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Article

Habitat-specific survival of golden-winged warblers *Vermivora chrysoptera* during the non-breeding season in an agricultural landscape

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Nearctic-Neotropical migratory birds are considered priority species for conservation because they are subject to threats at distinct breeding, migratory and stopover locations throughout their annual cycle, and many species have undergone severe population declines. Research during the non-breeding season has focused on identifying the locations and habitats that migrants use, but wintering migrants are known to occupy habitats of both high and low quality, especially when the best sites are saturated by conspecifics. Thus, the presence or abundance of a species may not be a reliable indicator of winter habitat quality. The habitat associations of the golden-winged warbler *Vermivora chrysoptera*, a Nearctic-Neotropical migrant bird species of elevated conservation concern, are relatively well studied, yet conservation efforts are hindered by lack of information about basic demographic rates. In particular, no published estimates exist for non-breeding season survival, which can be a key vital rate affecting population viability, nor how survival rates vary among habitats, which is important to designing conservation programs to support populations during the winter period. We studied a color-banded population of golden-winged warblers in Costa Rica over a three-year period and estimated overall survival rates, and the effects of habitat characteristics on survival. We found that monthly survival of juveniles (0.881) was lower than adult birds (0.978). Monthly survival during the non-breeding season (0.967) was higher than monthly survival during the rest of the annual cycle (0.930). Survival was negatively related to canopy height, and we observed a significant quadratic effect where survival peaked at intermediate levels of vine tangles and dead hanging leaves, which corresponds to habitat features associated with abundance in prior studies at this same site. Our findings contribute to our existing knowledge about the potential impacts of winter-season events on Nearctic-Neotropical migratory bird populations, and also informs potential conservation strategies for wintering golden-winged warblers.

Keywords: Avian, Costa Rica, habitat, Nearctic-Neotropical migrant, survival, winter

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Introduction

Long-distance migrants that travel between temperate and tropical regions are considered particularly vulnerable because they are subject to potential threats throughout their annual cycle at distinct breeding, migratory and stopover locations (Askins 1993, Sherry and Holmes 1996, Rosenberg et al. 2019). Furthermore, Nearctic-Neotropical species have undergone severe population declines in recent decades (King et al. 2006, Rosenberg et al. 2019). Although events on the non-breeding grounds may limit migrant populations (Rappole et al. 1989, 2003, Sherry and Holmes 1996, Strong and Sherry 2000, Studds and Marra 2005, Holmes 2007, Calvert et al. 2009), the winter ecology of most species is under-studied, relative to their breeding ecology (Faaborg et al. 2010a). As a result, understanding the habitat needs and other requirements of these species has been identified as a research priority by the international conservation collaborative 'Partners in Flight' (Donovan et al. 2002).

One migrant species of conservation concern is the golden-winged warbler *Vermivora chrysoptera*. Breeding Bird Survey data show an annual population decline of 2.6% year^{-1} over the past 45 years, with apparent extirpation in parts of their historic breeding range. This rate is slightly higher than the rate of decline for North American species as a whole (Rosenberg et al. 2016). Breeding ground factors, such as the reduction of effective population size due to hybridization with blue-winged warblers *Vermivora cyanoptera*, and the loss of early-successional breeding habitats (Litvaitis 1993, Gill 1997, Vallender et al. 2007) may contribute to these declines (Buehler et al. 2007). However, little is known about the extent to which population declines are impacted by events during the non-breeding season. Recent migratory connectivity work shows segregation in non-breeding distributions among geographically distinct breeding populations, with evidence that habitat loss and degradation in South America may have significantly contributed to observed declines in the Appalachian Mountain population of golden-winged warblers (Kramer et al. 2017, 2018, Bennett et al. 2019a).

Research on non-breeding golden-winged warblers has shown they are most abundant in disturbed forests with intermediate canopy heights, and high concentrations of vine tangles and hanging dead leaves, which are preferred foraging substrates (Chandler and King 2011, Bennett 2012). However, abundance and density can be misleading indicators of habitat quality, for example, when high numbers occur in sink habitats with lower fitness (Van Horne 1983, Gilroy and Sutherland 2007). This decoupling between habitat use and habitat quality is particularly pronounced in systems that have been altered relatively recently (Bock and Jones 2004). For example, in Neotropical landscapes in which forests has recently been converted to coffee, wood thrushes *Hylocichla mustelina* are known to select shade coffee over native forest, despite the fact that their survival is lower in shade coffee (Bailey and King 2019). It is therefore important to supplement estimates of occupancy and abundance with estimates of habitat-specific survival to ensure that they are valid indicators of non-breeding habitat quality (Johnson et al. 2006, Johnson 2007, Streby et al. 2016). In order to validate the current understanding of wintering habitat quality for golden-winged warblers based on abundance–habitat relationships (Chandler and King 2011, Bennett 2012), we conducted this study to estimate habitat-specific survival, and to establish baseline survival estimates for golden-winged warblers during the non-breeding season. This information will shed light on the factors that limit populations of this and other migrants throughout the annual cycle, and help conservationists target resources more effectively (Sillett and Holmes 2002, Streby et al. 2016).

Material and methods

This study took place between January and April of 2011 through 2013. Our population included a few individuals banded as early as 2006 by Chandler and King (2011), but encounter histories were generated from 2011 to 2013. An abbreviated four-week season was conducted in 2013 to help generate more robust estimates for annual and among season survival. Thus, the majority of effort was concentrated in 2011 and 2012. The study area consists of an approximately 30 km^2 mosaic of predominantly equal parts forest and cattle pastures located on the Pacific slope of the Tilarán mountain range in the Montes de Oro region of Costa Rica (N10°13′ W84°39′; Fig. 1). Small-scale coffee farms are also common in the area. Elevations range from 900 to 1500 m (Fig. 1). Forest types of the study area can be classified as montane wet forest (often referred to as cloud forest) above 1200 m, and premontane moist forest below 1000 m, with a transition zone in between (Holdridge 1947). The montane wet forest is characterized by an abundance of epiphytes and moss, and trees of a shorter stature than those at lower elevations on either side of the continental divide. The premontane moist forest has fewer epiphytes, and some deciduous trees that drop their leaves in the dry season. Most of our work took place in the transition zone between these forest types.

We estimated apparent survival of golden-winged warblers by systematically searching for uniquely marked individuals over time. Individuals were located for capture by searching all habitats in which golden-winged warblers had been located during a prior, systematic survey by Chandler (2010), including primary and secondary forest, forested ravines, abandoned pastures and orchards. Searches consisted of visually scanning habitat for individual birds or the mixed-species flocks that golden-winged warblers associate with (Chandler et al. 2016), and using playback periodically.

Once located, individuals were target-netted using playback and a decoy placed in front of mist nets. Captured birds were weighed, measured, sexed and aged as either second year birds (SY, less than 1-year old) or after second year (ASY) based on plumage characteristics (Pyle 1997), and marked with a USGS numbered band and a unique combination of color-bands. Individuals banded previously by Chandler and

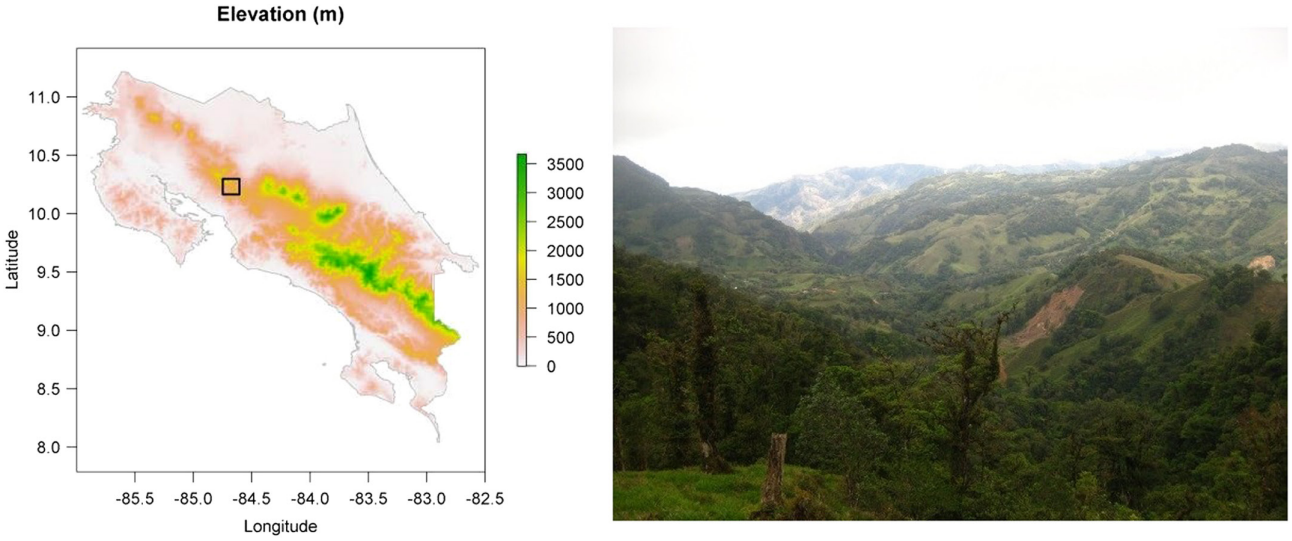

Figure 1. The study area is represented by the black square on the map of Costa Rica, and a typical view of the area, showing a mosaic of forest patches and pastures.

King (2011) were searched for and, if found, also included in the study.

To relocate individuals, a resight attempt was made using playback 50 m away from the initial capture location on a randomly selected bearing of 0, 120 or 240 degrees. Each resight attempt was 10 min long during which a recording of golden-winged warbler vocalizations was played at a standard volume (~100 dB at a distance of 1 m; Chandler and King 2011). If an individual was not detected, a second attempt was immediately made at another randomly chosen bearing of 0, 120 or 240 degrees (excluding the first used bearing), and if still not detected, at the initial capture location. This sequence of resight attempts constitutes one resight occasion, and totals no more than 30 min of effort. Each subsequent resight occasion was centered on where an individual was last detected, and the process of fanning out at randomly chosen bearings (0, 120 or 240 degrees) for resight attempts began again. In this way, new areas of each territory were identified. If two resight occasions passed without detection, on the following occasion a 30-min search of the area was undertaken using playback within the vicinity of the initial capture location. Following the capture of each individual, resight occasions took place every two weeks until just before the estimated departure date for spring migration (15 April). Resight occasions then resumed when the following season began in January. In 2013, our final season, we conducted up to three resight occasions for each individual over a four-week period to gather more information on annual and among season survival. This procedure generated an encounter history with which to estimate detection probability and survival, and also allowed a portion of the birds' home range to be identified and characterized.

At the location of each resight attempt, regardless of whether an individual was detected there, we recorded habitat variables reported to be associated with golden-winged warbler abundance at these sites (Chandler and King 2011). These variables were canopy height, the number of vine tangles > 1 m in diameter, and a dead hanging leaf index (0–10 low, 11–100 med, > 100 high) within an 8 m radius plot. Because individuals were possibly drawn to playback at point locations within a territory, we were unable to use these data to compare habitat at occupied versus unoccupied points. Instead, the mean of each habitat variable was used to characterize an individual territory, not to describe features selected within a territory. Golden-winged warblers exhibit high territoriality and aggressive behavioral responses to playback on our site (Chandler et al. 2016). Furthermore, they have large home range sizes (8.77 ± 0.92 ha), and no resight location was ever more than 50 m away from a point where a given individual was detected. Therefore, we are confident that individuals were not drawn outside of their territory by playback, and that our habitat measurements are representative of respective territories.

We calculated minimum convex polygons around resight locations to give a general sense of the proportion of a given territory's area that our field methods identified, considering a previously reported mean of 8.77 ha.

Cormack–Jolly–Seber (CJS) models were developed to estimate survival rates when detection probability is less than one (Cormack 1964, Lebreton et al. 1992). CJS models can be extended to investigate differential survival among individuals or groups, such as age class or sex, or environmental variables, such as vegetation structure and composition. We modeled apparent survival (ϕ) and resight probability (p) using a hierarchical formulation of the CJS model (Royle 2008, Royle and Dorazio 2008), described as follows:

$$z(i,t) \mid z(i,t-1) \sim \text{Bernoulli}\left(z\left(i,t-1\right)\phi\right)$$

$$y(i,t) \mid z(i,t) \sim \text{Bernoulli}\left(z\left(i,t\right)p\right)$$

where $z(i,t)$ is a partially-observed variable describing if individual i was alive on day t, and $y(i,t)$ is the observed encounter data. This model acknowledges the fact that an individual cannot be detected if it is not alive or if it has emigrated out of the survey area. Individuals that are alive and within the survey area are detected with a probability of p. In this formulation, covariates of both survival probability and detection probability can be accommodated.

This model does not distinguish between mortality and permanent emigration, and thus yields only estimates of apparent survival. However, evidence from our study area suggests very high site fidelity of individuals within and among seasons, regardless of age or sex (Chandler et al. 2016), making it less likely that survival estimates are confounded by emigration. Furthermore, permanent emigration indicates lower persistence, and since persistence is a useful correlate of survival (Faaborg et al. 2010b), it still provides information on the influence of habitat on demographic rates during the non-breeding season.

Encounter histories were set up by day (versus week or month), which provides estimates of daily survival. An individual receives either a '1' (detected) or '0' (not detected) for each resight occasion, and no entry (i.e. 'NA') for days without a resight occasion. By explicitly defining the wintering season (1 October–15 April, based on arrival and departure dates, Chandler 2010), daily survival rates are estimated for the entire 6.5-month non-breeding season. Individuals who return in subsequent years allow for the estimation of a survival rate for the 5.5-month period of time spent outside the wintering season (i.e. migrating and breeding), termed among season survival.

We modeled within season survival as a function of average canopy height, number of vine tangles and an index of dead hanging leaves, which were treated as individual random effects. Collinearity among these variables required a separate model for each. These variables were selected because they are known to be associated with golden-winged warbler use at our site (Chandler and King 2011), so are useful for determining whether selected habitat features are associated with greater survival, and thus represent habitat quality. As golden-winged warbler territories can encompass multiple habitat types (e.g. primary forest, secondary forest, and abandoned pasture), and the microhabitat features associated with golden-winged warbler use are not distributed differently by habitat type, we did not model survival by habitat category.

Songbirds are reported to experience lower survival in their first year of life (Gardali et al. 2003), and therefore age was included in survival models. Individuals in their first winter represented the juvenile age class, and all others were considered adults. Our sample included very few females, so we did not model differences between sexes.

We initially modeled detection probability as a function of canopy height, as birds in taller forests may be more difficult to detect. We also modeled the effects of exposure to playback as birds could become habituated and ignore the recordings. Neither was significantly associated with detection probability; thus, we kept that probability constant by not including these variables in our final models.

We used Bayesian inference and vague prior distributions. Convergence was assessed using visual inspections and Rubin–Gelman diagnostics (Gelman and Rubin 1992, Supporting information). Models were run in the program JAGS 4.2.0 (Plummer 2003) using the R2jags package in RStudio 0.99.892 (Su and Yajima 2014, <www.r-project.org>). Finally, we approximated the variances of derived parameters using the delta method (Powell 2007).

Results

We banded 23 male and 2 female golden-winged warblers in the 2011 season, and 19 males and 1 female during the 2012 season, for a total of 45 individuals. We were also able to locate five additional birds (four males and one female) banded previously by Chandler and King (2011). We excluded six individuals from the analyses that were banded but never re-sighted, assuming that they were transients, since they were banded late in the season in habitats not typically used by golden-winged warblers (thin riparian strips of forest, or in brushy areas far from a forest patch; Chandler and King 2011). This yielded 397 resight attempts for 44 individuals (40 males, 4 females). An average of 9.9 points were collected per individual (range: 6–20), with an average minimum convex polygon area of 1.07 ha (range: 0.28–3.93 ha; Fig. 2). These areas should be considered only a portion of home ranges, as our field methods were not meant to

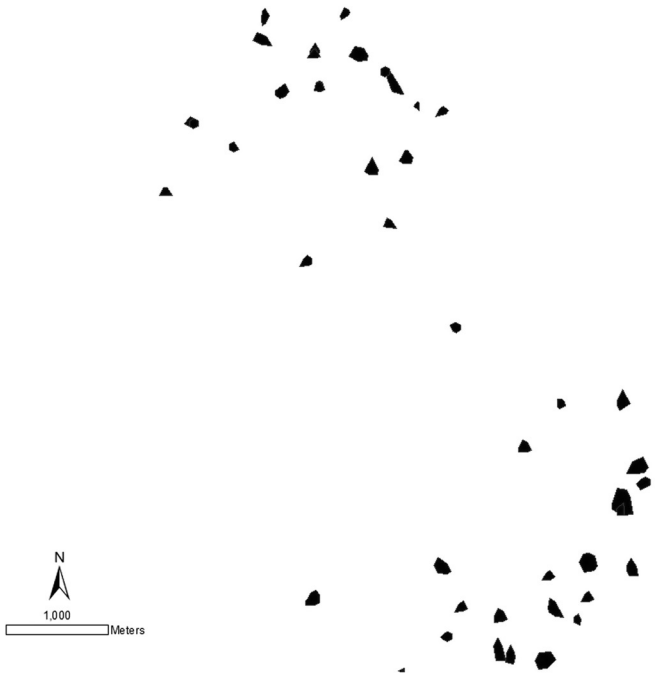

Figure 2. Minimum convex polygons around resight locations for golden-winged warblers (n = 44) in the Tilarán Mountains of Costa Rica, 2011–2013.

precisely measure the large home range sizes reported at our site (8.77 ± 0.92 ha, Chandler et al 2016).

The average canopy height across all individuals' resighting areas was 11.66 ± 4.4 m. We found that canopy height was positively correlated with the number of vine tangles ($r = 0.32$, $p = 0.4$), as well as the number of dead hanging leaves ($r = 0.41$, $p = 0.008$). Vine tangles and dead hanging leaves were also correlated ($r = 0.51$, $p = 0.0007$). The credible intervals around slope estimates in early models for the effect of canopy height ($\beta = -0.54$, CI −1.41 to 0.22) and exposure to playback ($\beta = -0.42$, CI −2.91 to 5.15) on detection probability contained 0, which indicates no significance.

Apparent monthly survival (daily survival raised to the 30th power) was 0.967 (SD 0.02), equivalent to a 0.804 (SD 0.11) probability of surviving the entire 6.5-month stationary non-breeding season. Detection probability was estimated to be 0.537 (SD 0.03). Eighteen individuals were encountered in multiple seasons. Two individuals survived for at least four seasons, four for three seasons and twelve for two seasons. Among-season apparent survival was estimated at 0.670 (SD 0.10), equivalent to a monthly survival of 0.930 (SD 0.01). This rate includes survival during the breeding season as well as both migratory periods. Annual survival was derived by multiplying the within season survival estimate by the among season survival estimate, yielding an annual apparent survival probability of 0.539 (SD 0.15).

We marked a total of 17 juveniles and 27 adults, and were able to estimate age-specific survival rates. Juvenile within season monthly survival (0.881, SD 0.07) was less than adult monthly survival (0.978, SD 0.02, $t(42) = 6.8135$, $p < 0.0001$). This equates to probabilities of 0.439 and 0.865 (juvenile and adult survival, respectively) for surviving the 6.5-month stationary non-breeding season. The survival rate of birds from the end of their first (i.e. juvenile) stationary non-breeding season until the start of the next stationary non-breeding season (0.725, SD 0.16) was not significantly different than that for birds that were adults at the start of this period (0.672, SD 0.13, $t(42) = 1.2335$, $p = 0.2242$).

Finally, the 95% credible interval for the slope estimate of canopy height did not contain 0, and indicated a significant negative association between canopy height and survival, and significant positive quadratic terms were observed for the number of vine tangles and dead hanging leaves (Table 1, Supporting information). Survival was estimated to be greatest at lower canopy heights, ~5–10 m. For the number of vine tangles, the greatest survival rate was at 1.58 vine tangles within an 8 m radius plot, or about 79 vine tangles per hectare. Survival was also greatest at moderate levels of dead hanging leaves (Fig. 3).

Table 1. Summary statistics of posterior distributions for all parameters in age- and habitat-specific models of golden-winged warbler survival in the Tilarán Mountains of Costa Rica, 2011–2013.

				95% CI	
Parameter	Mean	SD	Median	Lower	Upper
Canopy height slope	−0.66	0.37	−0.63	−1.48	−0.02
Quadratic vine tangles	1.00	0.51	0.95	0.17	2.16
Quadratic dead leaves	1.97	1.21	1.74	0.29	4.63
Juvenile within season monthly	0.91	0.06	0.93	0.75	0.99
Adult within season monthly	0.96	0.02	0.97	0.91	0.99
Among season survival	0.67	0.05	0.66	0.60	0.79
Variance	1.07	1.55	0.55	0.00	5.20
Resight probability	0.53	0.04	0.53	0.46	0.60

Discussion

The survival estimates we were able to generate in this study address key research priorities of quantifying demographic rates across the annual cycle, and identifying habitats and landscapes that promote the survival of Nearctic-Neotropical migrants across the annual cycle (Donovan et al. 2002, Sillett and Holmes 2002, Faaborg et al. 2010b, Streby et al. 2016). Including estimates of survival in non-breeding habitat studies is important because survival is reported to be decoupled from abundance in some cases (Rappole et al. 1989, Bailey and King 2019). However, we found general agreement between habitat associations based on abundance (Chandler and King 2011) and habitat-specific survival at these same study sites. For example, we found that survival was high at intermediate canopy heights, and positively associated with the presence of vines and dead leaves, which is generally consistent with the abundance-based habitat associations described by Chandler and King (2011). There were some minor contrasts – the canopy heights associated with the highest survival in this study were lower than those associated with maximum abundance, and the relationships of abundance with vines and dead leaves were linear (Chandler and King 2011) as opposed to the quadratic relationships we found with survival. All considered, both assessments – based on either abundance measures or survival – suggest that naturally disturbed primary forest and advanced second growth constitute high quality habitat for this species (Chandler and King 2011).

Differences in monthly survival rates among periods of the annual cycle can reveal when mortality is highest. For example, Jones et al. (2004), found that male cerulean warblers *Setophaga cerulea* had a higher breeding season monthly survival (0.98) than among season (0.93), indicating that most mortality occurs during migration or the overwinter period. We found the monthly rate of surviving the non-breeding season (0.967) to be higher than the monthly among season rate (0.930). The among season rate encompasses both migratory periods and the breeding season, which cannot be separated using our data. However, migratory songbirds likely experience the highest mortality during migratory periods (Sillett and Holmes 2002, Newton 2006, Calvert et al. 2009, Klaassen et al. 2012, Rockwell et al. 2017, Rushing et al.

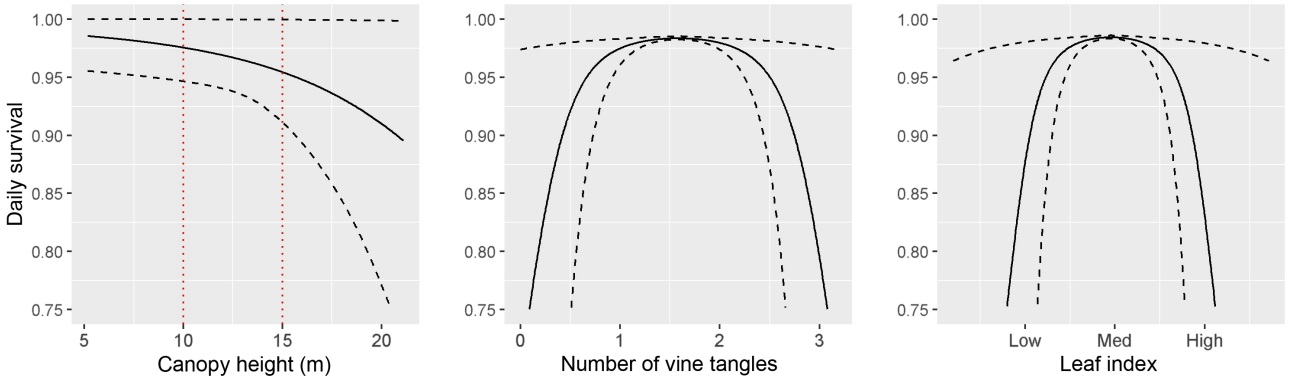

Figure 3. Daily survival estimates as a function of canopy height, quadratic vine tangles and quadratic dead hanging leaves with 95% credible intervals generated from an iterative mark–resight approach in the Tilarán Mountains of Costa Rica, 2011–2013. Canopy height terciles shown by red vertical lines.

2017). If this holds true for golden-winged warblers, the true breeding season monthly survival rate is higher than the monthly among season estimate provided here.

The annual survival rate for golden-winged warblers of 0.539 reported here is within the range (0.41–0.64) of other estimates for this species (Bulluck et al. 2013), and other Nearctic-Neotropical songbird migrants (Stutchbury et al. 2009, Calvert et al. 2010, Faaborg et al. 2010b, Wolfe et al. 2013, Rockwell et al. 2017, Bailey and King 2019). Most notably, our estimated survival rate is nearly identical to the value generated by Chandler (2010) for this same population (0.53). Although the survival rates we report are within the range of estimates for other non-breeding Nearctic-Neotropical migrants, it is important to note that some of these studies, including ours, were conducted in human-dominated landscapes with many degraded forests embedded within a matrix of villages and agricultural areas. These land cover types may expose birds to hazards affecting their survival, like pesticides, house cats, etc., as well as potential sub-lethal impacts associated with behavioral and physiological changes birds employ to reduce predation risk that may impact their fitness and population dynamics (Cresswell 2008). As a result, the survival rates we present may not reflect the survival rates in more remote landscapes, in which habitat occurs in the form of landslides, riparian areas and tree fall gaps (Chandler 2010), and thus these overwinter survival rates might differ from survival rates experienced by migrants wintering in more pristine conditions (Kramer et al. 2017).

Our estimates of age-specific survival are consistent with other reports that survival rates of juveniles are lower than those of adults' (Gardali et al. 2003). Low juvenile survival during the non-breeding season could be a key factor in the declines of some long-distance migrants, for example, the song thrush *Turdus philemelos* (Robinson et al. 2004). Marra and Holmes (2001) reported that lower juvenile American redstart *Setophaga ruticilla* survival could be caused by juveniles being disproportionately displaced into suboptimal habitat. However, the distribution of juveniles among habitats at our sites was similar to that of adults (Ritterson 2015). We also found no difference in among season survival between age classes. That is, juvenile birds that survived their first stationary non-breeding season subsequently had survival rates that were indistinguishable from adults. Furthermore, return rates at the start of stationary non-breeding seasons were similar (~41%) between birds that previously departed the wintering grounds as juveniles and those that departed as adults. Our finding that the overwinter survival of adult golden-winged warblers is higher than juveniles is similar to Rockwell et al. (2017) for wintering kirtland warblers *Setophaga kirtlandii*, but contrasts with the findings of Sillett and Holmes (2002) who reported that overwinter survival was similar between adult and first year black-throated blue warblers *Setophaga caerulescens*.

Our results indicate that the abundance of golden-winged warblers as determined by previous research at this site (Chandler and King 2011) does not correspond directly with habitat-specific survival, since they are less abundant in low-canopy habitats in which we found their survival to be higher. Perhaps this is because lower canopy habitats did not contain as many of the micro-habitat features selected for foraging (vine tangles, dead leaves; Chandler and King 2011), or do not support a suitable size or composition of mixed species flocks of which golden-winged warblers are near obligate participants (Chandler et al. 2016). Alternatively, golden-winged warblers may simply fail to perceive which habitats are actually of higher quality (Gilroy and Sutherland 2007). Survival was lowest at a canopy height of 20 m, which is similar to the height at which Chandler and King (2011) reported that abundance is highest (21 m). It should be noted that the average canopy height value (17 m) of Chandler and King (2011) was taller than this study (12 m), perhaps due to non-complete overlap of respective study areas. Alternatively, it is possible that some measurement error occurred in either or both studies. Thus, it may be useful to interpret these associations as relative values – low canopy conditions characteristic of dense-scrubby growth, medium canopy height typical of secondary forest and high canopy conditions characteristic of advanced second growth or virgin forest. There appears to be some correspondence between these ecologically recognizable structural stages and the terciles illustrated in Fig. 3 (5–10, >

10–15 and > 15–20 m). Notably, earlier analyses included canopy as a categorical variable, and the results were qualitatively the same.

The association between golden-winged warblers and areas with a high density of vine tangles and dead hanging leaves likely reflects their preferred foraging resources in the form of dry-leaf dwelling invertebrates (Chandler et al. 2016). Indeed, dead hanging leaves tend to be prevalent in vine tangles. The reason survival was low in areas with abundant leaves and vine tangles is unclear; one would expect food resources to enhance survival (Johnson and Sherry 2001, Sherry et al. 2005). Chandler and King (2011) documented one case of mortality in this population due to predation by a striped palm pit-viper *Bothriechis lateralis*. This species is associated with dense vegetation (Mehrtens 1987). Perhaps very dense vine tangles are selected because they offer abundant food, but at the cost of elevated predation risk. Similarly, Bailey and King (2019) reported that wintering wood thrushes selected heavily shaded coffee, apparently because of abundant food resources, but they were subject to higher predation. They suggest this decoupling between habitat selection and habitat quality was due to anthropogenic habitat alteration retaining features that served as cues for suitable habitat even though elements of the habitat that may have provided protection from predators (e.g. native understory vegetation) were absent. Our Costa Rican study area has been modified extensively by decades of agricultural and other activity (Chandler 2010), raising the possibility that a similar mechanism is causing some decoupling of habitat use and habitat quality for golden-winged warblers as well.

Quantifying variation in survival rates of migratory birds throughout the annual cycle and in relation to habitat conditions is key to understanding the ecology of these species and conserving their populations. For some species it is possible to map winter territories and generate capture histories by following individually-marked birds (Sillett and Holmes 2002). This approach is challenging for golden-winged warblers for a number of reasons. First, golden-winged warblers occupy larger home ranges within our study area (8.77 ± 0.92 ha) compared to other published estimates for wintering migrant songbirds (Chandler et al. 2016). Furthermore, golden-winged warblers forage in dense vegetation that reduces detectability (Chandler et al. 2016). Radio telemetry is an effective means for generating habitat-specific survival rates for large species like the wood thrush (Rappole et al. 1989, Bailey and King 2019), however radios small enough for golden-winged warblers have insufficient battery life to generate robust estimates of survival rates (Chandler 2010). Finally, point count data analyzed with hierarchical models for open populations can generate overall survival rates; however, generating habitat-specific survival rates may require an unrealistic investment in field sampling (Chandler and King 2011). The methodology we present here offers a useful tool for cryptic species occupying large areas of intractable habitats, and too small to bear radio transmitters with sufficient battery life.

The fact that naturally-disturbed primary forest and advanced second growth appear to provide high quality habitat will be useful for planning conservation and restoration activities for wintering golden-winged warblers in coffee growing regions since suitable second-growth forest remains in many of these landscapes, or regenerates rapidly, and initiatives that afford these lands protection in return for the purchase of carbon credits are promising (King et al. 2016). Although one implication of our results is that survival is lower in taller forests, we do not recommend managing mature or pristine forests to create habitat for golden-winged warblers, since suitable habitat can be readily produced through restoration or allowing fallow areas to re-grow, and because mature and pristine forests, and the species that depend on them, are more threatened in our study region than secondary forests.

It should be noted that habitat associations of this species appear to vary across their range, with birds occupying oak forests in the highlands of Honduras (Bennett 2012). Furthermore, although female golden-winged warblers were present within our study area (Chandler and King 2011), the population at our study sites appears to be male-biased, evidently because of broad-scale geographic segregation of winter habitats (Bennett et al. 2019b). Thus, the habitat associations reported here may not fully reflect the requirements of female golden-winged warblers.

Finally, differences in survival among habitats may be compounded by carryover effects, whereby conditions of the wintering grounds impact processes such as subsequent breeding territory acquisition (Marra et al. 2015). The impacts of wintering habitat use on breeding ecology would be a promising area of inquiry.

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Author contributions

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