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Assessing the effect of seasonal agriculture on the condition and winter survival of a migratory songbird in Mexico

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Migratory birds can spend 8 months of the year on their wintering grounds and the conversion of natural habitats to agriculture in Latin America has been implicated in population declines of several Neotropical migrants. Despite this, few studies have directly assessed the value of agricultural habitat for wintering migrants. We compared the condition and survival of Yellow Warblers (*Setophaga petechia*) occupying natural (riparian forest, scrub-mangrove) and agricultural habitat (annually cropped sorghum, corn, and chili-peppers separated by hedgerow) in western Mexico. We assessed condition with five metrics (daily and seasonal changes in size-adjusted body mass, leukocyte profiles, rectrix regrowth rate, rectrix quality, and dates of departure on spring migration). We used Cormack–Jolly–Seber models fitted to mark-resighting data collected over 4 years (2012–2015) to estimate January–May monthly survival rates. We found that birds occupying agricultural habitat and riparian forest had higher monthly apparent survival between January and May than birds in scrub-mangrove. Birds in agricultural habitat also grew higher quality feathers (i.e., rectrices with a higher barbule density) than those in natural habitat. In contrast, birds in agricultural habitat were lighter than those in riparian habitat. We found no detectable effect of winter habitat use on daily or season changes in size-adjusted mass and H/L ratios, although the effect of winter habitat use on departure rates differed for males and females. Our results demonstrate that agricultural habitat may provide suitable winter habitat for a long-distance migrant and suggest that feather quality can be an indicator of winter habitat quality.

KEYWORDS
agricultural habitat, feather quality, habitat quality, *Setophaga petechia*, wintering habitat, Yellow Warbler

1 | INTRODUCTION

Four billion birds from 250 species migrate between breeding grounds in North America and wintering grounds in the Neotropics (Berlanga, Kennedy, & Rich, 2010). The difficulty associated with following migratory birds throughout the four distinct periods of their annual cycle (breeding, autumn migration, winter, and spring migration) and the long standing notion that the reproductive period has the most influence over bird fitness and demography (Böhning-Gaese, Taper, & Brown, 1993) has led to a research bias towards the breeding period (Marra, Cohen, Loss, Rutter, & Tonra, 2015). Fewer studies have focussed on the winter period although it encompasses over 60% of the annual cycle. There is still a widespread need of assessment of which species spend the winter in which habitats, what the

demographic consequences are of that habitat occupancy, and the conservation value of many types of native and anthropogenic habitats (Faaborg et al., 2010).

Most research dealing with long-distance migrants wintering in anthropogenic habitats in the Neotropic found that diversity and abundance are higher in agroforestry systems than in unshaded monocultures or in natural habitats (reviewed by Johnson, Jedlicka, Quinn, & Brandle, 2011). Less is known about the condition and survival of the millions of birds wintering in these habitats in the Neotropic (Faaborg et al., 2010). Conditions during the winter period have been shown to influence the body condition (Angelier, Tonra, Holberton, & Marra, 2011; Johnson, Sherry, Holmes, & Marra, 2006; Smith, Reitsma, & Marra, 2010; Stirnemann, O'Halloran, & Donnelly, 2012) and survival (Studds & Marra, 2005) of long-distance migrants. Agroforestry systems, such as shade-grown coffee or citrus plantations, can provide suitable winter habitat for migratory songbirds (Johnson et al., 2006; Bakermans, Vitz, Rodewald, & Rengifo, 2009; but see Rappole, King, & Rivera, 2003). Migratory birds that overwinter in severely modified habitats (e.g., clear-cut logging, cattle pasture) have been found to be in poorer condition and have lower survival than those in natural habitats (Golden-cheeked Warbler [_Setophaga chrysoparia_; Rappole, King, & Leimgruber, 2000)] Wilson's Warbler [_Cardellina pusilla_; Ruiz-Sánchez, Renton, & Rueda-Hernández, 2017]).)Negative habitat effects on individual condition and survival can translate to negative demographic trends if habitat loss or modification affects large segments of the population (LaSorte et al., 2017).

Lowlands in Mexico are host to the highest density and diversity of long-distance migrants in the Nearctic-Neotropical migration system (Rich et al., 2004). Natural habitat in Mexico, however, has been converted to agriculture at an annual rate of 150,000 ha over the last 20 years (FAO, 2015). The most widespread crops in Mexico are corn and sorghum, with 8.1 and 1.7 million ha planted respectively (Johnson et al., 2011). The most productive areas for both crops are the lowlands (SIAP, 2017). However, very little is known about the condition and survival of Neotropical migrants wintering in annually cropped monocultures, to the best of our knowledge ours is the first study to assess how an annually cropped agricultural system influences the condition and survival of a Neotropical long-distance migratory songbird.

In this study, we investigated how winter habitat use in Western Mexico affects the physiological condition and survival of a long-distance migrant, the Yellow Warbler (_Setophaga petechia; aestiva_ group). We used five metrics (daily and seasonal changes in size-adjusted mass, leukocyte profiles, rectrix regrowth rate, rectrix quality, and departure dates on spring migration) to assess the condition of birds in riparian forest, coastal lagoon vegetation (hereafter scrub-mangrove), and annually cropped agriculture. We used a 4-year mark-resighting data to estimate overwinter survival in each habitat type. Based on previous studies in Caribbean Islands (Smith et al., 2010; Studds & Marra, 2007) we predicted that birds in mesic riparian forest would be in better condition and have higher overwinter survival than those in drier scrub-mangrove. In addition we predicted that birds utilizing the structurally simple seasonal agricultural habitats would be in poorer condition and have lower overwinter survival than those in natural habitats.

2 | MATERIALS AND METHODS

2.1 | Study species and study area

During the winter Yellow Warblers (_aestiva_ group) can be found across Central and South America, usually below 500 m above sea level, in a variety of natural (e.g., riparian forest, mangrove, evergreen forest) and human-modified habitats (e.g., coffee and palm plantations, cattle pasture, and various crops) (Lowther, Celada, Klein, Rimmer, & Spector, 1999; Valdez-Juárez et al., 2018). We studied Yellow Warblers in the lowlands of Jalisco, Mexico, adjacent to the Chamela-Cuixmala Biosphere Reserve in three field seasons (2012–2014) between January and March. Weather in the region has a marked seasonality; 80% of the precipitation (630.4 mm) falls from June to November, while less than 5% of the precipitation (39.4 mm) falls from January to May (IBUNAM, 2007). The predominant vegetation in this region is undisturbed tropical dry-forest with patches of mesic riparian forest along the Cuixmala and Chamela Rivers and patches of mangroves interspersed with scrubs near the coast. Agriculture is found mostly around the townships of Punta Pérula and Zapata (populations <1,500). Here, Yellow Warblers occupy riparian forest, scrub-mangrove, and agriculture, but not tropical dry-forest. Our previous work found no evidence of intraspecific habitat segregation by sex, age, or size (Valdez-Juárez et al., 2018). We established 2–2.5 ha study sites in each habitat occupied by Yellow Warblers (Figure 1). Study sites with natural habitats had most of the natural canopy remaining, human influence is limited to light cattle grazing in riparian forest and scattered beach houses in scrub-mangrove. Agricultural study sites had most of the natural cover converted to agriculture, save for 1–2 m wide hedgerows of native shrubs and trees that separated small irrigated fields (corn, sorghum, chili-peppers, and tomatoes) that were annually cropped and rotated. Our study plots were centered on the lanes around the crops.

2.2 | Banding and monitoring

We attempted to capture all Yellow Warblers present at each site. Mist-netting began at sunrise and ended at sunset, with a break between 1,200 and 1,500 hr. Capture effort was allocated evenly across all sites in 2012 and 2013, but for

FIGURE 1 Pictures from the six study sites in Jalisco, México. Each of the three habitat types are depicted; scrub-mangrove: (a) Careyitos Beach, (b) Xametla Beach. Riparian forest: (c) Cuixmala River, (d) Chamela River. Agriculture (e) near Zapata, (f) near Punta Pérula. Pictures on the left were taken near the start of the season (January–February) and pictures to the right near the end (April–May)

logistic reasons was higher in riparian forest and agricultural habitat than scrub-mangrove sites in 2014. We recorded time of capture and banded each bird captured with a Canadian Wildlife Service (CWS) aluminum band and a unique combination of three-color-bands. We used plumage coloration, molt limits, the presence of tapered feathers, and lower mandible color to determine sex and age (juvenile or adult) following Pyle (1997). We weighed all banded birds to the nearest 0.1 g with an Ohaus PS121 scale (Ohaus, Parsippany, NJ), measured tarsus to the nearest 0.1 mm with

callipers, and measured wing chord to the closest 1 mm with a wing ruler. We estimated body size with the first principal component (PC1) of a principal components analysis that included tarsus and wing length (Gosler, Greenwood, Baker, & Davidson, 1998). The PC1 explained 67.2% of the variance in tarsus and wing length. We assessed furcular fat (DeSante et al., 2016), but found most birds to be lean (93% of the birds had traces or no fat and 7% had <1/3 of the furcular cavity filled), and thus we did not include furcular fat in the results.

As part of a more detailed study on winter behavior, we attached a PicoPip AG337 (0.30 g) or a PicoPip AG317 (0.38 g) radio-transmitters (Lotek Wireless, Newmarket, Ontario) to 89 birds. We attached the heavier radio-transmitters to heavier birds such that radio-transmitters always weighed less than 4% of individual mass. We attempted to recapture birds to remove their radio-transmitters after 30 days.

We monitored color-banded and radio-tagged Yellow Warblers at each site between January–May in 2012, 2013, and 2014, and January through February in 2015. We typically visited each site every 2 days. We used the number of days spent in the field each month as a measure of resighting effort in our survival analyses.

2.3 | Metrics of physiological condition

We used five metrics (daily and seasonal changes in size-adjusted body mass, leukocyte profiles, rectrix growth rate, barbule density, and departure date) to assess the physiological condition of Yellow Warblers. Each metric reflects physiological condition over different timeframes. Daily changes in size-adjusted mass and leukocyte profiles reflect bird condition in the hours before capture (Brown, 1996; Davis, Maney, & Maerz, 2008). In contrast, seasonal change in size-adjusted mass, rectrix growth rate, rectrix quality, and departure date reflect the cumulative physiological condition over a longer period (DesRochers et al., 2009; Studds & Marra, 2007).

2.3.1 | Daily and seasonal changes in size-adjusted mass

Body mass has been often used as a condition index because it provides a single value that incorporates the levels of all body nutrients (Brown, 1996). However, body mass is typically correlated with structural size and might not be an accurate metric in sexually dimorphic species (Labocha & Hayes, 2012). We thus use size-adjusted mass as a metric of condition. There are currently two hypotheses that make nonoverlapping predictions about the relationship between size-adjusted body mass and habitat quality. The food limitation hypothesis predicts a direct relationship between size adjusted mass and food supply and thus body mass will be positively related to habitat quality (Sherry, Johnson, & Strong, 2005). Adaptive body mass regulation hypothesis posits that birds in habitats that are more likely to experience

food shortages may store fat in anticipation of energy deficits and thus have higher mass (Rogers, 2005). However, fat storages will also tend to be kept to a minimum because carrying fat will reduce flight performance and of predation risk (Cuthill & Houston, 1997).

We used a general linear model to assess whether size-adjusted mass (residuals from a mass-PC1 regression) varied with habitat. Habitat, sex, age, time of day, day of year (January 1 = 1), year, and all possible two-way interactions with habitat were included as explanatory variables. The "habitat × time of day" interaction allowed us to evaluate habitat effects on daily mass gain. Similarly, the "habitat × day of year" interaction allowed us to evaluate if habitat type influenced seasonal changes in size-adjusted mass. We only used the first set of data collected from birds recaptured within a season and excluded data from birds banded after March 31 to exclude transient birds likely to overwinter further south and pass through the area in April (Valdez-Juarez, personal observation).

2.3.2 | Leukocyte profiles

The ratio of two leukocyte types, heterophils and lymphocytes (hereafter the H/L ratio), has been widely used as metric of stress levels prior to capture (Davis et al., 2008). Bird H/L ratios are reported to increase with fasting (Włodarczyk, Podlaszczuk, Kaczmarek, Janiszewski, & Minias, 2018) and the frequency of antagonistic interactions with conspecifics (Mazerolle & Hobson, 2002).

We determined the H/L ratios within blood samples collected from the brachial vein of each bird captured following Podlesak, McWilliams, and Hatch (2005). Blood samples were smeared on glass microscope slides, air-dried, and stored in a dry and dark container prior to analysis. We used the May–Grünewald–Giemsa method to stain the blood smears, and then used a Nikon Eclipse E200 light microscope (Nikon, Minato, Tokyo, Japan) to assign 100 cells per smear to 1 of 5 cell types (heterophils, lymphocytes, eosinophils, basophils, and monocytes). The resulting H/L ratios were log-transformed to reduce skew (raw data skewness = 2.22, log-transformed data skewness = 0.32).

We used a general linear model to assess habitat, sex, age, time of day, day of year, and year effects on log-transformed H/L ratios. Habitat × time of day and habitat × day of year interactions were again included in models to allow examination of daily and seasonal changes in stress levels.

2.3.3 | Rectrix growth rate and quality

Feathers are nutritionally expensive as they are 95% protein and constitute between 4 and 12% of the mass of a bird (Murphy, 1996). Feather growth rate and quality therefore reflect nutritional state during the growing period (Broggi, Gamero, Hohtola, Orell, & Nilsson, 2011). We examined if habitat influenced the growth rate and quality of rectrices.

We first plucked a summer-grown rectrix (r1) from each captured Yellow Warbler. We then attempted to recapture these birds after 26 days had elapsed, and if successful, we noted whether or not the rectrix had regrown, measured its length (while still attached), and collected the replaced rectrix. Ongoing monitoring of color-banded and radio-tagged birds allowed us to confirm that individuals did not move among habitats during the regrowth period. We determined the growth rate of the replacement rectrix for birds captured within 52 days, the maximum duration of rectrix molt in Yellow Warblers (Rimmer, 1988).

We assessed the quality of the replacement rectrices by measuring barbule density (DesRochers et al., 2009) of a single randomly selected barb located at half the rectrix length. We counted all barbules from the selected barb, starting at rachis to the edge of the field of view and measured the distance from the first to the last counted barbule. We used the Infinity-analyze program and a 10× image to take all measurements and an Infinity 1-3C camera mounted on a Nikon Eclipse E200 microscope (Lumenera, Ottawa, Ontario, Canada) to take all pictures.

We used a Fisher's exact test to evaluate whether the probability that a bird replaced a rectrix varied with habitat, and a general linear model to examine habitat, sex, and age effects on rectrix growth rate and barbule density. The limited number of birds recaptured ($n = 28$) precluded us from including day of the year, year, or interaction terms in these models.

2.3.4 | Departure date

Migration schedules of long-distance migratory birds are regulated by endogenous mechanisms (Maggini & Bairlein, 2012). However, migratory birds can adjust the timing of departure from the wintering grounds according to ecological conditions (Marra, Francis, Mulvihill, & Moore, 2005) and each bird's ability to acquire the nutrient reserves required for long-distance migration (Smith et al., 2010; Studds & Marra, 2005). Birds wintering in habitats with limited resources delay migration onset, at the cost of decreased reproductive success (Marra, Hobson, & Holmes, 1998; Marra & Holmes, 2001; Rockwell, Bocetti, & Marra, 2012). Departure dates may therefore reflect habitat quality (Smith et al., 2010; Studds & Marra, 2005). We used departure dates of color-banded Yellow Warblers known to be alive on March 15 to assess if migration schedules varied with habitat. We visited each site every second day from March 15 to May 15, or until three consecutive visits to a site produced no sightings of any color-banded birds. We used the day after a bird was last observed as an estimate of their departure date. We used a general linear model that included habitat, sex, age, year, and all two-way interactions with habitat as explanatory variables to examine habitat effects on departure date.

2.4 | Data analysis

We used R 3.3.3 statistical computing environment (R Development Core Team, 2014) for all analyses.

We built all general linear models with the "lm" function in the built-in package "stats" and used the "ANOVA" function from the "car" package (Fox et al., 2012) to assess the significance of the relationships. We used the "lsmeans" package (Lenth, Love, & Lenth, 2018) to obtain the least square means, *SE*s, and 95% confidence intervals (CIs). These were calculated using the median values of the other terms in the model. We used diagnostic model plots to check for homoscedasticity, overly influential outliers, and to evaluate the distribution of the data.

2.5 | Monthly apparent survival

We used Cormack–Jolly–Seber models to estimate the monthly survival of Yellow Warblers in each habitat type. The mark-resighting dataset included data from 194 color-banded individuals (89 of those with a radio-transmitter) from the six field sites between 2012 and 2015. We compiled the data such that individuals could be marked/resighted in January, February, March, April, and May, leave and then return the following year, so time intervals between periods were either 1 or 8 months. The mark-resighting dataset included 573 capture/resighting events. On average, individuals were observed in 3 (range 1–13) of the 17 one-month resighting periods. Birds carrying radio-transmitters were observed more often than those without transmitters (radio-transmitters: mean = 3.8, range 1–13; without: mean = 2.1, range = 1–12).

We used program MARK 5.1 to calculate monthly apparent survival probability (ϕ) after controlling for the probability that Yellow Warblers were resighted or recaptured, hereafter described as resighting probablity (ρ). We first fit a global model that allowed the resighting probability to vary with sex, habitat, and month (January–April or May, when some individuals will have started to migrate). In the global model we allowed monthly survival in the month after capture (ϕ^1) to be lower and vary with habitat type (to control for the presence of transients and capture effects), and monthly survival during the winter (January–May, ϕ^2) and the rest of the year (ϕ^3) to vary with sex, age, and habitat. To best estimate habitat specific monthly survival for each sex/age class we did not allow ϕ^1, ϕ^2, or ϕ^3 to vary temporally. We subsequently used a hierarchical approach to first determine the best model structure for the resighting probability, then assess whether resighting probability increased with effort (the number of days per site in any given month) or was higher for birds carrying a radio-transmitter, and model monthly survival rates. This candidate set included the best model in the previous candidate set, and additive models where ϕ^1 was fixed or varied with habitat and ϕ^2, and ϕ^3 varied with (a) habitat, sex, and age or

(b) habitat and sex or age. We also included univariate models where ϕ^1, ϕ^2, and ϕ^3 only varied with habitat or sex or age, and null models where $\phi^1 \neq \phi^2 \neq \phi^3$ and $\phi^1 = \phi^2 \neq \phi^3$ ($n = 24$ candidate models, Supporting Information Appendix S1). Finally, we examined if there was any evidence that radiotransmitters reduced survival during the winter period (January–May), the subsequent period encompassing migration and the breeding season (May–January), or both. At each stage of the analysis we used Akaike's information criterion to rank competing models.

3 | RESULTS

We banded a total of 193 birds; 114 males and 79 females distributed across all habitats and of both age groups (Table 1). Although most of the birds sampled were males, the male skew was similar across all habitats (Valdez-Juárez et al., 2018).

3.1 | Metrics of physiological condition

3.1.1 | Daily and seasonal changes in size-adjusted mass

Yellow Warblers in our sample weighed between 6.9 and 9.6 g ($n = 186$). Males were larger and heavier than females (mean male PC1 = 0.45, $SE = 0.04$, $n = 111$; female PC1 = −0.74, $SE = 0.05$, $n = 75$; mean male mass = 8.44 g, $SE = 0.04$, $n = 111$; female = 7.95 g, $SE = 0.05$, $n = 75$). Size-adjusted mass was influenced by habitat type ($F = 7.29$, df = 2, 169, $p < 0.001$): Yellow Warblers captured in riparian forest were heavier than those in scrub-mangrove and agricultural habitat (Table 2). Males also had a higher size-adjusted mass than females ($F = 4.87$, df = 1, 169, $p = 0.03$; Table 2). However, we found no evidence that adult size-adjusted mass differed from that of juveniles ($F = 1.23$, df = 1, 169, $p = 0.27$), or that habitat interactions with age and sex influenced size-adjusted mass (all $p > 0.33$). Neither did we find evidence that size-adjusted mass differed by year ($F = 0.39$, df = 2, 169, $p = 0.68$).

Yellow Warblers gained mass at a rate of approximately 0.08 g per hour between 0:700 and 19:00 hr (time of day: $F = 17.65$, df = 1, 169, $p < 0.001$). We found no evidence that the gain in size-adjusted mass varied with habitat (habitat × time of day: $F = 0.23$, df = 2, 169, $p = 0.79$; Table 2) or seasonally across all habitats (day of year: $F = 0.75$, df =

1, 169, $p = 0.39$; habitat × day of year, $F = 1.11$, df = 2, 169, $p = 0.33$).

3.1.2 | Leukocyte profiles

H/L ratios ranged from 0.42 to 2.27 ($n = 81$). We found no evidence that H/L ratios (log transformed) were influenced by habitat ($F = 1.69$, df = 1, 64, $p = 0.19$; Table 2), sex ($F = 0.90$, df = 1, 64, $p = 0.35$; Table 2), age ($F = 0.19$, df = 1, 64, $p = 0.67$), or time of day ($F < 0.01$, df = 1,64, $p = 0.98$). However, H/L ratios increased over the course of the season (day of year: $F < 6.58$, df = 1, 64, $p = 0.01$) and were higher in 2014 than 2012 or 2013 ($F = 14.58$, df = 2, 64, $p < 0.001$). Habitat interactions with sex, age, time of day, and day of year were non-significant (all $p > 0.16$).

3.1.3 | Rectrix growth rate and quality

We recaptured 35 of the 193 banded Yellow Warblers: 28 had replaced the plucked rectrix, and 22 were recaptured while the rectrix was still regrowing (i.e., within 52 days). Habitat did not affect the probability that a plucked rectrix was replaced (Fisher's exact test, $p = 0.38$). New rectrices grew at an average rate of 0.89 mm per day ($SE = 0.08$). We found no evidence that rectrix growth rate was influenced by habitat ($F = 1.60$, df = 2, 16, $p = 0.23$; Table 2), sex ($F = 1.21$, df = 1, 16, $p = 0.29$; Table 2), or age ($F = 0.29$, df = 1, 16, $p = 0.60$).

The barbule density of the replaced rectrices, however, varied with habitat type ($F = 3.7$, df = 2, 23, $p = 0.04$; Table 2). Barbule density was highest in rectrices grown in agricultural habitat, intermediate when grown in riparian forest, and lowest in scrub-mangrove. Barbule density was also higher in male than female rectrices ($F = 4.9$, df = 2, 23, $p = 0.04$; Table 2). Barbule density did not vary with age within our sample ($F = 0.2$, df = 2, 23, $p = 0.7$).

3.1.4 | Departure date

Yellow Warblers appeared to depart between March 17 and May 9. On average, males left 4 days before females ($F = 3.56$, df = 1, 118, $p = 0.06$; $n = 86$ males, 44 females; Table 2). Habitat influenced the departure dates of females but not males (habitat × sex: $F = 3.86$, df = 2, 118, $p = 0.02$). On average, females left agricultural sites 3 days before females in scrub-mangrove sites and 13 days before females in riparian forest sites (Table 2). We did not

TABLE 1 Yellow Warblers captured in each habitat by age and sex

	Riparian forest		Scrub/mangrove		Agriculture		Total
	Male	Female	Male	Female	Male	Female	
Adult	23 (39.0%)	9 (15.3%)	10 (23.3%)	10 (23.3%)	29 (31.9%)	10 (11.0%)	91
Juvenile	17 (28.8%)	10 (16.9%)	13 (30.2%)	10 (23.3%)	22 (24.2%)	30 (33.0%)	102
Total	40 (67.8%)	19 (32.2%)	23 (53.5%)	20 (46.5%)	51 (56.0%)	40 (44.0%)	193

The % in the parenthesis is in relation to the total birds banded in each habitat.

TABLE 2 Habitat and sex effects on size-adjusted mass, daily change in size-adjusted mass, log heterophils/lymphocytes ratio (H/L), rectrix growth rate, barbule density, departure dates for migration, and monthly apparent survival of Yellow Warblers in Jalisco, Mexico

	Riparian[a]		Scrub-mangrove[a]		Agriculture[a]	
Condition metric[b]	Male	Female	Male	Female	Male	Female
Size-adjusted mass (g)[1,2,3,4]	0.21 ± 0.08 (0.05–0.37) $n = 39$	−0.03 ± 0.12 (−0.27 to 0.20. $n = 17$	−0.05 ± 0.11, (−0.26 to 0.16. $n = 25$	−0.05 ± 0.11, (−0.26–0.16) $n = 19$	−0.09 ± 0.08 (−0.24 to 0.06. $n = 47$	−0.22 ± 0.10 (−0.42 to −0.03) $n = 39$
Mass gain (g/h)[1,3,4]	0.061 ± 0.015 (0.056–0.065) $n = 39$	0.061 ± 0.016 (0.053–0.068) $n = 17$	0.049 ± 0.012 (0.049–0.050) $n = 25$	0.049 ± 0.013 (0.049–0.050) $n = 19$	0.036 ± 0.011 (0.034–0.038) $n = 47$	0.036 ± 0.011 (0.034–0.037) $n = 39$
H/L ratio[1,2,3,4]	−0.92 ± 0.19 (−1.31 to −0.54) $n = 17$	−0.88 ± 0.29 (−1.46 to −0.30) $n = 10$	−0.86 ± 0.26 (−1.37 to −0.34) $n = 10$	−1.16 ± 0.24 (−1.46 to −0.30) $n = 9$	−0.59 ± 0.24 (−1.31 to −0.54) $n = 18$	−0.78 ± 0.24 (−1.26 to −0.30) $n = 17$
Rectrix growth rate (mm/day)[1]	0.91 ± 0.15 (0.60–1.22) $n = 6$	0.71 ± 0.19 (0.31–1.11) $n = 2$	0.74 ± 0.21 (0.29–1.18) $n = 2$	0.54 ± 0.21 (0.09–0.99) $n = 2$	1.13 ± 0.15 (0.81–1.44) $n = 5$	0.93 ± 0.16 (0.58–1.28) $n = 4$
Barbule density (barbs/mm)[1]	30.97 ± 0.48 (29.97–31.97) $n = 10$	29.37 ± 0.76 (27.80–30.95) $n = 2$	30.06 ± 0.67 (28.69–31.44) $n = 5$	28.47 ± 0.89 (26.62–30.31) $n = 1$	32.20 ± 0.59 (31.09–33.51) $n = 6$	30.70 ± 0.67 (29.31–32.09) $n = 4$
Departure date (January 1 = 1)[1]	104.8 ± 2.1 (100.6–109.0) $n = 43$	119.2 ± 3.8 (111.6–126.8) $n = 14$	109.2 ± 4.0 (101.2–117.2) $n = 19$	110.7 ± 5.7 (99.4–122.0) $n = 8$	106.1 ± 1.9 (102.2–109.9) $n = 45$	105.6 ± 2.5 (99.4–110.7) $n = 30$
Apparent monthly survival (adults)	0.964 ± 0.022 (0.880–0.990) $n = 23$	0.946 ± 0.041 (0.782–0.989) $n = 9$	0.951 ± 0.030 (0.844–0.986) $n = 10$	0.927 ± 0.045 (0.712–0.985) $n = 10$	0.967 ± 0.020 (0.895–0.990) $n = 29$	0.948 ± 0.040 (0.788–0.989) $n = 10$
Apparent monthly survival (juveniles)	0.963 ± 0.021 (0.858–0.991) $n = 17$	0.940 ± 0.050 (0.734–0.989) $n = 10$	0.950 ± 0.037 (0.810–0.989) $n = 13$	0.919 ± 0.067 (0.659–0.985) $n = 10$	0.965 ± 0.025 (0.864–0.992) $n = 22$	0.942 ± 0.048 (0.743–0.989) $n = 30$

[a]Values reported are least square means with SEs, confidence intervals are presented in parentheses.
[b]Subscripts denote covariates that are controlled for in the analyses: age[1], time[2], date[3], and year[4].

observe an effect of age ($F = 0.25$, df = 1, 118, $p = 0.62$; age × habitat: $F = 0.69$, df = 2, 118, $p = 0.51$) or year ($F = 0.001$, df = 1, 118, $p = 0.97$ year × habitat: $F = 0.34$, df = 2, 118, $p = 0.71$) on departure dates.

3.2 | Monthly apparent survival

The global model describing monthly annual survival of Yellow Warblers between January 2012 and Febuary 2015 fit the data well and showed no evidence of overdispersion (median procedure, $\hat{c} < 1$). The top model in the candidate set examining temporal variation in resighting probability (ϕ^1 habitat ϕ^2 sex × age × habitat ϕ^3 sex × age × habitat, ρ May; $w_i = 0.55$; Appendix S1) indicated that the resighting probability was lower in May (0.12, $SE = 0.02$, 95% CI 0.08–0.17) than in January through April (0.58, $SE = 0.02$, 0.53–0.63). However, the top model was improved ($\Delta AIC_c = 8.04$) by the addition of covariates that described effort (the number of days in the field that month) and whether a bird was carrying a radio-transmitter or not (Appendix S2).

There was some model uncertainty in the candidate set examining variation in monthly apparent survival as seven models received strong support (Table 3). The top model indicated that ϕ^1 (apparent survival during the first month after capture) was lower than ϕ^2 (apparent monthly survival during January to May), and that ϕ^2 varied with sex and habitat type. The sex term was included in all strongly supported models describing ϕ^2 and had parameter likelihood

approaching 1. Age and habitat were included in three or four of the strongly supported models describing ϕ^2 and had parameter likelihoods of 0.58 and 0.67, respectively (Table 3).

Apparent monthly survival estimates for Yellow Warblers wintering in Mexico were influenced by sex, age class, and habitat. Monthly apparent survival estimates (ϕ^2) were lower for juveniles than for adults and lower for females 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, $SE = 0.016$). Model averaged monthly apparent survival estimates (ϕ^2) for birds in scrub-mangrove were lower than survival estimates for birds in riparian forest and agricultural habitat (Table 1). We found no evidence that radio-transmitters reduced Yellow Warbler survival, the top survival model in Table 3 was not improved by that addition of a term that allowed the apparent monthly survival of Yellow Warblers with radio-transmitters to differ from those without during the winter ($\Delta AIC_c = 0.78$), the subsequent period when birds were not monitored ($\Delta AIC_c = 0.20$), or both ($\Delta AIC_c = 0.78$). Furthermore, counter to expectation if radio-transmitters had a negative effect on survival parameter estimates for the radio-transmitter term were positive and had 95% CIs that bounded zero (winter: radio-transmitter = 0.504, $SE = 0.449$, CI = −0.376–1.383; subsequent period: radio-transmitter = 0.324, $SE = 0.234$, CI = −0.136–0.783) suggesting this term was a spurious variable and support for these model

TABLE 3 Summary of models in the candidate set examining variation in monthly apparent survival of Yellow Warblers in Jalisco, Mexico

Model[a]	Model statistics[b]					
	Dev	K	Model likelihood	AIC$_c$	ΔAIC$_c$	w_i
ϕ^1 . ϕ^2 sex + habitat ϕ^3., ρ May + effort + radio	1,353.23	10	1	1,373.63	0	0.18
ϕ^1 . ϕ^2 sex + age + habitat ϕ^3., ρ May + effort + radio	1,351.34	11	0.91	1,373.82	0.19	0.16
ϕ^1 . ϕ^2 sex + age + habitat ϕ^3 sex, ρ May + effort + radio	1,349.86	12	0.67	1,374.43	0.80	0.12
ϕ^1 . ϕ^2 sex + age ϕ^3. ρ May + effort + radio	1,356.12	9	0.67	1,373.44	0.81	0.12
ϕ^1 . ϕ^2 sex ϕ^3. ρ May + effort + radio	1,358.39	8	0.61	1,374.65	1.02	0.11
ϕ^1 . ϕ^2 sex ϕ^3 sex ρ May + effort + radio	1,356.76	9	0.48	1,375.09	1.46	0.09
ϕ^1 . ϕ^2 sex + age + habitat ϕ^3 age, ρ May + effort + radio	1,350.69	12	0.44	1,376.26	1.63	0.08
ϕ^1 . ϕ^2 sex + age + habitat ϕ^3 habitat, ρ May + effort + radio	1,349.78	13	0.24	1,376.45	2.82	0.04
ϕ^1 . ϕ^2 sex + age + habitat,ϕ^3 sex + age + habitat, ρ May + effort + radio	1,345.59	15	0.24	1,376.48	2.85	0.04
ϕ^1 . ϕ^2 sex + habitat ϕ^3 sex + habitat, ρ May + effort + radio	1,350.13	13	0.21	1,376.80	3.17	0.04
ϕ^1 habitat ϕ^2 sex + age + habitat ϕ^3 habitat, ρ May + effort + radio	1,345.38	17	0.03	1,380.51	6.88	0.01
ϕ^1 habitat ϕ^2 sex + habitat ϕ^3 sex + habitat, ρ May + effort + radio	1,349.99	15	0.03	1,380.88	7.24	0
ϕ^1 . ϕ^2 age + habitat ϕ^3., ρ May + effort + radio	1,363.66	10	0.01	1,384.06	10.43	0
ϕ^1 . ϕ^2 age ϕ^3., ρ May + effort + radio	1,368.27	8	0	1,384.53	10.90	0
ϕ^1 . ϕ^2 age ϕ^3 age, ρ May + effort + radio	1,367.41	9	0	1,385.73	12.10	0
ϕ^1 . ϕ^2 habitat ϕ^3, ρ May + effort + radio	1,368.05	9	0	1,386.38	12.75	0
ϕ^1 . ϕ^2 age + habitat ϕ^3 age + habitat, ρ May + effort + radio	1,359.85	13	0	1,386.52	12.88	0
ϕ^1 . ϕ^2. ϕ^3., ρ May + effort + radio	1,373.23	7	0	1,387.43	13.80	0
ϕ^1 . ϕ^2 habitat ϕ^3 habitat, ρ May + effort + radio	1,365.94	11	0	1,388.42	14.79	0
ϕ^1 habitat ϕ^2 age + habitat ϕ^3 age + habitat, ρ May + effort + radio	1,359.58	15	0	1,390.46	16.83	0
ϕ^1 habitat ϕ^2 habitat ϕ^3 habitat, ρ May + effort + radio	1,365.86	13	0	1,392.53	18.89	0
ϕ^1 . ϕ^2 sex × age × habitat, ϕ^3 sex × age × habitat, ρ May + effort + radio	1,336.16	29	0	1,397.46	23.83	0
ϕ^1 = ϕ^2 ϕ^3., ρ May + effort + radio	1,387.29	6	0	1,399.44	25.81	0
ϕ^1 habitat ϕ^2 sex × age × habitat, ϕ^3 sex × age × habitat, ρ May + effort + radio	1,335.96	31	0	1,401.73	28.10	0

[a]Model parameters: monthly survival in the first month after capture (ϕ^1). Monthly survival between January and May (ϕ^2). Monthly survival from May to January (ϕ^3) . ϕ may be constant (.) or vary with habitat, sex or age. Number of days in the field in any given month (effort). Whether a bird carried a radiotransmitter or not (radio). All models allow resighting probability to be lower in May (May), when some birds are expected to have left on migration.

[b]Model statistics: model goodness-of-fit is reported as the model deviance (Dev), total number of parameters in each model is indicated by (K). Better individual model performance, relative to the model candidate set, is indicated by lower Akaike Information Criterion scores, corrected for small sample size (AIC$_c$). Akaike weights (w_i) indicate the likelihood that a given model describes the observed data, relative to other models in the candidate set (cumulative probability of 1.0).

simply reflected their similarity to the top model (Burnham & Anderson, 2002).

4 | DISCUSSION

Population declines of several migratory songbird species have been attributed to the loss and degradation of winter habitat (Chandler & King, 2011; Rappole et al., 2003; Townsend, Rimmer, McFarland, & Goetz, 2012). Agricultural habitats that have a similar structure to natural habitats (e.g., coffee plantations) can constitute high quality winter habitat for Neotropical migrants (Bakermans et al., 2009; Johnson et al., 2011). Here, we show that even agricultural land that has been heavily modified and is annually cropped can provide relatively high quality winter habitat for a Neotropical migrant. Yellow Warblers overwintering in agricultural habitat were able to grow high quality rectrices and had

monthly survival rates comparable to those of birds in mesic riparian forest. Our results suggest that the conversion of natural habitats to agriculture in Mexico cannot explain the significant population declines observed among western Yellow Warbler populations (Partners in Flight Science Committee, 2017) thought to winter in western Mexico (Boulet, Gibbs, & Hobson, 2006).

Site or habitat quality can be assessed directly by estimating winter survival, but this takes considerable time and effort. Body mass (Marra & Holmes, 2001; Angelier et al., 2011), leukocyte profiles (Cīrule, Krama, Vrublevska, Rantala, & Krams, 2012), and dates of departure for spring migration (Marra & Holmes, 2001) have all been used as metrics of winter habitat quality for migratory birds. However, in our study none of these metrics reflected the observed differences in winter survival of birds in the three habitats. The disconnect between size-adjusted mass and

habitat quality in our study may be because birds adaptively adjust their mass in response to high predation risk (Rogers, 2015) by any of the eight avian predators present at our sites (Valdez-Juarez & Green, unpublished data). The lack of a relationship between size-adjusted mass and habitat quality in our results contrasts with the results obtained with American Redstarts (*Setophaga ruticilla*) wintering in Jamaica (Johnson et al., 2006; Marra & Holmes, 2001). However, the risk of predation may be substantially lower in Jamaica, with the mongoose (*Herpestes javanicus*) being the only occasional predator of migratory songbirds (Brown & Sherry, 2008).

Lack of differences in stress levels in our sample might be caused by cofounding influences in H/L ratios; starvation risk in low-quality habitat (Davis et al., 2008) and conspecific interactions in high-quality habitat (Mazerolle & Hobson, 2002). Departure date was also uninformative. Males left earlier than females, however that is more likely to reflect sex specific innate migration schedules (Maggini & Bairlein, 2012) than differences in condition between sexes. The fact that females in riparian forest left 14 days later than females in agriculture is unlikely to be caused by differences in habitat quality given the high survival rate and high quality of feathers grown by females in both riparian forest and agriculture. The small sample size or the effect of uncontrolled variables, such as breeding origin, might account for female differential departure times.

Yellow Warblers wintering in riparian forest and agricultural habitat grew rectrices with higher barbule density than birds in scrub-mangrove. Previous work with captive birds suggests that barbule density can be positively correlated with diet quality (DesRochers et al., 2009; Pap, Vágási, Czirják, & Barta, 2008) and to coccidian parasite infection (Pap, Vágási, Bǎrbos, & Marton, 2013). We believe our results likely reflect differences in diet quality. Pap et al. (2013) attributed the higher interbarbule density in feathers grown by birds with a coccidian infestation to high levels of blood glucocorticoids (Pap et al., 2013). However, H/L ratios are closely linked to levels of glucocorticoids circulation in the blood stream (Davis et al., 2008) and we did not find any differences in H/L ratios across habitats, thus we believe our results suggest that low barbule density in birds in scrub-mangrove is because of inadequate protein reserves. Admittedly, our sample size for feather quality is small, future studies can corroborate the validity of our results with a larger sample size and with additional measures of feather quality.

Population density can be an easy and inexpensive indicator of winter habitat quality for birds, although it has the potential to be misleading if competitive asymmetries relegate a large number of less competitive birds to suboptimal habitats (Johnson, 2007) or if features that are unfavorable to avian survival (e.g., high edge to area ratio, increased predation risk) lead to ecological traps (Battin, 2004). We have previously shown that there are no apparent competitive differences in Yellow Warblers occupying different habitats and that Yellow Warbler density is higher in agricultural habitat and riparian forest and lowest in scrub-mangrove (Valdez-Juárez et al., 2018). Our present work found that survival and feather quality follow the same pattern. Both are higher in agriculture and riparian forest and lowest in scrub-mangrove. These results suggest that density can be a good indicator of habitat quality for wintering migrants. This conclusion is supported by similar studies on American Redstarts in Jamaica (Johnson et al., 2006) and Wilson's Warblers in Mexico (Ruiz-Sánchez et al., 2017), but contrasts with work on Black-throated Blue Warblers (*Setophaga caerulescens*) in Puerto Rico (Wunderle, 1995). Given the potential disconnect between density and habitat quality, we advocate that density only be used as an indirect measure of habitat quality when combined with survival and condition metrics.

In this study we provide evidence that annually cropped agriculture may provide suitable winter habitat for some species of migratory songbirds in western Mexico. The field margins with hedgerows, tree lines, or remnant natural habitat increase biodiversity and abundance of resident, wintering, and migrating birds, in heavily modified agricultural landscapes (Foster, 2007; Heath, Soykan, Velas, Kelsey, & Kross, 2017). We found that birds overwintering in agricultural habitats where hedgerows and trees are present have survival and condition similar to that of birds wintering in natural habitat. Our results lend further support for policies to preserve remaining habitat and incentivize installation of woody hedgerows and trees. However, it is important to note that Yellow Warblers use a wide range of habitat types during winter (Lowther et al., 1999). Species with more specialized habitat requirements such as the Golden-cheeked Warbler may be more affected by winter habitat loss and modification (Rappole et al., 2000).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ACCESSIBILITY STATEMENT

The data is part of the Ph.D. thesis of S.O.V.-J. and will be available on the Government of Canada data repository at https://open.canada.ca/en/open-data once the thesis has been defended.

ETHICS STATEMENT

All feather and blood sampling was done in compliance with the applicable Mexican laws and within the limits set by the permits granted by Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT). The Simon Fraser University Animal Care Committee approved all field protocols.

AUTHOR CONTRIBUTIONS

All authors collaborated to the design of the study. S.O.V.-J., A.D., and D.J.G. collected data in the field. S.O.V.-J. and A.D. processed the samples. S.O.V.-J. and D.J.G. analyzed the data. All authors contributed to writing and editing the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.