = 0.35$), the pattern of male bias appeared to be stronger in the first 2 yr of the study. We observed 81 banded birds across years, 17 of which were recaptured. Among birds that we cross-checked across years, we had correctly sexed 95% of the males ($n = 61$ individuals) and 95% of the females ($n = 20$ individuals). We corrected the misclassifications before analyzing the data. Combining capture and resighting data, we found that sex ratios were uniformly male-biased in all land cover types (agriculture = 59 ± 11%, $n = 6$ site-years; riparian gallery forest = 72 ± 12%, $n = 6$ site-years; scrub mangrove = 60 ± 19%, $n = 4$ site-years; combined = 64 ± 16%; $\chi^2_2 = 3.63$, $P = 0.16$). Using the same dataset, we also found that age ratios tended to be adult-biased in all land cover types (agriculture = 56 ± 9% adults; riparian gallery forest = 70 ± 7% adults; scrub mangrove = 57 ± 18% adults; $\chi^2_2 = 4.44$, $P = 0.11$).

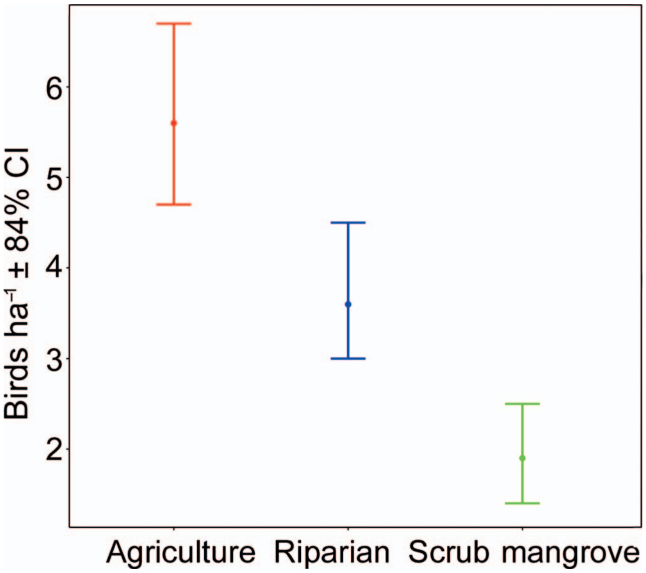

FIGURE 2. Yellow Warbler densities (mean ± 84% CIs) in 3 land cover types in Jalisco, Mexico.

We obtained δ^2H_f values from 205 summer-grown primary coverts (PC9) collected from 191 birds. Of the 14 birds recaptured across years, 6 birds were first captured as juveniles and 8 were first captured as adults. The δ^2H_f in the entire sample varied from –73.0‰ to –195.5‰ (–140.2 ± 1.3‰). Males and females had similar δ^2H_f values (males: –139.8 ± 2.1‰, $n = 127$; females: –140.9 ± 2.4‰, $n = 78$; $F_{1,203} = 0.14$, $P = 0.71$). Juveniles (–143.9 ± 2.2‰, $n = 98$) had significantly lower δ^2H_f values than adults (–136.9 ± 2.1‰, $n = 107$; $F_{1,203} = 6.98$, $P = 0.009$). We also detected an age effect in δ^2H_f values for the 6 individuals captured as juveniles and adults (mean difference = 23 ± 2.4‰ higher as adults; paired t-test = –3.8, $P = 0.004$).

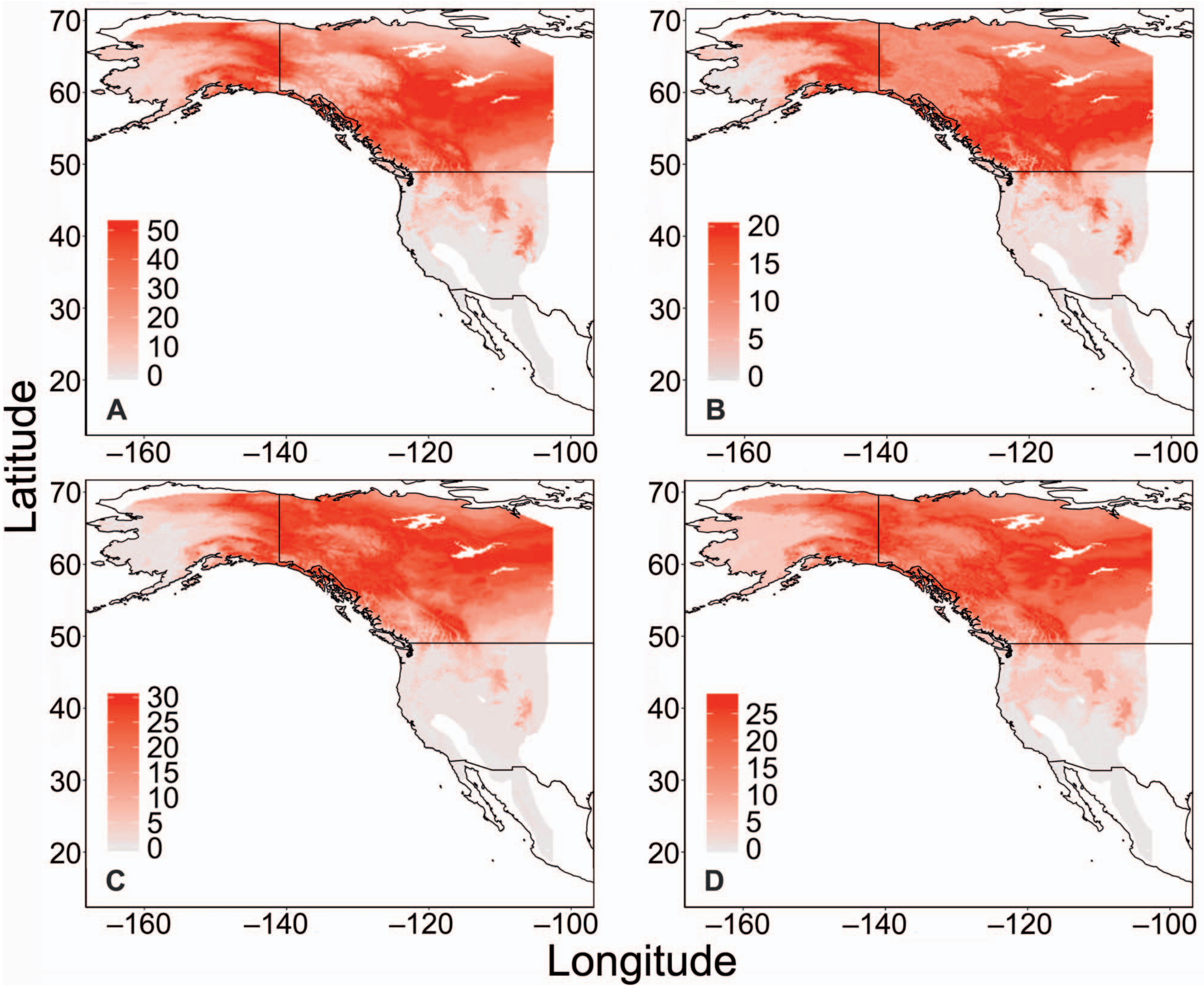

FIGURE 3. Probable breeding origins of (**A**) adult male, (**B**) adult female, (**C**) juvenile male, and (**D**) juvenile female Yellow Warblers overwintering in Jalisco, Mexico. Potential breeding origins were restricted to the portion of the range where >50% of Yellow Warblers from the western and southern lineages occur (Boulet et al. 2006). Scales indicate the numbers of individuals that were isotopically consistent with a similarly colored pixel within the breeding range.

Breeding Area Assignment

We found that the wintering population of adult Yellow Warblers in western Mexico was most likely to have had breeding origins in Canada or Alaska (USA), rather than the contiguous U.S. (Figures 3A and 3B). The majority of wintering adult males and females were likely to have come from the Canadian provinces of British Columbia, Alberta, and Saskatchewan, or from eastern Alaska in the U.S. Few adults were likely to have come from southwestern Alaska, the west coast, the Great Plains of the U.S., or the Sierra Madre Occidental in Mexico. Concordant with juvenile Yellow Warblers having lower δ^2H_f values than adults, we found that the wintering population of juveniles was most likely to have originated from eastern Alaska and the Yukon and Northwest Territories of Canada (Figures 3C and 3D).

Winter Use of Different Land Cover Types by Yellow Warblers

The multinomial logistic regression analysis that combined data for both sexes suggested that breeding origin had different effects on the use of the 3 land cover types by wintering female and male Yellow Warblers (δ^2H_f*sex, $\chi^2_2 = 5.76$, $P = 0.06$). Age and body size had no detectable effects on the use of the 3 land cover types by either female or male Yellow Warblers (age, $\chi^2_2 = 2.13$, $P = 0.34$; age*sex, $\chi^2_2 = 3.79$, $P = 0.15$; age*δ^2H_f, $\chi^2_2 = 0.64$, $P = 0.72$; size, $\chi^2_2 = 1.37$, $P = 0.50$; size*sex, $\chi^2_2 = 0.81$, $P = 0.42$; size*δ^2H_f, χ^2_2

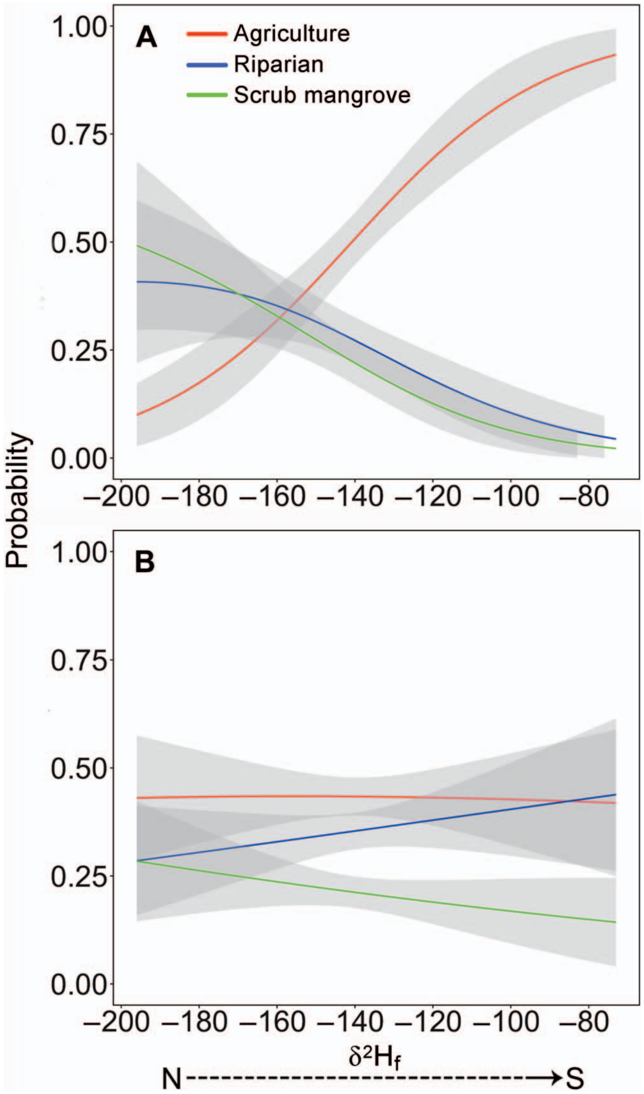

FIGURE 4. Relationship between the concentration of deuterium in primary covert feathers (δ^2H_f) and the use of sites with natural and anthropogenic land cover by (**A**) female and (**B**) male Yellow Warblers during the winters of 2012 to 2014 in Jalisco, Mexico. Lower δ^2H_f values indicate more northerly breeding origins of overwintering birds. Lines show predicted relationships from the minimal adequate model that included the main effects of sex and δ^2H_f and their interaction (sex*δ^2H_f). The shaded areas illustrate 95% CIs.

$= 0.46$, $P = 0.79$). The minimal adequate model predicted that the probability of females occupying sites with natural land cover (either riparian gallery forest or scrub mangrove) declined as δ^2H_f increased (Figure 4A). In contrast, the probability of males occupying sites with natural land cover did not change with δ^2H_f (Figure 4B). The post hoc analyses conducted for each sex separately confirmed that breeding origin had a significant effect on the use of the 3 land cover types by females (δ^2H_f, $\chi^2_2 = 10.38$, $P = 0.006$), but no effect on the use of the 3 land cover types by males (δ^2H_f, $\chi^2_2 = 0.79$, $P = 0.96$).

DISCUSSION

Migratory Yellow Warblers wintering in our study area occupied sites with both natural and anthropogenically modified land cover, but, somewhat surprisingly, we found the highest densities of Yellow Warblers in agriculture. This result contrasts with the wintering distribution of Wilson's Warblers (*Cardellina pusilla*), which are found in lower densities in agriculture relative to mature cloud forest (Ruiz-Sánchez et al. 2017). Irrigated agriculture may be attractive to Yellow Warblers in our study area as the natural land cover is xeric and dry conditions intensify as the winter and spring progress. Alternatively, the limited availability of natural land cover (e.g., riparian gallery forest and dry scrub mangrove; Figure 1) may force most birds to occupy agricultural areas.

Yellow Warblers wintering in the 3 studied land cover types could have had breeding or natal origins anywhere within the breeding range of the western and southern lineages (from the Canadian tundra to northern Mexico). However, most of the wintering population was likely to have had originated from the northern portion of the breeding range. Our finding confirms the results of earlier work that assigned the majority of Yellow Warblers wintering in northwestern Mexico to the western lineage that breeds in Canada (Boulet et al. 2006). Our results are also consistent with Boulet et al.'s (2006) conclusion that populations in the western lineage undergo a chain migration, with the northernmost population overwintering at the northern edge of the wintering range.

We found that the δ^2H_f of adults was higher than that of juveniles. Thus, juvenile birds were assigned to more northerly origins than breeding adult birds. This could reflect real differences in the natal and breeding origins of juvenile and adult Yellow Warblers, respectively, but could also be due to differences in δ^2H_f that are independent of origin. Previous studies with warblers of known natal and breeding origins found that nestling flight feathers had lower δ^2H_f values than flight feathers of adults from the same locations, possibly because of differences in their diets, water sources, or metabolic rates (Langin et al. 2007, Haché et al. 2012). If we correctly assigned juveniles to their natal origins, the differences in origin between age classes could have arisen because of a tendency of adult birds to disperse south of their natal origins to benefit from shorter migrations (Studds et al. 2008).

We found that Yellow Warblers captured in the northern portion of their wintering range in Jalisco, Mexico, were predominantly male. The male bias observed in our study (64%) is consistent with previous work describing a latitudinal gradient in the sex ratio of wintering Yellow

Warblers. Komar et al. (2005) found a male bias (65% males) for Yellow Warblers captured in Mexico, but equal sex ratios for those captured in Central America. Studies at a continental scale have often reported latitudinal gradients in sex ratios of Nearctic–Neotropical migrants on the wintering grounds, with males typically overwintering north of females (Cristol et al. 1999, Nebel et al. 2002, Komar et al. 2005). Latitudinal gradients in sex ratio could arise because males wintering farther north benefit from shorter migration distances, thus arriving earlier on the breeding grounds, or because larger males might competitively exclude females from preferred parts of the wintering range (Komar et al. 2005).

Winter segregation between ages or sexes can also arise at a local scale if competitive asymmetries determine which individuals occupy high-quality habitat (Marra 2000). However, we found little evidence that traits linked to dominance, such as size and age, influenced Yellow Warbler use of wintering sites with different land cover. This result contrasts with findings for American Redstarts (*Setophaga ruticilla*) and Black-throated Blue Warblers (*S. caerulescens*) wintering in the Caribbean. In both species, larger adult males were found more frequently in higher-quality habitats (Wunderle 1995, Marra 2000). Similarly, age influenced the winter habitat use of Cape May Warblers (*S. tigrina)* in the Caribbean, where adults of both sexes were predominant in higher-quality habitats (Latta and Faaborg 2002). The lack of sex, age, or size differences among Yellow Warblers wintering in sites with different land cover in our study suggests either reduced dominance interactions between classes of Yellow Warblers, or reduced habitat quality differences associated with land cover types compared with other studies.

We predicted that breeding origin would influence the use of sites with different land cover in winter because birds from more northerly latitudes precede southern conspecifics to stopover sites during fall migration (Kelly 2006, González-Prieto et al. 2011). Assuming that early migration predicts earlier arrival on the wintering grounds, we expected birds with more northerly origins to preferentially occupy the highest-quality winter sites. Our prediction was only partially supported, as breeding origin influenced only female use of sites that differed in land cover. Females with the lowest δ^2H_f values (less than –170‰), and thus with likely origins in eastern Alaska, Yukon, and the Northwest Territories, were most likely to winter in sites with natural land cover. This result suggests that riparian gallery forest and scrub mangrove either are high-quality habitats or are preferred by northern-origin females. Conversely, northern-origin females may have avoided agriculture. The latter explanation is more likely, given that scrub mangrove is xeric, supports the lowest density of Yellow Warblers, and presumably provides low-quality habitat. Females with higher δ^2H_f values (greater than –140‰) and likely origins in the contiguous U.S. or northern Mexico may have been more familiar with and had a preference for agriculture. Alternatively, if these females arrived late, they may have had fewer opportunities to settle in sites with natural land cover. Further work that includes arrival times at the wintering grounds is required to determine the causes behind the observed pattern.

Irrespective of the cause of the observed distribution of Yellow Warblers across sites with different land cover, our results suggest that winter habitat conversion to agriculture could have both localized and widespread effects on the population dynamics of Yellow Warblers. We have shown that the highest density of wintering Yellow Warblers occurs in agriculture, where anthropogenic stressors such as pesticide use could reduce winter survival or subsequent productivity (Mineau and Whiteside 2013). In addition, our finding that breeding and natal origins influence the winter distribution of female Yellow Warblers suggests that localized declines could occur either directly via survival differences or indirectly via carryover effects if condition or subsequent reproductive success differs between birds wintering in sites with natural land cover vs. agriculture. Further work on how demography varies with land cover on the wintering grounds will clarify the influence of agriculture on regional variation in the population dynamics of migratory songbirds.

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