Contrasting the suitability of shade coffee agriculture and native forest as overwinter habitat for Canada Warbler (Cardellina canadensis) in the Colombian Andes

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ABSTRACT

In the Neotropics, coffee production occurs on a large scale in some of the planet’s most biodiverse regions: tropical mountains. Coffee production systems involving shade trees are considered to have a lower impact on biodiversity than alternative sun coffee. To date, the majority of evidence for the value of shade coffee plantations has not taken into account the relative quality of this habitat compared to the native forests they replaced. We determined the suitability of shade coffee and forest as winter habitat for Canada Warbler (Cardellina canadensis) by comparing variation in the likelihood of capturing individuals, seasonal changes in body condition, and estimates of annual survival between the 2 habitats. We also determined the effect of the strong 2015–2016 El Niño event on survival. Males were relatively more likely to be captured in forest than females and this likelihood increased during drier years. Body condition change over the winter and apparent annual survival were similar for individuals that used forest and coffee. However, condition and survival decreased in both habitats during the El Niño year. Apparent survival was also lower for individuals carrying a radiotag or geolocator. Our findings suggest that shade coffee with high canopy cover and height offers similar benefits to forest in terms of body condition and survival. Landscape conservation approaches, promoting diverse matrices of structurally complex shade coffee and forest might best ensure long-term survival in Neotropical migrants like Canada Warbler.

Keywords: El Niño Southern Oscillation, forest, habitat quality, Neotropical migrants, shade coffee

Contrastando la conveniencia de la agricultura de café de sombra y del bosque nativo como hábitat de invernada para Cardellina canadensis en los Andes de Colombia

RESUMEN

En el Neotrópico, el café se produce a gran escala en algunas de las regiones más biodiversas del planeta: las montañas tropicales. Se considera que los sistemas de producción de café que incorporan árboles de sombra tienen un menor impacto en la biodiversidad que la alternativa de café al sol. Hasta la fecha, la mayoría de la evidencia del valor de las plantaciones de café con sombra no ha tenido en cuenta la calidad relativa de este hábitat comparada con la de los bosques nativos que reemplazaron. Determinamos la conveniencia del café con sombra y del bosque como hábitats de invierno para Cardellina canadensis comparando la variación en la probabilidad de captura de individuos, los cambios estacionales en la condición física y las estimaciones de supervivencia anual entre los dos hábitats. También determinamos el efecto del fuerte evento de El Niño en 2015–2016 en la supervivencia. Los machos fueron relativamente más probables de ser capturados en el bosque que las hembras y esta probabilidad incrementó en los años más secos. El cambio en la condición física durante el invierno y la supervivencia anual aparente fueron muy similares para los individuos que usaron bosque y café. Sin embargo, la condición y la supervivencia disminuyeron en los dos hábitats durante el año de El Niño. La supervivencia aparente también fue más baja para los individuos que cargaron un radiotransmisor o geolocalizador. Nuestros resultados sugieren que el café de sombra con alta cobertura y altura de dosel ofrece beneficios similares al bosque en términos de condición física y supervivencia. Estrategias de conservación a nivel del paisaje que promuevan matrices diversas de cafetales con sombra estructuralmente complejos y bosque podrían garantizar mejor la supervivencia a largo plazo de los migrantes neotropicales como C. canadensis.

Palabras clave: bosque, café con sombra, calidad de hábitat, El Niño-Oscilación del Sur, migrantes neotropicales

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INTRODUCTION

Migratory birds are declining globally due to threats associated with habitat loss, climate change, and human exploitation (Wilcove and Wikelski 2008). In the Western hemisphere, population declines in Nearctic–Neotropical migratory songbirds are particularly severe for species that overwinter in northern South America, including the Canada Warbler (Cardellina canadensis), Cerulean Warbler (Setophaga cerulea), Golden-winged Warbler (Vermivora chrysoptera), and Olive-sided Flycatcher (Contopus cooperi) (International Union for Conservation of Nature 2016, Sauer et al. 2017). These species depend on diverse montane habitats in the tropical Andes during the winter. However, extensive deforestation has occurred in this region with estimates suggesting that <10% of mid-elevation montane forest remains (Henderson et al. 1991). This loss of habitat is known to be driving numerous endemic species towards extinction (Rueda-Almonacid et al. 2004, Renjifo et al. 2016) and has recently been linked to declines in migratory species spending the winter in the Andes (González-Prieto et al. 2017, Kramer et al. 2018, Wilson et al. 2018).

With the extensive loss of native forests, shade coffee plantations, which include canopy trees, are one of the few remaining “habitats” with forest-like vegetation in many mid- to high-elevation mountain ranges in Latin America (Perfecto et al. 2005, González-Prieto 2018). The transformation of shade coffee to full-sun coffee plantations (i.e. those with no canopy trees) results in a much greater loss of biodiversity compared with the conversion of native forest into shade coffee (De Beenhouwer et al. 2013). This effect is particularly strong in Latin America compared with other coffee-producing regions of the world (De Beenhouwer et al. 2013). As such, conservation efforts for both resident fauna and overwintering migratory species are now focusing on shade coffee agroecosystems to address the widespread loss of natural habitats (Perfecto et al. 1996, Perfecto and Vandermeer 2008, Caudill et al. 2015). Several studies in the Caribbean and the Americas have shown that Nearctic–Neotropical migrants are equally or even more abundant in shade coffee compared with native forest (Wunderle Jr. and Latta 1996, Tejada-Cruz and Sutherland 2004, Bakermans et al. 2009), although with variation among species (McDermott and Rodewald 2014, Céspedes and Bayly 2019). However, the presence of individuals in a habitat alone does not necessarily indicate that the habitat is high quality (Van Horne 1983, Garshelis 2000) or contributes to the maintenance of populations. Assessing the effect of occupying shade coffee vs. native forest on the overwinter ecology and demographics of Neotropical migrants is critical if we are to identify the factors driving population declines or limiting population growth, and to predict how environmental changes will impact migratory populations.

The quality of winter habitat limits the maintenance and survival of Neotropical migratory songbirds during the winter (Sherry and Holmes 1996, Sherry et al. 2005, Studds and Marra 2005) and can produce residual effects that carry over to migration and breeding, influencing individual fitness and population dynamics (Marra et al. 1998, Norris et al. 2004, Wilson et al. 2011, Rushing et al. 2016). Habitat quality for Neotropical migrants is often assessed by measuring variables such as sex ratios, individual body condition, and survival (Johnson 2007). Higher proportions of dominant males are expected in the habitats of highest quality (Marra 2000), and this distribution pattern is expected to have demographic consequences. For example, American Redstarts (Setophaga ruticilla) occupying poor-quality female-biased habitats in Jamaica had a steeper decline in body condition over the winter and lower annual survival than individuals in high-quality male-biased habitats (Marra and Holmes 2001). The results of past studies on the overwinter condition of individuals in shade coffee are mixed. In the Venezuelan Andes, for example, Neotropical migrants occupying shade coffee during the winter increased their body condition through the season (Bakermans et al. 2009), whereas in the Caribbean, body condition of individuals in shade coffee was either constant or declined (Strong and Sherry 2000, Johnson et al. 2006). In the Colombian Andes, Neotropical migrants in shade coffee have been found to be in poor condition on average and condition through the winter improved only for some species (Colorado and Rodewald 2017). Fewer studies have examined the demographic consequences of shade coffee use by migratory birds. In Jamaica, overwinter and annual apparent survival of American Redstarts in shade coffee and natural habitats were comparable (Johnson et al. 2006). In the Dominican Republic, annual return rates for 3 Neotropical migrants were similar between shade coffee and natural forests (Wunderle and Latta 2000). To our knowledge no study has simultaneously estimated the survival of declining migrant birds in shade coffee and native forest in mainland areas of the Neotropics or in critical wintering regions of the tropical Andes.

One of the challenges in assessing the effects of occupying shade coffee vs. native forests during the winter is that individual condition and apparent survival can vary spatially and temporally due to a range of factors. In many regions of the Neotropics, for instance, climatic conditions related to phenomena such as the El Niño Southern Oscillation (ENSO) can have dramatic effects on moisture and food availability (Ropelewski and Halpert 1987, Jaksic 2001). In turn, these factors are important determinants of winter habitat quality for Neotropical migrant birds (Studds and Marra 2007, Smith et al. 2010). Because such effects vary over time and space, the best assessment of the habitat quality of shade coffee should include simultaneous...
measures in coffee relative to the local native forest from where those plantations were carved (Van Horne 1983, Vickery et al. 1992), while simultaneously testing for possible differential effects of climatic events such as ENSO.

In this study, we determined the relative quality of adjacent shade coffee plantations and native forest as winter habitat for Canada Warbler in the Eastern Andes of Colombia. Canada Warbler is listed under Canada’s Species at Risk Act and over 60% of the breeding population has been lost during the last 50 yr (Environment and Climate Change Canada 2017). Over 50% of the winter distribution of this species lies within the highly deforested and fragmented Andean forests of Colombia, where native forest and shade coffee plantations at mid-elevations are habitats widely used by the species (Céspedes and Bayly 2019). Canada Warbler shows longitudinal segregation across the Andes of Colombia, giving rise to moderate migratory connectivity between breeding and wintering populations (González-Prieto et al. 2017). Individuals spending the winter at our study sites were found to have likely origins mainly from steeply declining eastern breeding populations in North America (González-Prieto et al. 2017, Sauer et al. 2017, Wilson et al. 2018).

We assessed the relative quality of shade coffee as winter habitat by addressing 3 questions: (1) Is there variation in the likelihood of capturing individuals in shade coffee vs. forest? (2) Do individuals maintain body condition similarly over the winter in the 2 habitats? (3) Is apparent survival different for individuals occupying the 2 habitats during the winter? We hypothesized that the simplified vegetation composition and structure of shade coffee may be inappropriate to maintain overwinter energy demands. Therefore, we expected that individuals in shade coffee relative to native forest would (1) be predominantly females, (2) be in poorer body condition at the end of the winter, and (3) have lower apparent annual survival. We also determined the effect of the ENSO on the survival of birds occupying both habitats given the potential for climate to influence year-to-year patterns of individual condition and demography. The ENSO influences rainfall patterns in the study region with drier conditions during El Niño events (Ropelewski and Halpert 1987, Jaksic 2001). We expected drier than average conditions induced by El Niño to have a negative effect on apparent survival across habitats by lowering habitat quality. If our above 3 predictions about shade coffee being a poorer quality habitat are true, we also predicted that differences in condition and apparent survival for individuals in the 2 habitats would be accentuated during El Niño years.

METHODS

Study Sites
Fieldwork was carried out from December to March over 5 field seasons (2013–2014, 2014–2015, 2015–2016, 2016–2017, and 2017–2018) in 3 study sites located on the western slope of the Eastern Andes in Colombia (Figure 1): “Hacienda La Fragua” (shade coffee 1,400 meters above sea level [m.a.s.l.], forest 1,500 m.a.s.l.), “Los Vientos” (shade coffee and forest 1,350 m.a.s.l.), and “La Vuelta” (shade coffee 1,400 m.a.s.l., forest 1,700 m.a.s.l.). Sites were equidistant and separated by 5 km. In La Fragua, shade coffee and forest habitats were separated by 300 m, in Los Vientos by 500 m, and in La Vuelta by ~1 km. Shade in coffee plantations was provided by native trees remaining from the original native forest cover. Native shade species included Inga spp., Simarouba amara, Cordia alliodora, Trichanthera gigantean, Sebastiania commersoniana, Alfaroa colombiana, Anacardium excelsum, Senna spectabilis, and Hevea pauciflora. Across our study sites, the average canopy height in coffee plantations was mean ± standard deviation (SD) = 18.8 ± 3.6 m (n = 68) and the average shade cover was 44.5 ± 17.1% (n = 68) (Céspedes and Bayly 2019). Our sites did not include sun coffee plantations and hereafter we refer to shade coffee as “coffee”.

Individual Capture and Measurements
We carried out constant-effort mist netting at fixed banding stations from 1 December to 30 March during 8 days a month in each habitat. Weather permitting, 12–15 mist nets (30-mm mesh) were operated from 0600 to 1100 hours and from 1500 to 1730 hours. All captured birds were fitted with a U.S. Fish and Wildlife Service numbered aluminium band and processed and released at the capture site. We determined age and sex (Pyle 1997), and recorded body mass (±0.1 g, using an electronic balance) for each bird at first capture and for all birds recaptured. Individuals were aged as hatch year and after hatch-year during December, and as second year and after second-year after 31 December (Pyle 1997). We refer to hatch-year and second-year birds as immatures, and after hatch-year and after second-year as adults from herein.

Statistical Analysis
Likelihood of capturing individuals in forest vs. coffee. We used generalized linear models with habitat (coffee = 0, forest = 1) as a response variable to assess the likelihood of capturing a higher number of individuals in forest or coffee during the winter. We compared a set of 5 candidate models, including a null model, to test whether the likelihood of capturing individuals in each habitat varied by year, sex, the additive effect of sex on year, or the interaction of year and sex. We ranked candidate models by second-order Akaike’s information criterion (AIC,) and estimated the relative likelihood of each model with AIC weights (w). Models within 2 units of the top model were considered to have equal support, except in cases where they differed by only one parameter and the more parameterized model had a
higher AICc (Burnham and Anderson 2002). All analyses were performed in the statistical software program R (R Core Team 2019). Models were selected using package AICcmodavg in R (Mazerolle, 2017). We used the coefficients from the model with the highest support to obtain the odds, odds ratios, and converted odds ratios to percent change of the odds of being captured in forest. We checked model assumptions by visually examining deviations from uniformity.

**Seasonal change in body condition.** A Wilcoxon signed-ranks test indicated that males were structurally larger, having longer wings than females ($W = 3,101, P < 0.001$; males, mean ± SD = 63 ± 2.03 mm; females, 61 ± 1.59 mm). Mass and wing length in males (Pearson's correlation $r = 0.39, n = 133, P < 0.001$) and females (Pearson's correlation $r = 0.33, n = 123, P < 0.001$) were correlated. To assess seasonal changes in condition, we therefore used the residuals of the linear regression of mass on wing chord as an index of body condition to account for differences in structural size (Labocha and Hayes 2012). After pooling sites, we estimated seasonal body condition changes in the population based on all individuals measured at first capture during the winter. Day 1 was equal to December 1.

We conducted the analyses in a 2-stage process. We first assessed whether trends in seasonal condition were linear or nonlinear by running a linear model (I), a quadratic model (I + I²), and a polynomial model (I + I² + I³), where “I” was capture day (Supplementary Material Table S1). Model selection was carried out using AICc as described above. The model structure of the top ranked model (Supplementary Material Table S1) was selected to be included in stage 2 (see below).

In the first stage, model selection suggested that the pattern of seasonal change in body condition was
Annual apparent survival. There were a small number of cases where individuals switched habitats between years and, therefore, we modeled apparent survival using a multistate mark–recapture approach (Lebreton et al. 2009) in program MARK (White et al. 2006). A multistate framework provides an estimation of state-specific probabilities of apparent survival and recapture as well as the transition probabilities between states (i.e., habitats). With this framework, the encounter history for each individual at time \( t \) contained an “F” if it was in forest or a “C” if it was in coffee. As an example, we describe the probabilities for an individual \( i \) in forest at time \( t \). This individual can either survive between the winters of \( t \) and \( t + 1 \) and return to the study area with probability \((\phi_F)\) or it can die or emigrate with probability \((1 - \phi_F)\). The individual’s survival probability between years is thus conditional on the habitat it was in at the start of the interval. Also, note that we are estimating apparent survival in this analysis and cannot separate mortality from emigration outside of the study area in year \( t + 1 \). Thus, it remains possible that the habitat an individual is in at time \( t \) influences whether it returns to the study area in year \( t + 1 \). If the individual survives the interval and returns to the study area it may return to the same forest habitat with probability \( \psi_F \) or move to coffee with probability \( \psi_C = 1 - \psi_F \). Conditional on the individual surviving the interval and returning to the study area, it can then be recaptured at time \( t \) with probability \( p_F \) in forest or \( p_C \) in coffee.

We began by modeling recapture probability as a function of age, sex, and habitat; the recapture probability model with the greatest support based on AIC\(_c\) was then used to examine which factors influenced apparent survival. Because so few individuals switched habitats between years, the probability of movement between habitats was only estimated as a single average value without covariates.

While accounting for recapture and movement probabilities, we then modeled apparent survival as a function of habitat (coffee, forest), age (immature, adult), sex (male, female), site (Los Vientos, La Fragua, La Vuelta), tag effects, time, and ENSO effects. Tag effects were tested because ~33.3% of the individuals in the analysis had a coded very high frequency (VHF) radiotag (Model NTWB-2, 0.35 g) or a light-level geolocator (Model Intigeo-W30Z11-DIP, 0.32 g) during one year of the study, and research elsewhere has reported on the potential for negative effects of tracking technology on the apparent survival of migratory passerines (reviewed in Constantini and Möller 2013). We predicted that apparent survival would be lower for individuals in the year following application of the tag and this potential influence was included as an additive effect. A strong El Niño event occurred during the winter of 2015–2016 and we incorporated this event as a categorical variable in the model, allowing for differences in survival following the El Niño year vs. the other 3 years. We also included a time-dependent model, which allowed for a separate apparent survival estimate for each year.

Apparent survival probabilities for males and females in each habitat were obtained by model averaging using the same approach as for Marra et al. (2015). Because some models had annually variable survival due to covariate effects, model averaging yielded annual estimates of apparent survival. The average of these annual means is reported as the expected mean apparent survival probability for the group with standard errors obtained using the Delta Method (Powell 2007) in R (R Core Team 2019) with package emdbook (Bolker 2019). We did not use model averaging for the model coefficients because of the challenges in their interpretation (Cade 2015, Banner and Higgs 2017) and instead report the coefficient estimates and standard errors from the top model. We used a median \( \hat{c} \) test to examine model goodness-of-fit (GOF). Because it is not possible to test GOF with models that contain individual covariates in program MARK, we used the most parameterized model without individual covariates. We then corrected for overdispersion by adjusting AIC\(_c\) values to quasi-AIC\(_c\) if \( \hat{c} > 1.0 \) (Burnham and Anderson 2002).

### Table 1

| Model | \( k \) | \( \text{AIC}_c \) | \( \Delta \text{AIC}_c \) | \( w_i \) |
|-------|--------|-----------------|-----------------|--------|
| D:Year + D\(^2\):Year + Time | 11 | 295.45 | 0 | 0.98 |
| D:H:Year + D\(^2\):H:Year + Time | 19 | 303.29 | 7.83 | 0.02 |
| D + D\(^2\) + Time | 5 | 310.45 | 15 | 0 |
| D:H + D\(^2\):H + Time | 7 | 313.09 | 17.64 | 0 |
| D:Age + D\(^2\):Age + Time | 11 | 314.49 | 19.04 | 0 |
| D:Sex + D\(^2\):Sex + Time | 7 | 314.64 | 19.19 | 0 |
| D:H:Sex + D\(^2\):H:Sex + Time | 11 | 315.46 | 20 | 0 |
| Null | 2 | 340.54 | 45.09 | 0 |
RESULTS

Likelihood of Capturing Individuals in Forest vs. Coffee
We assessed the likelihood of capturing a higher number of individuals in forest or coffee in 284 Canada Warblers captured with a banding effort of 45,085 mist net hr over 4 winters (one mist net hour = one 12-m net open during 1 hr). Banding effort was 0.2% and 17% higher in forest than coffee during 2013–2014 and 2014–2015, respectively, and 4% and 12% higher in coffee than forest during 2015–2016 and 2016–2017, respectively (Supplementary Material Table S3).

The top ranked model had 61% of model weight and included an effect of year with the additive effect of sex (Supplementary Material Table S4). Captured females were more likely to be in coffee than in forest in most years whereas males were more likely to be captured in coffee in 2013–2014 and 2014–2015 and in forest in 2015–2016 and 2016–2017. Confidence intervals for both sexes overlapped 1 in all years but 2014–2015 (Figure 2; Supplementary Material Tables S4 and S5). Visual inspection of residual plots indicated that the top ranked model complied with the assumptions.

Seasonal Change in Body Condition
We modeled seasonal changes in body condition in 260 individuals captured over the 4 winters (2013–2014, n = 61; 2014–2015, n = 69; 2015–2016, n = 85; 2016–2017, n = 45). When years were combined, a quadratic model including a difference in seasonal gain in body condition between years received the greatest support (Table 1). A model including year and habitat was ranked below that containing just year, suggesting that habitat had no clear effect on the seasonal pattern of body condition change in Canada Warbler in our sample. However, when analyzing years individually, there was support for body condition being higher throughout the season in forest relative to coffee in 2013–2014 but not in other winters (Supplementary Material Table S2). In general, body condition declined from early to mid-winter and increased at the end of the season. Birds showed the lowest condition during 2015–2016 (Figure 3).

Apparent Survival
Estimates of apparent survival were based on 330 individuals marked between winter 2013–2014 and 2016–2017, including 228 immatures and 82 adults, 163 females and
167 males, and 197 individuals marked in coffee and 133 marked in forest. Of the 330 individuals, 93 had been fitted with a light-level geolocator or a radiotag in at least one year (see Supplementary Material Table S6 for further details). Forty-two individuals were recaptured the year after they were marked, 33 in just one year and 9 individuals in 2 subsequent years. Average annual recapture probabilities varied by sex and habitat and were higher for females than males and higher for individuals in forest than coffee (Table 2). Recapture probabilities did not vary by age at first capture (Table 3, Supplementary Material Table S7).

Two of the 44 individuals that survived and returned to the study area switched habitat types with an estimated transition probability of 0.028 ± 0.019. One of these individuals was a female first marked in forest and recaptured in coffee the following year, while the other was a male marked in coffee and recaptured in forest 2 yr later. GOF tests with the median ĉ procedure showed no evidence of overdispersion (ĉ = 0.70). We found evidence that individuals carrying radiotags or geolocators (i.e. tags) had lower average apparent survival than those without tags (λ̂β = −1.19 ± 0.63). The coefficients from the top model in Table 3 predicted that the apparent survival for an individual tagged in year 1 would be 0.12 lower than an individual without a tag, due to higher mortality and/or emigration. Because of this influence, tag effects were included as an additive effect in all models. While including these tag effects, we found little support for our prediction that apparent annual survival would be lower for individuals occupying coffee during the winter than those occupying forest (Table 2). Model-averaged estimates of apparent annual survival were slightly higher (5%) for males in forest than males in coffee but were the same for females in the 2 habitats (Table 2). Males on average had a 4% higher annual apparent survival relative to females in coffee and 13% higher in forest but there was uncertainty in these estimates and models with sex had lower support than models without sex (Table 3).

While a fully time-dependent model had the greatest support, there was also strong evidence for a negative influence of El Niño year on apparent survival (λ̂β = −1.69 ± 0.49, Table 3). The addition of ENSO led to a reduction in AICc of 11.95 units compared with the same model with only a constant time effect (Table 3). Apparent survival during the El Niño year was substantially lower than the other years, ranging from only 0.15 for females in coffee to 0.22 for males in forest (see Supplementary Material Figure S1). We predicted that negative effects of El Niño event would also be greater for individuals in coffee than forest but found no evidence for this effect (AICc of the interaction model was 1.78 units higher than the additive model; Table 3).
TABLE 2. Sex and habitat-specific apparent and survival recapture probabilities (mean ± SE) for Canada Warbler spending the winter on the western slope of the Eastern Andes of Colombia. Estimates were obtained by model averaging across the full candidate set in Supplementary Material Table S7. See Supplementary Material Figure S1 for annual estimates of apparent survival.

| Group          | Apparent survival | Recapture  |
|----------------|-------------------|------------|
| Male coffee    | 0.48 ± 0.12       | 0.15 ± 0.08|
| Male forest    | 0.53 ± 0.11       | 0.36 ± 0.12|
| Female coffee  | 0.44 ± 0.10       | 0.35 ± 0.11|
| Female forest  | 0.44 ± 0.10       | 0.65 ± 0.15|

TABLE 3. Summary of model selection results for the probabilities of annual apparent survival ($\phi$) and recapture ($p$) of Canada Warblers at 3 sites in Colombia. Models are those with 95% of model support (see Supplementary Material Table S7 for all candidate models tested). Variables include time = annual variation, ENSO = El Niño Southern Oscillation effect, tag = effect of radiotag or light-level geolocator, age = juvenile vs. adult, habitat = shade coffee vs. forest, and sex = male vs. female. Covariates were not included for movement among habitats between years (ψ). $k$ is the number of parameters; $\Delta$AIC, the change in Akaike’s Information Criterion; $w_i$ is the Aikake weight support for each model. The intercept only model for apparent survival with sex and habitat effects on recapture and no covariates for movement had a $\Delta$AIC of 20.36.

| Model                     | $k$ | $\Delta$AIC | $w_i$ |
|---------------------------|-----|-------------|-------|
| $\phi_{time\cdottag} \cdot P_{sex\cdothabitat} \cdot \psi$  | 9   | 0           | 0.21  |
| $\phi_{time\cdottag\cdotsex} \cdot P_{sex\cdothabitat} \cdot \psi$ | 10  | 0.59        | 0.16  |
| $\phi_{time\cdottag\cdothabitat} \cdot P_{sex\cdothabitat} \cdot \psi$ | 10  | 0.66        | 0.15  |
| $\phi_{ENSO\cdottag} \cdot P_{sex\cdothabitat} \cdot \psi$ | 7   | 0.97        | 0.13  |
| $\phi_{ENSO\cdottag\cdotsex} \cdot P_{sex\cdothabitat} \cdot \psi$ | 11  | 1.65        | 0.09  |
| $\phi_{ENSO\cdottag\cdothabitat} \cdot P_{sex\cdothabitat} \cdot \psi$ | 8   | 2.18        | 0.07  |
| $\phi_{ENSO\cdottag\cdotsex\cdothabitat} \cdot P_{sex\cdothabitat} \cdot \psi$ | 8   | 2.38        | 0.06  |
| $\phi_{ENSO\cdottag\cdotsex\cdothabitat} \cdot P_{sex\cdothabitat} \cdot \psi$ | 9   | 3.40        | 0.04  |
| $\phi_{ENSO\cdottag\cdotsex\cdothabitat} \cdot P_{sex\cdothabitat} \cdot \psi$ | 9   | 3.96        | 0.03  |
| $\phi_{ENSO\cdottag\cdotsex\cdothabitat} \cdot P_{sex\cdothabitat} \cdot \psi$ | 10  | 4.23        | 0.02  |

*Prior to testing variables affecting annual apparent survival, we examined how age, sex, and habitat affected recapture probability; sex and habitat were retained in the top model and used for all subsequent comparisons.

**DISCUSSION**

We determined the suitability of shade coffee plantations and native forest as winter habitat for the declining Canada Warbler by comparing sex-specific variation in the likelihood of capturing individuals in each habitat, seasonal changes in condition, and annual survival between the 2 habitats. Males were slightly more likely to be captured in forest than females, and there was no strong effect of habitat on seasonal change in body condition or apparent annual survival. Apparent survival during the El Niño year was substantially lower than the other years. However, we found no evidence for a greater negative effect of El Niño event for individuals in coffee. Taken together, our measures of winter habitat quality suggest that, relative to native forest, shade coffee plantations with optimal conditions such as those at our study sites (high canopy height and cover) can be suitable winter habitats for Canada Warbler.

Sex-specific habitat segregation during the winter, in which males and females occur in different proportions in different habitats, has been reported in several Neotropical migrants (Lynch et al. 1985, Wunderle 1995, Marra 2000, Wunderle and Latta 2000, Latta and Faaborg 2002). One of the mechanisms underlying this habitat distribution pattern is behavioral dominance, where individuals of varying abilities compete for access to critical resources such as food, resulting in a greater proportion of dominant males in the highest quality habitats (Marra 2000). We found some support for our predictions that males may be more likely to be captured in forest than females. For instance, the mean likelihood of capturing a male in forest was higher than that of females and increased to a greater extent during the driest years (2015–2016 and 2016–2017). This result may suggest temporal variation in habitat quality linked to precipitation and its effects on food availability (Studds and Marra 2007, 2011). However, further studies estimating density in each habitat in relation to quality would be needed to evaluate whether annual winter conditions influence sex-specific habitat segregation.

Patterns of change in body condition and survival are consistent with previous research on the Caribbean islands showing that the amount and timing of precipitation during the winter has major effects on habitat quality and overwinter performance of Neotropical migrants in several habitats including shade-grown coffee plantations (Strong and Sherry 2000, Studds and Marra 2007, 2011). For instance, seasonal decline in body condition in both habitats across years was synchronized with the progression of the dry season from the beginning of December until the end of February before slightly increasing from late February to the end of March with the onset of the rainy season.

During the winter, survival is the demographic measure most clearly linked to fitness, and therefore a robust indicator of winter habitat quality for population persistence (Johnson et al. 2006). Contrary to our expectations, we did not find differences in apparent annual survival between individuals that overwintered in coffee and those that overwintered in forest. Previous studies suggest that a decline in body condition during the winter is a strong predictor of annual survival probability in insectivorous birds overwintering in Jamaica (Marra and Holmes 2001, Johnson et al. 2006). While we found evidence for this effect in the influence of El Niño event, we did not observe this pattern among habitats, as in Jamaica (Johnson et al. 2006), which likely explains the similar apparent survival probabilities for individuals in forest and coffee.
One possible explanation for the difference between our study and those in the Caribbean is the earlier initiation of the rainy season in Colombia (March) relative to the Caribbean (May), which allowed individuals to recover body condition during late winter in both habitats such that there were no subsequent consequences for apparent survival. Alternatively, it remains possible that within-winter apparent survival is lower for individuals in coffee compared with forest but that this effect is minimized across the other stages of the annual cycle after Canada Warblers have departed from the wintering grounds. Further studies comparing within- vs. between-winter survival would be useful to examine these possibilities.

A decrease in apparent survival in individuals carrying tags (i.e. radiotags or geolocators) is consistent with previous research reporting a negative effect of geolocators on birds (Constantini and Moller 2013) but contrasts with recent findings suggesting only slightly negative effects of geolocators on survival (Brlík et al. 2019). In our study, 28% of marked individuals carried a radiotag or geolocator at least one year and of those that did, 63% carried a radiotag while 37% carried a geolocator. We did not separately examine the influence of each type as we were only attempting to control for the effects of tags that had been applied for other purposes over the course of this study. Further studies assessing the differential effects of geolocators vs. radiotags on small Neotropical migrant birds would allow us to better understand the impacts of this technology, including whether any observed decreases in apparent survival are due to an increase in mortality or a greater propensity to disperse elsewhere.

For Neotropical migratory songbirds, moisture and food availability are the main drivers of winter habitat quality (Sherry et al. 2005, Brown and Sherry 2006, Smith et al. 2010). In turn, these are some of the most important ecological factors limiting physical condition and survival of migrants during the winter (Sherry and Holmes 1996, Sherry et al. 2005, Studs and Marra 2005). We found evidence that drought conditions induced by the 2015–2016 El Niño event (Supplementary Material Figure S2) amplified the negative effects of seasonal variation in rainfall on physical condition and annual survival. For instance, during the El Niño year, the decline in body condition and survival was steeper in both habitats. Within the coffee region, our study sites are characterized by drier than average conditions, with a median precipitation of 1,103 mm/year (Cenicafé 2011). Precipitation in our study sites follows a bimodal pattern with 2 rainy seasons (March to June and September to November) and 2 dry seasons (December to February and July to August) (Cenicafé 2011). The El Niño event induced drought conditions in our study sites; precipitation in December 2015 was only 0.7 mm compared with 108 mm in 2013, and ~84 mm in both 2014 and 2016 (Cenicafé 2016a, 2016b, 2016c, 2017; Supplementary Material Figure S2).

Severe drought induced by El Niño events has been shown to have lethal effects on Neotropical migrants spending the winter in primary forest by decreasing food availability and habitat quality (Sillett et al. 2000). We suggest that the steep decline in precipitation during the 2015–2016 El Niño event further challenged the response of individuals to seasonal drought (Strong and Sherry 2000, Latta and Faaborg 2002, Studs and Marra 2007, Smith et al. 2010), resulting in negative consequences for body condition and annual survival in both habitats. However, contrary to our expectations, we did not find evidence that the negative effects of the extreme El Niño event on apparent survival of individuals was stronger in coffee than forest, supporting our overall results that the 2 habitats offer similar quality. Further study is needed to determine whether this is true at a broader scale and whether within-season survival is impacted differentially among habitats.

Our results highlight the role of shade coffee in the conservation of Neotropical migrants. Demographic measures in both habitats were similar, particularly apparent survival, the parameter most closely linked to population change. It should be noted that the minimum amount of shade recommended in our study region is 29%, contrasting with other Andean regions with heavy cloud cover and high rainfall where 20% shade is recommended, and several regions have no shade (Farfán-Valencia and Jaramillo-Robledo 2009). Consequently, coffee plantations in our study sites have diverse floristic and structural attributes, and a complex and diverse vertical stratification, which increases habitat suitability for Canada Warbler and other Neotropical migrants (Bakermans et al. 2012, Céspedes and Bayly 2019). Indeed, shade coffee plantations at our study site were characterized by high canopies (mean 18.8 m) and an average canopy cover of 44.4%, and may not reflect “average conditions” across shade coffee plantations in the Andes. Therefore, we may have found clearer evidence for differences in habitat suitability in plantations with less favorable management practices such as less diverse shade trees or lower canopy cover and height; such practices are widespread across the Andes.

Traditionally, coffee has been produced in rustic systems where the native canopy was maintained across much of the Neotropical region (Moguel and Toledo 1999). Since the 1970s, coffee plantations have been more intensively managed and transformed into open-sun production systems (Perfecto et al. 1996, Moguel and Toledo 1999, Rice 1999). For instance, by 1990, almost 50% of the traditional shade coffee had been converted to sun coffee in Latin America, and this decrease continued between 1990 and 2010 across the globe (Jha et al. 2014). In Colombia alone, the share of coffee production under shade decreased from...
The dramatic intensification of agricultural practices towards open-sun systems has resulted in a more severe loss of global biodiversity relative to the conversion of natural forest to agroforestry systems (De Beenhouwer et al. 2013), and undoubtedly in a decrease in winter habitat availability for Neotropical migrants. Despite the development of market-based conservation incentives to promote shade coffee retention, the remnants of this valuable agroecosystem are in danger of being lost across the Neotropics. Strategies aiming to conserve structurally complex shade coffee plantations from further intensification, and to diversify current open-sun systems, will enhance biodiversity and ecosystem services (Bakermans et al. 2012, De Beenhouwer et al. 2013) and habitat availability for Neotropical migrants such as the Canada Warbler. Recent models predict that reverting sun coffee to shade coffee maximizes farmers’ income by increasing pest control services provided by birds and potential price premiums for higher quality coffee, while offsetting lower yields associated with shade coffee production (Hernández-Aguilera et al. 2019). However, the effective implementation of such strategies depends, in part, on the development of financial and technical assistance programs to low-income smallholder farmers, and on the promotion of sustainable coffee among consumers (González-Prieto 2018, Hernández-Aguilera et al. 2019).

The conservation value of shade coffee plantations is likely enhanced by the presence of forest in the landscape and, in addition, forest is expected to provide additional ecosystem services (Ricketts 2004, Ricketts et al. 2004, Karp et al. 2013). While shade coffee might be beneficial for Canada Warbler, this might not be true for resident non-migratory Neotropical forest specialists, which are severely affected by the global transformation of forest to agroecosystems and by management intensification (Tejada-Cruz and Sutherland 2004, De Beenhouwer et al. 2013). Landscape conservation approaches, promoting diverse matrices maintaining both habitats, might best ensure long-term survival in both Canada Warbler and resident species, while simultaneously creating resilience and satisfying the economic needs of local communities.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *The Condor: Ornithological Applications* online.

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Ethics statement: All applicable institutional and national guidelines for the care and use of animals were followed. We captured and marked birds following Animal Use Protocol #20100084 approved by the University of Saskatchewan Animal Research Ethics Board. Research permits were issued by Agencia Nacional de Licencias Ambientales (Res. 0597).

Author contributions: A.M.G. conceived the idea. A.M.G., N.J.B., and K.A.H. designed the study. A.M.G. carried out the study and collected data. A.M.G. and S.W. analyzed data. A.M.G. wrote the manuscript with contributions and feedback from all co-authors.

Data depository: The datasets generated and analyzed during the current study can be found at González et al. (2020).

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