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Winter Territoriality of the American Redstart in Oil Palm Plantations

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Abstract: Aspects of territorial behavior of Nearctic-neotropical migratory birds during the nonbreeding period are poorly studied. Information about territoriality, site persistence, between-year site fidelity, and territory sizes are not available for most birds, especially in tropical agroecosystems. Given the rapid expansion of oil palm in the neotropics, determining how oil palm affects the territorial behaviors of overwintering migratory birds is an important line of inquiry with conservation implications. The American Redstart (*Setophaga ruticilla*) is considered a model species for the study of population dynamics in the neotropics; however, territory size for American Redstart has only been assessed in native habitats. In this study, we outfitted individual redstarts with radio tags, across two winter seasons, to determine variation in territory sizes across oil palm plantations and native forest patches in the State of Tabasco, Mexico. Average redstart territory size was 0.29 ha in oil palm plantations and 0.17 ha in native forest. Albeit presenting larger territories in oil palm plantations, which could indicate poorer habitat quality, the difference between both habitats was not statistically significant. Our results demonstrate, for the first time, that American Redstarts hold territories in oil palm plantations and that territory size may serve as an important indicator of relative habitat quality for redstart populations in tropical working landscapes.

Keywords: American Redstart; *Elaias guineensis*; Mexico; neotropical; oil palm; *Setophaga ruticilla*



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1. Introduction

Most Nearctic-neotropical migratory birds tend to adopt territorial behavior during the breeding season as well as between-year site fidelity to breeding territories [1]. Using the same site likely provides energetic advantages due to previous knowledge of the area, predator avoidance, and increased foraging success [2]. Relative to territoriality on the breeding grounds, the degree of territorial behaviors on the wintering grounds is more diverse, where some species routinely defend territories, others are facultatively territorial, while some exhibit no territoriality at all [3–6].

One neotropical migrant subject to a relatively large amount of study during the non-breeding season is the American Redstart (*Setophaga ruticilla*) which provided one of the earliest examples of carry-over effects, where habitat quality on the wintering grounds influenced reproductive success on the breeding grounds [7,8]. In the tropics, redstarts display territoriality and adult male dominance, whereby adult males often exclude females and young males from high-quality habitats like mangroves [7,9–12] and primary and secondary forests [13–15]. Subordinate redstarts are often relegated to suboptimal habitats [16] where they suffer from decreased fitness, characteristic of an ideal despotic distribution [17]. Moreover, experiments demonstrated that females and young males colonize the territories of dominant males after their removal from mangroves and dry limestone forest sites in Jamaica resulting in improved fitness [9,11].

Given that despotic individuals competitively exclude conspecifics from high quality habitats, measures of density could be misleading indicators of habitat quality, as high quality habitats may, in theory, have lower densities at small spatial scales [18]. Alternative indicators of habitat quality include distributional and individual measures, such as sex

and age ratios, indices of fitness (e.g., body condition index, fat, and muscle scores), spring departure date, seasonal survival rate, site persistence, rate of transient behavior, and territory size. Specifically, transient behavior occurs when otherwise territorial birds do not hold territories thereby acting as “floaters” within a wintering population [19]. Transient American Redstarts tend to be females and young individuals of both sexes [12,20,21] and are more common in poorer quality habitats [22–24]. Additionally, individuals in high-quality habitats move less distance to acquire food resources thereby resulting in an inverse correlation between habitat quality and territory size [25–27].

Although American Redstarts tend to select undisturbed forest habitats during the winter [28], populations will use a diversity of other habitats, from forest edges, young secondary forests, and regenerating pasture [29,30] as well as shade coffee plantations in Puerto Rico, Jamaica and Venezuela [14,20,31], cacao plantations in Mexico [32], citrus farms in Jamaica [31], and oil palm plantations in southern Mexico [33,34]. Oil palm cultivation is a rapidly expanding agroecosystem in the neotropics where it often replaces secondary forest or pasture [35]. To our knowledge, no information is available regarding territory size of American Redstarts in oil palm plantations. Understanding how territory size varies between forest and oil palm plantation habitats can provide insight into the value of oil palm to wintering birds; such information informs long-term conservation strategies for migratory species in human-modified landscapes [36]. In this study, we aimed to: (1) determine if American Redstarts held territories in oil palm plantations, (2) estimate territory size, and (3) compare territory size between oil palm and native forest habitats. Given territoriality and dominance hierarchies exhibited by redstarts in other parts of their winter range, we predicted that birds would maintain territories in both habitats and that individuals in lower quality habitat (i.e., oil palm plantations) would exhibit larger territories relative to higher quality forest (i.e., native forest), due to lower food resource availability.

2. Materials and Methods

This work took place in southeast Mexico in the state of Tabasco where the original moist tropical forest has largely been converted to cattle pasture, known as “potreros”, as well as crops like banana, corn, hardwood, and most recently oil palm plantations [37,38]. This process resulted in just a few secondary forest remnants in lower elevations. The climate in the region is characterized by an average temperature of 24° to 28 °C and precipitation ranging from 2500 to 4000 mm [39]. We collected data during two winter seasons, 2017–2018 and 2018–2019, and most of the fieldwork took place during the stationary migratory period (November–February) in the municipalities of Jalapa, Tacotalpa, and Teapa. Study areas included one secondary native forest site (17.6495° N, –92.8146° W) and three oil palm plantations (17.5788° N, –92.8526° W; 17.6992° N, –92.9488° W; 17.6473° N, –92.8304° W). The secondary forest patch was 60 ha and isolated from other woodlands; oil palm plantations ranged from 46 to 84 ha (mean 63.3), were characterized by similar age (~12 years), and presented no adjacent contact with native forest.

Mist-netting was used to capture birds to assess habitat quality through various indicators, including species abundance, community composition, fat loads, mass, and age and sex segregation [15,34]. Concurrently with bird captures (see Oliveira et al. [34]), we outfitted 16 American Redstarts with 0.3 g radio telemetry transmitters (Advanced Telemetry Systems model no. 2414) attached using eyelash glue on the trimmed lower back of the birds. To increase the chance that we were putting transmitters on territorial individuals, we only attached the tags on birds recaptured at least once on the same mist-net line. Tracked individuals were also color banded with a unique color combination to facilitate identification by resighting.

After release, birds were relocated using handheld radio receivers (ATS model 410) and a three-element Yagi antenna (ATS model 148-152). Because American Redstart relocation methodology was mainly constrained by the 14-day battery life of the transmitter, we based our tracking on burst sampling [40]. However, we spaced the interval between relocations every 5 min to give individuals enough time to move to any point in their territory. Cooper and colleagues [41] suggested that because American Redstarts have

relatively small territories in the winter, 30-s intervals between locations is sufficient for sampling independence. We tracked tagged birds until we could confirm a location visually or until the signal strength was sufficient that we were confidently within 10 m of the bird and recorded a GPS point (Universal Transverse Mercator). For birds without visual confirmation, we used a compass to determine an azimuth towards the individual based on radio signal to project the proximate point. Locations were recorded using a Garmin GPS unit (model GPSMAP 64). To minimize GPS error, we only recorded coordinates when the device showed an accuracy of ≤ 5 m. We relocated the individuals no less than three days apart and collected no more than five points per day. We stopped tracking individuals when the transmitter battery died, accidentally fell from the bird's back, no signal was located in the territory or within a 150 m radius from the last location.

We estimated territory size for individuals with at least 20 GPS relocations using a minimum convex polygon calculated by the package “adehabitatHR” [42] in program R [43]. Our sample size was constrained by the number of field assistants trained for radio telemetry, distance among sites, and the transmitters' battery life. Although there is no consensus for a minimum sample size when using the minimum convex polygon, the number of relocations can influence the territory size estimation as the method is sensitive to sample sizes and outliers [44]. Differences in territory size between oil palm plantations and native forest was compared using a *t*-test in program R [43]. Normality of the dataset's distribution was assessed prior to conducting the *t*-test [45].

3. Results

From the 16 individuals outfitted with radios, we were able to collect a minimum of 20 GPS point relocations (mean 30.7) for 10 birds. No females were captured at our native forest site. This way, we opted to use only male redstarts in our analysis, thereby controlling for sex variation. We estimated territory size for seven individuals in oil palm plantations and three individuals in the native forest patch. Overall territory size, including both native forest and oil palm plantations, was 0.25 ha (± 0.033 SE). Territory size ranged from 0.18 to 0.42 ha (mean 0.29 ± 0.035 SE) in oil palm plantations, and from 0.07 to 0.24 ha (mean 0.17 ± 0.052 SE) in native forest (Table 1). Our results suggested that, on average, American Redstarts had larger territories in oil palm plantations than in native forest patches (Figure 1); however, the difference was not significant (*t*-value = -1.93 , *p* = 0.09). Two individuals captured during the first season were recovered in the second season, both in oil palm plantations. The rate of inter-annual site fidelity could not be assessed with the relatively small sample size; however, we did estimate the territory size of one individual in both seasons. The bird was a young (first-cycle formative, FCF, following WRP; [46]) male during the first season and held a 0.34 ha territory, while in our second field season the territory was similarly sized at 0.29 ha (Figure 2). Additionally, although a year apart, the two home ranges included significant spatial overlap based on the minimum convex polygons (Figure 3).

Table 1. Territory size estimates of territorial American Redstarts (*Setophaga ruticilla*) during the non-breeding season in Tabasco, Mexico. Two estimates for the individual SR6 are reported, each one for a different season.

Bird	Territory Size (ha)	Vegetation	Sex	Age
SR1	0.421	Oil palm	Male	Adult
SR2	0.181	Oil palm	Male	Young
SR3	0.071	Native forest	Male	Adult
SR4	0.248	Native forest	Male	Adult
SR5	0.182	Native forest	Male	Adult
SR6	0.344	Oil palm	Male	Young
SR7	0.360	Oil palm	Male	Young
SR8	0.241	Oil palm	Male	Adult
SR6	0.292	Oil palm	Male	Adult
SR14	0.182	Oil palm	Male	Young

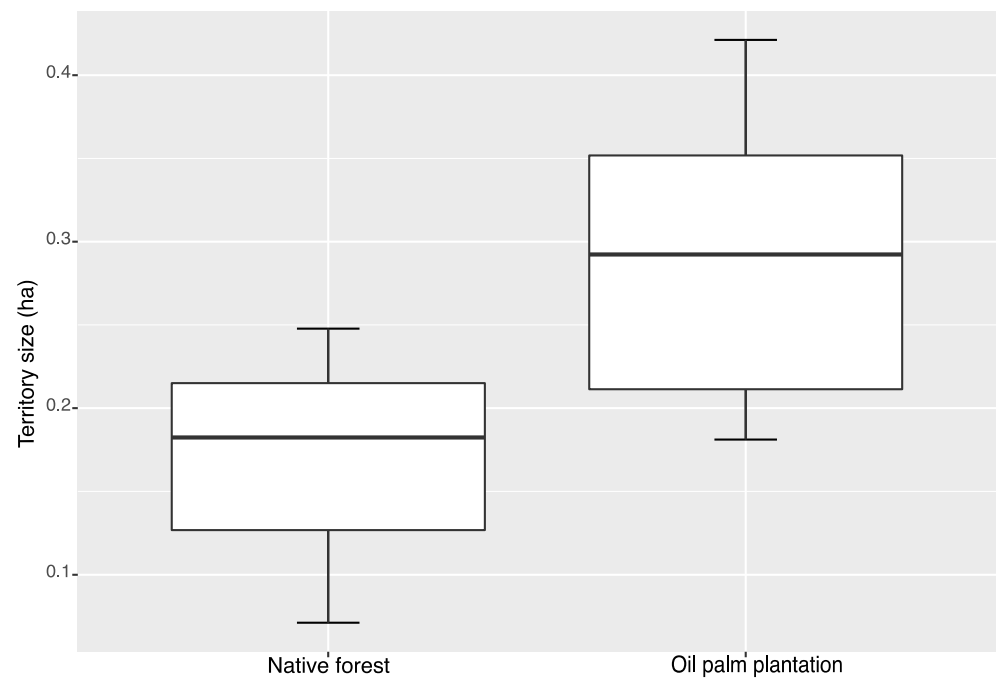


Figure 1. Boxplot of mean showing territory size of American Redstarts (*Setophaga ruticilla*) in oil palm plantations and in native forest in Tabasco, Mexico. Lines represent, in bottom-up order: minimum, first quartile, median, third quartile, and maximum.



Figure 2. Pictures of the first year male American Redstart (SR6) captures in the first (a) and the second (b) wintering season, in oil palm plantations, Tabasco, Mexico.

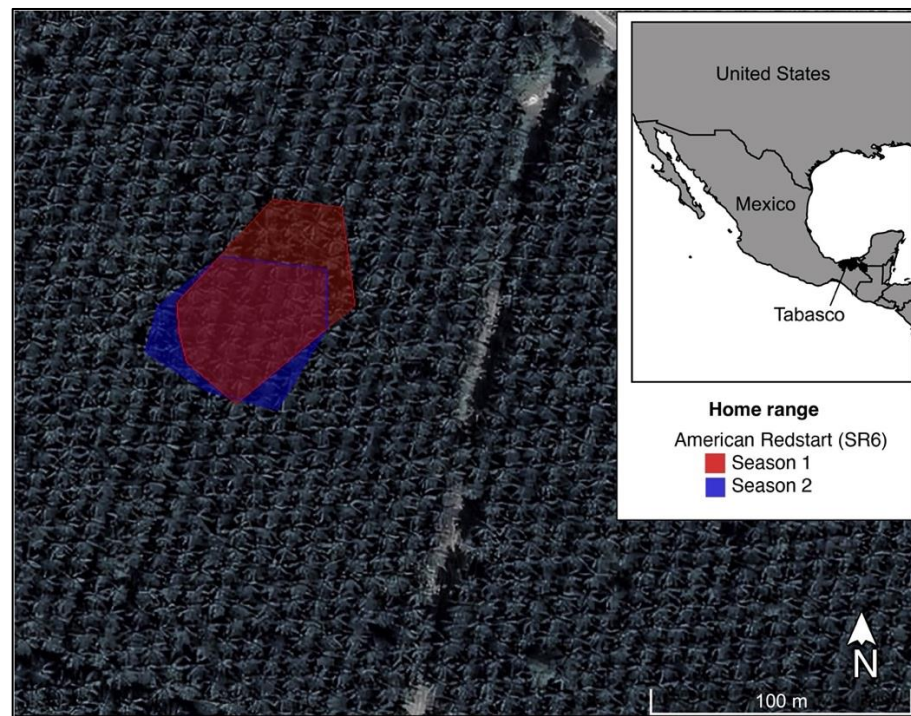


Figure 3. Oil palm plantation territory of the same American Redstart (SR6) on two consecutive wintering seasons, in the state of Tabasco, Mexico. The first season is represented by the transparent red polygon (0.34 ha) and the second season by transparent blue (0.29 ha).

4. Discussion

Although considered a suboptimal habitat for the American Redstarts in the wintering grounds, oil palm plantations were still commonly used whereby multiple individuals established territories [15,34]. Winter territoriality and sexual segregation have been shown to exist in American Redstarts overwintering in more natural forested habitats in the neotropics [9,31]. Our study is the first to identify territorial behavior in a non-native monoculture surrounded by other human-modified land covers, broadening our understanding of the diversity of habitats used by migratory birds on the wintering grounds.

Because they have been shown to arrange themselves according to an ideal despotic distribution, the density of redstarts at small spatial scales should not be used to assess habitat quality. This is a common misconception, especially for generalist birds with broader habitat tolerances [21]. In the case of the American Redstart, prey availability, influenced in part by humidity, play an important role in habitat quality for individuals inhabiting different forest types [41,47]. In Venezuelan shade coffee [14], citrus orchards in Jamaica [48], and oil palm plantations in Mexico [34,49], the observed higher densities of Redstarts, when compared with native vegetation could lead one to believe that these agroecosystems provide similar or higher quality habitats compared to native forest. Further assessments in citrus and oil palm plantations, using distributional and individual indicators, showed that these monocultures likely serve as poorer habitats for American Redstarts, as suggested by significantly lower body condition, sex and age segregation, and differences in territory size ([15,48], Figure 1).

Our overall territory size estimates, including native forest and oil palm plantations, was 0.25 ha, similar to the values reported for native vegetation in Jamaica, 0.25 and 0.3 ha [50,51] and Puerto Rico, 0.39 ha [23]. The mean territory size in the Tabascan native forest (0.17 ha) was also close to the value reported by Cooper et al. [41] in Jamaica, 0.16 ha. The area defended by territorial birds can be used as a proximate cue to assess food availability [25,52,53], and ultimately habitat quality. Our results suggest that, although not statistically significant, American Redstart territory size tended to be larger in oil palm plantations than in native

forests. Despite a small sample size, we observed a pattern suggesting that territory size varies between oil palm plantations and native forests, warranting further studies that directly assess habitat quality (e.g., food abundance and survival). This pattern of higher quality habitats resulting in smaller territories has been repeatedly shown in other Neotropical migrants. For example, overwintering Wilson's Warblers (*Cardellina pusilla*) in Veracruz, Mexico, defended smaller territories in protected forests than in disturbed lowland forest-covered sites [54]. On the breeding grounds, Red-eyed Vireos in West Virginia defended smaller territories in areas with more caterpillars [55]. Likewise, Ovenbirds in eastern Tennessee, held smaller territories in sites with higher prey abundance [52]. Conversely, sedentary Ovenbirds did not exhibit transient behavior, expand territory size, or move their territories when their food supply was experimentally reduced in Jamaica [56]. Similarly, in an experiment with food availability reduction in Jamaica, the American Redstarts showed no increase in territory size to acquire more food resources but instead became floaters (non-territorial) [41]. This suggests that other mechanisms may also influence territory size, such as agonistic interactions with adjacent sedentary individuals.

Inter-season winter site fidelity has been observed among American Redstarts [4,20,21,28,48,50,57,58]. Our work is the first to describe this behavior in oil palm plantations with the recovery of two individuals captured in the first winter season. Furthermore, the territory overlap exhibited by one individual monitored in two consecutive seasons suggests that American Redstarts exhibit high site fidelity even in what appear to be relatively poor-quality habitats, like the oil palm plantations [15]. Between-year site fidelity is considered advantageous as a result of individuals returning to a familiar site [1,2,59]. The rate of between-year return of wintering birds is expected to be highly correlated with food abundance and predictability, thus serving as an index of habitat quality [7,60–62]. Further long-term studies assessing populations in oil palm plantations would be helpful in determining what drives the habitat quality for the American Redstarts and whether these drivers could be managed. Such understanding could be used to assess the viability of the populations using this and other human-modified landscapes.

According to Sherry and Holmes [28], the American Redstart's preference for less disturbed forested habitats in most of its winter distribution suggests that human land use change in the wintering range has contributed to the documented decline of 12% over the last 45 years [63]. Because Nearctic-neotropical migratory birds overwinter in a region much smaller than the breeding grounds [64], the loss of quality habitat during the winter is especially troubling. Evidence indicates that some habitats occupied by redstarts in the Neotropics seem to be saturated due to elevated density [9,28,41,65]. Rushing et al. [66] suggested that reproductive success may ultimately be limited by the quality of the winter habitat. This emphasizes the importance of territory estimates, especially in agroecosystems, since the availability of high quality habitat may limit the population growth of the species.

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