# INTERSPECIFIC INTERACTIONS MODULATE SOCIAL FORAGING BEHAVIOUR AND HABITAT USE IN A NEOTROPICAL MIGRATORY WARBLER SPECIES DURING ITS NONBREEDING PERIOD

by

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# ABSTRACT

Spatial and temporal variation in biotic and abiotic conditions in any foraging environment prompts individuals to modify their strategies of space use and behavioral responses such as going from solitary to social foraging, as it occurs with flocking in forest birds. While asymmetric intraspecific competition determines differential habitat selection, the occurrence and foraging activity of others, conspecifics or even congeners, can also inform on fitness prospects and provide floaters or flock attendants additional foraging opportunities when searching for alternative habitats. Whether interspecific interactions between congeneric species modulate habitat use in a species that occurs at low densities during the non-breeding period remains less known. Here, I study two Neotropical migratory bird species that join flocks: the endangered Golden-cheeked warbler (GCWA; *Setophaga chrysoparia*) and the Townsend's warbler (TOWA; *S. townsendi*). The main objective was to describe social mechanisms underlying habitat preference in the former species by looking at foraging strategies and interactions with its congener that might influence its habitat selection. A secondary goal was to provide knowledge on the nonbreeding ecology of GCWA toward conservation recommendations. In Chapter 1, I present a literature review on social and environmental mechanisms underlying the spatial variation in densities of most migratory warbler species. In Chapter 2, I assess variation in habitat use (foraging substrates and home range) between individuals and species to obtain preliminary evidence for social dominance and its effects on flocking propensity. I then estimate foraging effort as daily use areas, travel distances and cumulative searching time to discern if these parameters vary as a function of intrinsic (sex and age classes) or extrinsic factors (habitat conditions) in both warblers. Differences in the use of foraging substrates were evident between species and sites, regardless of disturbance levels. Sex and age ratios in GCWA were adult male dominated, whereas TOWA ratios were balanced for males and females when in flocks. Home range and core areas of captured individuals (mostly of TOWA) belonged more often to adult males and these areas overlapped the spatial distribution of foraging flocks, suggesting a strategy to allow for additional foraging opportunities provided by flocks as resources in a territory decline over the winter. Foraging effort was higher in the less preferred habitats (more disturbed), whereas daily use areas, travel distances and searching times were smaller and shorter in the preferred habitats, often with higher resource abundance. In Chapter 3, I use Isodars (i.e., regression curves plotting competitor densities in two adjacent habitats) to test how interference and exploitative interactions at the intra- and interspecific levels affect habitat preference in GCWA across two

landscapes that differ in vegetation and disturbance levels. The single-species Isodars showed there is no apparent habitat preference in a relatively undisturbed forest landscape (Moxviquil), whereas density-dependent habitat selection occurred in a disturbed landscape (Encuentro). When densities of TOWA increased, two-species Isodar models showed that proportionally fewer GCWA individuals used the preferred habitat in Encuentro. The effect of TOWA on GCWA is likely as a function of site preemption by the TOWA in both landscapes. In Chapter 4, I tested if artificial social cues (playback calls) induce agonistic responses, or the opposite, if positive interactions measured as the increase in relative abundance are a local precursor of aggregation and habitat settlement. Territorial behaviour (agonistic responses) was more likely in the GCWA, for which a numerical response was not detected after playbacks. Conversely, TOWA was not as aggressive as GCWA, and TOWA increased its numerical responses locally. Site preemption by TOWA may limit settlement into territories for GCWA, while TOWA habitat preference is influenced more by information-mediated settlement. Foraging effort as a function of flocking seems to decrease fitness regardless of social hierarchies. Failing to account for interactions between species and disturbance effects on GCWA habitat use and foraging effort would erroneously inform managers on strategies for conservation of this species.

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# CHAPTER 1. INTRODUCTION

Seasonal migration in Neotropical birds is an evolutionary response to declining resources (e.g., arthropod prey) over the breeding season and further reduction in leaf productivity and cover due to a sharp decrease in temperature during winter (Somveille et al. 2015). These environmental changes underlie an annual fall migration to a nonbreeding range, the Mesoamerican pine-oak forest region and farther south, areas where plant productivity is higher on arrival during the wet season from September to November (Albert et al. 2020). In these forests, transition from a wet to a dry season from December to March again lowers the abundance of tropical arthropod prey, and this foraging context undoubtedly influences strategies of space use by birds to maximize their fitness (Janzen 1980; Smith et al. 2010). Survival for any organism is maximized by choosing an optimal strategy that will minimize energy expenditure and predation threats (Stephen and Krebs 1986). However, survival will not only depend on food availability and behavioral plasticity, but also on a forager's competitive abilities to secure a continuous food supply in the presence of other individuals, those posing intra- and interspecific competition or risk of predation (Lima and Dill 1990; Morris 2003). Assessing the social mechanisms that underlie differential habitat use and selection in focal warbler species under environmental change is crucial to identify how these interactions, either negative or positive, influence spatial variation in densities of migratory species during their nonbreeding period (Holmes 2007).

Climate-induced food limitation coupled with changes in land use (e.g., from forest to agricultural land) modifies food supply and wintering habitat for Neotropical migrants, and as a result the densities and distribution of birds (Sherry et al. 2005; Holmes 2007). Individuals in a warbler community are thus prompted to assess fitness trade-offs in maintaining a territory and defending it against intruders (Brown 1969), shifting their space use through adjustments in territory size (Davis and Houston 1984), floating (i.e., wandering without a fixed territory), or associating with other individuals in foraging groups (i.e., flocking) to increase fitness-enhancing opportunities (Brown and Sherry 2008). While territoriality (despotic behaviour) is an adaptive strategy in most species to maximize resource harvest and reduce predation risk (Marra 2000), shifting from solitary to flocking behaviour has been observed in some warbler species while wintering in the tropics (Rappole and Warner 1980). Individuals unable to secure a territory or inexperienced with novel environments are assumed to join flocks more often

(Winker 1998), but former territory-holders facing changes to habitat quality and availability may also join flocks (Powell 1985; Brown and Sherry 2008). Local movements and dispersal of birds between habitats, while a common component of their life history, influence social dynamics through the spatial dispersion of populations (Pulliam 1988). Despite our current knowledge on the suite of strategies used by migrant warblers during their nonbreeding period (Greenberg and Salewski 2005), the strength and direction of an interaction within and between species may change as a function of environmental heterogeneity. Studying the mechanisms that promote differential habitat selection during winter is thus relevant to enhance conservation strategies of focal species and their habitats during a crucial stage in the annual cycle, as differential survival during the nonbreeding period will contribute to population size and dynamics throughout the year.

## 1.1 Mechanisms underlying variation in space use by animals

Habitat selection is a behavioral process influenced by an individual's perception of environmental heterogeneity (i.e., spatiotemporal variation in abiotic and biotic factors) and the social context in which it exploits resources, reproduces, and survives (Brown 1988; Morris 1992). Habitat is defined as a spatially delimited area with similar quantitative characteristics (e.g., resource levels) and qualitative characteristics (e.g., species interactions), where at least one parameter associated with fitness differs with respect to another habitat (Morris 2003). The ability of the environment to provide conditions that guarantee survival and persistence of an individual has been interpreted as habitat quality (Hall et al. 1997). Population density is thus expected to increase in habitats where chances of survival are higher (Fretwell 1992), but fitness expectations will depend on the competitive interactions, often negative, between individuals occupying a patch of habitats (Rosenzweig 1981; Morris 1988). Spatial variation in densities within a population thus result in differential habitat selection and *per capita* contribution to population growth, measured through vital rates such as reproduction and survival, which may themselves differ as a function of the quality of a habitat occupied (Rodenhouse et al. 2003).

Strategies of habitat selection by individuals aiming to maximize fitness have been explained through distributional measures that conform with models of an Ideal Free Distribution (IFD) or Ideal Despotic Distribution (IDD). In the IFD model, a forager is assumed to be informed on resource distribution, while is free to move between patches (without social and environmental constraints), occupying a habitat until fitness is equalized with the value attained in the habitat the forager has left (Fretwell and Lucas 1969). A main prediction of the IFD model is that, for equal competitors, no individual can improve fitness by changing habitat. However, the IFD is rarely met, as individuals are usually unequal competitors and defense of territories in the highest-quality habitats ensures that the strongest competitors reap the greatest rewards (Parker and Sutherland 1986). Competition thus forces the less experienced and less competitive individuals to leave and search for less preferred habitats where fitness will be lower (Morris 1987).

When dominant individuals reduce the fitness of subordinates that they encounter through direct contest, the IDD model better explains the equilibrium density between high- and low-quality habitats (Fretwell and Lucas 1969; Johnson 2007). A special case of IDD involving interindividual differences in competitive ability and territoriality, the Ideal Pre-emptive Distribution (IPD) suggests that earlier selection of high-quality habitat maximizes fitness, but this outcome will vary when the density of competitors reduces the availability of these habitats (Pulliam and Danielson 1991). Unlike the IFD and IDD models, fitness through preemption of sites will depend on unoccupied space rather than through direct contests against other individuals, where dominant individuals should settle disproportionately in the highest-quality habitats (Pulliam 1988). Differentiating between the three distributional models is relevant to habitat management strategies for conservation of species of interest. Loss of high-quality habitats under an IDD model, for example, is known to significantly reduce the contributions of dominants to population growth (Pulliam and Danielson 1991), whereas in an IFD model, habitat quality would match density, and the habitats with the highest densities should be prioritized for conservation, regardless of the social status of occupants (Fretwell and Lucas 1969).

## 1.2. Habitat selection by wintering migratory birds

Selection of winter habitats by warblers aims to secure vital resources and reduce predation threats to maximize survival and minimize carry-over effects to the next breeding period (Norris 2005). For most Neotropical birds, moisture and food supply are the main drivers of habitat quality and important ecological factors influencing fitness (Steven et al. 2020). Asymmetric intraspecific competition occurs in most warbler species and is a social mechanism underlying segregation of subordinate individuals (e.g., often females and juveniles) into less preferred habitats (Sherry and Holmes 1996). Exclusion from higher-quality habitats by dominants (e.g., more competitive and/or experienced, often male adults) tends to be higher when competition for mutually preferred habitats increases as a function of changes in habitat quality and availability (Morris 1990; Holmes 2007). Density-dependent habitat selection often results in unbalanced sex-age ratios and unequal fitness traits such as body condition and survival, which are highly variable or lower in subordinates occupying less preferred habitats (Stutchbury 1994; Marra 2000; Sillet and Holmes 2002). Trait-based habitat segregation has consequences for population dynamics throughout the winter and for subsequent seasons, as it results in delayed departure times and higher mortality rates during spring migration, as well as late arrival and lower reproductive success on the breeding grounds (Runge and Marra 2005).

While intraspecific interactions often determine differential habitat selection and contributesto site-dependent regulation in populations of most migratory birds (Rodenhouse et al. 2003, Marra et al. 2015), positive associations may also occur when birds observe the behaviour others, either conspecifics or heterospecifics, to increase fitness (Stamps 1988). Facilitation arises when fitness benefits are accrued by settling in close neighbourhoods or by aggregating in foraging groups as a function of information transfer (Forsman et al. 2008; Goodale et al. 2017). Whether conspecific and heterospecific social cues first influence occurrence, with settlement solved afterwards through competitive interactions, remains less explored in the nonbreeding period. Moreover, assessing the effects of social interactions on behavioral strategies, habitat use and fitness (or its proxies) across heterogenous environments has been less studied despite their importance to inform on alternative strategies of habitat selection by migrant birds.

## 1.3 Alternative strategies of space use in migratory birds

Foraging aggregations in mixed-species flocks are common during the nonbreeding period, when migrant and resident birds move and feed together as a strategy to maximize fitness (Rappole and Warner 1980; King and Rappole 2000). Propensity to join flocks is best predicted by traits such as body size and risky behaviours (e.g., outer-branch foraging), and by environmental factors such as a reduction in habitat quality and availability (Elgar 1989). A main assumption is that flocking increases prey harvest rates through less time in vigilance and reduced predation risk mediated by collective defense, risk dilution and predator confusion (Dolby and Grubb 1998; Jullien and Clobert 2000). Engaging in flocks influences local foraging activity and habitat use across landscapes, but the outcomes of this behaviour in terms of habitat selection and fitness may depend on social hierarchies at the intraspecific level (Sherry et al. 1996). While aggregation increases competition, the best payoff for a forager may be to hold a spatial position within a flock where prey harvest and predation threats are higher and lower respectively (Smith 1976; Hirsch 2007), or to hold its own territory close to where a flock occurs (i.e., spatial overlap). However, these strategies have been shown only in few resident species and locations (Pomara et al. 2007; Darrah and Smith 2014), where the occurrence of individuals within flocks as a function of despotic behaviour informed on mechanisms underlying their spatial occurrence.

Interference and exploitative competition between ecologically similar species are also common interaction within mixed- species bird flocks (Goodale et al. 2017) and overlap in foraging niches between otherwise segregated species will occur when they forage in poor-quality habitats where resources are clumped (Kent and Sherry 2020). Rather than coexist within shared habitats through resource partitioning, diffuse exploitative competition has been demonstrated in wood warblers wintering in the tropics (Sherry et al. 2016). However, interactions among conspecifics and between species can change from negative to positive when expansion of foraging opportunities and shifts to better-quality habitat are facilitated by joining a flock (Harrison and Whitehouse 2011; Martinez and Robinson 2016). Whether interspecific effects on habitat use are stronger than intraspecific interactions in migrant birds is a question that has often not been considered for closely related species (i.e., congeners) despite their co-occurrence in mixed flocks during the nonbreeding period. Given a decline in habitat quality throughout the nonbreeding period and the assumption that congeners are more prone to compete for similar resources and safe space (Ricklefs and Schluter 1993), there is a need to assess the interactive effects of competition and facilitation among and between species before and after joining mixed flocks. This information may help to discern governing social mechanisms determining the variation in spatial densities in focal warbler species.

### 1.4 Facilitation as a mechanism underlying social foraging

Conspecific and heterospecific attraction have been shown to result from transfer of information where members of a single or of two or more species remain near others in networks of territories (Stamps 1988; Nocera and Betts 2010). In addition to their own foraging experience and from environmental cues, individuals can learn about fitness prospects across habitats of varying quality by observing the occurrence and foraging activity of conspecifics or species with similar ecological traits (Stamps 1988; Parejo and Aviles 2016). Such social information can provide a fast assessment of food supply, predation risk (i.e., location-based cues) and reproductive performance (i.e., public information *sensu* Dall et al. 2005), thereby influencing foraging decisions and habitat selection (Mönkkönen et al. 1999; Thomson et al. 2003). Facilitation arises when social information is shared in such a way that positive fitness outcomes result, e.g., when foragers settle according to the highest rewards (Forsman et al. 2002). However, the behaviour and fitness outcomes of information users will depend on the densities of interacting individuals where at low densities, social cues may be unavailable to guide habitat selection, whereas at high densities, crowding costs may outweighs benefits (Sepannen 2007). Benefits are therefore proposed to accrue at intermediate densities (Fletcher 2007) and serve as an incentive to settlement and social foraging (Goodale et al. 2010).

Aggregation economies in foraging groups such as monospecific and mixed-species bird flocks result from transfer of information (Gil et al. 2017), but aggregation also does not preclude negative interactions expressed through social hierarchies (Morse 1970). Prey harvest rates, for instance, are known to be reduced by interference (contest) and exploitative (scramble) competition when resources are limited and scattered (Hirsch 2007). To maximize fitness, an optimal forager should therefore assess trade-offs between establishing individual territories or joining groups where closely related species (congeners) co-occur (Alatalo and Moreno 1987; Martinez and Robinson 2016). While differences in foraging niches may or may not allow coexistence among flock members (Pomara et al. 2007; Kent et al. 2020), trade-offs between competition and benefits should also depend on resource levels (Terborgh 1990; Thiollay 2003). At lower resource abundance and higher predation threats, negative interactions are stronger where less competitive individuals are often excluded from a group or displaced to riskier positions where more time must be allocated to vigilance (Hamilton 1971; Krause 1994). Conversely, in rich habitats where food is more abundant and predation threat lower, interactions can be relaxed in smaller groups (Sridhar et al. 2009). Whether heterospecific dominants can restrict foraging opportunities for subordinates through interference that limits harvest rates within a flock, or whether they can impede access to a group through site preemption is less known. Given the effects that differential habitat selection may have on population size through differential contributions to survival, it is relevant to identify the strategies warblers may use. This kind of investigation could discern if observed patterns of distribution mediated by conspecific or heterospecifics interactions conform with an ideal free or a despotic distribution, and thus design effective conservation strategies for species and their habitats.

## 1.5 Study species

Two Neotropical warbler species were chosen to assess how habitat-dependent interactions influence the variation in strategies of space use, foraging behaviours, and differential densities. The first, the golden-cheeked warbler (*Setophaga chrysoparia*), is an endangered species of conservation concern that breeds in mature woodlands of Central Texas, U.S.A. (Birdlife International 2018). Habitat loss and degradation that mostly result from conversion of forests to agricultural land, cattle grazing, and urbanization are known to be the causes associated with declining in population size in the breeding grounds of the golden-cheeked warbler (Morrison 2010). Its occurrence in the reproductive grounds is best predicted by the availability of mixed oak-juniper woodland cover (Wahl et al. 1990), while its breeding success positively correlates with higher tree basal area and density of woody stems in the shrub understorey (Reidy et al. 2017). The species has seasonal stratification by sex and age in its use of vegetation as a function of territorial behaviour in the early and late stages of breeding (Smith-Hicks et al. 2016). While species-habitat associations and preference within the breeding grounds are thus well known, settlement patterns and variation in foraging behaviour in wintering areas occupied by the golden-cheeked warbler are less known. Despite current strategies to recover this species, its abundance in both breeding and wintering areas is still declining.

The golden-cheeked warbler winters in the Mesoamerican pine-oak forest ecoregion that extends from southern Mexico to northwestern Nicaragua, common nonbreeding areas for warblers, where a steady decline in abundance of most migratory species is partially explained by habitat loss and deterioration (Bennett et al. 2018; Albert et al. 2020). The golden-cheeked warbler seems to show latitudinal sexual segregation and occurs at low densities across its nonbreeding grounds. This species co-occurs at similar elevations (1200-2200 m) and environments (pine-oak forests) with its close relative, the Townsend's warbler (*S. townsendi*), the second study species. The Townsend's warbler breeds in mature coniferous forests in the northwestern U.S.A. (Wright et al. 1998; Komar et al. 2011). Both species join other migrants and residents in mixed-species flocks as a foraging strategy to deal with the variation in resource availability and predation risk throughout their wintering areas (Vidal et al. 1994). The golden-cheeked warbler is considered an oak tree specialist, because oaks provide critical habitat substrates for its persistence (King et al. 2012). The Townsend's warbler shows little specialization in foraging, occurring in both primary and secondary habitats, but will also forage over oak species (Greenberg et al. 2001).

Being congeneric, the two warbler species share ecological and morphological similarities, and may compete for resources such as prey located on same foraging substrates (Newell et al. 2014; Losin et al. 2016). To date, no study has assessed effects of co-occurrence with the Townsend's warbler on habitat use and selection by the golden-cheeked warbler. Assessing complementary effects of heterospecific interactions is expected to provide a better understanding of the social mechanisms that influence patterns of spatial variation in densities of an endangered warbler species during a crucial stage of its annual cycle.

## 1.6 Study area description

Data for this dissertation were obtained from two study sites in the municipality of San Cristobal de Las Casas, in the state of Chiapas, Mexico. Throughout Chiapas, agriculture, wood extraction, cattle grazing, and urbanization have created heterogeneous landscapes characterized by diverse interacting environments and land uses that include agricultural land, partially logged or secondary forest with different conditions in terms of vegetation structure and composition and cleared land with rural and urban settlements (Gaona et al. 2004). Of particular interest for this study is extraction of wood, which modifies forest vertical structure and tree composition, in turn limiting the availability of foraging substrates, tree cavities and epiphytes, all important components of a forest bird habitat (Vanderwel et al. 2011; Bautista et al. 2014). Human disturbance also induces changes in the age and size of forest fragments, number of standing dead and alive trees, their relative abundance, and the distance between forest fragments. These changes have been linked to decreases in the abundance of forest birds, modifications in their use of space, the strength of interspecific competition for higher quality habitats, and the overall structure of bird communities (Sekercioglu 2012).

Two study sites (landscapes) with different levels of disturbance (low *versus* high) were selected (Figures 1 and 2). These sites are separated by an average distance of 4.5 km and they are the closest sites from each other and where the occurrence of the study species and of mixed-species flocks has been previously described (Vidal et al. 1994). The value of these sites to this research owes to their variable complexity associated with different vegetation strata and plant species composition and the fact that they harbour important breeding habitats for many resident birds. Yet, little is known about how current habitat conditions translate into suitable nonbreeding habitat for migratory species. Research is thus needed to identify habitat management actions to enhance the availability of those sites where conservation of associated bird species may be secured in the long term.

The study sites resemble two conditions that span higher-quality (low disturbance site) to poorer-quality (high disturbance site) habitats:

Site 1) Moxviquil is a nature reserve with an area of 101 ha and average altitude of 2,200 m, where the dominant vegetation types are second-growth oak forest and pine-oak associations (Figure 1). Closed canopy forest dominates, and density of trees, especially oaks, is relatively high compared to other landscapes where the golden-cheeked warbler overwinters. Moxviquil is assumed to be a primary habitat for the golden-cheeked warbler.

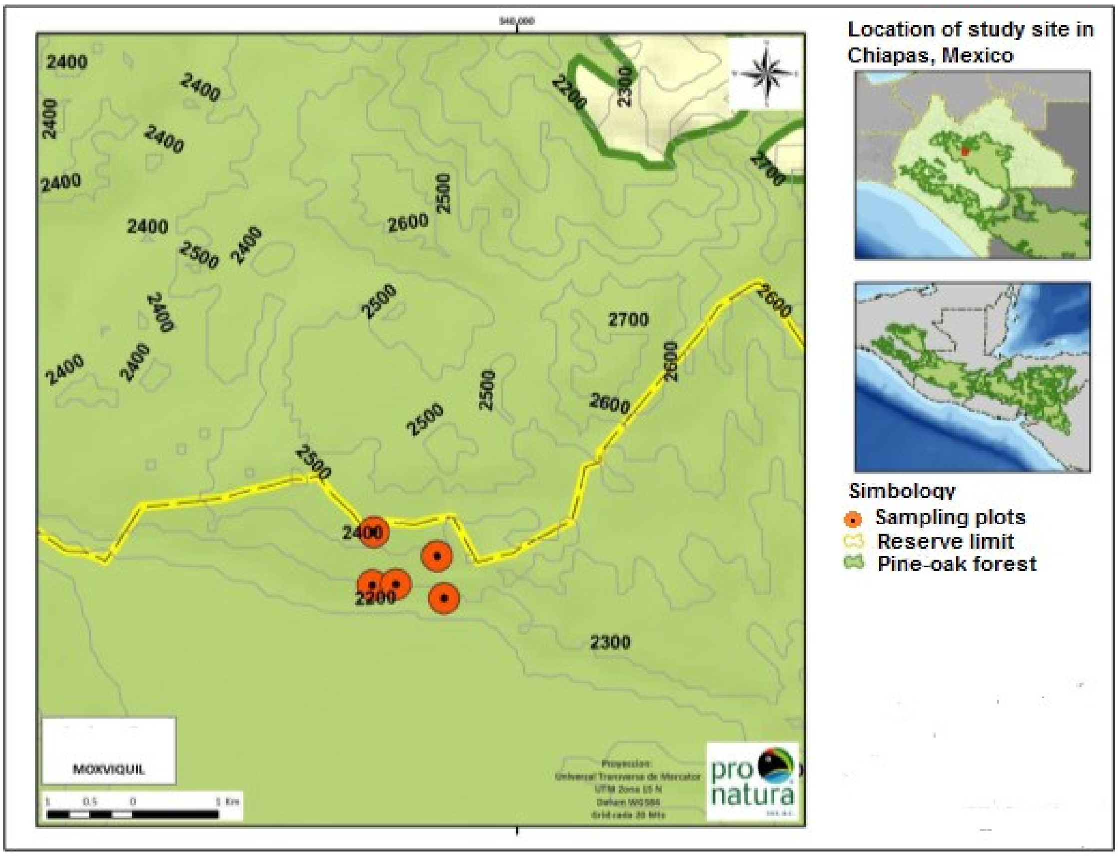

Figure 1. Location of sampling units/flock pairs in Moxviquil surveyed across three sampling years in San Cristobal de Las Casas, Chiapas, México

Site 2) Encuentro comprises remnant patches of pine-oak forest within land used largely for grazing, with semirural, scattered housing settlements (Figure 2). The forest has been used mainly for wood extraction, an activity that creates open areas and forest stands with non-continuous canopy cover and a lower density of trees than Moxviquil. Encuentro is considered a secondary habitat for the golden-cheeked warbler.

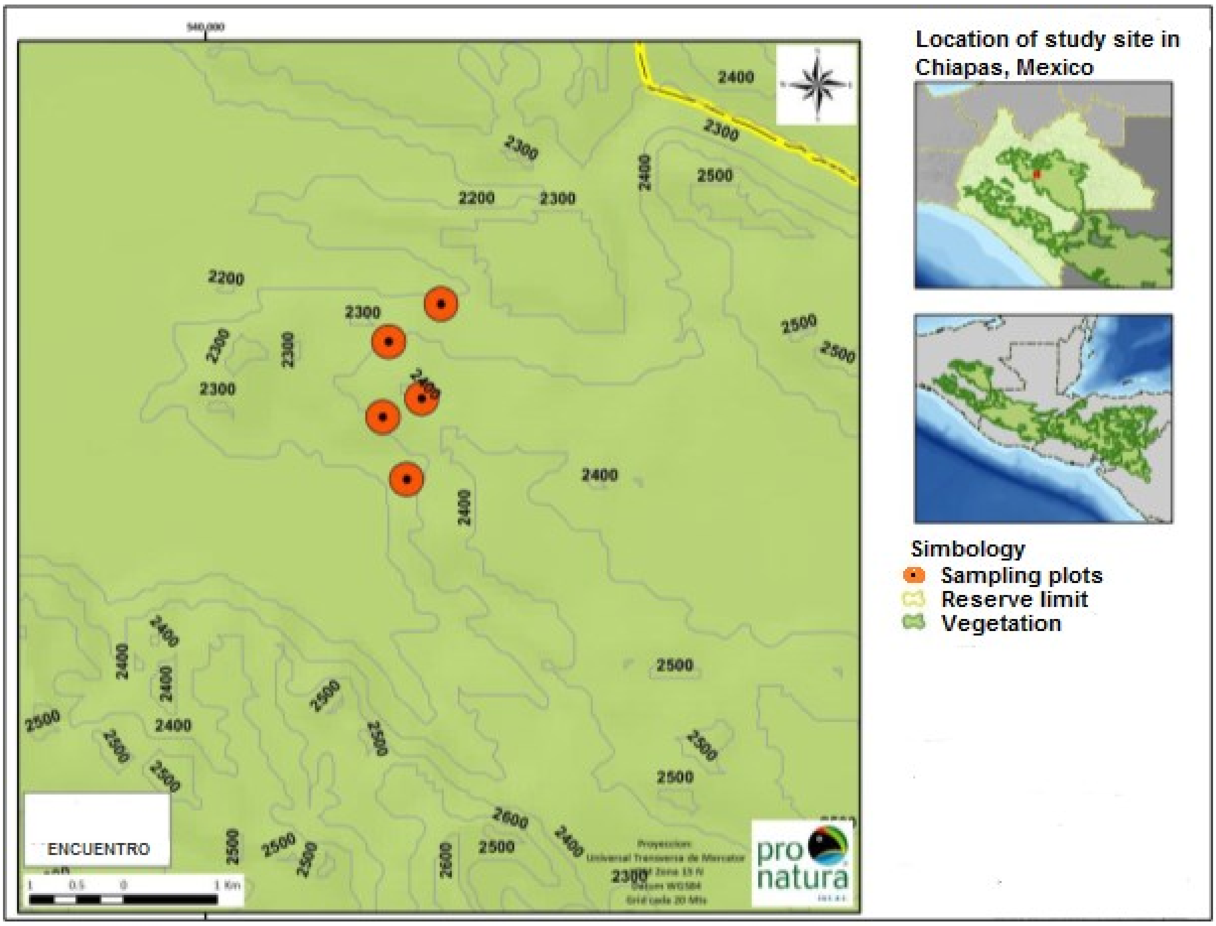

Figure 2. Location of sampling units/flock pairs in Encuentro site surveyed across three sampling years in San Cristobal de Las Casas, Chiapas, México.

## 1.7 Dissertation objectives and chapter synopses

This dissertation aims to identify social mechanisms and environmental factors that underlie variation in foraging behaviors, strategies of space use, and overwintering densities in two Neotropical migratory warbler species with its emphasis on an endangered species, the golden-cheeked warbler. The main goal is to test for the effects of intra- and interspecific competition on differential habitat use and associated foraging behaviours in two study sites that differ in vegetation structure and composition. The secondary goal is to provide research-based evidence to enhance habitat management strategies for conservation in the short- and long-term of the focal species.

In the next three chapters, different approaches were used to achieve the research objectives:

### Chapter 2. Foraging effort is influenced by habitat in two flocking warbler species during the nonbreeding period

I first assessed variation in space use and foraging effort when the two warblers (hereafter, golden-cheeked warbler, GCWA, and Townsend's warbler, TOWA) join flocks, comparing the two study sites described above. I then obtained estimates of sex and age ratios and described microhabitat use. I estimated home ranges to describe how territorial ownership is linked to flocking propensity. Daily use areas, travel distances and cumulative searching time were larger and longer in the more disturbed area, Encuentro. Flocks were dominated by adult males, and sex and age ratios differed between the two sites for GCWA, but not for TOWA. Differences in use of foraging substrates were evident between species and sites, with lower levels of overlap than were predicted, regardless of vegetation type and disturbance levels. Home ranges of tracked individuals (mostly TOWA), a proxy for territories, overlapped the areas used by mixed-species flocks. Home range size did not increase through time, suggesting a potential benefit of retaining a territory where additional opportunities provided by flocks are available. Dominance of TOWA over GCWA is linked to its higher occurrence in flocks.

### Chapter 3: A close competitor shapes intraspecific competition in an endangered warbler

I estimated densities of the two warbler species in several sampling units/flock pairs that spanned higher to lower disturbance or preferred versus less preferred habitats within the two study sites. I then constructed single and two-species Isodar equations (i.e., regression curves plotting competitor densities in adjacent habitats), the first set to explore intraspecific effects on GCWA habitat preference, and the second set to discern how TOWA occurrence may affect GCWA habitat preference. GCWA perceived quantitative differences between plots and habitats (sampling units) in Encuentro and its habitat choices in this site was density dependent. When TOWA density was included in a second Isodar equation, its increased density in GCWA secondary habitats in Encuentro increased GCWA preference for its primary habitats both in Moxviquil and Encuentro. Because TOWA does not behave aggressively towards GCWA, site preemption may be a cryptic factor explaining the two-species Isodar.

### Chapter 4: Behavioral and numerical responses by focal warbler species to experimental attraction by conspecifics and heterospecifics

I used an audio playback experiment at the two study sites to test how different types of information may determine numerical and behavioral responses in the two closely related warbler species, i.e., as putative competitors. The goal was to determine if territorial behaviour precludes site preemption over time, or if a positive response (facilitation) through co-occurrence without aggression influences the formation of foraging groups (flocks). Territorial behaviour measured through aggressive bouts (e.g., chasing, constant calling towards speaker) was higher in GCWA when conspecific songs were played. A numerical response in GCWA was not detected after the audio treatments. TOWA, on the other hand, did increase its relative abundance after the same audio treatments, very often responding by occupying treatment plots without displaying aggressive behaviour. Site preemption negatively affecting GCWA may describe occupancy of territories in the low-disturbance site, Encuentro, whereas TOWA may be more tolerant to the presence of both conspecifics and heterospecifics.

# CHAPTER 2. FORAGING EFFORT IS INFLUENCED BY HABITAT IN TWO FLOCKING WARBLER SPECIES DURING THE NONBREEDING PERIOD

Environmental heterogeneity prompts foragers to modify their behaviours and space use to increase prey harvest rates, reduce predation risk and maximize fitness (Lima and Zollner 1996). Individuals unable to secure a territory (subordinates) or inexperienced with a novel environment may join foraging groups to maximize fitness (Goodale et al. 2017), but even dominant individuals such as adult foragers may also leave a defended territory to join nearby groups (Powell 1985). Joining a group is expected to increase feeding efficiency while reducing foraging costs associated with energy expenditure and predation risk; however, benefits should vary between habitats (Jullien and Thiollay 1998; Sridhar et al. 2009). Flocking in birds is an alternative strategy of space use that differs from maintaining and defending an exclusive territory, and interactions while in a flock can positively or negatively influence fitness rewards (Elgar 1989). The net *per capita* effect of group foraging on fitness depends on the balance between prey harvest rates and the density of interacting individuals (Caraco 1981; Sih et al. 2004). This statement is supported by the idea that solitary foragers defend high-quality territories where energy expenditure and exposure to predators while foraging is lower (Brown 1969; Stephen and Krebs 1986). Conversely, poorer-quality habitats might support non-exclusive territories, with increased energy expenditure and exposure to predators along with more intra- and interspecific competition (Davies and Houston 1984). Declines in habitat quality may, however, prompt former territory owners to shift their foraging behaviour and space use, opting to occur in flocks (Krebs 1973), but it is still less is known if benefits will differ between subordinates and dominants when they join flocks.

While individuals aggregate to flocks expecting to increase fitness (Gardner 2004), competition for favoured positions within flocks reduce prey harvest rates if individuals increase vigilance to minimize predation risk when foraging at the periphery (Hamilton 1971; Smith 1976; Alatalo and Moreno 1987; Fernandez-Juriric and Beauchamp 2008). Foraging in areas without protective cover or along forest edges may increase exposure to predators, particularly when prey forage in secondary forests (Rodriguez et al. 2003; Mokross et al. 2018). Interference competition may also increase predation risk in open habitats where species with risky behaviours such as outer branch foraging in warblers (Remsen and Robinson 1990) expand this risk to suffer early detection by predators (Warfe and Barmuta 2004; Hirsch 2007). For forest-dwelling birds, reduction in forest patch area and in canopy cover, along with an increase in the distance between forest patches, also influences the behavioral activity and characteristics of flocks in terms of distance of movements, flock size, and species composition (Telleria et al. 2001; Maldonado-Coelho and Marini 2004). Perceived predation risk, higher in open areas, exerts non-lethal effects on flocks by inducing changes to group size (McNamara and Houston 1992; Gil et al. 2017). Larger flocks are stronger when foraging and defending against predators (Elgar 1989; Courchamp et al. 1999), but in mixed flocks, the less abundant species may be more conspicuous to predators, increasing apparent competition with the more abundant species (Holt and Lawton 1994; Laundré et al. 2010).

While fitness benefits are accrued through anti-predatory advantages provided by groups (Jullien and Clobert 2000), an increase in group size will influence interference and exploitative competition, as well as change the size of daily use areas and travel distances, especially when prey density is sparse (Gillespie and Chapman 2001; Pollard and Blumstein 2008). Given that group size and foraging effort (i.e., searching time, daily use areas, and travel distances) are expected to increase as a function of habitat degradation and resource location (Hutto 1988; Sridhar et al. 2009), it is thus useful to assess how energy expenditure or its proxy (e.g., foraging effort) varies across individuals and sites that differ in suitability when warblers join flocks. While flocking propensity is common (Terborgh and Janson 1986; Greenberg and Salewski 2005), owning a territory where a flock spatially overlap may reduce foraging costs and then represent an optimal strategy for wintering habitats (Brown 1969; Sherry 2005).

In this chapter, I test whether despotic or preemptive behaviours are underlying differences in microhabitat use and flock formation in warblers (GCWA and TOWA) during the nonbreeding season, and how positive effects on fitness might result for flocking individuals, through lower foraging effort, measured by travel distances, size of daily use areas, and cumulative searching times during foraging. Finally, I assess if differences in microhabitat use between species and individual home range size relates to flock occurrence; I also describe spatial overlap between flocks to discern whether competitive interactions through dominance within and between two congeneric warbler species might limit their access to these flocks. Differences will be explored across two study sites, one the preferred with lower anthropogenic disturbance (Moxviquil) and one suboptimal with higher anthropogenic disturbance (Encuentro). I predict that lower density of trees, canopy cover and height conditions within Encuentro should force longer searching times and travel distances, as well as larger daily use areas, predicted in part as a function of bigger flock size. In this case, I will confirm that changes in habitat characteristics imposes higher foraging costs. Opposite responses are expected at the low-disturbance site, Moxviquil. Lastly, I predict that dominant individuals (adult males and females) preferentially hold territories with high spatial overlap with areas of flock occurrence expressed through age- and sex-biased strategies of space use. Subordinates will occur in the most disturbed habitats and at a lower proportion in flocks.

## METHODS

*Habitat data.* Before collecting data on vegetation characteristics, I first mapped the movements and areas used by flocks and by the two focal warbler species using a spot mapping technique based on minimum convex polygons (MCP; Bibby et al. 2007). Vegetation data were obtained where movements of focal warbler species and flocks were continuously recorded in each study site: Moxviquil (low disturbance) and Encuentro (high disturbance). Based on previous knowledge on the two focal species and occurrence of flocks, I established 10 plots (0.1 ha in size) in the two study sites (Moxviquil, *n* = 5, and Encuentro, *n* = 5). Because the objective was to measure densities of each species, we focus our attention on individuals occurring in flocks. In each survey plot, I described and measured the following variables: oak tree species density (no. ind./per 1000 $m^2$), average oak tree height, tree canopy cover, and abundance of epiphytes (average number per tree). All variables were measured using standard techniques in forest mensuration (Kershaw et al. 2016).

*Flock size, sex and age ratios.* Sampling seasons were from November to March when migrants were assumed to be occupying winter habitats and not migrating farther southward. Sampling was carried out in 2018-2019 and 2019-2020 for estimation of group size. Additional information from two previous seasons (2016-2017 and 2017-2018) was provided by a local organization (Pronatura Sur AC) to increase sample size for density estimation and site settlement between seasons. Information was obtained using the same field methods as in this study. Based on where the occurrence of the two focal warbler species was confirmed during the survey seasons, I searched for flocks starting at dawn (06:00 local time) to match the peak activity of birds. Once I located a flock (i.e., a group of individuals of at least two or three different species moving and foraging together), I followed it for four hours or until flock members abandoned the formation. I counted and classified by sex and age (i.e., immature or first year, second year and adult) every individual for each species and flock to obtain densities and group size. Flocks were mostly foraging in the upper canopy, but we remain silent at a safer distance of 50m and reduce our speed while following the flocks to avoid interfering with their activity.

*Flock travel distance, size of daily use areas, and cumulative searching time*. I first located foraging flocks and confirmed the occurrence of the two focal warbler species within the flock. I then followed each flock by visually tracking and recording their geographic positions every few minutes using the "tracklog" function of a GARMIN eTrex 22x GPS unit (precision ±5m) Sampling frequency with GPS was about 60 fixes during a period of flock cohesion, which ranged from about two to three hours (fixes range:40 to 60). However, we only used data with the lowest number of fixes when a flock was feeding because this reduced the number of overlapping points. We acknowledge that number of locations could have influenced differently the results. The points dataset then was used to obtain minimum travel distances, calculated as the sum of distances between each set of coordinates. I used the geographic boundaries from the same coordinates to create a set of MCP for 10 flocks that were surveyed across three seasons at the two sites. To estimate size of daily use areas, I took readings every five minutes with a GPS unit (Garmin eTrex, 5m) to delineate a polygon (Minimum Convex Polygon) per every flock surveyed in each study site. Average size was obtained by summing all MCP and divided between the total polygons area. Given that as it was not possible to differentiate between feeding and moving time, I obtained the average cumulative searching time, daily used areas and travelled distance as proxies for foraging time which were estimated for every flock by pooling search times across all surveyed flocks by season and study site.

*Foraging traits and micro-habitat use.* Observations in periods of 60 s were conducted in focal warbler individuals spotted in flocks. To describe foraging by these individuals, I counted observations on various substrate locations (outermost leaves, outer twigs 2-4 m from trunk, inner major branches 0-2 m from trunk, and trunk) and heights within the tree canopy (vertical layers: in shrubs or 0-1 m from the forest floor, in the understorey 1-2 m from the forest floor, at mid-level 2-8 m from the forest floor, and in the tree canopy). Sample sizes of individuals in Moxviquil were $n$ = 53 TOWA and $n$ = 16 GCWA; in Encuentro, they were $n$ = 54 TOWA and $n$ = 10 GCWA.

*Home range*. I obtained a banding permit from the Secretary of Natural Resources and the Environment (SEMARNAT in Mexico) and approval from the Animal Care Committee at Lakehead University respecting the Canadian Council on Animal Care guidelines. I then captured birds belonging to the two focal species using mist-nets; they were captured with audio playbacks of their calls and were likely in defended territories at the time they were captured. The sample individuals were fitted with aluminum bands and nano-transmitters (Model LB-2X, Holohil Systems Ltd.) using a harness made from elastic thread. Transmitter weight was 0.31g equivalent to less than 5% of the weight range in the two species (9-15 g), aimed to avoid movement constraints and unnecessary energetic demand on birds. I tracked the individuals with a Telonics R-4 receiver and a hand-held antenna. Tracking began 24 h after capture and ran continuously until the battery life of the transmitter ended (seven weeks on average). Search effort was limited to the undisturbed site (Moxviquil) due to logistic constraints, although I was able to follow both the focal warblers and five flocks when accompanied by a technician. This allowed me to record geographic locations throughout the survey season. I estimated MCP for flocks and Kernel Utilization Distributions (KUD), generating a 95% volume contour for the home range and a 50% volume contour for the core foraging area. This information was used to assess the spatial overlap between individual home ranges and the flocks mapped previously and concurrently. The difference in the approach relies on the assumption that flocks and individuals forage and move, differently.

*Statistical analyses.* To assess if residuals were normally distributed in all vegetation variables, I used Chi-square goodness-of-fit tests. To compare vegetation and flock size between Moxquivil and Encuentro, I used Analysis of Variance (ANOVA) for group size and tree density, a test of homogeneity for epiphyte abundance (count data), and a Kruskal Wallis for the variables with data not normally distributed (tree height and canopy cover). To compare the proportional use of foraging substrates and vertical forest layers between species in both study sites, I used Chi-squared tests of association. To compare travel distances, daily use areas and cumulative searching times between sites I used ANOVA and a Generalized Linear Mixed Model (GLMM) with survey year (visit) as a random variable and tree canopy cover percentage and group size as explanatory variables to test for the relation between foraging effort variables and group size. Results are presented as means and standard errors. All differences were considered significant at $\alpha = 0.05$. Analyses were performed with JMP® statistical software.

# RESULTS

*Habitat data.* Vegetation differed between sites, but not between plots at each site (Table 1). Moxviquil had the expected conditions associated with low disturbance: higher density of mature oak trees, higher average tree height, denser canopy cover, and higher abundance of epiphytes. Encuentro was typical of an area of high anthropogenic disturbance.

*Sex and age ratios.* At Moxviquil, across three survey seasons, 16 GCWA individuals were found. Nine were males, seven were females, a ratio of 1.2 males: 1 female. While this is not different than a 0.5 expectation in most adult birds, here is relevant due to adult dominance over juveniles in flocks. Eleven were adults (nine males and two females), and five (all females) were immatures, a ratio of 2.2 adults: 1 immature. At Encuentro, adult GCWA males dominated; ten individuals were males (all adults), alongside only one immature female. At Moxviquil, 53 TOWA individuals were found, 28 males and 25 females, a ratio of 1.1 male : 1 female. Age was only assessed in 32 of these because plumage similarities between juvenile male and females made assessment of the other 21 individuals difficult; 29 were adults and only three were immatures, a ratio of 9.7 adults : 1 immature. Fourteen were adult males, and 15 were adult females. In the immature category, two were males, and one was a female. At Encuentro, 54 TOWA individuals were found, 37 males and 17 females, a sex ratio of 2.1 male : 1 female. Forty-three of these were aged; 30 were adults and three were immatures, one an immature male and two immature females, a ratio of 3.0 adults : 1 immature. In sum, for both focal species, age ratios differed (adults dominated) at Moxviquil, while both sex and age ratios differed (males and adults dominated) at Encuentro.

Table 1. Vegetation characteristics and comparisons between two study sites, Moxviquil, a higher-quality habitat for GCWA, and Encuentro, a lower-quality habitat. Mean includes the the standard error as measure of variation.

| Variables | Study sites |  | Test statistic | *P* |
|---|---|---|---|---|
|  | Moxviquil | Encuentro |  |  |
| Number of oak trees /1000 m$^2$ | 98 ± 17 | 46 ± 5 | $F_{1,8} = 8.82$ | 0.02 |
| Average height of oak trees (m) | 13.0 ± 0.7 | 10 ± 1.1 | $Z = -2.91$ | 0.003 |
| Mean abundance of epiphytes | 2780 ± 650 | 480 ± 70 | $\chi^2 = 7.9$ | <0.001 |
| Canopy cover (%) | 80.0 ± 0.2 | 63.6 ± 0.5 | $Z = -15.2$ | <0.001 |

*Flock characteristics.* Mean number of individuals per flock did not differ between plots at either site, but flocks were larger at Encuentro (35 ± 3 individuals) than at Moxviquil (27 ± 2 individuals; $F_{1,28}$=5.64, $P$=0.02). Group size varies from 13 to 40 individuals in Moxviquil and 20 to 45 in Encuentro. Focal species number of individuals was 1 to 2 in GCWA and 1 to 7 individuals in TOWA in surveyed flocks. Flock size was not correlated with any vegetation variable at Moxviquil, but it was significatively associated with canopy cover percentage (F = 6.37, $P$ = 0.02) at Encuentro. The two focal species were tightly associated when moving together during foraging bouts at both study sites. The number of species in the mixed flocks was similar for Moxviquil (15 species) and Encuentro (16 species). The most abundant other species in flocks were the hermit warbler (*Setophaga occidentalis*), crescent-chested warbler (*Oreothlypis superciliosa*), Hutton's vireo (*Vireo huttoni*) and blue-headed vireo (*V. solitarius*), all forest dependant migratory species. While flocks were numerous at both sites, densities of focal species were lower (i.e., one or two GCWA individuals and three to five TOWA individuals per flock) in the most disturbed site (Encuentro) when compared with Moxviquil.

*Flock travel distance, size of daily use areas, and cumulative searching time.* Daily average travel distances by flocks differed between sites ($F_{1,28}$ = 5.21, $P$ = 0.03), where they were lower at Moxviquil (1.02 ± 0.80 km) than at Encuentro (1.30 ± 0.12 km). This difference was explained as a function of increased group size (t=6.65, P<0.001). Daily use areas were not statistically different ($F_{1,28}$ = 2.09, $P$ = 0.15) between Encuentro (3.27 ± 2.94 ha) and Moxviquil (2.03 ± 0.16 ha), but two areas at Encuentro were much larger (6.9 and 12.3 ha) than the average size at this site. Cumulative searching times were lower ($F_{1,28}$ = 6.6, $P$ = 0.01) at Moxviquil (160 ± 8 min) than at Encuentro (194 ± 11 min).

*Effects of flock size and vegetation characteristics on foraging effort.* Travel distances, daily use areas and cumulative searching times were highly correlated, so only the latter was used as a proxy for foraging effort. Cumulative searching times increased as a function of flock size, and accounting for this effect in the GLMM resulted in significant differences in cumulative searching times across the two study sites (Table 2). Vegetation variables were not associated with cumulative searching times.

Table 2. Generalized Linear Mixed Model results showing a positive effect of flock size on cumulative searching times and direction of non-significant explanatory variables.

| Term | Coefficient | Std. error | *t* | *P* |
|---|---|---|---|---|
| Intercept | 77.26 | 37.92 | 2.03 | 0.05 |
| Site | –9.32 | 32.18 | –0.29 | 0.77 |

| | | | | |
|---|---|---|---|---|
| **Flock size** | **2.40** | **0.69** | **3.48** | **<0.01** |
| Flock size × site | 0.53 | 0.95 | 0.56 | 0.58 |
| Canopy cover class | 0.14 | 0.50 | 0.28 | 0.77 |
| Number of oak trees | 0.03 | 0.27 | 0.12 | 0.90 |
| Tree height (m) | 5.81 | 10.75 | 0.54 | 0.59 |
| Number of epiphytes | –0.39 | 0.58 | –0.68 | 0.50 |

*Foraging traits in the focal warbler species.* Proportional use of foraging substrates at Moxviquil did not differ between warbler species ($\chi^2 = 5.09$, $df = 3$, $P = 0.16$). However, GCWA frequently foraged near the outermost leaves and the outer twigs, whereas TOWA allocated effort to inner branches and trunks (Figure 3). At Encuentro, use of foraging substrates did differ between warbler species ($\chi^2 = 16.0$, $df = 3$, $P = 0.001$), with the same pattern as at Moxviquil. At both Moxviquil ($\chi^2 = 16.53$, $df = 3$, $P < 0.001$) and Encuentro ($\chi^2 = 13.7$, $df = 3$, $P = 0.003$), use of vertical forest layers differed between species (Figure 4). GCWA was more often observed in the upper layers, and TOWA mostly in the lower layers.

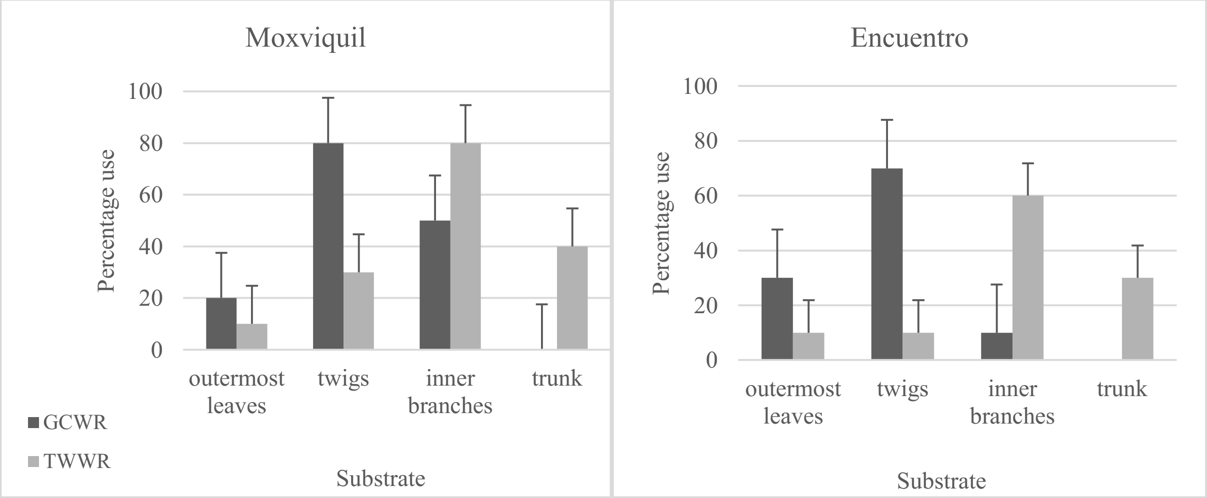

Figure 3. Time spent (percentage) foraging by habitat substrate for golden-cheeked warblers (GCWA; dark bars) and Townsend's warblers (TOWA; light bars) at two study sites.

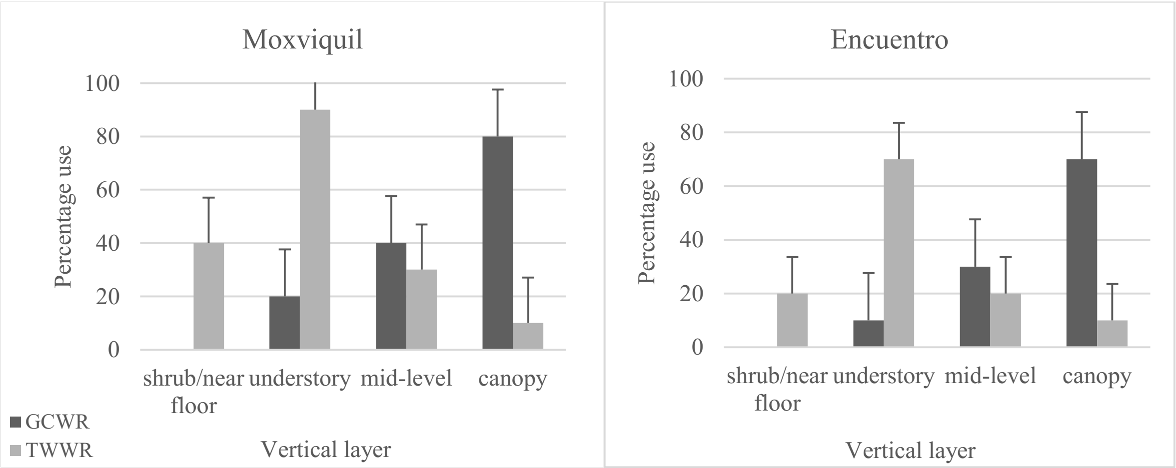

Figure 4. Time spent foraging by vertical forest layers for GCWA (dark bars) and TOWA (light bars) at two study sites.

*Home ranges in focal warblers at Moxviquil*. Fifteen adults were captured (GCWA, *n* = 1; TOWA, *n* = 14), ten of 14 TOWA males and the GCWA a female. Median daily use area (MCP) for all tracked individuals was 4.5 ± 0.8 ha; median home range (90% KUD) and core area (50% KUD) were 4.6 ± 0.7 ha and 1.4 ± 0.3 ha, respectively. Male home ranges (95% KUD for ten captures) were smaller (3.5 ha, 1.6–5.5 ha 95% CI) than those of females (four captures; 6.8 ha, 4.1–9.6 ha; *t* = 2.40, *P* = 0.03). Overlap between flocks and home ranges was observed in four out of five flocks (Figure 5). The GCWA individual and eleven TOWA individuals out of fourteen (80%) overlapped their home range either with one or two flocks, and the mean area of overlap was 0.76 ± 0.20 ha. Each home range overlapped a mean of 4.3 other home ranges, and individuals overlapped their home range more often in two of the four flocks observed.

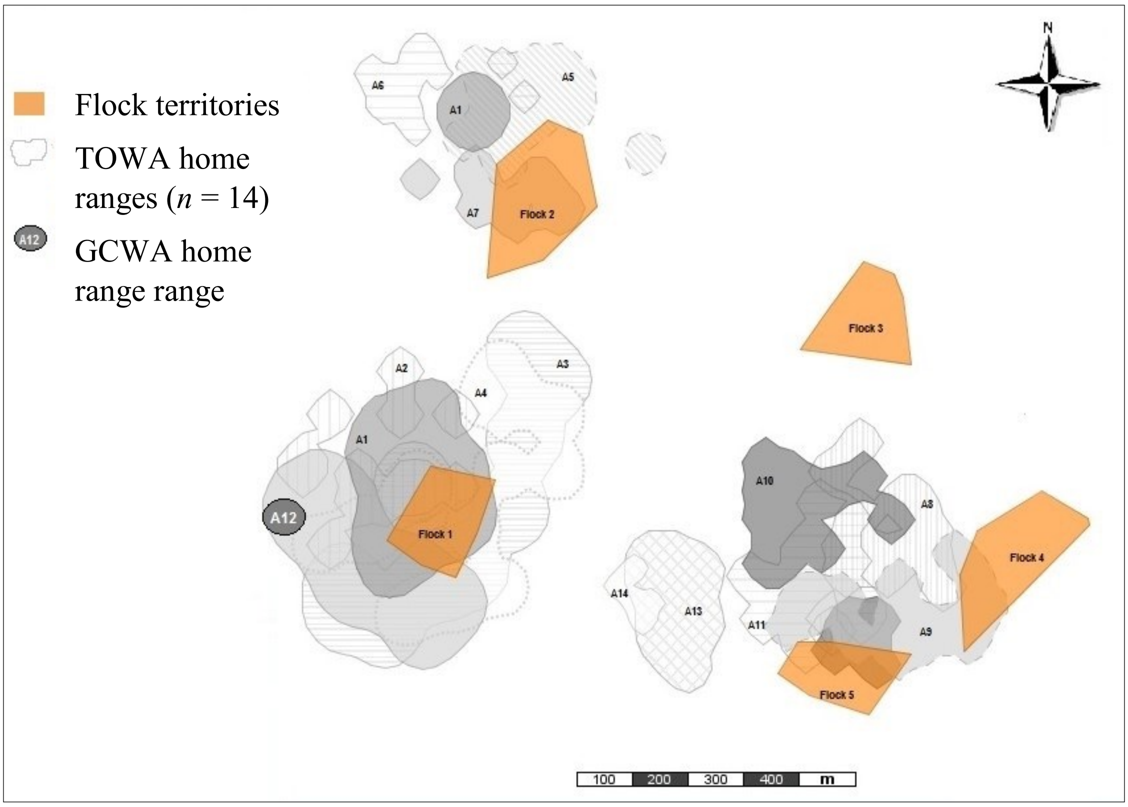

Figure 5. Home ranges of 1 GCWA individual and 14 TOWA individuals, mapped together with flock territories monitored at Moxviquil.

## DISCUSSION

Both focal warbler species were found together at both sites in mixed flocks. Flocks were larger at Encuentro, as predicted for a more disturbed landscape. For both species, adult individuals dominated flocks, mostly males at Encuentro, and males and females in Moxviquil in equal proportions, suggesting that intraspecific competition within flocks is stronger in the lower-quality habitat (Encuentro). All monitored individuals also occurred regularly in flocks, despite theory predicting advantages of securing territories during unfavourable seasons, here, the relatively dry winter season. While I predicted higher densities of subordinates in the more disturbed landscape, subordinate GCWA females and juveniles were found in similar proportions at both sites. Some researchers have suggested latitudinal segregation in GCWA, where males occupy the northernmost nonbreeding grounds and females occur as far south as Nicaragua (Vidal et al. 1994). However, male dominance is also higher within the southernmost sites (Komar et al. 2011). In this study, one adult female was continuously recorded and captured while defending a territory at Moxviquil, where predominance of adult TOWA males in contiguous territories was higher. The generalist behaviour of TOWA and its foraging preferences such as on trunks and inner branches of oak trees, may underlie a winning strategy in competition for microhabitats and insect resources, influencing thereby GCWA shifts in habitat use, as shown by Greenberg et al. (2001) for the black-throated green warbler (*Setophaga virens*), another congener.

As predicted, GCWA has risky foraging traits associated with outer branch maneuvers. On the other hand, GCWA used inner branches at a lower proportion at the disturbed site, suggesting that at Encuentro, TOWA may better defend and dominate inner branch and trunk microsites that pose less predation risk, where these microsites are also less abundant in a disturbed forest landscape. An alternative explanation, that TOWA is a better competitor for food, runs contrary to the models of flocking propensity (Pomara et al. 2007). On the other hand, the use of vertical forest layers differed between species regardless of overall site quality; GCWA foraged more often in higher layers around the canopy and mid-levels of trees, while TOWA allocated its foraging to understorey layers. Habitat partitioning and differences in foraging traits are thus described both as an outcome of competition for areas with lower predation risk (Whittingham and Evan 2004) and as a means for coexistence of closely related species (Greenberg et al. 2001). Interpretation of a higher number of outer branch maneuvers by GCWA at Encuentro may nevertheless be related to prey scarcity; and thus, measuring differences in prey abundance is a logical extension of this study to differentiate habitat segregation from other factors acting on foraging efficiency and predation risk.

Foraging effort increased with flock size, while daily use areas, travel distances and searching time were larger or longer in the more disturbed site. However, density of trees, canopy cover percentage and potential prey supply linked to leaf cover were only associated with variation in flock size and foraging effort at the site scale and not at the microsite scale in this study. Elsewhere, flock size has been shown to increase as a function of conditions associated with resource location and higher predation risk, often associated with higher rates of forest cover loss, but at the landscape scale (Maldonado-Coelho and Marini 2004). One explanation is that vegetation characteristics within a site are not a factor that influences competitive interactions; when individuals join flocks, the landscape-scale size of areas traversed allows them to increase prey harvest rates, at the same time lowering competition for foraging substrates at the microscale; this explanation follows models of flocking propensity (Pomara et al. 2007). While increases in flock size may provide information on prey location at a site like Encuentro, more competitors could also deplete foraging areas more rapidly (Gil et al. 2017). However, the increase in foraging effort at Encuentro is proposed here as an indirect effect of vegetation structure, where reduced density of trees and lower canopy cover forces groups to allocate more time to searching for food over longer distances. Conversely, at Moxviquil, where habitat quality is higher, lower scramble or contest competition should be occurring in the smaller flocks, predictions to be tested by further field observation.

Home ranges that overlapped with flock territories were smaller than those that did not, suggesting that joining flocks does not require a larger home range. The smaller ranges, together with the fact that adult males, presumably dominant individuals, held most of them, may be the outcome of a recognized benefit of maintaining a fixed territory when a flock shows site fidelity or occurs in the same areas across different seasons (Darrah and Smith 2014). Tropical bird flocks have been shown to be stable in composition and size, occupying and defending the same foraging areas through several seasons (Martinez and Robinson 2016). A further interpretation is that subordinate individuals do not have a flock near their home range, or do not hold a home range, as relatively few females and no immatures were captured during the study. Most captured individuals occupied home ranges coincident with the territory of one or more flocks. Thus, a dual strategy, in which territory-holders may forage locally and may also regularly opt for group foraging, may be the case for these warblers where variation in food supply occurs both spatially and temporally, especially where environmental changes also occur rapidly (Greenberg and Salewski 2005). As previously done for the wedge-billed woodcreeper (*Glyphorynchus spirurus*; Darrah and Smith 2014), increasing the survey window in future study of the two warblers will allow a test of the idea that not only do some overwintering warblers adhere to territories, illustrating despotic behaviour, but they also position their territories to limit the occupation of flocks by subordinates, in this case preemptive behaviour.

Elsewhere, floating behaviour has been shown to compensate for lack of territories when flocks are not available or when competition within them is strong (Winker 1998). The cost-benefit ratio for territory owners was not evaluated or compared to that of subordinates without a fixed territory in this study. To test the idea that dominant individuals should settle disproportionately in the highest-quality habitats and strategically position their home ranges near flock territories, a next step will be to examine the relationship between habitat quality, density, and fitness or its proxies.

# CHAPTER 3. A CLOSE COMPETITOR SHAPES INTRASPECIFIC COMPETITION IN AN ENDANGERED WARBLER

Intraspecific competition influences habitat selection by Neotropical warblers during the nonbreeding season (Holmes et al. 1996). Social ranks create differential survival rates within tropical habitats of differing quality, limiting a warbler population size during winter, with possible carryover effects on reproductive success during the subsequent breeding period (Rodenhouse et al. 2003; Norris et al. 2005). Interspecific competition between ecologically similar species over limited resources such as prey and safe space from predators may also influence habitat choices if a subordinate species cannot outcompete another species (Morris 1998). Most warblers mediate their coexistence through specialization in their foraging niche and habitat selection to reduce such competitive interactions (MacArthur 1958; Marra et al. 2015). Dietary overlap, however, suggests that interspecific competition between warbler species still occurs, and it is often overlooked during the nonbreeding period (King and Rappole 2000). Consumption of shared prey may limit its availability and thus affect prey harvest rates of the least successful or less abundant forager (Wilson 2010; Kent and Sherry 2020). Opportunism by generalists drives convergence in foraging behaviour and overlap in resource use that exacerbates competition among conspecifics or between species (Sherry et al. 2016). Foraging success and habitat use will thus depend on how competition among warblers occurs during periods of scarcity that can occur during the dry season in the wintering grounds.

Divergence in use of foraging substrates is often interpreted as evidence of distinct preferences in diet and habitat use (Martinez and Robinson 2016), but vegetation characteristics also influence habitat preferences by individuals in a manner to diminish threats from predators, e.g., where protective leaf cover is dense (Whittingham and Evans 2006). When habitat quality diminishes, foragers adjust their foraging strategies, patterns of microhabitat use or preference for alternative habitats (Stephens and Krebs 1986; Lima and Dill 1990). With current rates of habitat loss in the wintering grounds of Neotropical migrants, changes in species densities due to dispersal are expected to modify species interactions and their patterns of space use as competition for the most suitable habitats increases (Johnson 2007; Birdlife International 2018). Overlap in habitat use by unequal competitors may still occur if their joint densities are below their carrying capacities; thus, assessing how foragers spatially segregate when co-occurring may show competitive interactions and solutions for coexistence (Morris 2009). Accounting for mechanisms other than intraspecific competition is further relevant because an increase in interspecific competitors due to reduced habitat quality may influence habitat selection and observed densities in a focal species.

The golden-cheeked warbler (GCWA) and the Townsend's warbler (TOWA) occur in sympatry and within flocks during their nonbreeding periods, but their interactions may be modified when their densities within the habitats they co-occupy are not at equilibrium, as might be described by Isodar theory (Morris 1988). Shifts in strategies of space use at several scales are known to change as a function of habitat quality, but also when the densities of putative competitors and predators increase (Martinez and Robinson 2016). As a result, one species may mediate microhabitat use (e.g., from inner to outer tree foliage) through dominance over the other (Krebs 1973; Suhonen 1993). Intraspecific dominance when in flocks has been documented in black-capped chickadees (*Poecile atricapillus*; Smith 1976) and tropical antbirds (Thamnophilidae; Colorado et al. 2015), but interactions between interspecific warbler competitors and their influence on space use in flocks has not yet been evaluated. Moreover, less is known about whether species co-occurrence might be determined through intra- and interspecific dominance behaviours that ultimately influence habitat selection. While the GCWA's breeding ecology is well understood, there is scarce information about the effects of varying densities on its nonbreeding habitat preference at different spatial scales (within and between habitats), specifically when uncertainty in availability of preferred habitats is high due to natural and human-induced environmental disturbance.

*Isodar theory*. Ideal habitat selectors are expected to choose among a set of habitats with contrasting conditions (e.g., in prey, predator and competitor densities) in a manner to maximize fitness (Fretwell and Lucas 1969). However, the occurrence of competitors within preferred and less preferred habitats may reduce expected fitness and thus induce density-dependent changes to habitat preference in the less competitive species (Rosenzweig 1981). While coexistence of two species is possible when they are below their joint carrying capacities (Morris 2003), species A (GCWA, for instance) may co-occur with species B (TOWA) in its less preferred habitat (forest and edge areas), despite having preference for less a disturbed habitat (forest interior). Coexistence of species A and B in a secondary, disturbed habitat is thus possible when the density of species B is low. However, both species may still compete for resources or overlap in habitat use and thus solve their coexistence through differential habitat preference as a function of their densities (Tarjuelo et al. 2016). Assessing the mechanisms that influence habitat use may show how behaviour and habitat choices are modified when conspecific dominance is high or when two species co-occur. Isodars, or linear regressions for a set of densities for the same or two species in pairs of habitats that differ in quality, can be decomposed to describe competitive interactions, either among conspecifics or between species (Morris 1999). The partial regression coefficients of an Isodar are used to assess the effects of exploitative or interference competition on habitat choices (Morris 1990).

The set of joint densities in two habitats at different population sizes defines a species' habitat Isodar (regression curve):

$N_{A1} = c + b\, N_{A2}$ [Equation 1],

where the density (N) of species A in habitat 1 is predicted by its density in a second habitat 2. The coefficient *c* (the regression intercept) represents the quantitative difference in resource renewal rate, and *b* (the slope) represents the strength in habitat preference as changes in population density in each habitat. An effect of a second species B on the behaviour of species A can be incorporated by modifying Equation 1 (Morris 1989; Tarjuelo et al. 2016):

$N_{A1} + \alpha N_{B1} = c + b\, (N_{A2} + \beta N_{B2})$ [Equation 2],

rearranging to:

$N_{A1} = c + bN_{A2} + b\, \beta N_{B2} - \alpha N_{B1}$ [Equation 3],

The coefficients α and β represent the partial regression terms accounting for interspecific exploitative competitive effects on the fitness of species B over species A. To account for interference competition between species, it is possible to incorporate an interaction term into Equation 3, $N_{A2} \times N_{B2}$ with a new coefficient $\gamma$, which may then used as an alternative two-species model:

$N_{A1}= c + b\, N_{A2} + b\, \beta N_{B2} + b\, \gamma N_{A2} \times N_{B2} - \alpha N_{B1}$ [Equation 4].

An Isodar intercept with a slope of 1 indicates that fitness of individuals is equal in two habitats and no preference for either habitat is present. If the slope of an Isodar is steeper than 1, it indicates that individuals increase their relative use of the most preferred habitat, but fitness of individuals should decline with any increase in conspecific or heterospecific densities in that habitat or in the secondary if competitor density is higher (Fretwell and Lucas 1969, Morris 1988).

To assess intraspecific and interspecific effects of competition on GCWA in its wintering grounds (for this case, in two main landscapes with independent sampling units or pair of habitats in each landscape), I fitted density data from each species to first create single-species Isodars (following Equation 1). If density dependence drives differential habitat selection in these species, then I expect to find density-dependent habitat preference among conspecifics. According to assumptions of territoriality during resource scarcity, females and immatures should occur more frequently in a secondary habitat (here, forest edges, areas of higher road density, and urban areas or other areas with less vegetation cover); they should also occur more frequently in the landscape with higher disturbance (Encuentro). I then fitted density data from GCWA and TOWA together to create two-species Isodars, one for each site (Equations 3 or 4). The main prediction here is that variation in density of GCWA when comparing its preferred and secondary habitats is also a function of the density of TOWA. This effect would be explained by an apparent preference by GCWA for its secondary habitat, as a result of interference competition with TOWA in its primary habitat, possibly due to site preemption, either from individual territory-holders or from flocks. Lastly, I compare Isodar results across landscapes, as they differ in vegetation characteristics and levels of disturbance.

## METHODS

*Study site description.* Counts were obtained from 6 pairs of flocks at two study landscapes, Moxviquil (Figure 6) and Encuentro (Figure 7) that differ in vegetation structure and disturbance level. Within each landscape, I selected sampling stations that were divided into two habitats occupied by different flocks. I surveyed flock 1 in Habitat 1 (forest interior) and flock 2 in Habitat 2 (forest edge, roads, and urbanized areas) and so on, until completing three pairs of flocks for each site to obtain densities of the focal species in adjacent habitats. There were in total three sampling stations (pairs of habitats/flocks) for each study landscape ($N = 6$ flocks per site), surveyed over three years, 2018 to 2020. The occurrence of flocks were restricted to forested areas and the fact that flocks occurred separately (more than 500 lineal meters) allowed to estimate, with independence, densities of focal species, that were pooled after. Simultaneous surveys on different flocks occurring in both landscapes were carried to satisfy independence of data. Habitat data was taken from three vegetation plots located within Minimum Convex Polygons delineated for each flock surveyed and described differences in the vertical and horizontal structure for each habitat type were flocks occurred. Habitat type 1 (less disturbed) was considered the preferred habitat where higher density of oak trees was identified as the main variable explaining GCWA occurrence and long-term occupancy (King and Rappole 2000; Komar et al. 2011). Habitat type 2 (disturbed) included forested areas near other land uses (i.e., edges) associated with human activities such as roads, areas for wood extraction, and housing areas.

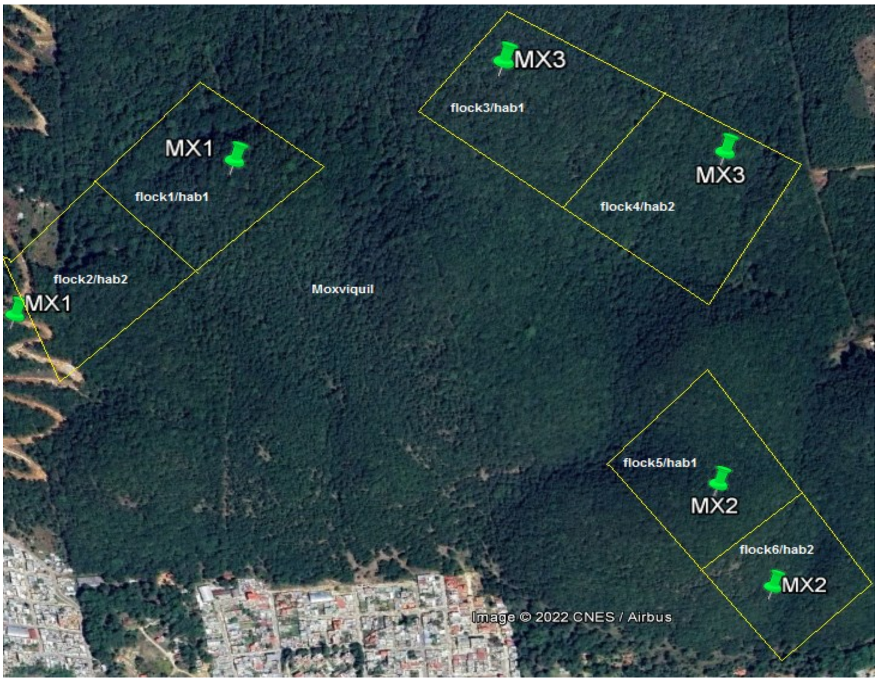

Figure 6. Sampling units, i.e., flock pairs in contiguous habitat 1 (forest interior as preferred habitat) and habitat 2 in Moxvquil (forest edge, roads and urbanization).

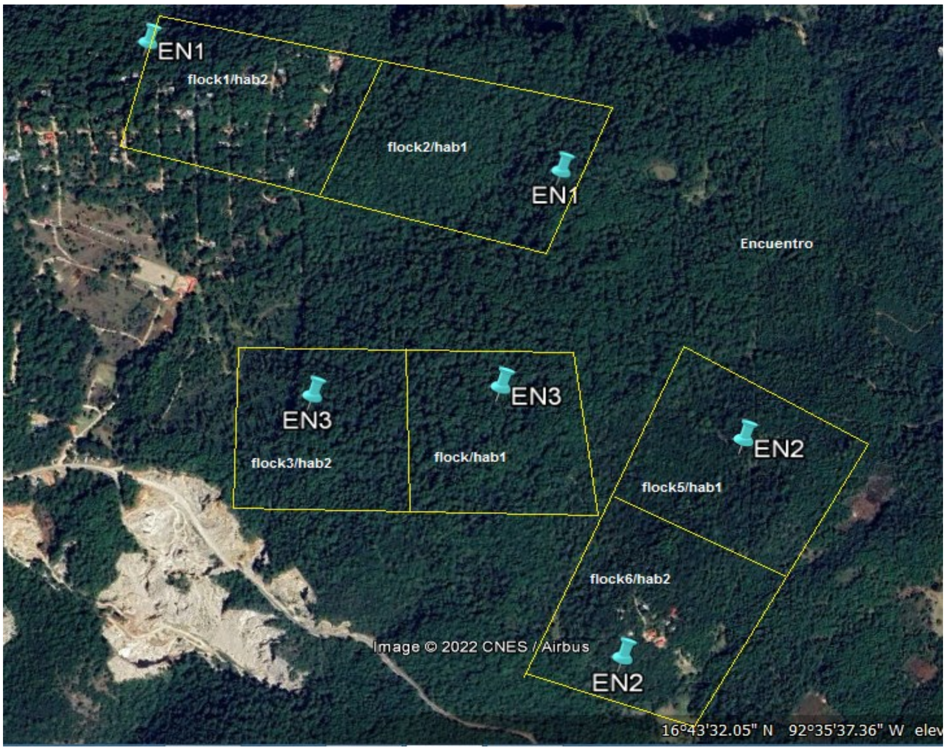

Figure 7. Sampling units, i.e., flock pairs in contiguous habitat 1 (forest interior as preferred habitat) and habitat 2 in Encuentro (forest edge, roads and urbanization).

Standard vegetation variables were measured in each plot within habitat type, starting with number of oak trees, average height of oak trees, mean abundance of epiphyte and canopy cover percentage. To account for disturbance in plots where edges were present, I included: level of human disturbance explained through measured variables such as number of open areas for housing, and number of roads (walking trails and vehicle transit routes).

*Bird species densities*. I used binoculars and followed Sibley (2014) to identify plumage characteristics of individuals foraging in flocks at both study sites. To estimate densities, I identified their occurrence in foraging flocks and counted every individual of both warbler species. Sampling stations and flock pairs at each landscape were assessed within two days, and over a period spanning from January through February, during which time leaf cover declined, as did densities of both warblers. I delineated the Minimum Convex Polygon (MCP) for each flock based on observations of their foraging movements during a period of two to four hours, or up to the time when the flock disbanded. The same procedure was repeated for three years. To estimate densities of each species per plot and year ($N = 3 \times 3 = 9 \times 2 = 18$), I divided the number of individuals in a flock by its MCP area, using the assumption that flock densities correlate with plot densities. Normality assumptions on density data distributions were assessed with Chi-square goodness-of-fit tests.

*Isodars.* I fitted Isodars with linear regression (for the one-species model, Equation 1) and Generalized Linear Mixed Models (GLMM) with Gaussian error distributions, with flock pair and year as random effects (for the two-species models, Equations 3 and 4). The better of the two Equations 3 and 4 was determined by the statistical significance of the interaction term in Equation 4. I presented the outcome of the better GLMM visually in a three-dimensional plot with a prediction surface "mesh" showing the effect of TOWA density on habitat preference of GCWA. I used the lme4 and rgl packages in R to run the models and to build the three-dimensional plot.

## RESULTS

*Habitat data.* Vegetation structure at Moxviquil differed between habitat types except for oak canopy cover (Table 3). Number and height of oak trees, epiphytes and canopy cover were higher than in Encuentro, where the differences across Habitats 1 and 2 were limited to distance to open areas and the presence of roads, lower and higher respectively in the preferred habitat.

Table 3. Vegetation characteristics and comparisons between habitat types in Moxviquil, a higher-quality habitat for GCWA, and Encuentro, a lower-quality habitat. Mean includes the the standard error. Open areas include mainly housing; roads are trails mainly used by vehicles.

| **Variables** | **Sampling plots** | | **Test statistic** | ***P*** |
|---|---|---|---|---|
| | **Moxviquil** | | | |
| | **Habitat 1** | **Habitat 2** | | |
| Number of oak trees /1000 $m^2$ | 128 ± 7 | 55 ± 4 | $F_{1,16} = 70.2$ | 0.001 |
| Average height of oak trees (m) | 14.4 ± 0.9 | 9.2 ± 1.3 | $Z = 7.93$ | 0.005 |
| Mean abundance of epiphytes | 4092 ± 811 | 686 ± 216 | $\chi^2 = 18.0$ | <0.001 |
| Canopy cover (%) | 75 ± 5 | 65 ± 5 | $Z = 1.88$ | 0.16 |
| Distance to open areas (m) | 346 ± 41 | 128 ± 26 | $F_{1,16} = 0.17$ | <0.001 |
| Presence of roads | 0.11 ± 0.11 | 0.67 ± 0.16 | $F_{1,16} = 7.69$ | 0.01 |
| | **Encuentro** | | | |
| | **Habitat 1** | **Habitat 2** | | |
| Number of oak trees /1000 $m^2$ | 49 ± 2 | 38 ± 4.3 | $F_{1,16} = 0.01$ | 0.93 |
| Average height of oak trees (m) | 11.5 ± 0.5 | 10 ± 1 | $Z = 1.45$ | 0.22 |
| Mean abundance of epiphytes | 520 ± 82 | 396 ± 87 | $\chi^2 = 0.62$ | 0.53 |
| Canopy cover (%) | 50 ± 5 | 35 ± 5 | $\chi^2 = 2.0$ | 0.15 |
| Distance to open areas (m) | 203 ± 36 | 49.3 ± 2.3 | $F_{1,16} = 12.5$ | 0.003 |
| Presence of roads | 0.56 ± 0.17 | 1.89 ± 0.26 | $F_{1,16} = 18.0$ | 0.001 |

*Warbler densities.* Sixteen GCWA individuals were found at Moxviquil and 11 were found at Encuentro across the three years. All individuals were found foraging in mixed-species flocks. GCWA densities were not different between its preferred (0.71 ± 0.14 $ha^{-1}$) and secondary habitats (0.65 ± 0.12 $ha^{-1}$) within Moxviquil ($F_{1,16} = 0.11$, $P = 0.74$). TOWA densities were not different between habitats at Moxviquil (3.1 ± 0.6 $ha^{-1}$ and 3.2 ± 0.7; $F_{1,16} = 0.03$, $P = 0.99$). In Encuentro, densities of GCWA were higher in its preferred habitat (0.67 ± 0.1 $ha^{-1)}$ than within its secondary habitat (0.37 ± 0.7 $ha^{-1}$ ; $F_{1,16} = 3.5$, $P = 0.08$). TOWA densities did not differ between habitat types in Encuentro (2.5 ± 0.67 $ha^{-1}$, 1.7 ± 0.35 $ha^{-1}$; $F_{1,16} = 1.07$, $P = 0.31$).

*Isodar analysis.* The test for density-dependent habitat selection in GWCA at Moxquivil resulted in an Isodar with a non-significant intercept (0.51 ± 0.31; $t = 1.6$, $P = 0.14$) and a positive slope <0.5, indicating no preference for either habitat (0.29 ± 0.42; $t = 0.71$, $P = 0.49$; Figure 8). This may also indicate that this species does not perceive qualitative and quantitative differences between its assumed preferred versus less preferred habitat. Crossover regulation (mixed preferences) suggests that there is an effect of a dominant competitor, here assessed by including a second species, TOWA.

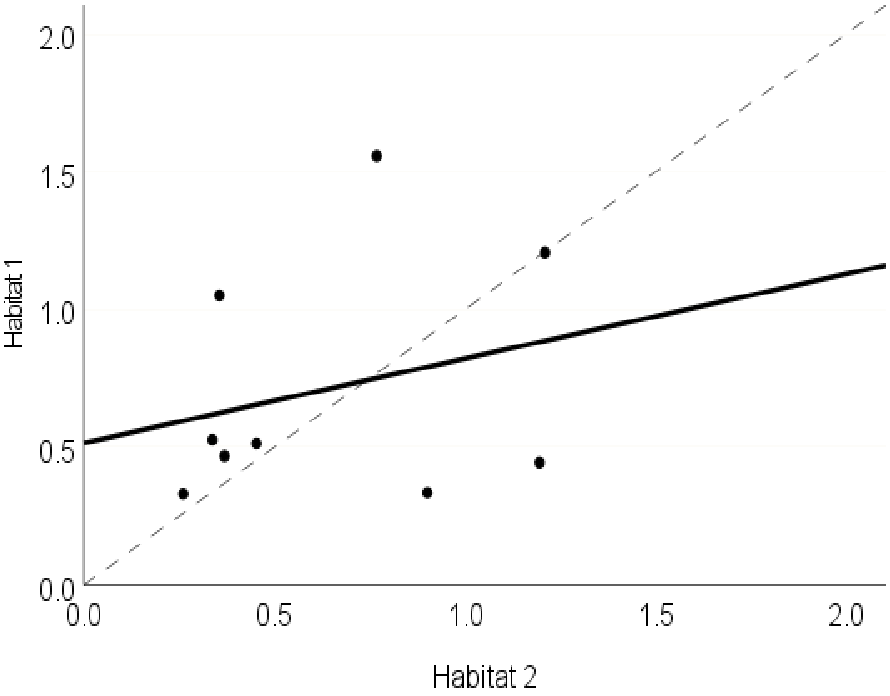

Figure 8. Linear regression of GCWA density (ha$^{-1}$) in its preferred habitat 1 (forest interior) against density in its secondary habitat (forest and edge) within sampling units/flock pairs in Moxviquil.

Opposite to the results at Moxviquil, the test for density-dependent habitat selection in GWCA at Encuentro resulted in an Isodar with a non-significant intercept (0.14 ± 0.21; $t = 0.69$, $P = 0.5$) and a positive slope (1.43 ± 0.45; $t = 3.17$, $P = 0.02$; Figure 9), corresponding to density-dependent preference for Habitat 1, which is quantitatively the preferred habitat beginning at intermediate densities. This assumes that GCWA conspecific competition is stronger and dominated by adult individuals. When regressing TOWA densities within Habitats 1 and 2 in each site, there were no significant effects or density-dependent preference for either habitat as a function of densities (Moxviquil Isodar slope: 0.4 ± 0.29; $t = 1.37$, $P = 0.21$; Encuentro Isodar slope: 0.77 ± 0.76; $t = 1.02$, $P = 0.34$).

Neither of the two models testing the effect of TOWA densities on the GCWA Isodar was preferred, comparing AIC alone (Equation 3, AIC = 27.91; Equation 4, AIC = 27.28). Equation 3 without the interaction term showed a positive effect of TOWA densities on GCWA densities within its preferred habitat, although no effect of the congener was present in GCWA secondary habitats at Moxviquil (Table 4). At Encuentro, Equation 3 without the interaction term showed a stronger positive effect of TOWA densities on GCWA densities within both preferred and less preferred habitats (Table 5). Also, the positive effect of GCWA conspecific densities in Habitat 2, suggest a competitive pressure by both conspecifics and heterospecifics where anthropogenic disturbance is higher.

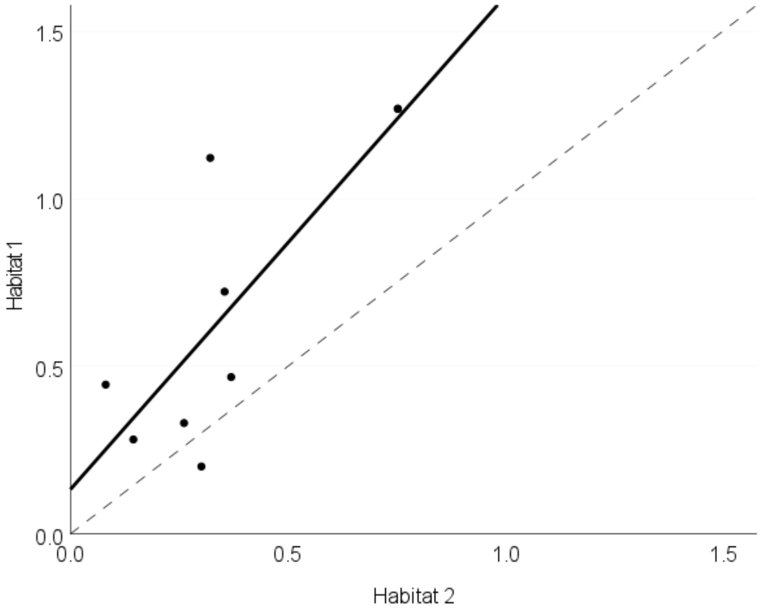

Figure 9. Linear regression of GCWA density (ha$^{-1}$) in sampling units within sampling units in Encuentro: preferred versus less preferred habitats (i.e., 1 and 2).

Table 4. GLMM of GCWA density in its preferred habitat ($\mathrm{GCWA}_{\mathrm{Hab1;\ dependent\ variable}}$), following Equation 3. Independent variables include GCWA density in its secondary habitat ($\mathrm{GCWA}_{\mathrm{Hab2}}$), density of TOWA in both habitats, and two random factors (sampling unit/flock pair and year) in sampling units/flock pairs in Moxviquil.

| Term | Coefficient | Std. error | *t* | *P* | 95% conf. int. | |
|---|---|---|---|---|---|---|
| Intercept | 0.21 | 0.19 | 1.13 | 0.33 | –0.36 | 0.79 |
| $\mathrm{GCWA}_{\mathrm{Hab2}}$ | –0.11 | 0.34 | –0.33 | 0.76 | –1.46 | 1.23 |
| $\mathrm{TOWA}_{\mathrm{Hab2}}$ | –0.06 | 0.05 | –1.08 | 0.33 | –0.21 | 0.09 |
| $\mathrm{TOWA}_{\mathrm{Hab1}}$ | **0.24** | 0.05 | 4.42 | **<0.001** | 0.10 | 0.38 |

Fitting the warbler densities to Equation 4 created an Isodar that suggests a competitive heterospecific relationship described by a significant effect of TOWA densities over GCWA in its less preferred habitat at Moxviquil (Table 6). Higher TOWA densities at Encuentro correspond to an apparent lack of preference of GCWA for Moxviquil even at low densities, while maintaining crossover regulation (mixed preferences), presumably involving TOWA (Figure 10). At Encuentro, Equation 4 resulted in a positive interaction term that suggests a competitive heterospecific relationship between TOWA and GCWA in its preferred Habitat 1 (Table 7). However, a significant effect of TOWA densities over GCWA still occurs in Habitat 2, and when combined with an increase of GCWA conspecifics in Habitats 1 and 2, the effect remains (Figure 10).

Table 5. GLMM of GCWA density in its preferred habitat ($GCWA_{Hab1;\ dependent\ variable}$), following Equation 3. Independent variables include GCWA density in its secondary habitat ($GCWA_{Hab2}$), density of TOWA in both habitats, and two random factors (unit/flock pair and year) in sampling units/flock pairs in Encuentro.

| Term | Coefficient | Std. error | *t* | *P* | 95% conf. int. | |
|---|---|---|---|---|---|---|
| Intercept | 0.38 | 0.20 | 1.96 | 0.19 | –0.45 | 1.23 |
| $GCWA_{Hab2}$ | **–0.38** | 0.08 | –4.93 | **0.02** | –0.63 | –0.13 |
| $TOWA_{Hab2}$ | **0.13** | 0.002 | 63.2 | **<0.001** | 0.12 | 0.14 |
| $TOWA_{Hab1}$ | **0.08** | 0.01 | 9.90 | **0.002** | 0.05 | 0.11 |

Table 6. GLMM with dependent variable ($GCWA_{Hab1}$) and independent variables as in Table 3, as well as a species interaction term for densities at Moxviquil ($GCWA_{Hab2} \times TOWA_{Hab2}$), following Equation 4.

| Term | Coefficient | Std. error | *t* | *P* | 95% conf. int. | |
|---|---|---|---|---|---|---|
| Intercept | 0.06 | 0.52 | 0.12 | 0.90 | –1.40 | 1.53 |
| $GCWA_{Hab2}$ | 0.06 | 0.69 | 0.09 | 0.92 | –1.85 | 1.99 |
| $TOWA_{Hab2}$ | **0.24** | 0.05 | 4.06 | **0.01** | 0.07 | 0.40 |
| $TOWA_{Hab1}$ | –0.001 | 0.19 | –0.007 | 0.99 | –0.54 | 0.54 |
| $GCWA_{Hab2} \times TOWA_{Hab2}$ | –0.05 | 0.18 | –0.30 | 0.77 | –0.57 | 0.46 |

Table 7. GLMM with dependent variable ($GCWA_{Hab1}$) and independent variables as in Table 3, as well as a species interaction term for densities at Encuentro ($GCWA_{Hab2} \times TOWA_{Hab2}$), following Equation 4.

| Term | Coefficient | Std. error | *t* | *P* | 95% conf. int. | |
|---|---|---|---|---|---|---|
| Intercept | 0.24 | 0.05 | 4.46 | 0.02 | 0.06 | 0.42 |
| $GCWA_{Hab2}$ | –0.24 | 0.26 | –0.93 | 0.42 | –1.07 | 0.58 |

| | | | | | | |
|---|---|---|---|---|---|---|
| $\text{TOWA}_{\text{Hab2}}$ | **0.13** | 0.007 | 16.98 | **0.000** | 0.10 | 0.15 |
| $\text{TOWA}_{\text{Hab1}}$ | –0.10 | 0.03 | –3.19 | 0.06 | –0.22 | 0.01 |
| $\text{GCWA}_{\text{Hab2}} \times \text{TOWA}_{\text{Hab2}}$ | **0.44** | 0.08 | 4.98 | **0.01** | 0.18 | 0.71 |

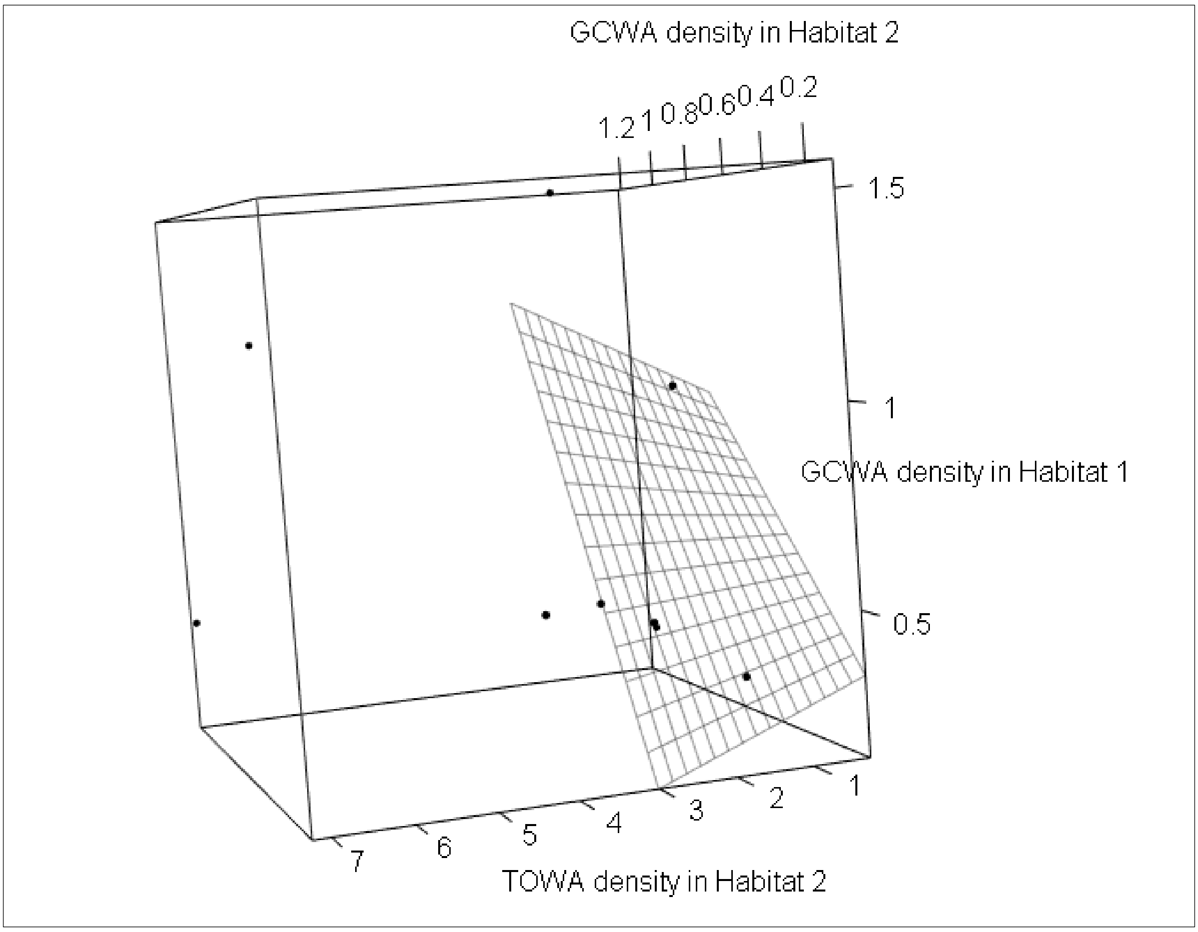

Figure 10. Three-dimensional plot with added surface (mesh) of predicted values based on a Generalized Linear Mixed Model (Isodar Equation 4) with densities of GCWA in low disturbance habitats (in Moxviquil) as a function of densities of conspecifics and heterospecifics (TOWA) in high disturbance habitats (in Encuentro).

# DISCUSSION

In most migratory species, intense intraspecific competition results in site preemption, especially where food resources are stable and when predation risk, space use and energy expenditure are to be minimized (Marra 2000). Occupying environments driven by winter food limitation, as is the case for migratory warblers in their nonbreeding season, should then progressively segregate less competitive individuals into lower quality areas (Fretwell and Lucas 1969). In this study, GCWA densities were higher at Moxviquil than Encuentro, the assumed preferred landscape with less disturbance (King and Rappole 2000). However, differences in densities were not significant within pair of surveyed habitats in Moxviquil and incorporating disturbance levels into isodars may show if a gradient of habitat quality on each pair of flocks is linked to density-dependence and its variation between pair of habitats (Hodson et al. 2010) Bias in GCWA sex and age ratios toward adult males and females in some flocks in both study landscapes now suggests intraspecific competition over microhabitats where higher cover of oak trees and lower anthropogenic disturbance indicate higher suitability. The fact that most GCWA individuals were found in flocks further suggests that occupation of fixed territories may be occurring less often than expected. Sex and age ratios in TOWA, on the other hand, were not biased toward males or adults, and its density was not different between landscapes.

Difference in densities across landscapes often corresponds to variation in habitat suitability and to adjustments to home ranges forced by other individuals (Jones 2001; Gaona 2004). While competition between species may be solved to an extent by segregation and differential habitat use or territorial acquisition, competitors may still overlap in habitat use if their densities are below a habitat's carrying capacity (Morris 1999). It is possible, as in this study, that patch choices of a subordinate individual or species are modified when the density of its dominant competitor increases in response to temporal variation in habitat use due to reduced food supply or other factors. The strong association of GCWA adults with mixed flocks and the potential lack of territories in this species are scenarios that imply density-dependent effects of exploitative competition among conspecifics, and interference with a closely related species when occupying winter habitats of declining quality. This fact is supported on the assumption of stronger competition among congenerics (Connell 1980), being these species similar in their ecological requirements and patterns of niche overlap as shown in previous studies on Setophaga warblers (Greenberg et al. 2001, Komar et al. 2011). However, this association does not discard other interactions between flocking warblers that may occur but not detected so far.

Competitive asymmetries and differential habitat use in GCWA may be mediated by traits associated with variation in sex, age, personalities (e.g., aggressive, tolerant) or a combination. A potential explanation for observed distributions in GCWA would be to argue that this species follows a despotic distribution where conspecific dominance and site preemption by its congener mediate access to flocks (intraspecific effects) or influence differential habitat use (interspecific effects). On the other hand, facilitation, likely in flock formation, appears as a possibility arising from co-occurrence with TOWA in the less disturbed landscape, as GCWA densities were positively associated with densities of TOWA at Moxviquil in the Isodar that accounted for a competitive effect (Equation 4). Intraspecific competition is known to cap local density (Brown 1969), and thus release available resources not exploited by conspecific competitors, which in turn may allow more heterospecifics to use available food or space (Brown and Orians 1970). However, in this study, this proposed positive effect changed as a function of higher environmental disturbance associated with lower tree canopy cover, suggesting a need to account for negative interactions or density-dependence even in habitats or sites considered to be suitable early in the winter. Ultimately, interspecific competition would further decrease food supply and habitat quality (Holmes 2007). While intra-specific territoriality or dominance may cap the abundance of GCWA individuals, most instances of interspecific territoriality in Parulidae appear more strongly related to phylogeny than to resource use (Losin et al. 2016). This may explain why interspecific competition was also present in this study species and system and more importantly, that phylogenetic similarities would not preclude other effects on fitness or demographic parameters (Kent and Sherry 2022).

While GCWA densities differed between habitats in the disturbed site, Encuentro, the lower abundance of GCWA compared with TOWA and the possible interference from additional co-occurring species may have limited the assessment of habitat preference and its density dependence. Experimental removal of the most abundant putative competitor has been shown to reveal a preference for a certain habitat type (Morris 1998) but using this kind of test on flocks is restricted by the difficulty of capture of individuals of a given species. While facilitation in flocks seems to be a mechanism that may facilitate species co-occurrence, interspecific competition negatively impacts perceived habitat quality (Jones 2014). Territorial ownership would thus be expected to reduce foraging costs, although alternatives to site preemption, such as opting for floating, may be selected by dispersing individuals, former territory owners or subordinates (Brown and Sherry 2008). Less competitive individuals, not found among the GCWA tracked in this study, may be surveyed by a more comprehensive assessment across wintering areas. In this case, construction of Isodars using a range of densities over a larger area of forest may confirm the intriguing reversal of expected habitat preference when an Isodar accounts for co-occurrence of a rare species with a putative competitor, its congener.

The two-species Isodar constructed here can be hypothesized as evidence for site preemption of subordinate individuals of GCWA by TOWA, even when joining flocks might facilitate foraging efficiency in both species. That this might occur more frequently at the more disturbed site is explained as increased densities of TOWA in its less preferred habitat when its preferred habitat is increasingly occupied. In terms of conservation, maintaining a suite of habitats of varying quality where each differentially contributes to overall population size may best represent the precautionary principle, a target in most conservation programs involving Neotropical migratory birds. The potential for TOWA effects on GCWA habitat use indicates that management of winter habitats should secure the maintenance of primary habitat with higher amount of oak forest cover, where the GCWA reaches higher densities. Although females may have differential preference because of site preemption or competition for favoured positions when in flocks, survival within secondary sites still contributes to overall population size in the nonbreeding season. Conservation policies should, therefore, target all habitats occupied by this species despite apparent effects of competition and facilitation.

# CHAPTER 4. BEHAVIORAL AND NUMERICAL RESPONSES TO EXPERIMENTAL ATTRACTION IN TWO MIGRATORY WARBLER SPECIES

Social cues, in addition to personal experience, are known to increase knowledge on mate availability and reproductive success during the breeding period (i.e., public information, Dall et al. 2005), and to provide information on food supply and predation threats year-round (i.e., location-based cues, Nocera and Betts 2010). Transfer of information on habitat quality is predicted to increase with overlap in behaviour when benefits derived from information outweigh the costs of competition (Danchin et al. 2004; Sridhar et al. 2012). To be profitable, information must be acquired from individuals limited by the same factors; often they are conspecifics (Stamps 1988). Others argue that use of interspecific cues is advantageous because differences in foraging traits between species reduce niche overlap (Schoener 1974; Parejo and Aviles et al. 2016). Conspecific and ecologically similar species often increase their co-occurrence by settling in close neighborhoods or by aggregating in foraging groups as a function of information transfer (Valone 2007). For example, an increase in the relative abundance of a migratory bird species (a numerical response) occurred following experimental augmentation of a resident species when information on reproductive success was provided (Mönkkönen et al. 1999). Networks of information transfer between flocking species increase social foraging and fitness benefits, reflecting the adaptive value that information transfer has on communities of tropical birds (Martinez et al. 2016). However, it remains less clear whether using such cues accurately reflects ecological interactions at intra- and interspecific levels that influence realized habitat selection and shifts in foraging traits, such as shifting from solitary to social behaviour.

Transfer of information from sentinels or leaders among bird species, usually foragers with conspicuous colour patterns, vocalizations, or foraging behaviours, often mediates the formation of bird flocks (Goodale et al. 2010). However, the benefits of attraction and the costs of aggregation create fitness trade-offs that are assessed whenever foragers choose among available opportunities (Forsman et al. 2008). Previous assessment of dominance traits in putative competitors has shown that use of information for settlement (i.e., the choice to occupy an area) and other behavioral decisions further depends on social context (Morinay et al. 2020). Behavioral traits inherent to the source of information will influence a competitor's willingness to use available information, and therein decisions on settlement or aggregation (Goodale et al. 2010).

While provision of social cues (e.g., calls and songs) has been used to influence settlement in migrant bird species in areas occupied by resident species and other migrants arriving earlier to breeding grounds (Forsman et al. 2007; Farrell et al. 2012), less is known if different types of calls (e.g., from aggressive *versus* tolerant individuals) in the nonbreeding grounds can induce territorial behaviour or numerical responses in ecologically similar species. An experimental approach to fill this gap may determine the value of certain information to making initial foraging decisions that may later influence habitat choices (Dall et al. 2005), and it can be used to test whether occupancy rules correspond with despotic behaviour that influences habitat selection. In migratory birds exempt from the demands of breeding during the winter season, available information from any neighbours may guide their foraging decisions and influence their patterns of space use (Mönkkönen and Forsman 2002). In the focal species, the golden-cheeked warbler (GCWA), occurrence is known to result from conspecific attraction on their breeding grounds (Campomizzi et al. 2008; Farrell et al. 2012), whereas associations with others in foraging flocks has been shown to influence its winter habitat use (Komar et al. 2011). The congeneric Townsend's warbler (TOWA) also joins flocks during the nonbreeding season, but it may also occur as solitary individuals across its winter range (Greenberg et al.2005). The types of cues to which individuals are responsive could thus influence behaviour such as shifting space use from a solitary situation involving defending a territory (e.g., conspecific neighborhoods) to joining flocks that expand home ranges and may facilitate foraging (Goodale et al. 2017).

In this chapter, I describe the outcome of an experiment to assess how aggressive and nonaggressive calls, under different environmental contexts, create different responses, explained best by agonistic behaviour interpreted as territoriality, or by nonaggressive behaviour and numerical responses (i.e., local increases in density) interpreted as the propensity to settle or join others and forage in a flock. Although both focal species in this study are highly social throughout the nonbreeding period, social hierarchies may modulate their differential occupancy and propensity to join flocks. Given that competitive asymmetries between individuals may underlie differential patterns of habitat use (see chapter 2), agonistic interactions among conspecifics in both species is expected to result from playbacks in low-disturbance habitats. Conversely, tolerance and coexistence with reduced aggression rates may be more common in high-disturbance habitat, where territories are not strongly defended due to unpredictable predation risk and food supply (Komar et al. 2011). This latter scenario may result in increased local densities in both species (i.e., more individuals being prone to attraction) regardless of the type of information provided by conspecifics or heterospecifics.

## METHODS

I performed a playback experiment at two study sites, Moxviquil (low disturbance) and Encuentro (high disturbance), which differ in vegetation structure and composition (described in chapter 2). At each site, in each of the five plots (1 ha in size, described in chapter 2), I established a calling station. Plots were spatially separated by an average distance of 500 m. Vegetation structure was held as constant as possible within each site where the stations were established, to avoid confounding effects on warbler responses. Vegetation data for this chapter is taken from data presented in chapter 2. To confirm absence of both species in each plot before treatments, I conducted point counts at all calling stations for one month and later compared responses with those in plots where abundance was estimated post-treatment.

Playback treatments were applied before spring departure (during January-February). Treatments consisted of songs and calls of GCWA, TOWA, and the greater pewee (*Contopus pertinax*, GRPW). The latter species was included because it often initiates group formation, i.e., as a sentinel species (Goodale et al. 2010). Songs and calls were downloaded from the Xenocanto website (www.xenocanto.com). Song recordings were specific to the breeding season, although chirping calls were also included as they are more common than territorial songs during the nonbreeding season. Alarm calls were left out of the treatments because several attempts at using predator calls did not influence responses in any plot, and because neither predation events nor predator occurrence was observed during surveys, except for one isolated attack by a Cooper's hawk (*Accipiter striatus*). Data were processed using Audacity® Version 1.2.6 (http://audacity.sourceforge.net), which produced tracks for each species in the playback experiment. Treatments were applied during 60 noncontinuous days (i.e., 25 days of calls followed by 5 days off, repeated twice for each species and study site). They were timed before sunrise to simulate the dawn chorus assumed to start flocking.

At each calling station, a 10-minute loop was played of the songs and calls of the two warblers (6 min) and GRPW (2 min) followed by a period of silence (2 min). I stayed at the calling points to wait for visual and acoustic responses. It took one survey day to cover each of the five plots at both sites, visiting all plots five times over 25 days. I summarized the number of aggressive or territorial displays (i.e., when an individual responded with constant vocalization moving towards the speaker) in response to playback calling. Constant aggressive calling was considered territorial defense and evidence of site preemption. Silent behaviour or chirping without clear agonistic bouts was considered as a negative response to playbacks. Possible aggregation was recorded as frequency of settlement, i.e., attraction to the calling station, and recorded as changes in relative abundance between plots and study sites. To obtain an index of relative abundance (average number of individuals observed divided by total time observing per visit), I surveyed all calling stations to obtain pre-treatment relative abundance in both warbler species. To obtain relative abundance post-treatment, I compared responses before and after treatments to look for an effect of manipulation of social cues. The numerical response or changes in relative abundance by species was obtained through visual or acoustic evidence of presence.

*Statistical analysis.* To analyze differences in numerical responses (i.e., change in relative abundance before and after treatments) and compare frequency of agonistic bouts at the two study sites, I used ANOVA and goodness-of-fit tests, respectively. A nominal logistic regression was used to explore relationships between vegetation variables (presented in chapter 2) and responses to the playback calling. Frequency of settlement were modeled as a function of vegetation covariates as proxies for visible exposure to predators and lower resource abundance in the more disturbed habitat (Encuentro). Interactions were considered significant at $\alpha = 0.05$. Analyses were performed with JMP® statistical software.

# RESULTS

*Numerical responses in the warblers.* There was no effect of playbacks on the average number of GCWA individuals observed per hour (i.e., its relative abundance) at either site. The number of TOWA individuals increased in the treatment plots at both Moxviquil ($F_{1,28} = 23.7$, $P < 0.01$) and Encuentro ($F_{1,28} = 22.8$, $P < 0.01$).

*Effects of playbacks on settlement and behaviour of GCWA individuals.* Settlement occurred for GCWA on hearing playback calls of GRPW more often than in response to its own calls or calls of TOWA at Moxviquil, but these differences did not occur at Encuentro ($\chi^2 = 7.1$ $df = 2$, $P = 0.03$; Table 8). GCWA was aggressive in response to its own calls at both sites, infrequently aggressive in response to TOWA calls, and never aggressive after GRPW calls ($\chi^2 = 11.7$, $df = 2$, $P = 0.02$).

Table 8. GCWA settlement and behavioral responses to playback treatments at the low-disturbance (Moxviquil) and high-disturbance (Encuentro) sites. Asterisk (*) shows where the greater pewee (GRPW) calling had the most significative effect on GCWA responses.

| **Treatment** | **Settlement** | | **Behaviour** | |
|---|---|---|---|---|
| **Moxviquil** | Not detected | Present | Silent | Aggressive |
| GCWA | 25 | 5 | 22 | 8 |
| TOWA | 28 | 2 | 28 | 2 |
| GRPW* | 20 | 10 | 30 | 0 |
| Total number of playbacks applied | 73 | 17 | 80 | 10 |
| **Encuentro** | Not detected | Present | Silent | Aggressive |
| GCWA | 23 | 7 | 20 | 10 |
| TOWA | 19 | 11 | 27 | 3 |
| GRPW | 21 | 9 | 30 | 0 |
| Total number of playbacks applied | 63 | 27 | 77 | 13 |

Table 9. TOWA settlement and behavioral responses to playback treatments at the low-disturbance (Moxviquil) and high-disturbance (Encuentro) sites. Asterisk (*) shows where aggression in TOWA occurs more often to its own calls.

| **Treatment** | **Settlement** | | **Behaviour** | |
|---|---|---|---|---|
| **Moxviquil** | Not detected | Present | Silent | Aggressive |
| GCWA | 11 | 19 | 30 | 0 |
| TOWA* | 13 | 17 | 26 | 4 |
| GRPW | 14 | 16 | 30 | 0 |
| Total number of playbacks applied | 38 | 52 | 86 | 4 |
| **Encuentro** | Not detected | Present | Silent | Aggressive |
| GCWA | 17 | 13 | 27 | 3 |
| TOWA* | 4 | 26 | 24 | 6 |
| GRPW | 8 | 22 | 30 | 0 |
| Total number of playbacks applied | 29 | 61 | 81 | 9 |

*Effects of playbacks on settlement and behaviour of TOWA individuals.* TOWA individuals responded to settle more often after all playback calls at Moxviquil, and especially after its own calls and GRPW calls at Encuentro; settlement occurred much more often than for GCWA in all cases (Table 9). More aggressive responses in TOWA occurred when its own calls were played ($\chi^2$=8.4, $df$ = 2, $P$ = 0.02), with only three cases of aggression after the GCWA calls at Encuentro and no aggression after GRPW calls. Treatment effects were significatively different between the two sites ($\chi^2$ = 13.53, $df$ = 2, $P$ < 0.01).

*Relationship between vegetation variables and settlement.* Density of oak trees at both sites influenced detection by both species, with occurrence being less likely at higher tree density (Table 10). Settlement was more likely in areas with greater tree density and height at Moxviquil and lower tree density at Encuentro.

Table 10. Output of logistic regressions relating vegetation variables and settlement responses combined across species and treatments at Moxviquil and Encuentro.

| | **Moxviquil** | | | | **Encuentro** | | | |
|---|---|---|---|---|---|---|---|---|
| Term | β | S.E. | *T* | *P* | β | S.E. | *t* | *P* |
| Intercept | 65.7 | 40.5 | 2.6 | 0.10 | 48.3 | 36.1 | 1.8 | 0.10 |
| Density of oak trees | **-0.8** | **0.3** | 5.7 | **0.01** | **-0.9** | **0.4** | 4.4 | **0.03** |
| Average tree height | **2.3** | **1.1** | 4.0 | **0.04** | -2.0 | 2.2 | 0.8 | 0.30 |

# DISCUSSION

Local settlement, especially by TOWA individuals as a function of all the playbacks, regardless of source, confirms that attraction among conspecifics and between species is a factor that influences habitat choices. Habitat use is often mediated by interactions with conspecific or interspecific competitors with similar ecological niches (e.g., preferred foraging substrates; Greenberg et al. 2001). Similarity in ecological requirements and predation threats also underlie an individual's reliance on cues created by the occurrence of other foragers. Aggressive responses to conspecific calls occurred at both sites in this study, supporting the hypothesis of dominance-mediated defense of a territory in both species. Site preemption may be a mechanism by which settlement occurs, but because settlement was more likely in plots with lower density of oak trees and lower potential abundance of prey, preemption may be limited to a mechanism that occurs within flocks, away from better habitats. In flocks, dominance of adult males was higher, especially in the subordinate GCWA, but in TOWA, preemption seems to act through increased abundance rather than direct aggression on either territories or flocks. TOWA is likely a more generalist species, explaining why individuals of this species responded approximately equally to all playback treatments with less agonistic behaviour at both sites. That it responded with an increase in abundance and occupancy of shared habitats when co-occurring with GCWA supports its putative role in preemption, especially in the more disturbed landscape (see chapter 3).

The source of information, coming from a conspecific or a heterospecific, may promote differential effects on patch choices as a function of the interactions between the information source and a receptor (Thomson et al. 2003). In this study, conspecific playback served to attract and induce initial settlement, probably in those individuals without a fixed territory that are more likely to join flocks. Thus, reliance on social cues may promote temporary associations aiming to reduce foraging costs in terms of searching time when resources are scattered outside defended territories (Galef and Giraldeau 2001; Ahlering et al. 2010). Meanwhile, competition for resources and safer spaces should force subordinates to leave potential territories for foraging opportunities elsewhere (Johnson 2007). Social cues strongly influence the process of habitat selection, but the availability of social information and its value may further depend on the social hierarchies within the context where information is gathered (Fletcher et al. 2007; Szymkowiak et al. 2017). In this study, GCWA individuals responded aggressively towards conspecifics, a trend observed in foraging flocks but not known in solitary individuals. Higher density of dominant individuals and aggressive behaviour towards intruders has been shown to impede access to potential information on habitat quality through limited use of sites where fitness rewards may be higher (Sepannen 2007). If interference to obtain information is intense among conspecifics or between species, a subordinate forager may then decide to search for another opportunity to reduce negative interactions and increase fitness-enhancing opportunities elsewhere.

Density of trees showed a significant interaction and was an important variable that influenced GCWA and TOWA settlement and responses to playback, but territorial behaviour seems to limit any increase in relative abundance of GCWA at the Moxviquil site. The playback experiment supports the hypothesis based in Isodar theory that site preemption as a result of increased abundance might be a common strategy used by TOWA, especially where resources are limited, as the case for Encuentro. This disturbed landscape still maintains remnant oaks, but GCWA adults were predominantly found foraging along with mixed-species flocks (see chapter 2). Aggregation may thus depend on individual personalities, where tolerant individuals or dominant and territorial individuals provide and limit access to opportunities, respectively (Morinay et al. 2020).

Experimentally provided social cues through callings have been used by some land managers to increase abundance or influence patterns of spatial distribution in some bird species as a conservation measure (Ahlering et al. 2010). In this study, despotic behaviour seems to influence behavioral responses and occurrence of subordinates in the endangered GCWA as this species responded aggressively, more often towards conspecifics. While sample size was low, frequent occurrence of adult GCWA males and females in flocks or territories supports this fact. I did not, however, test whether application of playbacks without a dominant trait (e.g., non-territorial songs) and differences in timing of playbacks (e.g., on arrival instead of during a settlement period) may influence distributions. Calls during the arrival period may have a different response that needs to be evaluated if attraction is to be settled to increase relative abundance in protected areas (Nocera and Betts 2010). Given the generous amount of remaining habitat in disturbed sites in Chiapas, like Encuentro, there is still opportunity for land managers to increase abundance of GCWA by use of artificial cues, considering the strong gradient of disturbance (i.e., resulting in differential habitat selection) across available sites would be important to avoid ecological traps (Gilroy and Sutherland 2007; Betts et al. 2008). This research shows that maintenance of flock sentinel species across sites may increase GCWA occurrence, regardless of interactions with its potential competitors.

# CHAPTER 5. CONCLUSIONS

Different strategies of space use may coexist within populations of migrants across habitats of varying quality. Flocking behavior is an important foraging trait in the GCWA warbler during its nonbreeding period and maintaining large tracts of forests in the wintering areas would secure the persistence of groups and attendants such as the GCWA in the long term. Group behaviour, although considered a helpful strategy to adopt for subordinates, was a function of male dominance and despotic behaviour in GCWA at both study landscapes, as shown by their occurrence in flocks and aggression towards conspecifics. Flocks transit through defended territories and dominant individuals, more likely among the congener TOWA, is perhaps more likely as habitat quality declines during a winter period. TOWA females also occur in flocks, but their home ranges were larger in comparison to males, suggesting that males increase the benefit-cost ratio more than females when joining flocks. An observed pattern of intraspecific territoriality, where GCWA avoided conspecifics, confirms a despotic distribution of wintering populations, explained by adult individuals that were more evenly spaced in flocks than randomly dispersed across habitats in the wintering grounds. These results are relevant because despotic distributions are often linked to reduced equilibrium densities (Lopez Sepulcre and Kokko 2005).

Social behaviour and intraspecific competition in GCWA may explain why this species presents a patchy distribution and low density during the nonbreeding period. The two-species Isodars constructed in this study suggest that habitat preference in GCWA is dissipated as densities of its congener increase. In this sense, both solitary (territorial) and social systems for GCWA should be managed in their nonbreeding grounds, because facilitation over shared resources would favour coexistence in both preferred and less preferred wintering habitats. A conclusion of this study is that data on occurrence of females and immatures are still lacking to predict how individuals maximize fitness in their wintering grounds. Landscape and habitat conditions likely influenced the variation in foraging effort and potential energy expenditure in GCWA, but it seems that adults found more often in flocks within the disturbed site, Encuentro, are trading off foraging efficiency and higher threat of predation for larger group sizes (Krause and Ruxton 2002; Gil et al. 2017). This response calls to test for additional effects on foraging effort on flocking individuals because dominants are assumed to secure the higher quality habitats with reduced foraging costs (Marra et al. 2015). Additionally, canopy cover influenced group size and, thereby, the amount of time GCWA and TOWA spent foraging in flocks, especially in the more disturbed landscape. Larger groups, on the other hand, may affect prey harvest rates if interspecific competition is higher between phylogenetically related flocking species. The opposite may be expected in non-territorial systems, or systems with less competition such as in Moxviquil, where flocks where smaller and sex-age ratios were more even.

Overall, the availability of social information influenced the occurrence of conspecifics and heterospecifics among the two warbler species targeted in this research. However, traits associated with dominance mediated the use of available information and habitat choices in terms of settlement and numerical responses among GCWA and TOWA. Site preemption may limit settlement into territories for the golden-cheeked warbler, where the best territories (e.g., where flocks occur, or survival is higher) are selected first and then defended. Selecting non-breeding habitats with higher density of competitors such as adult males, should thus outweigh the benefits of aggregation (Rodenhouse et al. 1997). On the other hand, TOWA, Townsend's warbler, habitat preference was influenced more by information-mediated settlement, but this species was not aggressive as GCWA in both study landscapes. Being an opportunistic species may explain why it does not rely on site preemption. Its response to congeners, in terms of implications to conservation of GCWA, suggests that without knowledge of densities of competitors across available habitats, we will erroneously inform managers on strategies for conservation. As interspecific interactions influence habitat use, is thus important to assess quantitative thresholds on abundances of direct and putative competitors as the variation in their densities across sites of varying quality would differentially influence habitat use in the focal species.

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