Consequences of habitat selection by two species of *Thryothorus* wren in a coffee agroforestry landscape

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Abstract of the Dissertation

Consequences of habitat selection by two species of *Thryothorus* wren in a coffee agroforestry landscape

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Alternative habitats for birds are areas modified by human activities that replace natural ecosystems, but provide the resources and conditions necessary for survival and reproduction. Empirical support that shade coffee is an alternative habitat comes mainly from occupancy patterns, but few studies have examined habitat selection and its consequences in shade coffee agroecosystems. The goal of the research presented here was to evaluate the consequences of habitat selection by the rufous-and-white wren, *Thryothorus rufalbus*, and the plain wren, *Thryothorus modestus,* on reproduction in a coffee agroforestry landscape in Nicaragua. The first section of this study used compositional analysis to evaluate habitat selection at two scales, the territory and the nest, and found that *T. rufalbus* exhibits strong selection of shade coffee at both scales, while *T. modestus* selects modified forest at the scale of the territory, but shows little habitat selection preferences at the scale of the nest. The second section of this study studied the reproductive consequences of that habitat selection, and found that productivity was extremely low in shade coffee for *T. rufalbus,* while habitat selection had little effect on productivity in *T. modestus*. The final section of this study examined how host specificity of *T. naevia excellens* for *T. rufalbus* may explain differences in the productivity of the study species. Shade coffee may provide alternative habitat for some, but not all, species with high abundances in this agroforestry crop. The conservation implications of these findings are discussed.

Dedication

This dissertation is dedicated to my family and friends who have always supported me. My mother, who encouraged me, my stepfather, who always cheered me on, my sisters who inspired me, and my father who nurtured my interests. To my friends, who have been a foundation of strength and patience, and to Gonzalo, whose positive attitude and love get me through each day. This dissertation was made possible by my primary advisors, Charles Janson who let me choose my own path, and Catherine Graham, who guided me through to the finish. Special thanks to the people of Miraflor, who welcomed me into their communities. Finally, this body of work was in large part due to my incredible field assistants, who amazed me every day with their inventiveness, tenacity, and hard work.

In memory of my father, Dennis Randall Mark.

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Chapter 1. Introduction

The destruction of habitat, and the associated fragmentation and degradation of landscapes, are major threats to avian biodiversity in Mesoamerica, where over 80% of the region’s original forest cover has been cleared or strongly modified (BirdLife InternationalMittermeier, Bowles et al. 1998; Brooks, Mittermeier et al. 2006; 2009). Mesoamerica is a biodiversity hotspot, home to 1,120 species of birds, and a crucial overwintering and stop-over area for migratory birds (Mittermeier, da Fonsec et al. 2003). Biodiversity hotspots are defined as areas with high species richness and endemism that have lost at least 70% of the original habitat (Myers 2003). Conservation action to mitigate the impacts of habitat loss on avian species richness in Mesoamerica has the potential to positively benefit other species living in the region.

Deforestation has been so extensive in the Mesoamerican region that it is virtually impossible for the remaining areas to serve as habitat for all forest bird species. The small amount of remaining forest has compelled biologists to examine the conservation value of countryside landscapes (Hughes, Daily et al. 2002; Luck and Daily 2003). In recent years, ecologists have focused much research on the potential of shade crop agriculture to protect biodiversity in rural Mesoamerican landscapes (Moguel and Toledo 1999; Petit and Petit 2003; Greenberg, Perfecto et al. 2008; Perfecto and Vandermeer 2008). Shade coffee, in particular, has been the subject of much research, because of organic and bird friendly certification criteria that increase both biodiversity and profitability (Gordon, Manson et al. 2007; Philpott, Bichier et al. 2007). The conversion of forest to shade coffee results in the loss of forest specialist species, but the new habitat supports high numbers of generalist species and Neotropical migrants (Tejeda-Cruz and Sutherland 2004; Harvey and Villalobos 2007; Tscharntke, Sekercioglu et al. 2008). Bird species richness is highest in shade coffee plantations adjacent to forest and managed as rustic or shaded monoculture coffee. Generally, rustic and shaded monoculture coffees are characterized by high structural complexity of the understory and high levels of canopy cover (Perfecto 2007).

Shade coffee is promoted as an alternative habitat for birds, but empirical support for this comes mainly from occupancy patterns. Few studies have critically examined whether shade coffee is a high quality habitat that benefits species, as is presumed (Lindell and Smith 2003; Cohen and Lindell 2004; Gleffe, Collazo et al. 2006; Pangau-Adam, Waltert et al. 2006; Cruz-Angon, Sillett et al. 2008). Coffee agroforesty ecosystems, although human modified environments, can be evaluated as high or low quality habitat using the general principles and theories of ecology. One of the most frequently studied phenomena in ecology is habitat selection, or the disproportionate use of resources by living organisms. Habitat selection is the ability to distinguish and select among habitats of varying quality, which results in non-random distribution of individuals in the landscape (Holt 1985). Habitat selection evolves when individuals experience variation in fitness among habitats, and individuals prefer high quality habitats that confer the highest fitness (Fretwell and Lucas 1970; Jaenike and Holt 1991). Individuals cannot directly evaluate expected fitness when selecting a habitat, and so the quality is often assessed using environmental cues that correlate to high fitness (Stamps and Krishnan 2005).

The evidence that rustic and shaded monoculture coffee serves as high quality alternative habitat for generalist forest bird species is based almost exclusively on studies of density (Komar 2006). The use of density as an indicator of habitat quality has long been criticized by ecologists since many scenarios can result in high density but low quality areas (Van Horne 1983). One such scenario, which has been the focus of much attention in modified landscapes, is known as the ecological trap, whereby the cues indicating habitat quality become dissociated from their fitness benefits (Schlaepfer 2003). It is therefore surprising that shade coffee has been almost universally embraced for its contribution to the preservation of avian diversity as there have been few critical studies on the survival, fitness, or productivity of birds in coffee (Komar 2006). It is unclear if this shade crop can contribute to the long term preservation of biodiversity in agroforestry landscapes.

I used habitat choice theory to examine the attractiveness and quality of shade coffee for two species of understory birds, *Thryothorus modestus* and *Thryothorus rufalbus* to determine if coffee agroecosystems can serve as alternative habitats. The first component of this study evaluates the environmental cues used to select habitat at two scales. As mentioned, habitat selection is a scale sensitive process, and the fitness costs and benefits of selection change with scale (Mayor, Schneider et al. 2009). The study species are territorial, and habitat selection should take place at two levels, the territory and the nest. These two scales differ in their population limiting factors, and habitat selection must optimize fitness among a series of scale-dependent choices (Rettie and Messier 2000). The interaction of habitat selection at different scales may have special consequences for species living in modified landscapes where the cues that indicate quality may be uncoupled from fitness at one scale but not another. The focus of this study was individual selection, and not population level dynamics. As such, this study does not address source-sink dynamics in the landscape, but rather the consequences of habitat selection.

The second component of this study quantifies the consequence of habitat selection on reproductive success. Habitat selection is adaptive if it results in increased fitness. Variation in avian fitness across habitats is typically approximated through measurements of reproductive success (Misenhelter and Rotenberry 2000; Arlt and Part 2007; Chalfoun and Martin 2007). If selection of a certain habitat is adaptive, then individuals that choose to set up territories or place nest sites in these habitats should show higher productivity; but if preference is maladaptive, then productivity will be low (Kristan 2003). Maladaptive habitat choice results in ecological traps, which differ from population sinks in that individuals will prefer low quality habitat even when high quality habitat is available. Ecological traps can result when individuals exhibit a preference for one habitat over another, and a surrogate measure of individual fitness (reproductive success) is equal to or lower than that of individuals in other habitats (Battin 2004). This study examined the impact of habitat selection at two different scales on reproductive success. For shade coffee to be considered a high quality alternative habitat, and not an ecological trap, individuals should experience the same or higher reproductive success as in the original habitat (Pulliam 1988; Pulliam and Danielson 1991).

Finally, this study examined behavioral dynamics between *Thryothorus rufalbus* and the brood parasite that is a threat to reproductive success in shade coffee. The striped cuckoo subspecies found at the study site, *T. naevia excellens,* had a strong negative impact on reproductive success in *T. rufalbus,* but never parasitized *T. modestus*. The rate of parasitism experienced by *T. rufalbus* was influenced by habitat choice made at the scale of the territory, but this did not account for parasitism of one species and not the other. *T. naevia* is divided into three subspecies that utilize at least 20 known host species, including both *T. rufalbus* and *T. modestus*, yet the population consequences of parasitism for hosts are unknown (Payne 2005). Brood parasitism has been shown to decrease reproductive success in birds living in human modified temperate landscapes (Lloyd, Martin et al. 2005; Tewksbury, Garner et al. 2006). However, brood parasitism by New World cuckoos has been virtually unstudied in modified landscapes, despite the fact that *T. naevia,* had expanded its range concomitant with deforestation. The final section of this study focused on host specificity in *T. n. excellens* at the study site, and host defense strategies in *T. rufalbus.*

This study represents one of the first attempts to gain a detailed understanding of the consequences of habitat selection in shade coffee agroecosystems at multiple scales. The results for the study species suggest that shade coffee may be an ecological trap for *T. rufalbus*, but not *T. modestus* and that characteristics of shade coffee that benefit certain species may be detrimental to others. While *T. modestus* experienced lower productivity in shade coffee, it was not significantly lower than other habitat types, and shade coffee may provide a good alternative habitat for *T. modestus*. The conservation utility of shade coffee agroecosystems must be assessed on a species specific basis, and high abundances of birds in coffee cannot be taken as a proxy for habitat quality.

Chapter 2. The effect of scale on avian habitat selection in a coffee agroecosystems

ABSTRACT

Birds are thought to use shade coffee as an alternative habitat, but few studies have examined the habitat choices that result in bird use of coffee in agroforestry landscapes. I used the framework of habitat choice models for two species of understory birds to evaluate if shade coffee is chosen as an alternative habitat by *Thryothorus rufalbus* and *Thryothorus modestus*. Specifically, I examined how scale influences habitat selection in a coffee agroecosystem. *T. rufalbus* selected shade coffee for territory location as well as nest placement, but nest site selection is mediated by attraction to vegetation variables most common in coffee. *T. modestus* selected modified forest over shade coffee for inclusion in the territory, but the vegetation variables preferred for nests sites are found in most available habitats, and so this species places its nest in most habitats. Habitat choice studies in coffee agroecosystems need to explicitly evaluate the scale at which individual decisions are made, since scale can affect the outcome of individual based models and the conservation recommendations drawn from them.

2.1 INTRODUCTION

A habitat is an area that a species occupies because it contains all the resources and conditions necessary for survival and reproduction (Hall, Krausman et al. 1997). Alternative habitats are areas modified by human activities that replace natural habitats, yet serve the same function (Railsback and Harvey 2002). Shade coffee is one such alternative habitat for birds, and species richness can be as high or higher in shade coffee as in native forests (Philpott, Arendt et al. 2008; Sanchez-Clavijo, Arbelaez-Alvarado et al. 2008). Development and conservation organizations promote the establishment of shade coffee because it both preserves biodiversity and secures a livelihood for impoverished farmers (Petit and Petit 2003; Philpott and Dietsch 2003; Philpott, Bichier et al. 2007; Greenberg, Perfecto et al. 2008). Empirical support that shade coffee is an alternative habitat for resident Neotropical birds comes mainly from occupancy patterns, but few studies have examined the habitat choices that result in bird use of coffee in agroforestry landscapes (Petit, Petit et al. 1999; Jones 2001; Petit and Petit 2003; Rappole, King et al. 2003; Tejeda-Cruz and Sutherland 2004) but see (Lindell and Smith 2003; Lindell, Chomentowski et al. 2004; Cruz-Angon, Sillett et al. 2008).

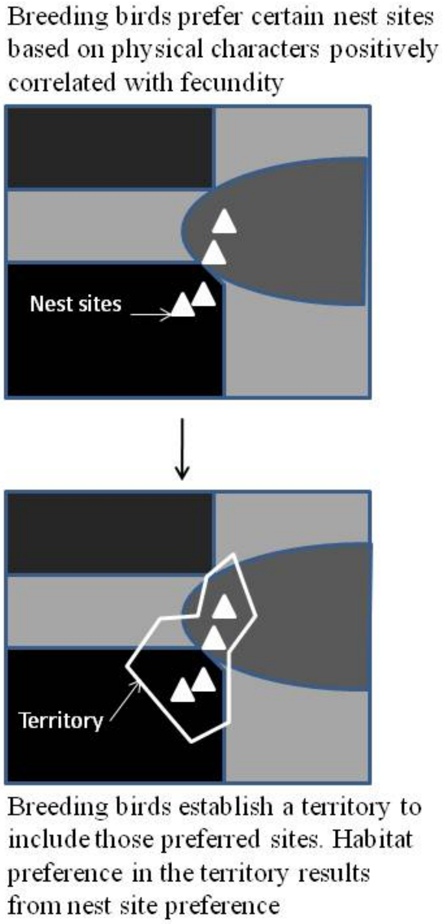
Studies on habitat choice in unaltered landscapes are usually conducted within the framework of optimal habitat choice models. These models assume that organisms actively select the highest quality areas available, and high quality habitats confer high expected fitness (Fretwell and Lucas 1970; Pulliam 1988; Pulliam and Danielson 1991). Individuals cannot directly evaluate expected fitness when selecting a habitat, and so quality is often assessed using environmental cues that correlate to high fitness

(Schlaepfer, Runge et al. 2002). However, in coffee agroecosystems, the attractiveness of a habitat can become decoupled from its quality, leading to an ecological trap (Kristan 2003). For shade coffee to aid in the preservation of avian biodiversity, it must be an attractive breeding habitat and must confer high fitness.

The goal of this study was to examine the first requirement, that shade coffee is a preferred habitat for territory establishment and nesting of breeding birds. Habitat choice can result from selection for cues at different scales, and species can vary in their scale of selection (Pearman 2002; Chalfoun and Martin 2007; Wheatley and Johnson 2009). Resident birds breeding in coffee agroecosystems make habitat selection decisions at two scales: the habitat composition of the territory, and the placement of the nest. Unlike temperate birds, territories are defended throughout the year, and selection different scales can interact to produce occupancy patterns (Wheatley and Johnson 2009). For example, selection of suitable nest site could determine the habitat composition and location of the territory (Fig. 1a), or habitat selection at the scale of the territory could limit the number and location of nest sites (Fig. 1b). These habitat choices in turn affect occupancy patterns, which are commonly used to promote shade coffee as alternative habitat.

In order to assess the influence of scale on habitat selection and occupancy patterns, I asked the following questions: (1) Do territorial birds select certain habitats over others at the scale of the territory in a coffee agroecosystem landscape? (2) Do breeding birds select certain habitats for nest sites within the territory? (3) Do vegetation variables in the habitats influence nest site selection? (4) Does habitat selection by breeding birds at one scale influence the choice made at another scale? I asked these questions on two species of Neotropical wren, *Thryothorus rufalbus* and *Thryothrus modestus*. Both species are territorial insectivorous birds frequently found in shade coffee and native forest. *T. rufalbus* is most often found in the interior of coffee plantations and woods, while *T. modestus* is an edge specialist. These species also vary in both nest structure and placement in the canopy. The varied habitat use patterns of the two species in coffee suggest that they use different physical cues to assess habitat quality, and I predict that the species will differ in territory and nest site selection.

a)



b)

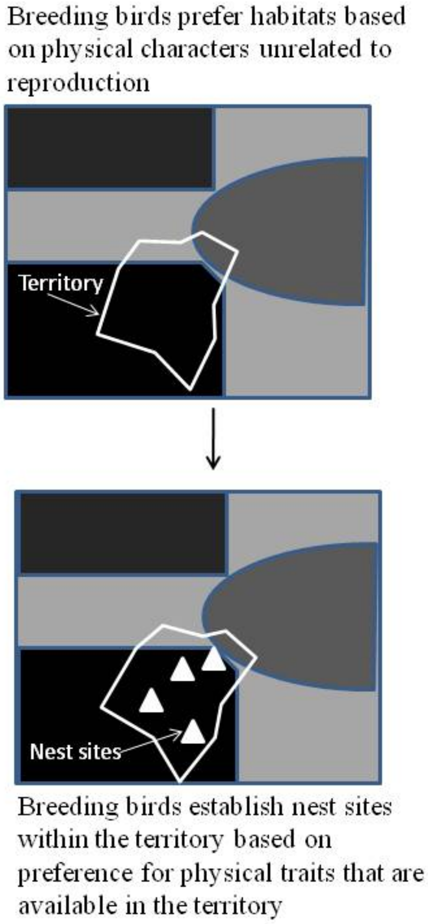


Figure 1a. Nest site selection can drive territory establishment. Shades of gray represent different types of habitat available to a bird in a hypothetical landscape.

Figure 1b. Habitat selection at the scale of the territory can drive nest site placement. Shades of gray represent different types of habitat available to a bird in a hypothetical landscape.

I examined the first question by using compositional analysis to evaluate if certain habitats are selected disproportionately to what was available in the study site. The second question I examined by using compositional analysis to determine if nest sites were selected disproportionately to what was available in the study site. I addressed the third question through a comparison of vegetation variables measured at the nest and those same variables sampled from random transects in the different habitats. I addressed the final question by dividing the territories according to nest site and comparing the habitat composition of these territories.

2.2 STUDY SITE AND SPECIES

This study took place in Reserva Miraflor (UTM WGS 84 1467524N 165751289E) in the Pacific Slope of Nicaragua, at an altitude of 1100-1280m (Fig. 2). The reserve is a mixture of semi-deciduous montane forest fragments and shade coffee plantations interspersed with pasture and agricultural areas. Conservation regulations in the reserve area limit the cutting of trees and restrict timber harvesting in watersheds.

Thryothorus rufalbus and *Thryothorus modestus* are foliage gleaning insectivores that utilize different heights in the understory, reducing interspecific competition (M. Mark, pers. obsv.) At the study site, both *T. rufalbus* and *T. modestus* are common, although habitat use differs between the species. *T. modestus* is an edge species, and prefers dense scrub along the borders of forest or shade coffee and open areas, while *T. rufalbus* nest most commonly along streams, in secondary forest, and in shade coffee plantations. *T. rufalbus* constructs closed retort-shaped nests at 1.5-15m from the ground, while *T. modestus* constructs domed nests less than 1m from the ground. Both species exhibit pair defense of the territory year round (Stiles and Skutch 1989).

2.3 METHODS

2.3.1 Habitat Classification

The study site is 584 ha in size and is composed of a mosaic of 0.5-5 ha plots subject to different levels of human modification. Because the goal of this study was to evaluate shade coffee as a habitat, I classified the study site into five categories of land-use. These categories will be considered as potential habitats and referred to as such. The category of fields includes both fallow and actively farmed plots of corn and beans. The shade coffee category is organic and cultivated in a rustic manner where the upper forest canopy is left intact, with some trees selectively removed, while the understory is cleared and planted with rows of coffee that vary between 0.5-2.5m in height. In shade coffee plots, farmers will often plant agriculturally valuable trees in order to increase shade cover and provide fruit and wood. The modified forest category is forest that has been subject to low levels of selective logging and firewood collection. The category of intact forest is composed of forest areas that have been protected by individual landowners from logging and firewood collection. I assigned the category secondary forest to all forest re-growth on previously cleared land.

I created a raster based map of habitat categories from a supervised classification of ASTER satellite images (United States Geological Survey Global Visualization Viewer, http://glovis.usgs.gov/). I performed the classification on ENVI 4.7 (Research Systems, Inc) using information from ground truthing and maps of agricultural areas to inform the classification (Fig. 3a). I used ArcView 9.3 (ESRI) to calculate the percent area of each habitat in the study site. Because *T. rufalbus* exhibits an affinity for water, I mapped all natural and artificial water sources onto the classified raster image. I scored territories for presence or absence of water sources and compared the number of territories with water between species using Student's t-test.

2.3.2 Habitat selection in the territory

In 2006 and 2007 I mapped the territories of 109 pairs of *T. rufalbus* and 53 pairs of *T. modestus* following the procedure developed by the British Trust for Ornithology (BTO), but with reduced census effort because all territorial birds were banded (Bibby, Burgess et al. 2000). Territory mapping resulted in clusters of points where territorial, nesting, and foraging behaviors were recorded. I used these clusters as vertex points to draw minimum convex polygons representing the territory. A polygon represents the core area of the territory and does not overlap with neighbors. I used Arc View 9.3 (ESRI) to calculate the area of each habitat type in the territory polygons. I used compositional analysis to compare the proportion of habitat in a territory to the habitat available in the study site. Compositional analysis quantifies proportional habitat use accounting for non-independence of the proportions of habitat used and available (Aebischer, Robertson et al. 1993). In compositional analysis, habitat use and habitat availability were converted to log ratios. Pair-wise differences between matching log ratios were calculated to create habitat ranking (ln (Ui/Uj) – ln(Ai/Aj), where *i* and *j* are two habitat types, and U is the percent proportion of a habitat within a territory, and A is the proportion of that habitat in the study site). The available habitat was determined by the borders of the study area. Although this may not be an accurate representation of the available habitat as perceived by the birds, individuals were documented throughout the extent of the study area, and the identification of the entire study site as potential habitat and was consistent with observations and historical information on habitat use in this species as well as with other studies of habitat selection (Garshelis 2000; Fernandez-Juricic 2001; Graham 2001; Morris 2003; Johnson 2007). To determine if the habitat ranking differed from random, I conducted permutation tests using SAS 9.1 (SAS Institute, North Carolina)(Aebischer, Robertson et al. 1993). Habitat composition of the territory and habitat rankings were compared between species.

2.3.3 Nest site selection

Nest site habitat

In order to rank habitat preference for nest sites, I conducted a compositional analysis on nest site locations for each species. In this case, rather than area, I created log ratios from the number of nests in a particular habitat and the total number of nests in the study site. Again, the significance of the ranking was assessed by conducting permutation tests on SAS 9.1 (SAS Institute, North Carolina).

Vegetation at the nest site

Vegetation characters around a nest can have a high impact on fecundity in birds, and so are likely to be used as physical cues to evaluate habitat quality (Lima 2009). In order to determine if birds exhibited preference for certain vegetation characteristics at the nest, I compared vegetation quantified around the nest to vegetation quantified from 50m vegetation transects placed in each habitat type. Transects were placed randomly within the field site, therefore the number of transects in each habitat reflected the total proportion that habitat contributed to the landscape. I established 10m-diameter circles along the transects, and 10m circles around nest sites, within which I sampled the vegetation according to the protocol for the Breeding Bird Survey (BBS) for Biology Research and Monitoring Database for North American birds (Martin 1997). BBS protocol measures vegetation characteristics that influence nest success, and preference for these physical cues may influence the choice of nest habitat.

The percent coverage of different vegetation types in the lower understory, including green vegetation, live stems, vines and lianas, dead leaves, dead stems, and ferns, were estimated by sight in four quadrants within the circle, up to a height of 1m. Values for the quadrant were averaged to obtain a rating for the entire sampling plot. To evaluate structural complexity of the upper understory, percent coverage of woody stems between 1 and 3m was estimated using a concave densiometer. Densiometer readings were taken from 8 points within the sampling plot and averaged. The average canopy cover above 3m was measured using a concave densitometer at 4 points within the sampling plot. The number of trees and their family was recorded for each plot. I also measured leaf litter density on the floor by taking the average of 12 points where leaf litter density was sampled with a pin.

Similarity of nest site and transect vegetation

To compare the nest vegetation variables selected by the two *Thryothorus* species, I created a multidimensional scaling (MDS) plot of based on a similarity matrix of variables measured at the nests of *T. rufalbus* and *T. modestus* in all habitat types. I used ANOVE to determine if there were differences in mean vegetation values measured around the nest. For within each species, I compared vegetation variables measured at the nest and vegetation variables measured on transects for each habitat type to assess if birds used a nonrandom set of vegetation variables within a habitat. I created a multidimensional scaling (MDS) plot of based on a similarity matrix of variables measured at the nest and the variables measured on transects in each habitat. The correlation of each of the variables to the values that determined the first two scalar dimensions indicates which variables most influenced the distribution of the sampling points, and are presented with the plots. I also performed a stepwise discriminate function analysis of the correlation matrix the variables measured at the nest and on the transect for each habitat type, to determine which vegetation variables contributed the most to the separation between these groups of sampling points. In this procedure, variables are added to discriminate functions until the addition of further variables does not improve discrimination. MDS procedures were performed on Primer 6.7.1 (Primer-E). All other statistical analyses were performed on SPSS 17.0 (IBM).

2.4 RESULTS

2.4.1 Question 1: Habitat selection at the scale of the territory

I evaluated if the study species exhibit preference at the scale of the territory. First, I examined the relative proportions of the habitat types in the territories and the study site. I then performed compositional analysis and ranked habitats according to preference.

The study site was composed of approximately 26% fields, 29% modified forest, 22 % shade coffee, 17% secondary forest and 6% intact forest (Fig. 4). The average territory size of *T. rufalbus* territories was 4321m2 (n=103, SD=1963, CI 95%=379.3). *T. rufalbus* used no pasture in their territories and showed a strong negative correlation between the proportion of coffee and the proportion of modified forest in the territory (Pearson's correlation coefficient, r=-0.82). *T. rufalbus* territories where water was present had a higher proportion of modified forest than any other habitat type, and a lower proportion of secondary forest (ANOVA, p=.028, p=0.012). Seventy one percent of *T. rufalbus* territories included water.

The average size of *T. modestus* territories was 2808 square meters, (n=53, SD=1684, CI 95%=453.6) and territory size significantly differed between the two species (Student's t-test, p<0.05). The territories of *T. modestus* showed no strong correlations between the proportions of any habitats. *T. modestus* used less shade coffee and more secondary forest in their territories than *T. rufalbus* (p<.0001, p<.0001). Both species utilized similar proportions of modified and intact forest (p=0.08, p=0.64), and *T.*

modestus used less field habitat than what was available in the study site (Fig. 4). *T. modestus* was significantly less likely to include water on their territories than *T. rufalbus* and only 34% of *T. modestus* had water present on the territory (Chi-square, p<0.0001).

From the compositional analysis, I ranked the proportion of habitat in all *T. rufalbus* territories to the proportion available in the study site and found that habitat use was ranked as follows: shade coffee > modified forest > intact forest > secondary growth > fields (Tbl. 1a). The proportion of habitats within the territory compared to the proportion of habitats available in the landscape differed significantly from random for all habitats (Tbl. 1b). *T. rufalbus* exhibited disproportionately high use of shade coffee, modified forest, and intact forest while avoiding secondary forest and fields (Fig. 4).

For *T. modestus,* the rank proportions of habitat in all territories to the proportion available were: modified forest > shade coffee > intact forest > secondary growth > fields (Tbl. 2a). *T. modestus* was more likely to include modified forest in the territory over secondary forest and fields, and also more likely to include shade coffee at the expense of fields, secondary forest, and intact forest (Tbl. 2b). Intact forest was avoided by *T. modestus* (Tbl.2b).

2.4.2 Question 2: Habitat selection at the scale of the nest

T. rufalbus was more likely to place its nests in shade coffee, and did not lay nests in fields or secondary forest (Fig. 5a). *T. modestus* placed slightly more nests in shade coffee and modified forest than any other habitat type, and did not lay nests in intact forest (Fig 5b). Compositional analysis produced nest site preference rankings for both species. Nest site preference rank for *T. rufalbus* was shade coffee > modified forest > intact forest > secondary growth > fields. *T. rufalbus* was significantly more likely to place nests in shade coffee than any other habitat type (p=0.01). *T. rufalbus* were more likely to place their nests in modified forest than intact forest (p=0.02). *T. rufalbus* did not place nests in secondary forest or fields. Nest site preference rank for *T. modestus* was shade coffee > modified forest > field > secondary forest > intact forest, but none of these relationships were significant.

2.4.3 Question 3: Selection for nest site variables

Habitat selection at the scale of the territory or the nest site could be the result of preference for physical cues characteristic of a habitat. Around the nest, *T. rufalbus* maintained higher than average canopy cover and lower than average percent cover of green vegetation and dead stems in all habitats, while *T. modestus* maintained higher than average green vegetation in all habitats (Fig. 6, Fig. 7). *T. rufalbus* maintained higher than average percent cover of dead leaves around the nest in intact forest only, and both species selected higher percent cover of vines and ferns around the nest that what was average for the habitat (Fig. 6, Fig. 7). The correlation table of variables and the MDS scalar axes indicate that percent cover green vegetation, percent cover dead leaves, and canopy cover, contributed the most to the separation of nests of the two species into two groups (Fig.10). One way analysis of variance (ANOVA) on these variables shows *T. rufalbus* nests had a higher canopy cover and lower percent coverage of green vegetation than nests of *T. modestus* (p=0.001, p=0.017). Both *T. modestus* and *T. rufalbus* maintained higher than average percent cover of vines and ferns in all habitat types (Table 5). When plotted with transect data for habitats, *T. modestus* nests showed greater dispersion for variable values across all habitats that *T. rufalbus* indicating *T. rufalbus* used a more specific subset of variables for nesting sites than *T. modestus* (Fig. 11).

MDS plots for individual habitats show that *T. rufalbus* nests in modified forest and intact forest had vegetation characteristics that differed from what was typical for those habitats, most obviously for modified forest (Fig. 9). Stepwise discriminate analysis (DA) of vegetation samples from both nests and transects in shade coffee resulted in 3 main variables, canopy cover, percent cover dead stems, and percent cover vines, loaded onto one function that explained 92% of the variance between nests and transects (Fig. 12a). Seventy-eight percent of the variation between nest and transect sites in intact forest was explained by percent cover dead leaves and canopy cover loaded onto two functions (Fig. 12c). In modified forest, 56% of the variation between transect and nest samples was attributable to canopy cover, percent cover of dead leaves, percent cover of dead stems loaded onto one function (Fig. 12b). *T. rufalbus* maintained high canopy cover, high percent cover of dead leaves, and low levels of percent cover of green vegetation and dead stems in all habitat types (Table 5). In contrast, the nests of *T. modestus* were mostly typical of the vegetation in the habitat, according to the MDS plots and associated correlations as measured by the transect (Fig. 11). Discriminate function analysis of vegetation samples from nests of *T. modestus* and transects in modified forest show that 82% of the variation was explained by canopy cover (Fig. 13b). Sixty-eight percent of the variation between nest sites and transects in shade coffee was attributable to percent cover of dead stems, percent cover of dead leaves, and canopy cover (Fig. 13a). Eighty percent of the variation between nest sites and transects in secondary forest was attributable to percent cover green vegetation, percent cover vines, and percent cover ferns loaded onto two functions (Fig. 13c). In field habitat, 79% of the variation between the nests and the transects was attributable to canopy cover, percent cover vines and percent cover ferns (Fig. 13d).

2.4.4 Question 4: Interaction of habitat choice made at different scales

Habitat selection at broader scales may constrain selection at lower scales. To assess if habitat choice at the scale of the territory influenced nest site selection, I used an ANOVA to compare habitat composition between territories with different nest site habitats. For *T. rufalbus,* pairs that placed nest sites in intact forest exhibited a rank habitat preference in their territory of modified forest > intact forest > shade coffee > secondary forest/field (Fig. 8). Compared to territories with shade coffee nests or nests in modified forest, these territories had a significantly higher proportion of modified forest, resulting in a lower proportion of shade coffee and secondary forest (shade coffee: p=0.003, p=0.001; modified forest: p=0.0001, p=0.038; Tbl. 3). Territories with nests in modified forests had habitat proportion ranking of modified forest > shade coffee >intact forest > secondary forest/field (Fig. 8). Territories with nests in shade coffee habitat had a habitat proportion ranking of shade coffee > modified forest > intact forest > secondary forest/field (Fig. 8). Territories with nests in shade coffee had a significantly higher proportion of shade coffee than territories with nests in modified forest, resulting in a significantly lower proportion of modified forest, intact forest, and secondary forest (p=0.004, p=0.007, p=0.0001; Tbl. 3).

Selection for habitat composition of the territory influenced nest site selection in *T. modestu* as well, albeit not as strongly (Fig. 9). For territories with nests in field, the proportion of habitat compared to the proportion available was ranked: field > secondary forest > modified forest > intact forest > shade coffee (Fig. 9). Compared to territories with nests in modified forest, these territories incorporated a significantly higher proportion of field and secondary forest at the expense of modified forest and shade coffee (field: p = 0.003, p = 0.002; secondary forest: p = 0.01, p=0.014; Tbl. 4). Compared to territories with nests in secondary forest, territories with nests in field had reduced proportion of modified forest, concomitant with an increase in field and secondary forest (p=0.004, p=0.003; Tbl. 4). Compared to territories with nests in shade coffee, territories with nests in field also reduced coffee proportion in favor of modified forest, intact forest, and reduced these habitats in favor of field and secondary forest (p=0.007, p=0.0001, p=0.0001, p=0.001, p=0.004; Tbl. 4). Territories with nests in shade coffee showed an increased proportion of shade coffee and areduced proportion of modified forest, secondary forest, and field compared to territories with nests in modified forest (p=0.011, p=0.017, p=0.004; Tbl. 4). Compared to territories with nests in secondary forest, territories with nests in shade coffee showed increased proportion of shade coffee, with a reduction in all other habitats (p=0.0001, p=0.0001, p=0.008, p=0.026; Tbl. 4).

2.5 DISCUSSION

Coffee agroecosystems can help to preserve biodiversity in areas where little natural forest remains (Perfecto and Vandermeer 2008). However, not all coffee agroecosystems contribute equally to the preservation of avian diversity. A recent study by Philpott et. al (2008) found that the diversity of understory birds decreased with intensification of shade coffee management. This indicates that certain physical characteristics affected by management influence the suitability of shade coffee as an alternative habitat. Occupancy of a potential habitat by breeding birds is the result of habitat selection at two different scales: the territory and the nest (Misenhelter and Rotenberry 2000). Little is known about how territorial Neotropical birds exhibit habitat choice in modified landscapes, however, scale has been shown to influence habitat choices of birds in modified rural landscapes in temperate areas (Chalfoun and Martin 2007). Habitat selection in coffee agroecosystems can influence the conservation value of shade coffee plots (Petit and Petit 2003; Komar 2006; Tscharntke, Sekercioglu et al. 2008). The goal of this study was to gain a better understanding of how scale affects habitat selection in coffee agroecosystems, and to identify some of the physical cues used by birds to identify suitable habitat. An understanding of how individual birds select their territories and nest sites within coffee agroecosystems is necessary if we are to maximize avian diversity through directed management of the physical cues influencing preference.

My first two questions aimed at evaluating if *T. rufalbus* and *T. modestus* exhibited habitat selection at the level of the territory or the level of the nest. *T. rufalbus* exhibited the strong preference for shade coffee and modified forest, with a strong aversion to fields (Table 1). *T. modestus* exhibited a strong preference for modified forest and a weaker preference for shade coffee (Table 2). These results demonstrate that both species display habitat preference at the level of the territory, but that preference is much stronger in *T. rufalbus*. Only *T. rufalbus* demonstrated strong disproportionate nest site selection for shade coffee, but the two species differed in the nest site habitats avoided (Fig. 5).

The study species exhibited habitat preference at the scale of the territory and the nest site, and the interaction of these scales was the subject of question four. Interestingly, the preference for physical cues (question three), mediated this interaction. *T. rufalbus* selected shade coffee over all other habitat types for inclusion in the territory, and the majority of *T. rufalbus* nests sites are also in shade coffee. When a territory has a high proportion of shade coffee the nests were placed in this habitat, and when a territory has a high proportion of forest, either modified or intact, nests are mostly placed in forest (Fig. 8). Detailed examination of physical cues at the nest site suggests that *T. rufalbus* preference for shade coffee is more complex than simply using the most available habitat in the territory. It appears that that the proportion of habitat types within the territory limits the number and location of suitable nesting sites for *T. rufalbus,* which are evaluated by the vegetation variables around the nest. In all habitat types, pairs attempt to maximizes preferred vegetation variables (Fig. 6).

T. rufalbus attempts to target preferred vegetation characteristics for nest sites regardless of habitat. Vegetation characteristics at the nest and on sampling transects for each of the three nesting habitats (intact forest, modified forest, shade coffee) indicates a tendency to maximize vine cover, dead leaves cover, and canopy cover, while minimizing the amount of understory cover due to green vegetation and dead stems at the nest (Table 5, Fig. 8). Preference for these variables can be explained by nesting and antipredator behavior in *T. rufalbus*. *T. rufalbus* use specific species of ferns as nesting materials and often place nests near or on vine tangles. At the study site, *T. rufalbus* does not generally avoid nest predators by hiding nests in dense foliage. Instead, nests are placed in plain view on trees with spines or near wasps' nests. Avoidance of dense understory may serve to limit contact with terrestrial predators, while a strong canopy cover may help to reduce avian predation. Given that these preferred variable values are common in coffee, territories with a high proportion of shade coffee may have more suitable nest sites in this habitat. This indicates that selection at the broader scale (territory) is driving selection at the smaller scale (nest). However, selection at the scale of the nest should not be overlooked, since strong affinity for nest site variables determines which nest site habitats are suitable.

In contrast to *T. rufalbus*, *T. modestus* exhibited significant preference for modified forest over intact forest, and a non-significant preference for modified forest over shade coffee. Despite exhibiting habitat preference for modified forest, *T. modestus* did not exhibit a strong preference for placing nests in one habitat more than any other (Fig. 5). No *T. modestus* nests were placed in intact forest, and it appears that while this habitat may be suitable for foraging and predator avoidance, it is unsuitable for reproduction. *T. modestus* exhibits weaker selection of habitats on all scales compared to *T. rufalbus*, and as such, the interaction between selection at the scale of the nest and selection at the scale of the territory is also weaker. *T. modestus* place their nests in the most common habitat type available in the territory, except for some pairs in territories with a large area of modified forest that placed nests in secondary forest (Fig. 9). This is most likely due to nests being placed in secondary growth areas bordering modified forest. The only vegetation variables for which *T. modestus* showed a strong affinity at nest sites was a high percent cover of green vegetation and a high percent cover of vines (Fig. 7). The emphasis on the latter variable may be explained by nesting behavior. *T. modestus* prefers to place nests in dense foliage and vine tangles, as they are generally lower to the ground and may experience high predation pressure (Lima 2009). Since nesting sites with a high percent cover of green vegetation could be found in almost any habitat, nest site selection by *T. modestus* was less constrained by selection at the level of the territory. Although not explicitly examined in this study, it is interesting to note that *T. modestus* maximized canopy cover in the only habitats (secondary forest and field) where nest sites did not overlap with *T. rufalbus*, indicating that interspecific competition may play a role in habitat choice (Table 5). Both study species chose nest sites based on the presence of certain physical cues. Some of these cues are the same for both species, such as the percent coverage of vies and ferns, as these are important nest building material for both species. Both species also maintained similar values for leaf litter, and both forage on the ground for important food items during the breeding season, such as Lepidoptera larvae. However, the values of vegetation variables that determine a good nesting site for *T. modestus* appear to be less restrictive and are found in a greater variety of habitats than those for *T. rufalbus.* Even closely related species in the same foraging guild and with similar reproductive strategies can vary in the strength of selection they exhibit in a modified landscape.

2.6 CONCLUSIONS

True alternative habitats that contribute to conservation will contain the resources and conditions necessary for survival and reproduction, with species exhibiting selection for these habitats. Individual selection exhibited at different scales can alter the effectiveness of shade coffee as an alternative habitat. For example, both study species preferred shade coffee for nesting habitat, yet favored different vegetation characteristics. Efforts to maximize avian diversity in shade coffee should focus on maintaining diverse microhabitats within areas of production. In this way, bird species that exhibit strong selection for nest site variables may find suitable nesting sites within shade coffee, even if researchers have not been able to identify what the preferred nest vegetation characteristics are. Other studies in shade coffee have shown that avian diversity is related to patch level variables such as epiphyte density, trees richness, canopy cover, and canopy height (Tejeda-Cruz and Sutherland 2004; Philpott, Arendt et al. 2008). Optimal habitat choice models can provide a good theoretical framework for understanding habitat selection in coffee agroecosystems (Cruz-Angon, Sillett et al. 2008). As shown in this study, the scale at which habitat selection occur can greatly affect the outcome of these models and conservation recommendations drawn from them. For the two study species, habitat composition of the territory and selection for vegetation variables at the nest site influenced nest site selection but the effect of a number of other factors, including food availability, competition, and landscape features on territory composition were not analyzed.

For one species, *T. rufalbus*, strong preference for physical cues typical of shade coffee resulted in strong selection for this habitat. Although not explicitly measured in this study, the preference for nest scale vegetation could be associated with the strong affinity *T. rufalbus* has for waterways. In the reserve, watershed management has left old stand trees around streams, and streams are often located in shade coffee, where understory vegetation is less dense. This affinity for water may reduce habitat availability in the landscape from the point of view of *T. rufalbus*; future studies on occupancy patterns and habitat use near waterways is recommended. *T. modestus* also prefers to place nests in shade coffee, but in areas with higher understory foliage, as is typical along the edges of coffee fields. Shade coffee is attractive to both species but each I prefers a different set of vegetation variables, which creates a management dilemma. For this and other species, management of shaded crops to benefit one species may reduce the attractiveness of the habitat to other species. Further study is necessary to determine if potential alternative habitats such as shade coffee are preferred because they are of high quality and confer higher fitness than other habitats in the landscape.

Figure 2. The location of Paisaje Terrestre Intervenida Miraflor-Moropotente on northwestern Pacific slope of Nicaragua

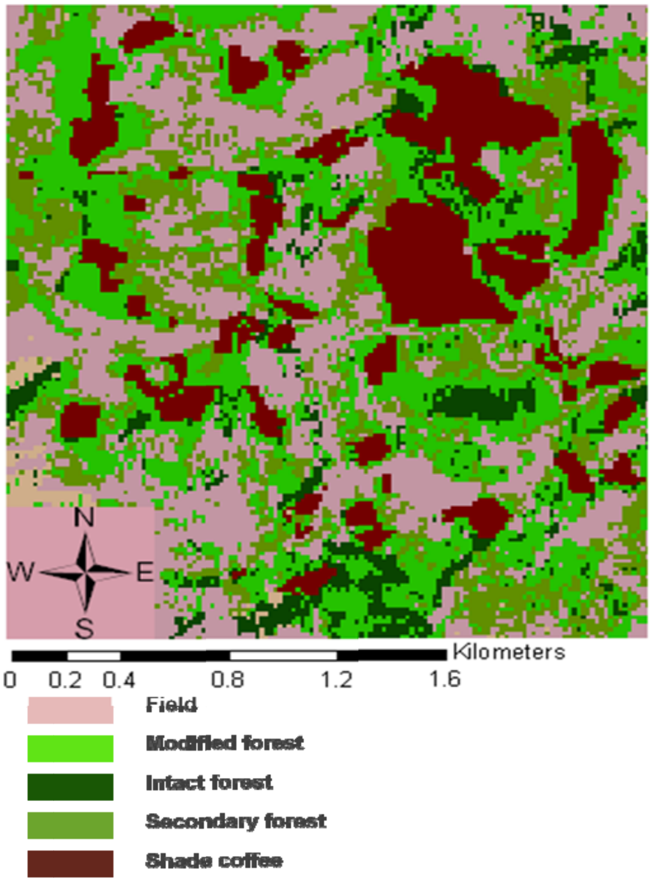


Figure 3a. The study site was classified into 5 habitat categories using ground-truthing, satellite images, and aerial photographs in ArcMap 9.2.

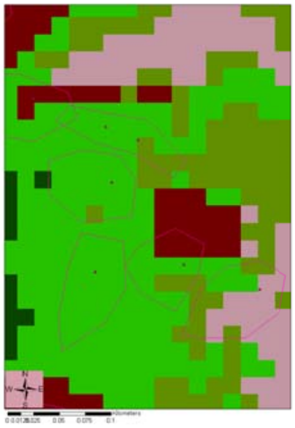


Figure 3b. The habitat composition of individual territory maps was calculated in ArcView 9.

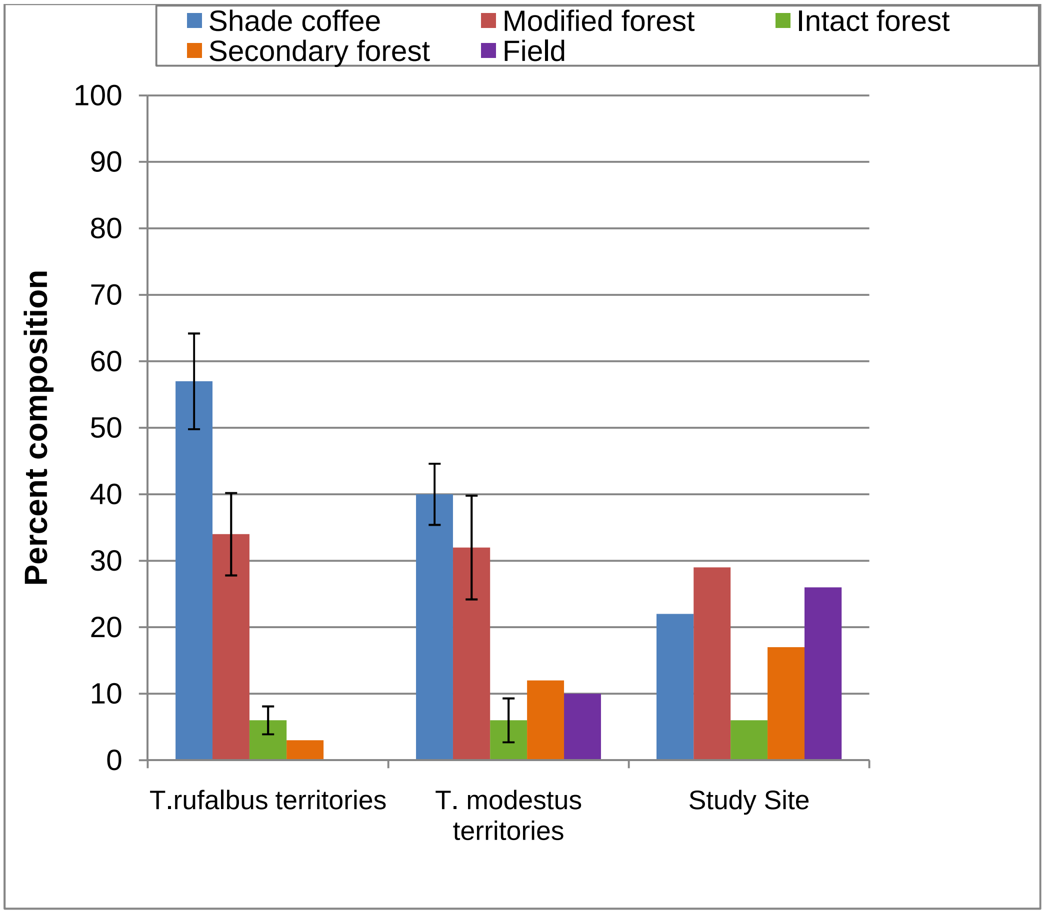


Figure 4. Percent composition of the 5 habitat types in the territories of *T. rufalbus*, *T. modestus*, and the study site.

	Shade Coffee	**Secondary forest**	**Intact Forest**	**Modified Forest**	**Fields**	Sum Rank
a) Rank means ± SE						
Shade coffee		4.45 ± 0.30	2.18 ± 0.40	1.29 ± 0.43	5.27 ± 0.24	13.19± 0.24
Secondary Forest	-4.45 ± 0.30		-2.27 ± 0.31	-3.16 ± 0.30	0.82 ± 0.15	-9.04 ± 0.26
Intact Forest	-2.18 ± 0.40	2.26 ± 0.31		-0.90 ± 0.28	3.09 ± 0.26	2.270± 0.31
Modified Forest	-1.29 ± 0.43	3.16 ± 0.30	0.90 ± 0.28		3.98 ± 0.29	6.75 + 0.32
Fields	-5.27 ± 0.24	-0.82 ± 0.15	-3.09 ± 0.26	-3.98 ± 0.29		-13.16± 0.24
b) Ranking matrices						
Shade coffee		+++	+++	+++	+++	
Secondary forest	---		---	---	+++	
Intact forest	---	+++		---	+++	
Modified forest	---	+++	+++		+++	
Fields	---	---	---	---		

Table 1. Habitat use patterns for all territories of *T. rufalbus:* (a) Ranking matrix of means and SE; (b) simplified ranking matrices of habitat preference. Each mean element in the matrix was replaced by its sign (+/-), and +++/--- denotes a significant deviation from random at P < 0.05 using a t-distribution.

	Shade coffee	**Secondary forest**	**Intact forest**	**Modified forest**	**Field**	**Sum Rank**
a) Rank means ± SE						
Shade coffee		1.37 + 0.59	0.91 + 0.511	-0.22 + 0.55	2.03 + 0.59	4.09 + 0.56
Secondary forest	-1.37 + 0.59		-0.46 + 0.54	-1.58 + 0.38	0.665 + 0.345	-2.74 + 0.47
Intact forest	-0.91 + 0.51	0.46 + 0.54		-1.21 + 0.42	1.125 + 0.502	-0.44 + 0.49
Modified forest	0.22 + 0.55	1.58 + 0.38	1.12 + 0.42		2.247 + 0.468	5.17 + 0.45
Field	-2.03 + 0.59	-0.67 + 0.35	-1.13 + 0.50	-2.25 + 0.47		-6.07 + 0.48
b) Ranking matrices						
Shade coffee		++	+	-	+++	
Secondary forest	--		-	---	+	
Intact forest	-	+		---	++	
Modified forest	+	+++	+++		+++	
Field	---	-	--	---		

Table 2. Habitat use patterns for all territories of *T. modestus*: (a) Ranking matrix of means and SE; (b) simplified ranking matrices of habitat preference. Each mean element in the matrix was replaced by its sign (+/-). A double sign denotes a significant deviation from random at 0.05>P>0.01, and +++/--- denotes a significant deviation from random at P < 0.01.

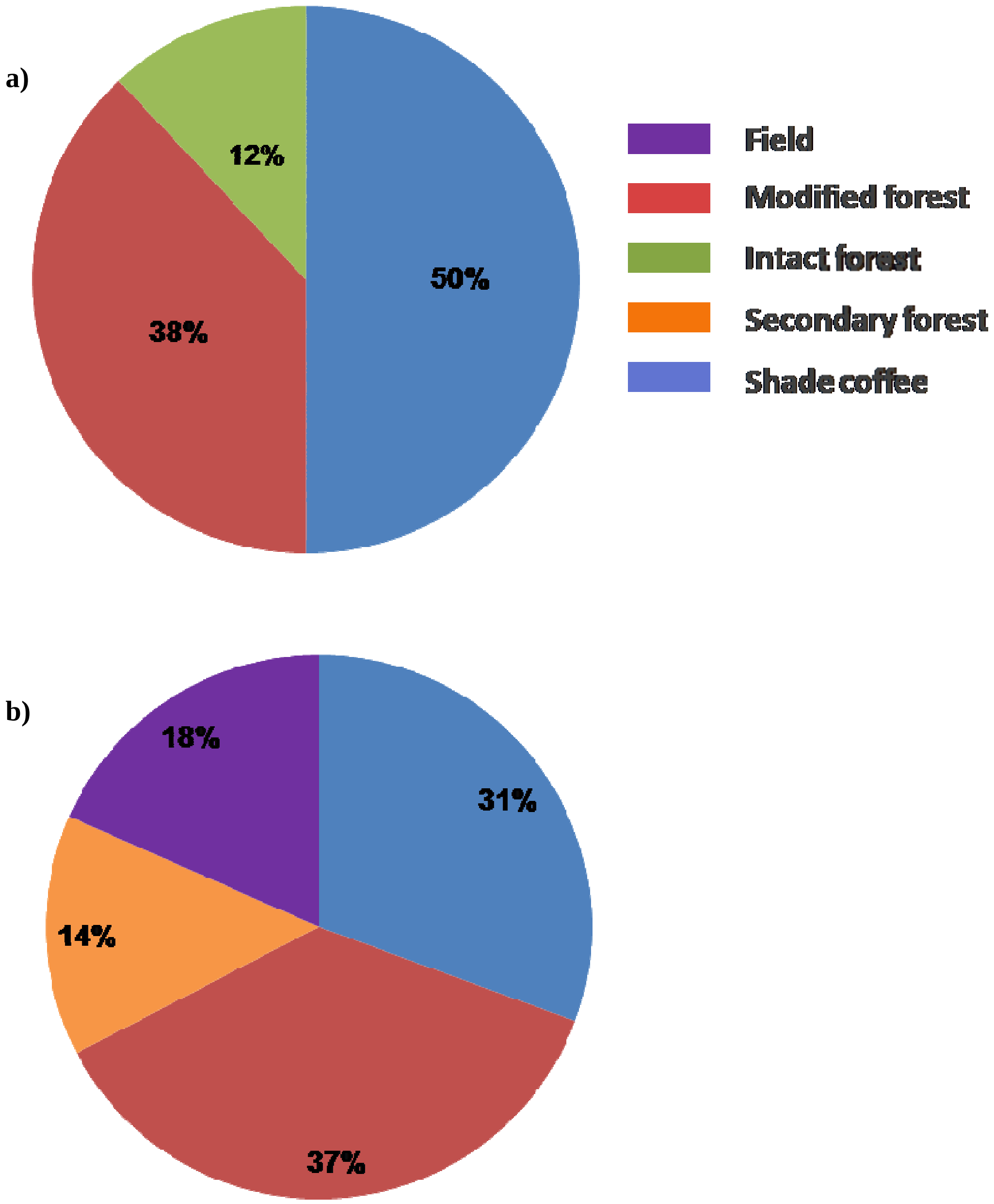


Figure 5a. The percentage of *T. rufalbus* nest sites in each habitat type.
Figure 5b. The percentage of *T. modestus* nest sites in each habitat type.

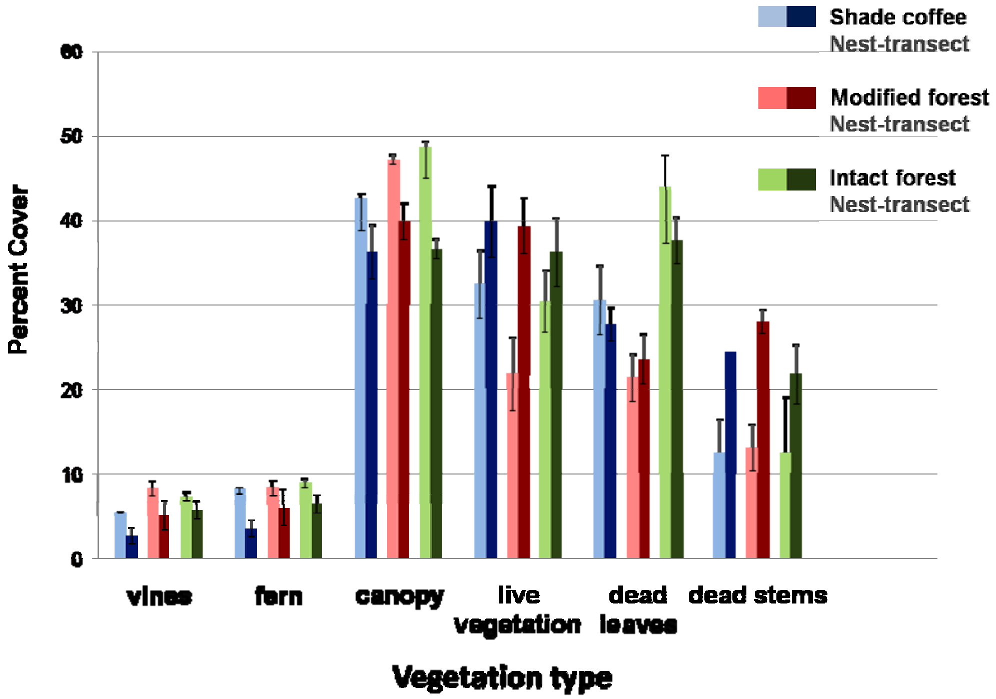


Figure 6. Vegetation variables measured at the nest sites of *T. rufalbus* and along habitat transects. For each color-coded habitat, the light shade corresponds to the nest and the dark shade corresponds to the transect.

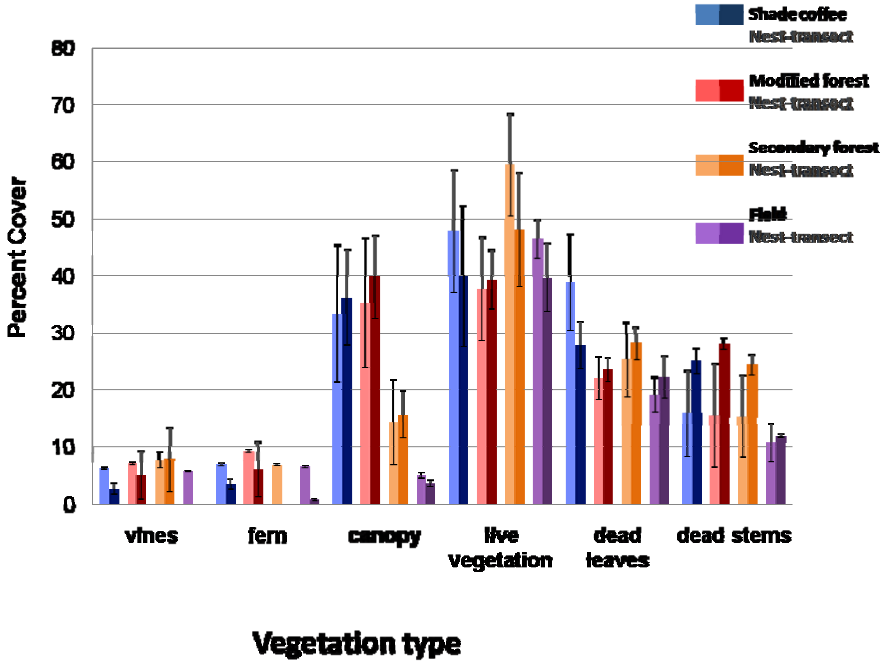


Figure 7. Vegetation variables measured at the nest sites of *T. modestus* and along habitat transects. For each color-coded habitat, the light shade corresponds to the nest and the dark shade corresponds to the transect.

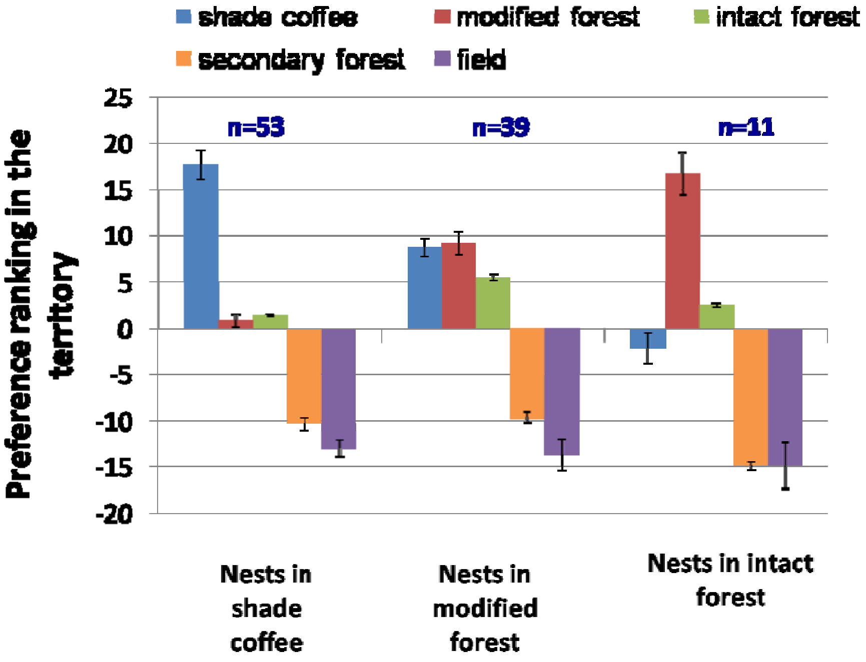


Figure 8. The habitat preference ranking for *T. rufalbus* territories with different nest locations.

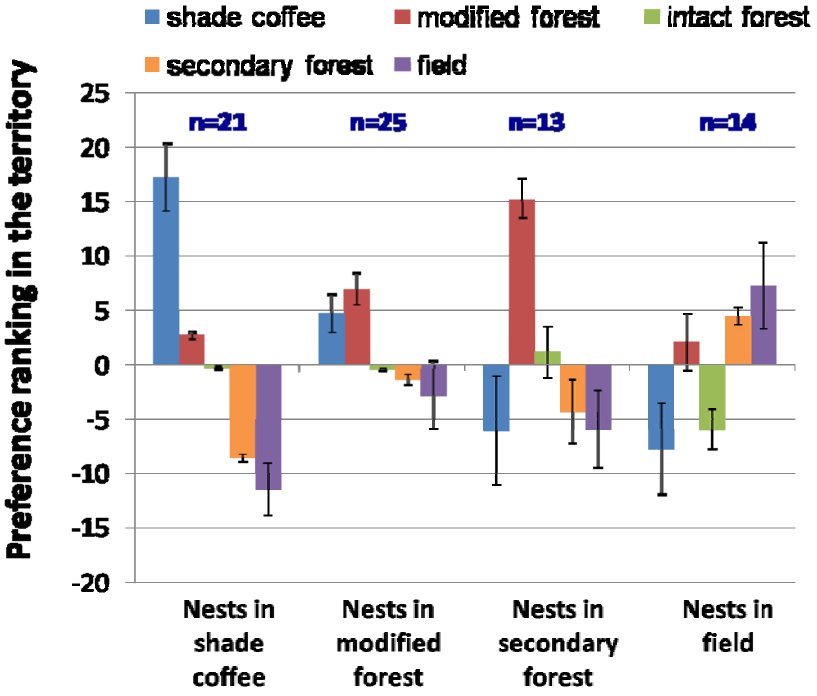


Figure 9. The habitat preference ranking for *T. modestus* territories with different nest locations.

	Shade coffee	**Secondary forest**	**Intact forest**	**Modified forest**	**Field**
Nests in shade coffee (n=55)					
Shade coffee		+++	+++	+++	+++
Secondary forest	---		---	---	+++
Intact forest	---	+++		+	+++
Modified forest	-	+++	-		+++
Field	---	---	---	---	
Nests in modified forest (n=41)					
Shade coffee		+++	+	-	+++
Secondary forest	---		---	---	+++
Intact forest	-	+++		-	+++
Modified forest	+	+++	+		+++
Field	---	---	---	---	
Nests in intact forest (n=13)					
Shade coffee		-	-	+++	+++
Secondary forest	+		++	+++	+++
Intact forest	-	--		++	+++
Modified forest	---	---	--		+
Field	---	---	---	-	

Table 3. Simplified habitat ranking matrices for *T. rufalbus* as a function of nest placement; (a) territories with nest in shade coffee(b) territories with nests placed in modified forest; (c) territories with nests placed intact forest . Each mean element in the matrix was replaced by its sign (+/-). A double sign denotes a significant deviation from random at 0.05>P>0.01, and +++/--- denotes a significant deviation from random at P < 0.05.

	Shade coffee	**Secondary forest**	**Intact forest**	**Modified forest**	**Field**
Nests in shade coffee (n=55)					
Shade coffee		+++	+++	+	+++
Secondary forest	---		-	---	+
Intact forest	---	+		-	+++
Modified forest	--	+++	+		+++
Field	---	-	---	---	
Nests in modified forest(n=18)					
Shade coffee		+	+	-	+++
Secondary forest	-		-	--	+++
Intact forest	-	+		-	+
Modified forest	+	++	++		+++
Field	---	---	-	---	
Nests in secondary forest (n=7)					
Shade coffee		-	-	---	-
Secondary forest	+		-	---	-
Intact forest	+	+		--	++
Modified forest	+++	+++	+		++
Field	+	-	-	--	
Nests in fields (n=9)					
Shade coffee		-	-	-	-
Secondary forest	+		+	+	-
Intact forest	+	-		-	-
Modified forest	+	-	+		-
Field	+	+	++	+	

Table 4. Simplified habitat ranking matrices for *T. modestus*; (a) territories with nests placed in coffee; (b) territories with nests placed in modified forest; (c) territories with nests in secondary forest; (d) territories with nests in fields. Each mean element in the matrix was replaced by its sign (+/-). A double sign denotes a significant deviation from random at 0.05>P>0.01, and +++/--- denotes a significant deviation from random at P < 0.05.

Intact forest	**Transect**		***T. rufalbus***	
Vegetation variable	mean	variance	mean	variance
Leaf litter	4.10	3.16	3.92	3.25
Percent cover live vegetation	36.16	7.64	30.34	13.69
Percent cover vines	5.69	1.17	7.27	0.24
Percent cover dead leaves	37.53	12.38	43.98	45.25
Percent cover fern	6.41	1.42	8.86	0.48
Percent cover dead stems	21.82	3.61	12.39	0.22
Canopy cover	36.56	16.90	48.64	13.82
Number of trees	4.17	4.72	3.52	3.47

Table 5a. Means and variances for vegetation variables measured at the nests and transect in intact forest.

Modified forest	**Transect**		***T. rufalbus***		***T. modestus***	
Vegetation variable	mean	variance	mean	variance	mean	Variance
Leaf litter	3.82	1.84	3.95	3.00	4.61	4.58
Percent cover live vegetation	39.31	9.13	21.79	7.78	37.72	21.10
Percent cover vines	5.06	4.27	8.27	0.83	7.09	0.21
Percent cover dead leaves	23.51	2.09	21.35	8.25	22.06	3.73
Percent cover fern	6.00	4.75	8.27	0.33	9.22	0.28
Percent cover dead stems	28.05	11.13	13.01	1.22	15.47	0.98
Canopy cover	39.83	11.32	47.18	19.41	35.31	11.40
Number of trees	3.39	2.89	3.29	3.09	3.69	4.74

Table 5b. Means and variances for vegetation variables measured at the nests and transect in modified forest.

Shade coffee	**Transect**		***T. rufalbus***		***T. modestus***	
Vegetation variable	mean	variance	mean	variance	mean	variance
Leaf litter	3.55	4.30	4.86	1.93	4.17	0.99
Percent cover live vegetation	39.81	18.38	32.47	16.91	47.72	20.71
Percent cover vines	2.62	0.95	5.35	0.02	6.22	0.15
Percent cover dead leaves	27.76	4.12	30.48	16.22	38.83	10.46
Percent cover fern	3.49	0.93	8.16	0.40	6.89	0.32
Percent cover dead stems	24.97	7.54	12.42	0.57	15.83	2.25
Canopy cover	36.19	10.39	42.55	15.43	33.33	12.00
Number of trees	3.50	2.22	3.34	4.21	2.70	0.79

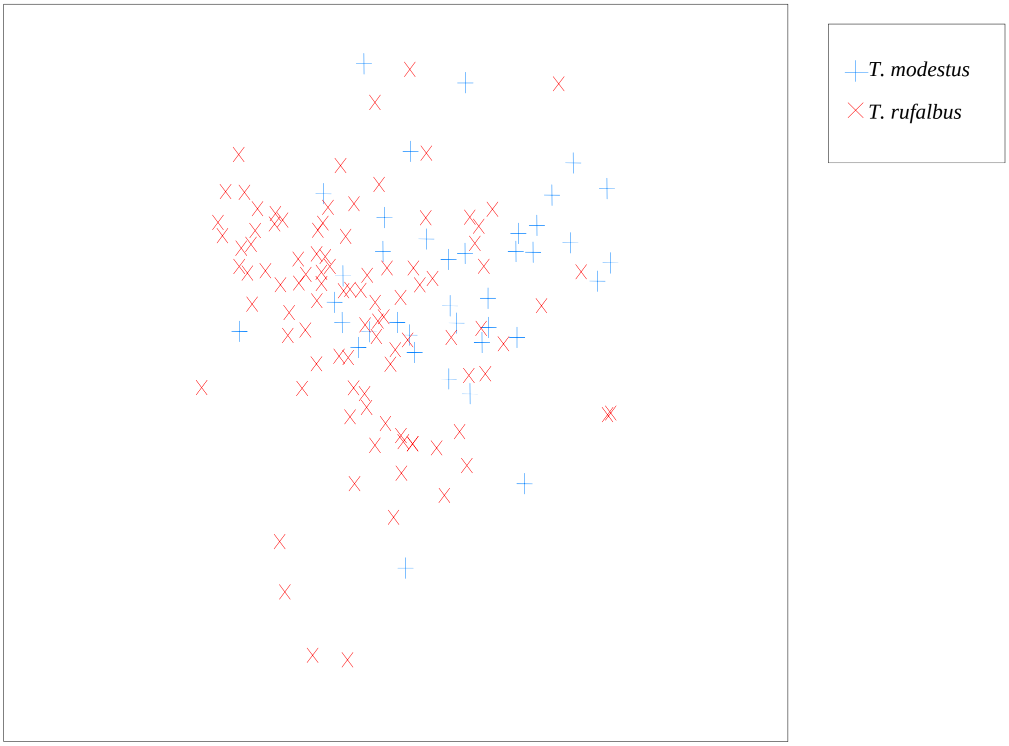
Table 5c. Means and variances for vegetation variables measured at the nests and transect in shade coffee

Secondary forest	**Transect**		***T. modestus***	
Vegetation variable	mean	variance	mean	variance
Leaf litter	3.10	8.07	4.44	3.44
Percent cover live vegetation	48.06	30.20	59.43	19.04
Percent cover vines	7.78	6.66	7.64	1.42
Percent cover dead leaves	28.13	5.86	25.29	7.69
Percent cover fern	0.00	0.00	6.86	0.14
Percent cover dead stems	24.31	15.15	15.36	3.87
Canopy cover	15.63	6.13	14.29	10.48
Number of trees	3.11	2.48	3.94	6.22

Table 5d. Means and variances for vegetation variables measured at the nests and transect in secondary forest

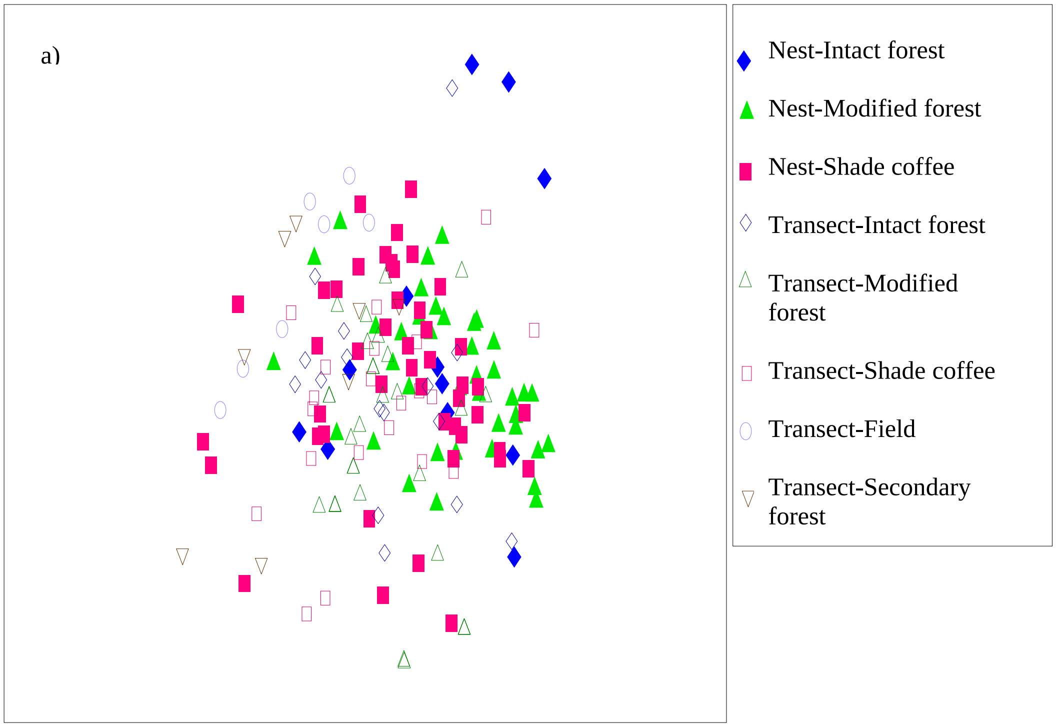
Field	**Transect**		***T. modestus***	
Vegetation variable	mean	variance	mean	variance
Leaf litter	3.10	2.96	3.05	0.41
Percent cover live vegetation	39.68	28.98	46.40	13.45
Percent cover vines	0.00	0.00	5.70	0.10
Percent cover dead leaves	22.22	3.70	19.10	3.10
Percent cover fern	0.79	0.18	6.50	0.20
Percent cover dead stems	11.90	6.35	10.75	0.24
Canopy cover	3.57	0.57	5.00	0.50
Number of trees	2.79	9.74	2.10	0.80

Table 5e. Means and variances for vegetation variables measured at the nests and transect in fields.



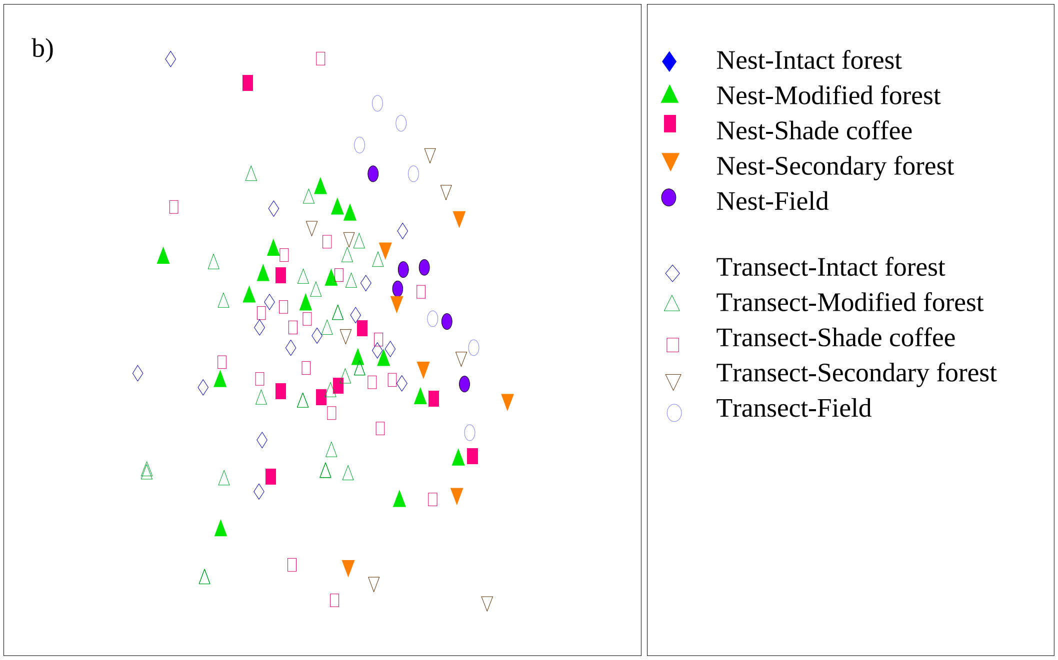
	Leaf litter	Percent cover green vegetation	Percent cover vines	Percent cover dead leaves	Percent cover ferns	Percent cover dead stems	Canopy cover	Number of trees
Scalar axis 1	0.17	0.79^{**}	-0.11	0.17^{*}	0.05	0.20^{**}	-0.81^{**}	-0.40
Scalar axis 2	-0.18^{**}	-0.42^{**}	-0.12	-0.74^{**}	0.07	-0.10	-0.34^{**}	0.38^{**}
T. rufalbus mean	4.25	28.58	6.72	28.58	8.28	12.68	42.6	16.7
T.modestus mean	4.25	46.18	6.98	26.31	8.00	14.80	26.18	3.27

Figure 10. MDS plot of all nests of *T. rufalbus* and *T. modestus* and the correlation matrix of the variables around the nest and the two MDS scalar axes. Two tailed significance of Pearson's correlation $p<0.01$(**) and $0.01<p<0.05$ (*).



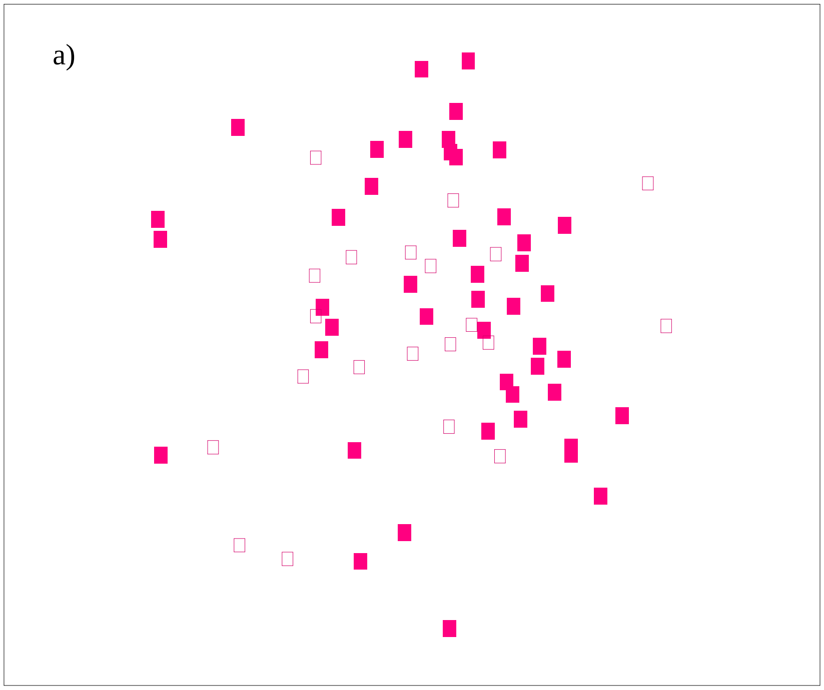
	Leaf litter	Percent cover green vegetation	Percent cover vines	Percent cover dead leaves	Percent cover ferns	Percent cover dead stems	Canopy cover	Number of trees
Scalar axis 1	-0.030	0.75**	-0.16*	0.14	-0.24**	0.27**	-0.76**	-0.11
Scalar axis 2	0.050	-0.54**	-0.24**	0.28**	-0.25**	-0.40**	-0.57	-0.30

Figure 11a. MDS plot of habitat transects and all nests of *T. rufalbus* with the correlation matrix of the variables around the nest and the two MDS scalar axes. Two tailed significance of Pearson’s correlation p<0.01(**) and 0.01<p<0.05 (*). Solid symbols are nests and open symbols are transect for each habitat.



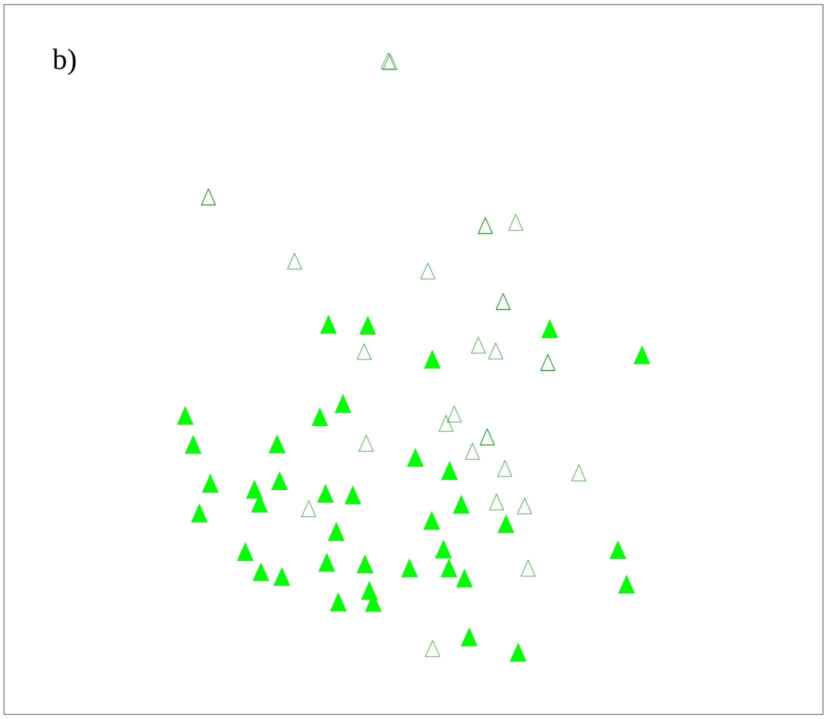
	Leaf litter	Percent cover green vegetation	Percent cover vines	Percent cover dead leaves	Percent cover ferns	Percent cover dead stems	Canopy cover	Number of trees
Scalar axis 1	-0.29^{**}	0.57^{**}	-0.13	-0.21^{*}	-0.40^{**}	-0.25^{**}	-0.85^{**}	-0.43^{**}
Scalar axis 2	-0.04	-0.79^{**}	-0.35^{**}	-0.02	-0.24^{*}	-0.40^{**}	0.45^{**}	-0.19^{*}

Figure 11b. MDS plot of habitat transects and all nests of *T. modestus* with the correlation matrix of the variables around the nest and the two MDS scalar axes. Two tailed significance of Pearson's correlation p<0.01(**) and 0.01<p<0.05 (*).Solid symbols are nests and open symbols are transect for each habitat.



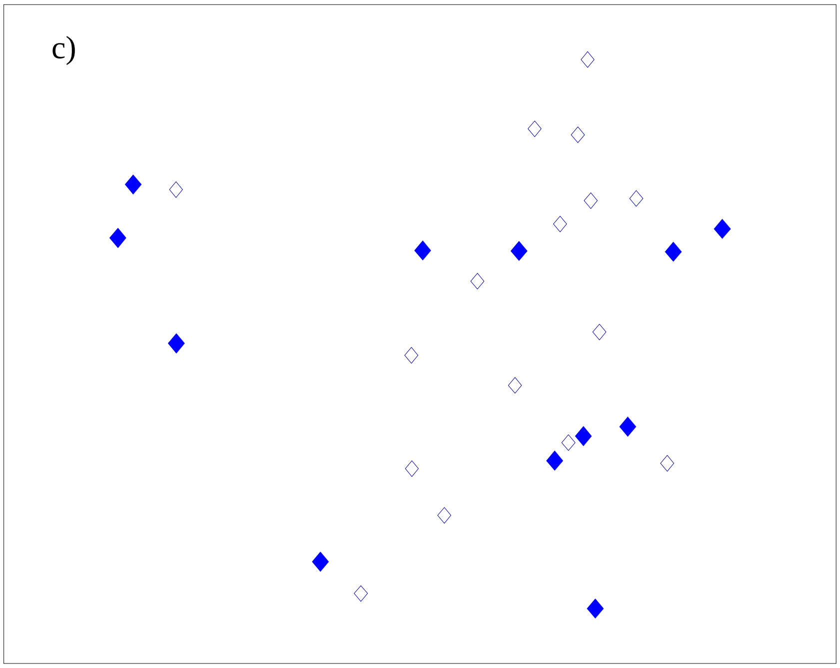
	Leaf litter	Percent cover live vegetation	Percent cover vines	Percent cover dead leaves	Percent cover fern	Percent cover dead stems	Canopy cover	Number of trees
Scalar axis 1	-0.05	-0.92^{**}	-0.12	-0.30^{*}	-0.16	-0.36^{**}	0.41^{**}	-0.08
Scalar axis 2	0.15	-0.33^{**}	-0.19	0.38^{**}	0.06	-0.26^{*}	-0.81^{**}	-0.29^{*}

Figure 12a. nMDS plots and correlation matrix for nests of *T. rufalbus* in shade coffee. Two tailed significance of Pearson’s correlation p<0.01(**) and 0.01<p<0.05 (*).Solid symbols are nests and open symbols are transect for each habitat.



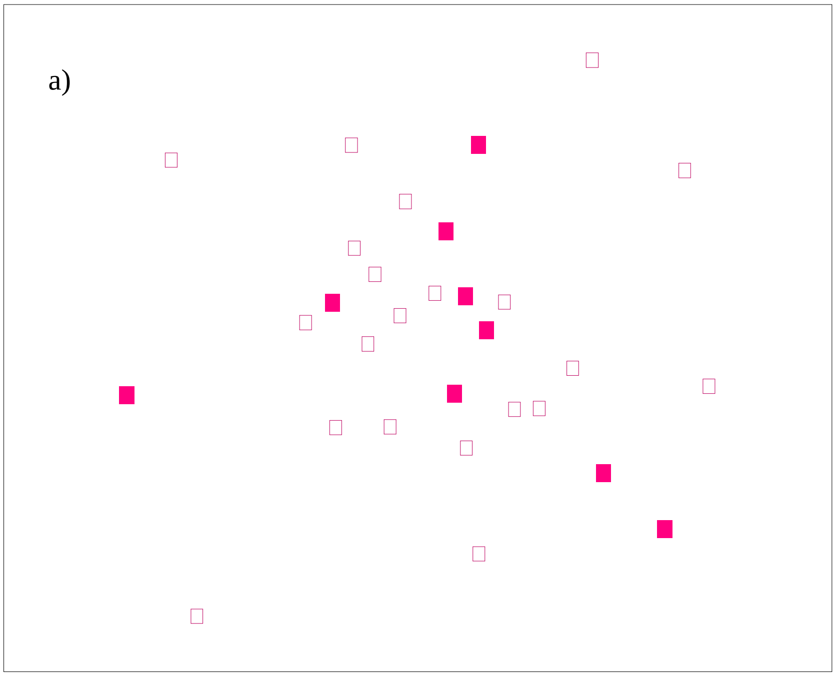
	Leaf litter	Percent cover live vegetation	Percent cover vines	Percent cover dead leaves	Percent cover fern	Percent cover dead stems	Canopy cover	Number of trees
Scalar axis 1	0.11	0.34**	-0.36**	0.45**	-.330**	0.30*	-0.93**	-0.23
Scalar axis 2	0.10	0.80**	0.01	0.07	.327**	0.63**	0.24	0.12

Figure 12b. nMDS plots and correlation matrix for nests of *T. rufalbus* in modified forest. Two-tailed significance of Pearson's correlation p<0.01(**) and 0.01<p<0.05 (*).Solid symbols are nests and open symbols are transect for each habitat.



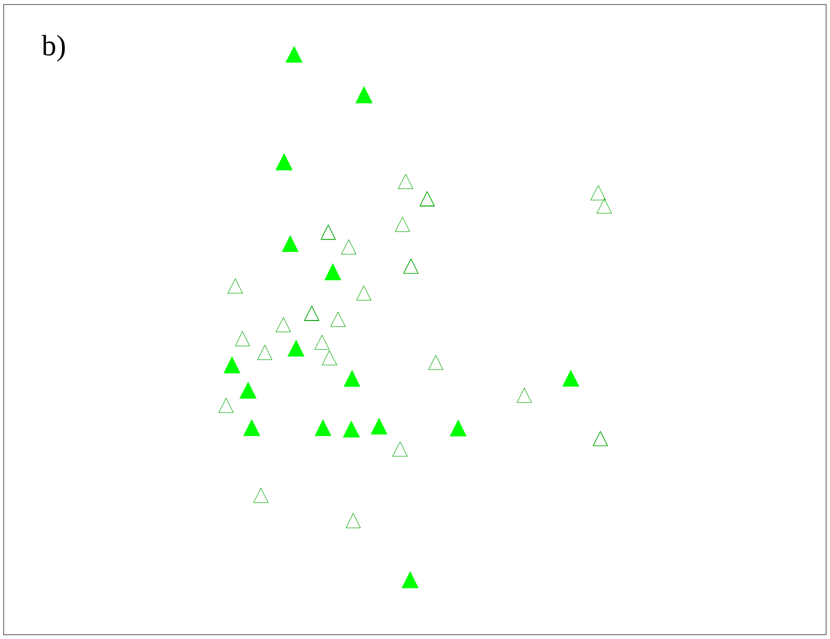
	Leaf litter	Percent cover live vegetation	Percent cover vines	Percent cover dead leaves	Percent cover fern	Percent cover dead stems	Canopy cover	Number of trees
Scalar axis 1	-0.71^{**}	0.51^{**}	-0.31	-0.95^{**}	-0.17	0.11	-0.41^{*}	-0.10
Scalar axis 2	-0.03	0.32	-0.54^{**}	0.29	$-.45^{*}$	0.18	-0.88^{**}	-0.57^{**}

Figure 12c. nMDS plots and correlation matrix for nests of *T. rufalbus* in intact forest. Two tailed significance of Pearson's correlation p<0.01(**) and 0.01<p<0.05 (*).Solid symbols are nests and open symbols are transect for each habitat.



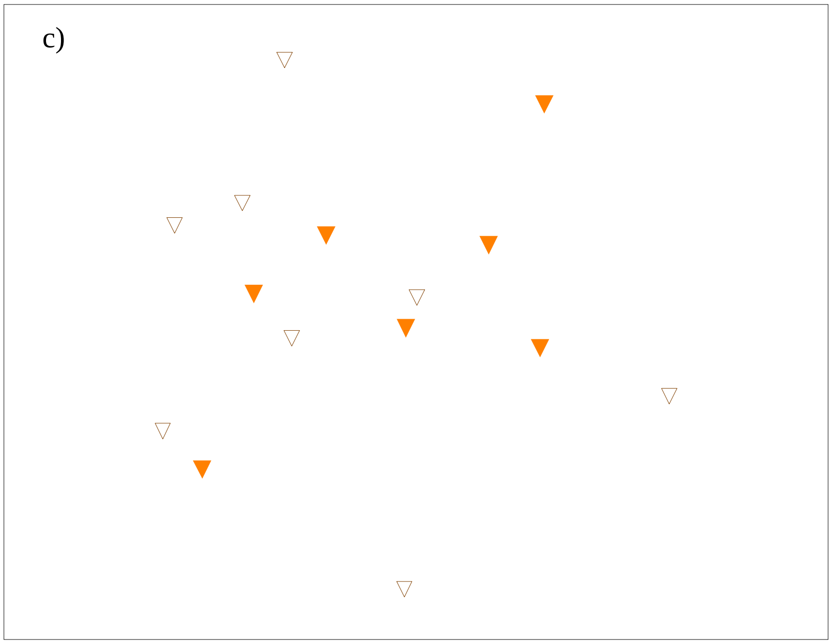
	Leaf litter	Percent cover live vegetation	Percent cover vines	Percent cover dead leaves	Percent cover fern	Percent cover dead stems	Canopy cover	Number of trees
Scalar axis 1	-0.18	0.94**	0.28	-0.32	0.08	0.32	-0.14	-0.41*
Scalar axis 2	0.01	-0.06	0.46*	0.24	0.04	0.50**	0.91**	0.24

Figure 13a. nMDS plots for nests of *T. modestus* in shade coffee. Two tailed significance of Pearson's correlation p<0.01(**) and 0.01<p<0.05 (*). Solid symbols are nests and open symbols are transect for each habitat.



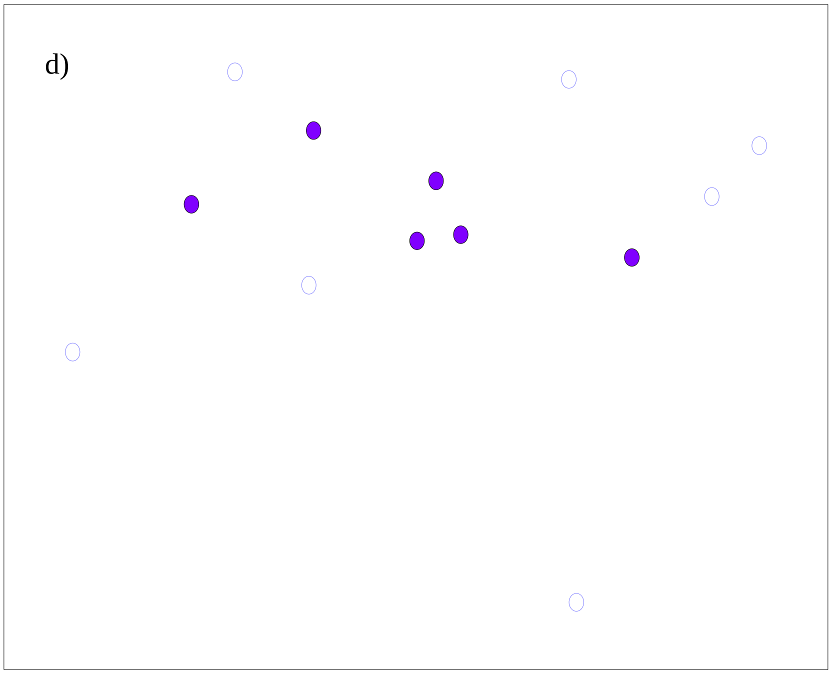
	Leaf litter	Percent cover live vegetation	Percent cover vines	Percent cover dead leaves	Percent cover fern	Percent cover dead stems	Canopy cover	Number of trees
Scalar axis 1	-0.38^{*}	-0.26	-0.47^{**}	-0.01	-0.60^{**}	-0.44^{**}	-0.88^{**}	-0.55^{**}
Scalar axis 2	-0.22	0.78^{**}	-0.20	0.53^{**}	0.01	0.41^{**}	-0.34^{*}	-0.31^{*}

Figure 13b. nMDS plots for nests of *T. modestus* in modified forest. Two tailed significance of Pearson's correlation $p<0.01$(**) and $0.01<p<0.05$ (*). Solid symbols are nests and open symbols are transect for each habitat.



	Leaf litter	Percent cover live vegetation	Percent cover vines	Percent cover dead leaves	Percent cover fern	Percent cover dead stems	Canopy cover	Number of trees
Scalar axis 1	-0.28	0.96**	0.18	-0.25	0.04	-0.22	0.46	0.37
Scalar axis 2	-0.43	-0.16	-0.38	-0.77**	0.08	-0.79**	0.05	0.56*

Figure 13c. nMDS plots for nests of *T. modestus* in secondary forest. Two tailed significance of Pearson's correlation $p<0.01$(**) and $0.01<p<0.05$ (*). Solid symbols are nests and open symbols are transect samples for each habitat.



	Leaf litter	Percent cover live vegetation	Percent cover vines	Percent cover dead leaves	Percent cover fern	Percent cover dead stems	Canopy cover	Number of trees
Scalar axis 1	0.23	-0.10^{**}	-0.15	-0.23	-0.06	0.54	-0.52	0.070
Scalar axis 2	-0.58^{*}	0.19	0.02	-0.51	-0.32	0.03	0.24	-0.92^{**}

Figure 13d. nMDS plots for nests of *T. modestus* in fields. Two tailed significance of Pearson's correlation p<0.01(**) and 0.01<p<0.05 (*). Solid symbols are nests and open symbols are transect for each habitat.

Chapter 3.The effect of habitat selection on nest success wrens in a shade coffee agroecosystem

ABSTRACT

Conservation biologists suggest that shade coffee can serve as an alternative habitat for many bird species. There are few studies on the consequences of selection of shade coffee on the productivity of birds, and it is unclear if this shade crop can contribute to the long-term preservation of avian biodiversity. Optimal habitat choice theory can provide a useful framework for evaluating the fitness impacts of habitat selection in shade coffee agroecosystems. Previous work suggests that *Thryothorus rufalbus* selects shade coffee habitat in both the territory and as a nesting site, while *T. modestus* exhibits weak disproportionate selection of habitat types in the territory. This study focused on the reproductive consequences of habitat selection in the territory and as a nesting site. A high percentage of shade coffee in the territory was associated with low nest success for *T. rufalbus*. Shade coffee nest sites experienced high nest loss and high rates of brood parasitism by *Tapera naevia excellens*. Preferred vegetation at the nest was associated with high reproductive success for intact forest only. *T. modestus* experienced highest nest success in the least preferred nest site habitat, but productivity was high across all sites, and three times greater than that of *T. rufalbus.* There was no effect of either territory composition nor nest-scale variables on nest success for *T. modetus*. The consequences of living in an agroforestry landscape for a bird species is dependent upon the strength of scale dependent habitat selection.

3.1 INTRODUCTION

In recent years, ecologists have focused much research on the potential of shade crop agriculture to protect biodiversity in rural landscapes (Greenberg, Perfecto et al. 2008). Many tropical birds maintain high abundances in shade coffee agroecosystems, prompting conservation biologists to suggest that shade coffee can serve as an alternative habitat for these species (Philpott, Arendt et al. 2008). Studies to evaluate shade coffee as habitat have examined the influence of taxonomic group, vegetation structure, landscape composition, management intensity, profitability, and certification category on species diversity and abundance (Petit and Petit 2003; Philpott and Dietsch 2003; Rappole, King et al. 2003; Ricketts, Daily et al. 2004; Schulze, Waltert et al. 2004; Tejeda-Cruz and Sutherland 2004; Gordon, Manson et al. 2007; Perfecto 2007; Philpott, Bichier et al. 2007; Tscharntke, Sekercioglu et al. 2008; Hernandez-Martinez, Manson et al. 2009). However, few studies that focus on the processes by which birds select coffee as a habitat or the consequences of habitat selection. Without studies on the survival, fitness, or productivity of birds in coffee, it is unclear if this shade crop can contribute to the long term preservation of biodiversity in agroforestry landscapes (Komar 2006). High abundances can be misleading, and do not necessarily reflect the quality of a habitat(Pulliam 1988).

High density and reproductive success have been shown to correlate negatively for birds nesting in human modified temperate areas (Bock and Jones 2004). Human modified landscapes can also create high density ecological traps, whereby individuals are attracted to habitats that confer low fitness (Kristan, Johnson et al. 2007). Direct studies of the fitness consequences of living in shade coffee have produced mixed results. Pangau-Adam et al. (2006) found higher predation on nests in shade coffee than in natural forest areas, while Gleffe et al. (2006) found few differences in nest success between shade coffee and secondary forest but that these differences were species specific. One of the few studies on survival and patch level variables in shade coffee showed monthly survival for birds in shade coffee plots positively correlated with epiphytic plants (Cruz-Angon, Sillett et al. 2008). The relationship between vegetation structure in shade coffee and individual fitness is relatively unknown.

Optimal habitat choice theory can provide a useful framework for evaluating the conservation value of shade coffee. Optimal habitat choice theory states that individuals should select high quality habitats that contribute to high lifetime fitness (Fretwell and Lucas 1970). For shade coffee to be considered an alternative habitat, individuals should experience the same or higher fitness as in the original habitat (Pulliam 1988; Pulliam and Danielson 1991). Fitness can be influenced by a number of factors, and is often difficult to measure in natural populations. Typically, measurements of survival and reproduction over multiple years are combined to give an estimate of fitness. Although incomplete, measurements of survival or reproductive success alone can be sufficient to indicate that a habitat preference will negatively or positively influence a population (Misenhelter and Rotenberry 2000; Kristan 2003; Arlt and Part 2007).

In this study I examined how nest success and the number of chicks fledged was influenced by habitat selection in *Thryothorus modestus* and *Thryothorus rufalbus,* two species of understory insectivores commonly found in shade coffee agroecosystems. Previous research has shown that *T. rufalbus* selects shade coffee over forest for both territory location and nesting sites, while *T. modestus* exhibits weak selection for shade coffee in the territory and little disproportionate selection of nest sites (Mark Chapter 1). Nest site selection was mediated by a preference for vegetation structure and both species optimized preferred nest-scale variables in all habitat types. This study focused on the reproductive consequences of selection of shade coffee in the territory and as a nesting site. In addition, I evaluated the interaction between selection at the scale of the territoryand selection at the scale of the nest on nest success. The main causes of nest loss in this study were predation and nest parasitism by the striped cuckoo, *Tapera naevia excellens* on *T. rufalbus* only. I found that brood parasitism was a major contributor to nest loss in shade coffee, and so I examined the relationship between territory composition, nest site, and nest parasitism. *T. rufalbus* and *T. modestus* are territorial species where both members of a pair defend a territory throughout the year and exhibit high territory fidelity, even after nest loss events (pers. obsv.) These species also exhibits high levels of bi-parental care. Because of these traits, these species should suffer greater negative consequences of poor habitat selection than a more mobile species. Territoriality and bi-parental care are typical of many Neotropical birds, and results from these species likely reflect the reality of other understory birds living in shade coffee agroecosystems.

3.2 STUDY SITE AND SPECIES

3.2.1 Study site

This study took place in Reserva Miraflor (UTM WGS 84 1467524N 165751289E) in the northern Pacific Slope region of Nicaragua. This area is jointly managed by a cooperative of residents, the UCA Miraflor, and the Ministry of the Environment and Natural Resources (MARENA). Conservation regulations in the reserve area limit the cutting of trees and restrict timber harvesting in watersheds. Residents are not permitted to clear forest for open agriculture, and the production of organic shade grown coffee is an important source of income. The study site is 384 ha area within the reserve and is composed of a mosaic of 0.5-10 ha plots subject to different levels of human modification. Since the goal of this study was to evaluate the quality of shade coffee as a habitat in a modified landscape, I classified the study site into five categories of land-use. These categories will be considered as potential habitats and referred to as such. The category of fields includes both fallow and actively farmed plots of corn and beans. The shade coffee category is organic and cultivated in a rustic manner where the upper forest canopy is left intact, with some trees selectively removed, while the understory is cleared and planted with rows of coffee that vary between 0.5-2.5m in height. In shade coffee plots, farmers will often plant agriculturally valuable trees in order to increase shade cover and provide fruit and wood. The modified forest category is forest that has been subject to low levels of selective logging and firewood collection. The category of intact forest is composed of forest areas that have been protected by individual landowners from logging and firewood collection. I assigned the category secondary forest to all forest re-growth on previously cleared.

3.2.2. Study Species

Historical accounts of *T. rufalbus* describe it as a forest-dwelling species that prefers secondary growth near streams and forest edges, but it is commonly reported in shade coffee ecosystems (Stiles and Skutch 1989; Brewer 2001). Within the study site, *T. rufalbus* is frequently found in shade coffee, the interiors of forest patches and forested streams, and in areas between coffee and forest. *T. modestus* is described as an edge species that prefers secondary forest and dense vine tangles at forest edges and in shade coffee. Both species are foliage gleaning insectivores which forages from the forest floor up to five meters in the canopy, with *T. modestus* foraging at lower heights than *T. rufalbus* when found together. *T. rufalbus* constructs closed retort-shaped nests at 1.5-15m from the ground and *T. modestus* constructs dome-shaped nests form 0-1.0 meters from the ground (Stiles and Skutch 1989). Mates defend territories year round, and exhibit bi-parental care during nestling and post-fledgling care, which may last up to 6 weeks (pers. obsv.). The average territory size at the study site is 4321 square meters for *T. rufalbus* and 2808 square meters for *T. modestus* (Mark Ch. 1)

The striped cuckoo, *T. n. excellens*, is a little studied member of the New World ground-cuckoos. They are obligate nest parasites, and at the study site exhibit host specificity for *T. rufalbus* (Mark Chapter 3). *T. n. excellens* forages on the ground in scrub areas and shade coffee, but calls from high perches (Davies 2000). A successful parasitism event results in complete brood loss for the host, as the hatched cuckoo chick apparently kills its nestmates (Morton and Farabaugh 1979).

3.3 METHODS

Nest outcome was measured during the breeding season of April to October for 2005-2007. Field assistants and I searched for breeding birds using behavioral cues, such as singing and alarm calls (Martin 1997). Nests were monitored every three days until nest loss or hatchlings fledged. We classified if nests were active by either checking for eggs or identifying reproductive stage through changes in behavior and song patterns. Mayfield survival estimators were not reported because many of the enclosed nests were located high in the canopy and/or near wasp nests, precluding accurate identification of nest contents. The estimates presented here are for apparent nesting success (Bibby, Burgess et al. 2000). Nests which could not be accurately identified as active were not used in this study. Nests that were abandoned during the construction phase were not included in this study. Only the first nest attempts were included in the analysis resulting in a sample size of 150 nests for *T. rufalbus* and 86 nests for *T. modestus* . I classified nests as either lost or fledged, and then assigned a cause of nest loss: predation, parasitism, or disturbance. Cause of nest loss was determined from physical inspection of the nest, parent behavior, and unique vocalization of *T. n. excellens* chicks. The number of chicks fledged was based on either the number of chicks at the last nest revision prior to fledging or by finding the chicks on the territory post-fledging. Territory composition for breeding pairs in 2006-2007 was evaluated in Mark, Chapter 1 (Fig. 1). A total of 109 territories for *T. rufalbus* and 53 territories for *T. modestus* and their corresponding nests were used in the analysis of habitat composition and nest success.

Vegetation variables were measured around the nest once the nest fate was recorded for 116 nests of *T. rufalbus* and 62 nests of *T. modestus* from 2005-2007. Following the protocol for the Breeding Biology Research and Monitoring Database, percent coverage of the following structures around the nest were measured: green vegetation, woody stems, grass, vines and lianas, dead leaves, dead branches, ferns, moss, water, and rocks (Martin 1997). Percent coverage was estimated by sight in four quadrants within an 11.3m diameter circle, up to a height of 1m. I measured the height of the nest substrate and the nest height either directly, or calculated the height (height = cos ø*dist) using a clinometer to measure the angle to the tree apex and the distance to the tree. I estimated the percent leaf coverage around the nest and classified the plant type as a tree, woody shrub, vine tangle, or herbaceous growth. If the substrate was a tree or woody shrub, I identified its family. I measured percent coverage of woody stems between 1 and 3m, estimated using a convex densitometer. Readings were taken from 8 points within the sampling plot and averaged. The average canopy cover above 3m was measured using a concave densitometer at 4 points within the sampling plot. The number of trees was measured within each plot, and tree family diversity was calculated using the Shannon diversity index (SDI) (Bibby et. al, pp. 266). The number of woody stems was measured within each plot and shrub family diversity was calculated using SDI. I also measured leaf litter density on the floor by taking the average of 12 points where leaf litter density was sampled with a pin.

3.3.1 Statistical analysis

The relationship between habitat composition of the territory and nest success for both species could not be analyzed directly with linear regression models because of high multicollinearity between variables. The contribution of individual habitats to territory composition is correlated because a reduction in one variable necessarily means an increase in another. A correlation matrix of the habitat composition variables displayed strong correlations between shade coffee, modified forest, and intact forest for T. rufalbus, and between shade coffee fields, modified forest, and secondary forest for T. modestus. In order to reduce multicollinearity, I used the covariance matrix among the percent habitats to generate a principal components analysis (PCA). The resulting principal components are combinations of habitats that had the highest contribution toward variance in habitat composition (see results below). To test whether nest success was predicted by habitat composition of the territory, I performed generalized linear models (GdLM) with the scores of the orthogonal principal components as predictor variables and nest success as the response variable (Graham 2003). I used a GdLM with a binomial distribution and negative log-log function to explain the variation in nest success as a function of the principal components. This function was used because the estimated probability of success was asymmetric, with zero success being the more probable outcome. To test whether the number of chicks fledged from successful nests was influenced by territory composition, I used a linear regression model with the log transformed number of chicks as the dependent factor, and the principal components as covariates.

Nest success (0-no fledglings, 1-at least one fledgling) in different nest site habitats was evaluated with a Pearson's Chi-square test. The contribution of nest site habitat to the differences in the mean number of chicks fledged per nest was evaluated with a nonparametric Kruskal-Wallis analysis of variance (ANOVA) test and by applying nonparametric Mann-Whitney U tests to pairs of habitats. I used a multinomial regression model to determine if habitat composition (principal components of the factor analysis) of the territory predicted nest site habitat.

In order to see which of the vegetation variables measured around the nest predicted nest success, as well as variation in the number of chicks fledged from successful nests, I used GdLM and linear regression analysis, respectively. Certain vegetation variables were correlated, and multicollinearity between these variables was reduced by regressing one variable against all other the correlated variables, using the single variable and residuals in the final analysis. For variables with strong negative or positive correlations ($r^2>0.8$), I used only one of the variables in the analysis. To test the role of these adjusted variables on variation in nest success I used a GdLM with a binomial distribution and negative log-log function. To test if these variables were good predictors of the number of chicks fledged from successful nests, I used a linear regression model with the log-transformed number of chicks as the dependent factor, and the vegetation variables as covariates.

To assess the explanatory power of habitat composition in the territory, nest site habitat, and vegetation variables on nest success, I performed a stepwise backward logistic regression using all three principal components, nest site habitat, and all vegetation variables that had a strong effect on nest success to construct the model.

For *T. rufalbus*, the association between cause of nest loss (parasitism or predation) and nest site habitat was examined using Pearson's chi-square test. To explain variance in the cause of nest lost among territories I used an ANOVA on the principal component of territory composition, with nest outcome (fledged, parasitism, or predation) as the fixed factor with post-hoc Tukey comparisons. To explain the variance in cause of nest loss between nest sites, I used backward stepwise binomial logistic regression to compare the nest vegetation variables, nest site habitat, and territory composition between successful nests and parasitized nests, and successful nests and predated nests, and parasitized nests and predated nests. All statistical analysis was performed on SPSS 17.0 (IBM).

3.4 RESULTS

The year had a small effect on nest success for *T. rufalbus*, with the lowest nest success occurring in 2007 (Pearson's Chi-square, p=.030). Combined nest loss for all three years across the study site was 90%. The mean number of chicks produced per nest for all nests in the study site was 0.24. There was no year effect for *T. modestus,* and nest loss across the study site for all three years was 70%. The mean number of chicks produced per nest for all nests in the study site was 0.77.

3.4.1 Nest success and territory composition for *T. rufalbus*

Habitat composition within the territory differed between successful and unsuccessful nests (Fig. 2a, 2b). The PCA of habitat composition in the territory resulted in three components that accounted for all of the variation in territory composition, with two components that accounted for 95% of the variance. Principal component one (PC1) accounted for 85% of the variance, and modified forest and shade coffee loaded onto this component (Table 1). As the PC1 value for a territory increased, so did the proportion of modified and intact forest, while the proportion of shade coffee decreases (Fig. 3). Shade coffee, modified forest, and secondary forest loaded onto principal component two (PC2) which accounted for 10% of the variance (Table 1). As the PC2 value for a territory increased, so did the proportion of secondary forest in relation to all other habitat types (Fig. 3). Principal component three (PC3) accounted for 5% of the variance and shade coffee, modified forest, and intact forest loaded onto this component (Table 1). As the PC3 value for a territory increased, so did the proportion of intact forest, while the proportion of shade coffee decreased. Modified forest had a strong negative relationship with shade coffee and a weak negative relationship with secondary forest (r^2= -0.895, p=0.001; r= -0.504, p=0.194). Modified forest had a significant positive correlation with intact forest (r^2= 0.285, p= 0.002).

The results of the binomial negative log-log regression show that nest success for *T. rufalbus* was accurately predicted by the factor values of the first and second components (PC1: b= -1.11, p=0.003; PC2: b= -0.523, p<0.001) . The third component did not accurately predict nest success (b= -0.273, p=0.241). Unsuccessful nests had a higher proportion of shade coffee in their territories than successful nests, which had a higher proportion modified forest (Fig. 4). Linear regression did not show any relationship between the number of chicks fledged from successful nests and the habitat composition of the territories(PC1: p=0.089; PC2: p=0.525; PC3: p=0.032).

3.4.2 Nest success and nest site habitat for *T. rufalbus*

Nest success was significantly lower for nest sites in shade coffee and significantly higher for nest sites in intact forest (Chi-square: p<0.001, p=0.007) (Fig.5a). The habitat type at the nest site had a strong effect on the number of chicks produced per nest (Kruskal-Wallis ANOVA: df=2, p <0.001). The mean number of chicks produced per nest was 0.09 for nest sites in shade coffee, 0.33 for nests in modified forest, and 0.86 for nests in intact forest (Fig. 5b). Territory composition accurately predicted nest site habitat (Fig. 6a, 6b).

The proportion of intact forest in the territory (PC3) predicted nest placement in intact forests with near significance (B= -1.087, p=0.054). The proportion of shade coffee to modified forest (PC1), and the proportion of intact forest (PC3) predicted nest placement in shade coffee (B= -1.065, p<0.001; B=-0.989, p=0.013). Shade coffee nests were in territories that had a higher proportion of shade coffee to modified forest and a lower proportion of modified and intact forest . The proportion of modified forest to shade coffee (PC 1) and the proportion of intact forest(PC 3) predicted nest placement in modified forest (B= -1.065, p<0.001; B= -0.989, p=0.013).

3.4.3 Nest success and patch variables for *T. rufalbus*

Of the nest associated variables measured at the nest, only one, percent coverage of dead leaves (HOJ), was significantly positively related to nest success (b=0.214, p=.005). None of the vegetation variables showed a relationship with the number of chicks fledged from successful nests. The percent cover of dead leaves is significantly higher in intact forest (Mark Chapter 1). However, even controlling for habitat type, the percent cover dead leaves still had a significant positive relationship with nest success (p=0.005) (Fig. 7).

To determine which scale best predicted nest success, a backwards stepwise regression model was constructed with PC1, PC2, nest site habitat, and the percent coverage of dead leaves. Evaluation of Akaike Information Criteria (AIC) demonstrated that percent dead leaves and nest site habitat created the best fitting model to predict nest success. The removal of territory composition did not affect the model, most likely due to its indirect effect on nest success via its influence on nest site habitat.

3.4.4 Nest success and territory composition for *T. modestus*

Habitat composition did not differ between territories of *T. modestus* with successful or unsuccessful nests (Fig. 8a, 8b). The PCA of habitat composition in the territory resulted in five components that accounted for all of the variation in territory composition (Table 2). Each component captured variation between territories for a single habitat type (Fig. 9). The first principal component (PC1) accounted for 47% of the variation between territories and modified forest loaded onto this component. The second principal component (PC 2) accounted for 23% of the variation between territories and fields loaded onto this component. The third principal component (PC 3) accounted for 16% of the variation between territories and intact forest loaded onto this component. The fourth principal component (PC 4) accounted for 9% of the variation between territories and secondary forest loaded onto this component. The fifth principal component 5 accounted for 4% of the variation and shade coffee loaded onto this component. Modified forest had a strong negative relationship with shade coffee and a strong negative relationship with secondary forest (r^2= -0.643, p< 0.001; r= -0.348, p=0.006). Fields had a strong positive relationship with secondary forest (r^2= 0.533, p< 0.001). Territory composition had no effect on nest success or productivity (Fig. 10). None of the principal components of territory composition predicted nest success (PC1: p=0.886; PC2: 0.498; PC3: 0.125; PC4: 0.536; PC5: 0.100). There was no relationship between territory composition and the number of chicks fledged from successful nests (PC1: p=0.384; PC2: 0.205; PC3: 0.371; PC4: 0.147; PC5: 0.109).

3.4.5 Nest success and nest site habitat for *T. modestus*

Nest success was significantly lower in secondary forest nest sites than any other habitat types (Chi-square: p <0.001) (Fig. 11a).. Nest site habitat did not predict the number of chicks produced from successful nests (Kruskal-Wallis ANOVA, df=2, p >0.5). The number of chicks produced per nest was 1.4 in fields , followed by 1.0 in shade coffee and 0.6 in modified forest sites (Fig. 11b).

The proportion of shade coffee in the territory was the only habitat that predicted nest site location. A high proportion of shade coffee in the territory predicted nest placement in shade coffee habitat (B=1.976, $p<0.001$). There were 25 nests placed in modified forest, 21 nests placed in shade coffee, 13 nests placed in secondary forest, and 14 nests placed in fields.

3.4.6 Nest success and nest vegetation variables for *T. modestus*

None of the vegetation variables measured at the nest were able to predict nest success nor did they have a relationship with the number of chicks fledged per successful nest. I did not use a stepwise multinomial regression analysis to analyze which scale was best able to predict nest success, as only nest site habitat showed a relationship with nest success.

3.4.7 Cause of nest loss for *T. rufalbus*

For all active nests from 2005-2007, parasitism was the cause of nest loss for roughly 33% of unsuccessful nests and predation was the cause of nest loss for 63% of unsuccessful nests (Fig. 12). Overall, there was a significant relationship between the fraction of failed nests lost to cuckoos vs. predators and the habitat where the nest was located (based on data associated with Fig. 12; G-test, Chi-square = 6.85, df = 2, P = 0.033). Parasitism caused nest loss in coffee more than any other habitat, but territory composition did not influence the cause of nest loss (Fig. 13). There was no difference in habitat composition between territories with parasitized or predated nests (ANOVA

PC1:p=0.996; PC2: p=0.994; PC3: p=0.707). The variance in predation vs. parasitism based nest loss was in part explained by one nest-associated variable, nest height (b=0.111, p= 0.028). Nests that suffered from parasitism were placed lower in the canopy than either predated nests or successful nests, but the difference was only significant between parasitized and successful nests (Fig. 14).

To determine which scale best predicted nest parasitism and nest predation, I constructed three backwards stepwise multinomial regression using PC1, nest site habitat, and all nest vegetation variables as predictor variables: parasitism vs. successful nests, predation vs. successful nests, and all nest outcomes. Evaluation of Akaike Information Criteria (AIC) demonstrated that nest height and the number of trees at the nest site constructed the best fitting model for nest parasitism (p=0.014, p=0.011). Evaluation of Akaike Information Criteria (AIC) demonstrated that nest site habitat and the percent cover of dead leaves at the nest site constructed the best fitting model for nest predation (p=0.007, p=0.046). Nest outcome (predation, parasitism, or fledged young) was best predicted by nest site habitat, nest height, and the percent cover of dead leaves at the nest site (p=0.011, p=0.03, p=0.04).

3.5 DISCUSSION

Optimal habitat choice theory predicts that individuals should select habitat that positively affects individual fitness, when available. The habitat that is most often selected by *T. rufalbus*, shade coffee (Mark, Chapter 1), produces both the lowest nest success and the lowest average number of chicks fledged (Fig. 4, Fig.5). The amount of shade coffee in a territory likewise had a negative impact on nest success. In fact, all successful nests had less than 50% coffee in the territory. *T. rufalbus* prefers to include shade coffee in the territory at the direct expense of modified forest, the one territory component that was positively correlated with fecundity (Fig. 4). *T. rufalbus* also showed a preference for placing nests in shade coffee habitat, and this too had negative consequences for nest success (Fig. 5a). Nest site habitat was predicted by habitat composition of the territory, such that an increase in the proportion of shade coffee in the territory led to a higher propensity to place nests in shade coffee, and an increased proportion of modified forest and intact forest in the territory increased the likelihood of nest placement in intact forest (Fig. 6a, 6b). Mark (Chapter 1), demonstrated that intact forest was the least selected nesting site, and the associated high percentage of modified forest in the territory were the least preferred habitats. Yet nests placed in intact forest in territories with a high proportion of modified forest had a higher success rate than nests in other habitats (Figs. 4, 5a). The amount of intact forest in a territory does not increase the likelihood of nest success, as much as the amount of shade coffee in a territory reduces it. Habitat composition of the territory influences nest site habitat selection, and this may be the pathway through which habitat composition of the territory predicts nest success.

The only local nest-associated vegetation variable that was positively correlated to nest success in *T. rufalbus* was the percentage cover of dead leaves, which is also one of the few measured variables for which *T. rufalbus* displays a preference (Ch 2). Although cover of dead leaves was highest in intact forest, the positive effect of dead leaves cover on nest success was the same in all habitats (Fig. 7). When values at the scale of the territory and the scale of the nest are analyzed simultaneously, nest site habitat and percentage cover of dead leaves at the nest site are the best predictors of nest success. Habitat composition at the scale of the territory predicts nest success via its influences on nest site habitat, which may explain why it does not increase the prediction value of the model that includes variables as all scales. This may indicate that nest site selection depends upon a threshold proportion of a given habitat in the territory, and above this threshold, composition in the territory has no effect on nest success. In this species, habitat selection at the broader scale constrains selection of nest site habitat, but individuals optimize nest site vegetation variables in all habitats. Although selection at broader scales may be important for studies of habitat selection in this species, selection at smaller scales should not be ignored as these behaviors can occur independently of broader scale selection processes.

Like *T. rufalbus, T.modestus* experienced reduced nest success at nest sites in shade coffee compared to other nest site habitats, although this nest site was not selected significantly more than other nest site habitats. *T. modestus* experienced the highest nest success at nest sites in field habitat, and significantly lower nest success for nest sites in secondary forest (Fig. 11a). However, since *T. modestus* placed relatively equal number of nests in the four appropriate nesting habitats, and that productivity was high for all nest site habitats, the placement of some nests in less productive nest sites did not have a strong negative effect on the average number of chicks produced by all nests in the landscape (Fig. 11b). *T. modestus* produced three times as many chicks per nest in the landscape than *T. rufalbus* (0.77 vs. 0.24). Habitat composition was similar for territories with successful and non-successful nests, and even though *T. modestus* showed disproportionate selection of shade coffee and modified forest for territories, this had no impact on nest success (Fig. 8a, 8b).

While in *T. rufalbus,* the disproportionate selection of certain vegetation types had little effect on nest success, in *T. modestus* there was no relationship between nest-scale vegetation and nest success. T. *modestus* did exhibit disproportionate use of high percent cover of green vegetation and low canopy cover at the nest, but there was no relationship to nest success or the number of chicks fledged per successful nest. In addition, territory composition had no significant effect on nest success, which is not unexpected since territory composition had little ability to predict nest site habitat. Only the proportion of shade coffee in the territory predicted nest site habitat, and territories with a higher proportion of shade coffee were more likely to have nests in shade coffee as well. This species exhibited weak selection for habitat variables at either the scale of the territory or the nest. Nest success was highest in the least preferred nest site, yet was still high in the preferred nest site habitat of shade coffee (1.4 vs. 1.0 chicks per nest).

This study demonstrates how habitat selection at different scales can interact to influence productivity of birds in modified agroforetry landscapes, and that this effect is strongest when a species exhibits strong disproportionate selection of habitat. In the case of *T. rufalbus,* highly disproportionate selection of shade coffee at the scale of the territory results in negative consequences for reproduction. This species excluded modified forest from territories, the habitat positively correlated with fecundity, in favor of shade coffee (Fig. 2a, 2b). A high proportion of shade coffee in the territory predicted a high number of nests in shade coffee, which produced the lowest number of chicks.

However, *T. modestus* showed weak disproportionate selection of shade coffee and modified forest habitat in the territories, and only the proportion of shade coffee predicted nest site location. Although *T. modestus* did place more nests in the less productive shade coffee than in highly productive fields, and experienced complete high nest loss in secondary forest, the consequences for making non-optimal nest site selection were not as severe as for *T. rufalbus.* This was due to the fact that productivity in shade coffee was still relatively high, and weak nest site preference led to roughly proportionate distribution of nests in all suitable habitats. In agroforestry landscapes, the strength of habitat selection at different scales may determine the productivity of birds using modified habitats. The strength of habitat selection can be influenced by density, and it is possible that the selection intensity for shade coffee by *T. rufalbus* was because all suitable sites in other habitats were occupied. Although I did not test the relationship between density and habitat selection, anecdotal evidence suggests that *T. rufalbus* exhibits an affinity for establishing territories near streams, and there were many stream areas in modified forest that were unoccupied for the duration of the study. In addition, the replacement rate of pairmates for birds that left the study site or died was shorter for territories in shade coffee plantation than territories in modified forest, indicating that shade coffee was not selected less often than modified forest.

The ability of habitat composition to predict nest site habitat in *T. rufalbus* supports the assertion of Rettie and Meisser (2000) that selection at broader constrains selection at lower scales. However, selection of vegetation variables around the nest was consistent across all nest site habitats and had a strong impact on nest success, indicating that researchers should not focus on broad scale selection behaviors alone. Also, for some species selection may only occur at smaller scales, as shown by *T. modestus,* which selected vegetation variables at the nest, but did not exhibit strong selection for nest site habitat or territory composition. The relationship between the selected variables and nest success for both species was little to none, indicating that perhaps selection of vegetation variables around the nest is more strongly related to survival of the adults or juveniles than to nest success. Previous work on *T. modestus* demonstrated that this species selected low canopy cover and high coverage green vegetation at the nest, yet neither of these variables related to nest success nor the number of chicks fledged from successful nests. Previous work demonstrated that *T. rufalbus* has a preference to place nest sites in areas of high canopy cover, high coverage of dead leaves, low coverage of green vegetation, and low density of woody shrubs (Ch 2). A high percentage of dead leaf cover in the understory was positively associated with nest success in all habitats , yet dead leaf cover was highest at nest sites in intact forest and shade coffee, two nest site habitats with vastly different results for nest success. While preference for dead leaf cover may contribute to nest success in forested habitats, other factors overwhelmed this benefit in shade coffee nest sites, where only four percent of nests fledged chicks (Fig. 5b).

Nest parasitism by the striped cuckoo, *T. n. excellens*, may explain why selection for dead leaf cover was associated with high nest success in intact forest but not shade coffee. The major causes of nest loss were brood parasitism by *T. n. excellens*, and nest predation by avian, reptile, and mammalian predators. The percent cover of dead leaves was significantly different between predated and successful nests, but it was another variable, nest height, that predicted parasitism. This is explained by the relative risks of parasitism and predation for nest sites in different habitats. *T. n. excellens* was only observed on forest edges, but entered into shade coffee plots to forage, often moving along riverine corridors. Nest site habitat and the percent cover dead leaves best predicted whether nests were predated or successful. The reduced risk of nest parasitism in intact forest meant that selection for nest variables that reduced predation (percent cover dead leaves) was a successful strategy in this habitat alone, resulting in high productivity from nests in these sites. Nest height and the number of trees best predicted whether nests were parasitized or successful. In shade coffee, both nest predators and parasites threaten nests, yet *T. rufalbus* did not select nest variables that decreased the risk of parasitism. *T. rufalbus* may not select nest height to avoid nest loss to parasitism but rather to minimize song degradation of males singing from a perch above the nest (Barker et. al). Lower nest height and fewer trees around the nest may increase visibility of nests to *T. n. excellens*, and the relationship between nest site variables and the risk of parasitism warrants further study. The stepwise regression model for all nest outcomes found that nest site habitat, percent cover of dead leaves, and nest height constructed the model with the best fit. The lack of any relationship between habitat composition of the territory and the cause of nest loss may be due to the small number of parasitized nests. If territory composition only influences nest outcome indirectly by predicting nest site placement, a larger sample size may be needed to demonstrate a measurable effect between composition and the cause of nest loss.

It has been suggested that human modified environments may become ecological traps for forest-dwelling birds, whereby the vegetation cues that are used to indicate high quality nesting habitat in relatively undisturbed habitats are no longer associated with the expected outcome of high reproductive success (Schlaepfer, Runge et al. 2002; Kristan 2007). Ecological traps may be more likely to occur in species that exhibit strong selection for habitat variables (Part, Arlt et al. 2007). Agroforestry landscapes may result in ecological traps for *T. rufalbus*, a species with strong selection for habitats with low productivity. For species that exhibit weaker selection tendencies, such as *T. modestus*, human activities can provide additional habitats with little effect on productivity in the landscape.

Ecological traps would only occur if both productivity and survival were low compared to other areas, and this study focused solely on reproductive success. Mark-recapture data from the field site, as well as from intact dry forest in Costa Rica, gives lifespan estimates for *T. rufalbus* wrens of between 2-5 years, with yearly survival estimates of 0.62 at the study site (Mark, unpubl. Data, D. Mennill pers. comm.). Reported survival rates for tropical understory insectivores range from 0.48-0.94 for intact forest and 0.64-0.74 for forest fragments, and estimate lifespan for understory foliage gleaners to be about 3 years (Karr, Nichols et al. 1990; Brawn, Karr et al. 1995; Morton and Stutchbury 2000; Blake and Loiselle 2008; Rangel-Salazar, Martin et al. 2008; Vogeli, Laiolo et al. 2008). Nest success for understory insectivorous birds ranged from 8-42%, with lower values generally in disturbed or fragmented forests, and the cause of nest loss predation for the majority of cases (Morton and Stutchbury 2000; Ahumada 2001; Roper 2005; Stutchbury, Morton et al. 2007; Rangel-Salazar, Martin et al. 2008; Salgado-Ortiz, Marra et al. 2008; Stutchbury and Morton 2008; de Lima and Roper 2009; Franca and Marini 2009). Nest success over two years for *Thryothorus rufalbus* and *Thryothorus leucotis* in a disturbed forest in northern Colombia was 67%

and 36% respectively(Ahumada 2001). In this study, nest success for *T. rufalbus* was significantly lower, at 10% while approximately the same for *T. modestus*, at 30%. Ahumada (2001) reported similar rates of nest parasitism by *T.n. excellens* on *T. rufalbus* of 28% in modified forest, and in the present study the rate of parasitism was 24% in modified forest and 41% in shade coffee. In most studies in intact forests, low productivity was offset by high survival rates, and survival was the primary demographic parameter determining population growth rates (Morton and Stutchbury 2000; Roper 2005; Rangel-Salazar, Martin et al. 2008). Anecdotal evidence suggests that survival rates of *T. rufalbus* may not be high enough to compensate for low productivity in shade coffee. Further research is needed on both survival and reproduction before it can be determined if shade coffee is an ecological trap for this species. In addition, the characteristics of shade coffee that make it attractive to *T. n. excellens* warrant further study, as this brood parasite was the cause of considerable nest loss in shade coffee habitats.

3.6 CONCLUSIONS

Due to its focus on habitat selection and fitness, optimal habitat choice theory provides a useful framework to evaluate the contribution of shade coffee to the preservation of biodiversity. The results of this study indicate that use of shade coffee as a habitat is a non-optimal reproductive choice that results in low nest success for the species with strong selection behavior, while shade coffee provides additional nesting habitat for the species with weak selection behavior. Non-optimal selection behavior in modified habitats, such as coffee agroecosystems, can result in sink populations or ecological traps, both of which can negatively affect species presence in the landscape (Kokko and Sutherland 2001; Kristan 2003). Additionally, non-optimal selection can combine negative effects across scales. In the case of *T. rufalbus,* selection of shade coffee in the territory increased the likelihood of placing nest sites in shade coffee, where they were exposed to nest parasites, and selection for variables around the nest that decreased predation but did not deter parasites, increasing the risk of parasitism. Although low nest success in a selected habitat such as shade coffee could be offset by increased survival of adults or fledglings, I suggest that further study is needed before shade coffee can be labeled as alternative habitat for forest-dwelling birds. The spatial scale at which individuals make decisions should be explicitly considered in future work, as the integration of habitat selection across scales can produce different opportunities for maximizing fitness (Misenhelter and Rotenberry 2000; Chalfoun and Martin 2007; Wheatley and Johnson 2009). Additional work on species survival in shade coffee would increase our understanding of the population viability of birds living in shade coffee agroecosystems. Also, I would suggest further study on brood parasitism by *T. n. excellens*, which was a major cause of nest loss in shade coffee in the present study, far above rates of parasitism in modified forest in this and other studies

Shade crops as alternative habitats are an attractive idea because they represent one of the few development strategies that can reconcile profitability and biological conservation (Sherry 2000; Philpott and Dietsch 2003; Ricketts, Daily et al. 2004; Philpott, Bichier et al. 2007). For some species, such as *T. modestus,* shade coffee may provide additional, and alternative habitat. Unfortunately, there may be few a priori reasons to assume that one abundant species found in shade coffee benefit while another species experiences negative effects. As shown here, even closely related species in the same foraging guild found in similar abundances in shade coffee plantations can experience large difference in productivity. Without careful evaluation of the survival and reproductive success of species living in shade coffee, the promotion of such shaded crops may undermine long-term conservation goals, at least for some target species, especially if such an emphasis comes at the cost of diminished protection for intact undisturbed forest. The conservation of common species in modified landscapes necessitates scale specific demographic studies on birds in both intact and disturbed habitats, with specific attention to variables that can be manipulated in managed areas, such as shade coffee, to increase survival and productivity.

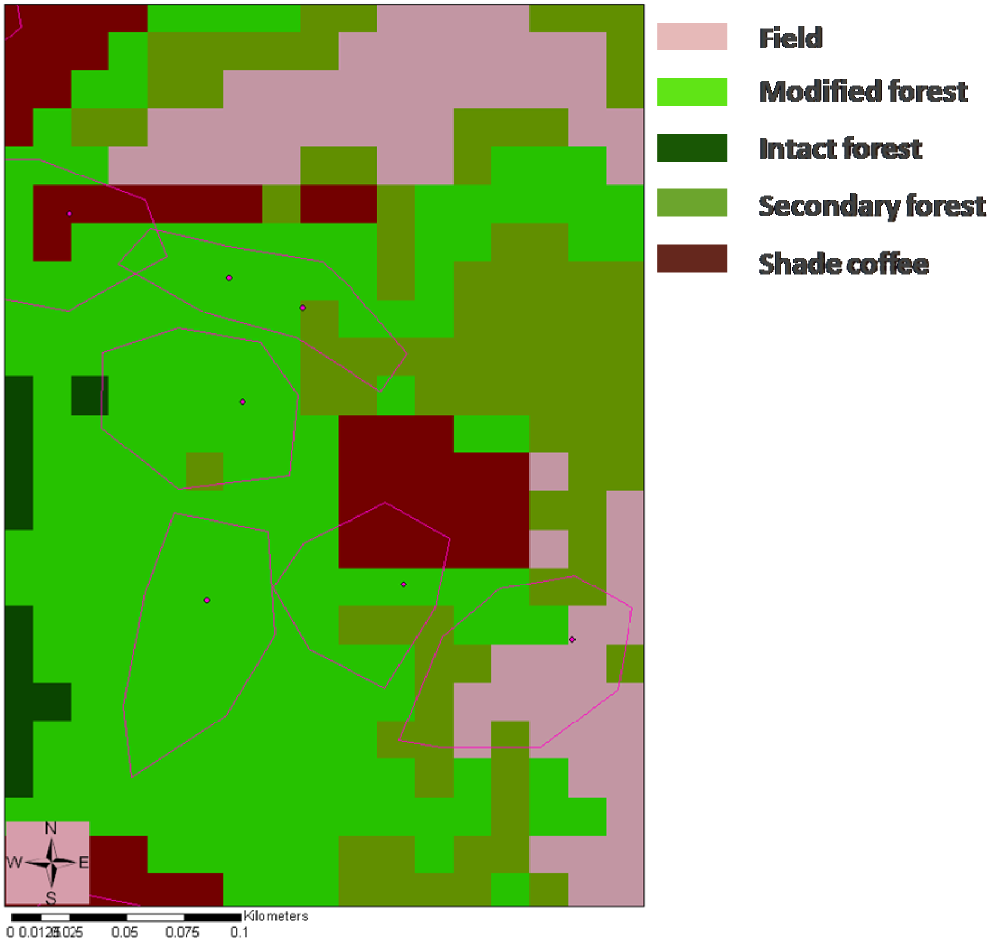


Figure 1. The study site was classified into 5 habitat categories using ArcMap 9.2. The habitat composition of the individual territory maps calculated using ArcView 9.

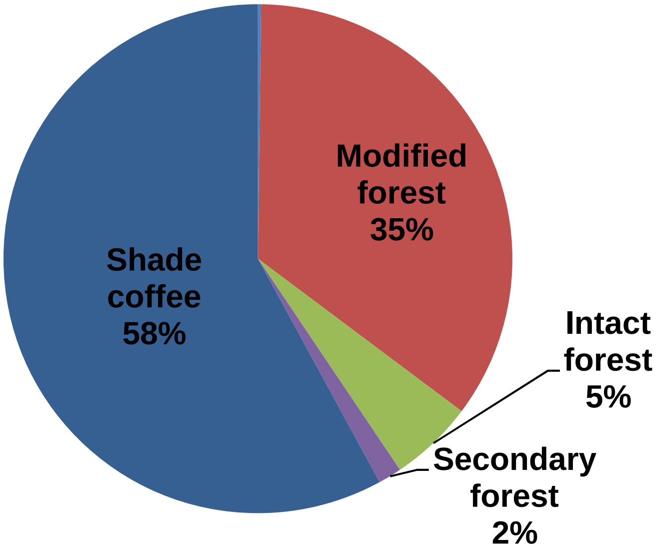


Figure 2a. Mean proportion s of habitat types in territories of *T. rufalbus* that produced no chicks

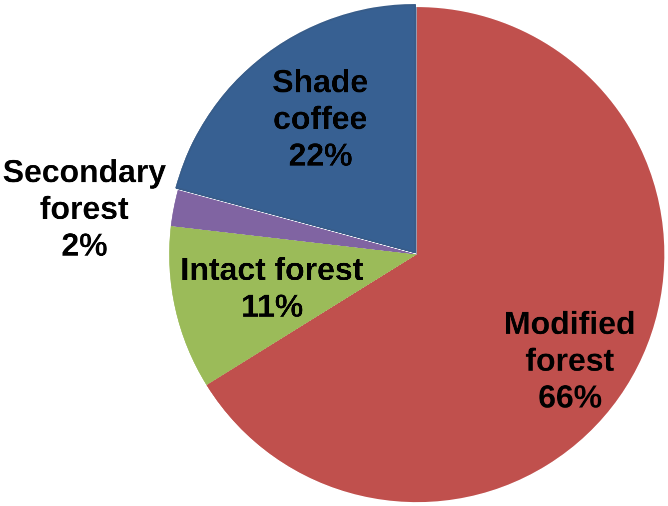


Figure 2b. Mean proportions of habitat types in territories of *T. rufalbus* that produced at least one chick

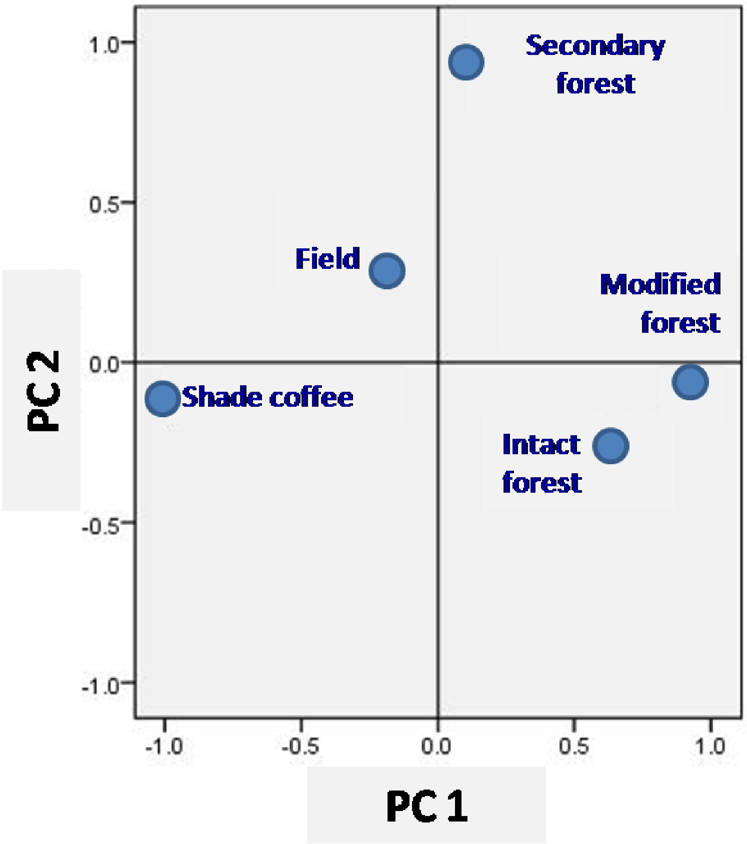


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Figure 3. As the PC1 value for a territory increases, so does the proportion of modified and intact forest to shade coffee decreases. As PC 2 value increases, so does the proportion of secondary forest. As PC3 (not shown) increases, so does the proportion of intact forest while shade coffee decreases. PC 1 explains 85% of the variance in habitat composition among territories. PC 2 explains 10% of the variance. PC3 explains 5% of the variance.

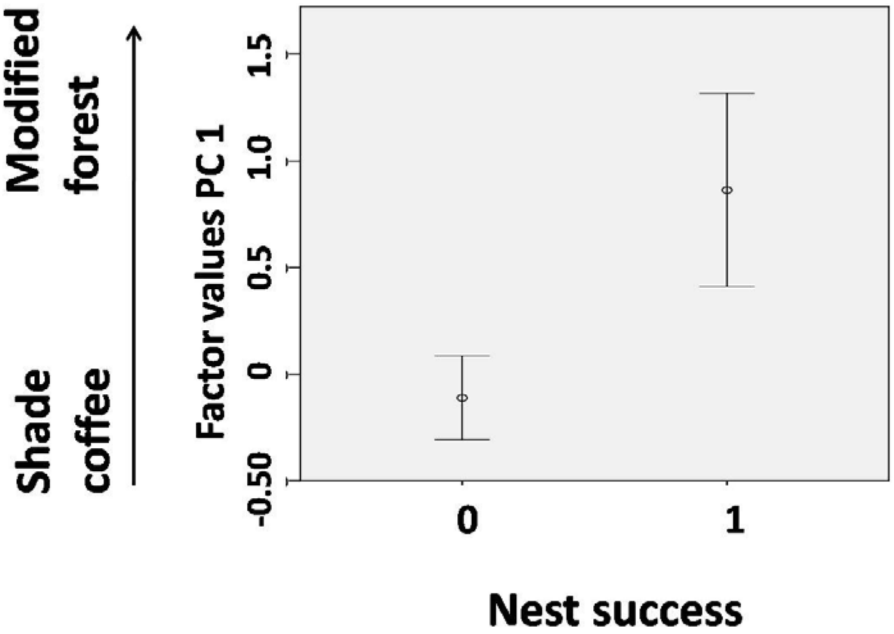


Figure 4. The mean factor values from PC 1 for territories containing nests that fledged no chicks (nest success=0), and nests that fledged at least one chick (nest success=1). Territories with successful nests had significantly more forest an less coffee in the territory than unsuccessful nests.

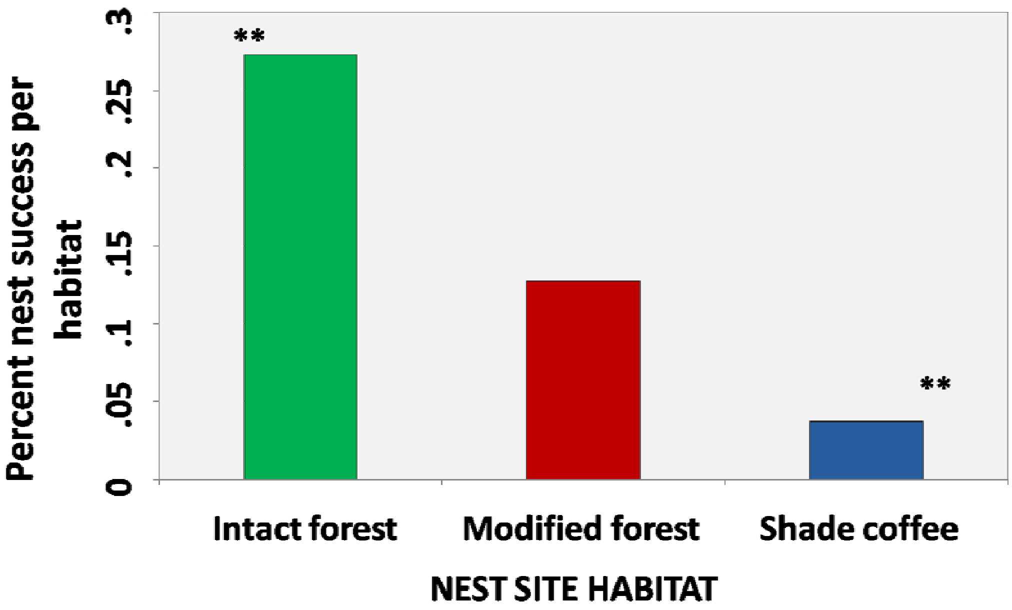


Figure 5a.Nest success for *T. rufalbus* was significantly higher in intact forest and lower in shade coffee (**, p <0.001).

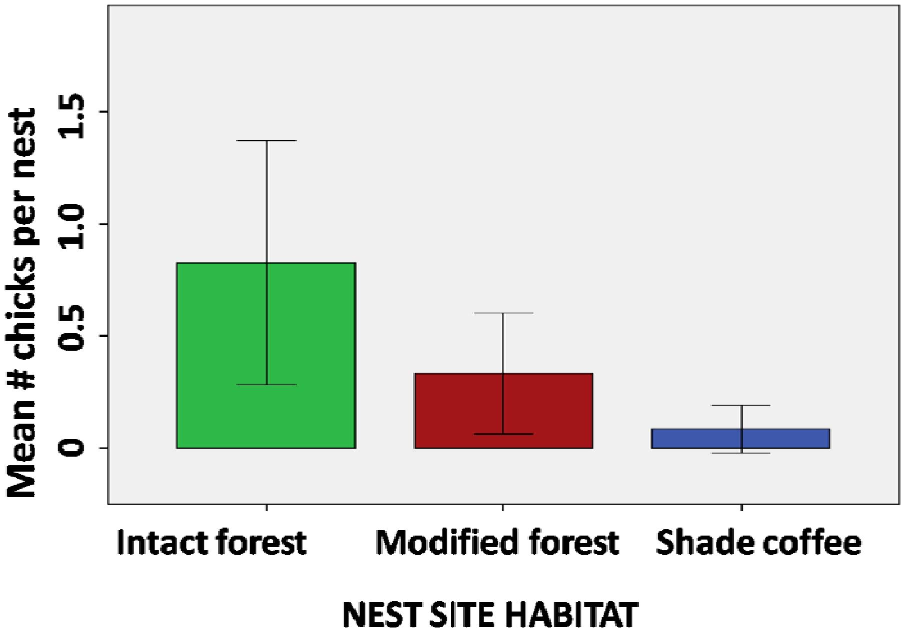


Figure 5b. The mean number of chicks fledged per nest for *T. rufalbus* was significantly different between modified forest (0.33), intact forest (0.86), and shade coffee (0.06). The habitat type at the nest site had a strong effect on the number of chicks produced per nest (Kruskal-Wallis ANOVA: df=2, p <0.001).

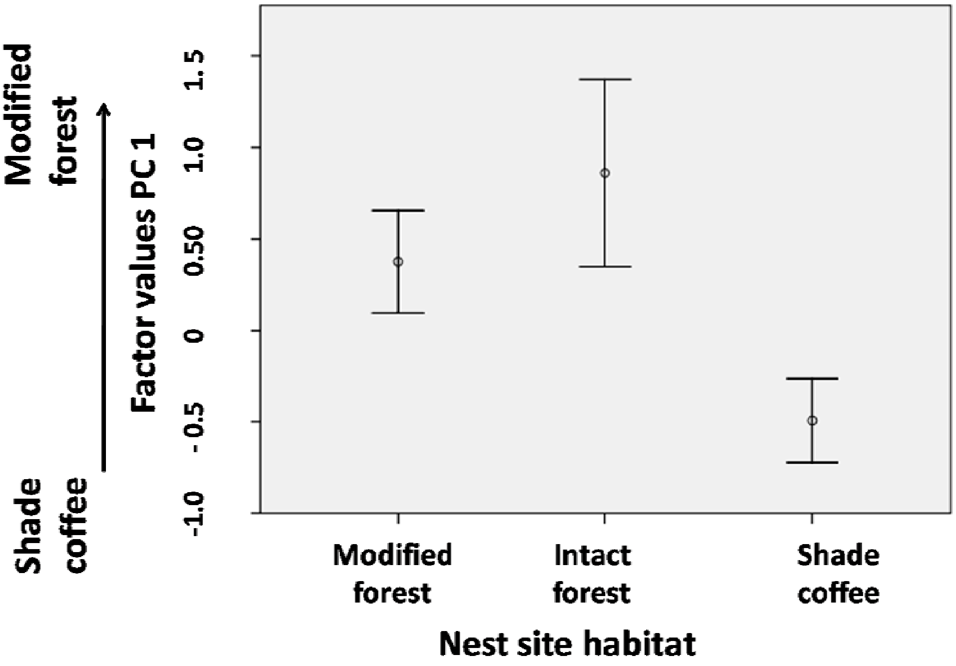


Fig 6a. The proportion of shade coffee and modified habitat in the territory (PC1) predicts nest site habitat for all nest sites.

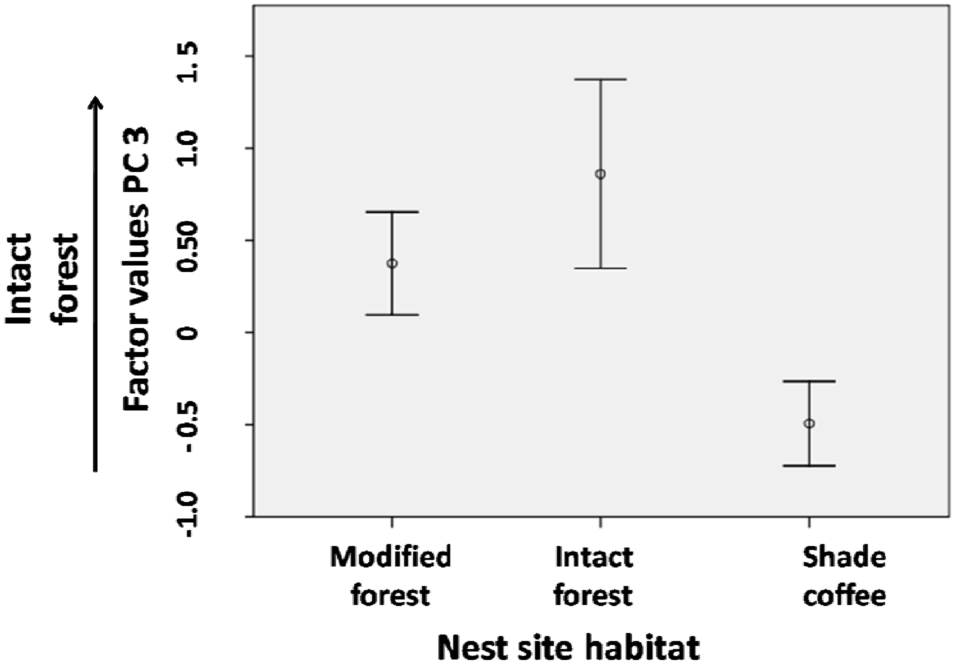


Fig 6b. The proportion of intact forest in the territory (PC 3) predicts nest site habitat for all nest sites.

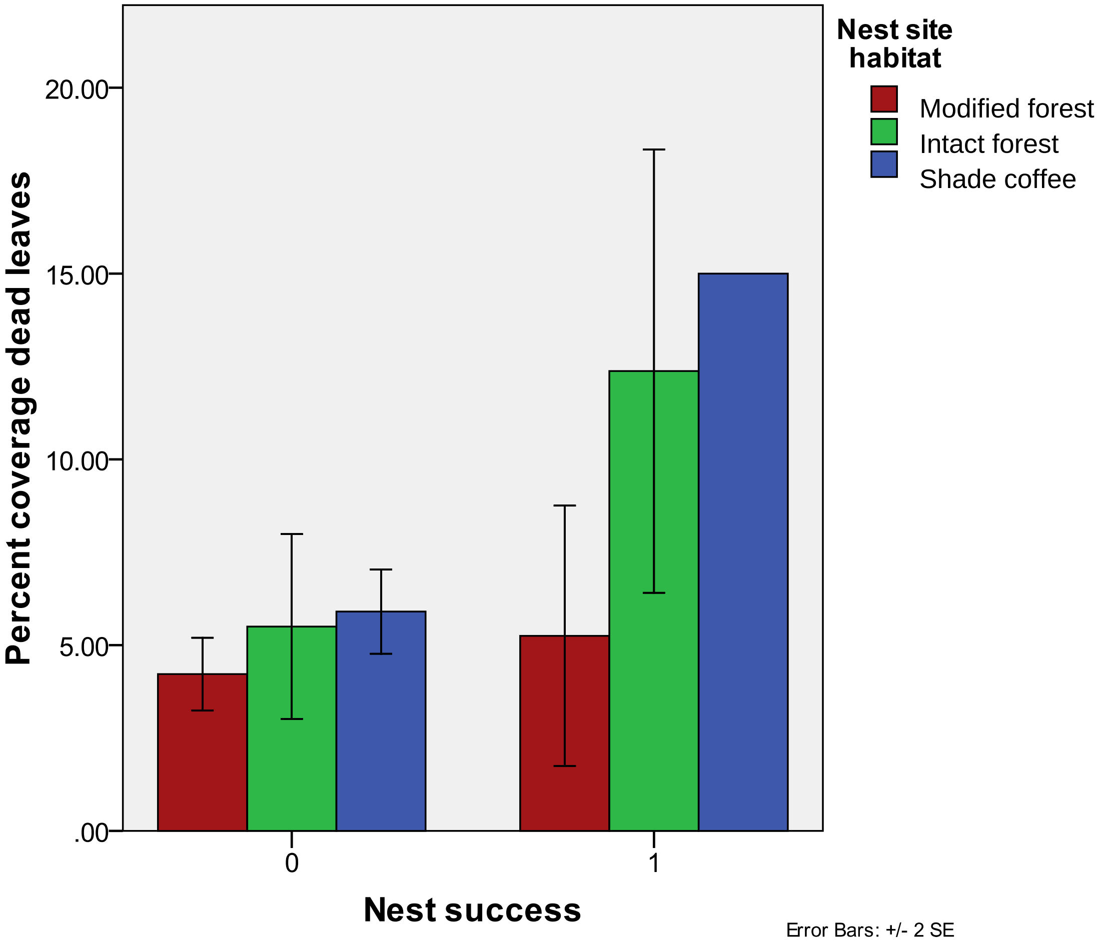


Figure 7. The mean percent cover of dead leaves around nests of *T. rufalbus* that fledged no chicks (nest success=0), and nests that fledged at least one chick (nest success=1). The percent cover of leaves was higher for successful nests in all habitats.

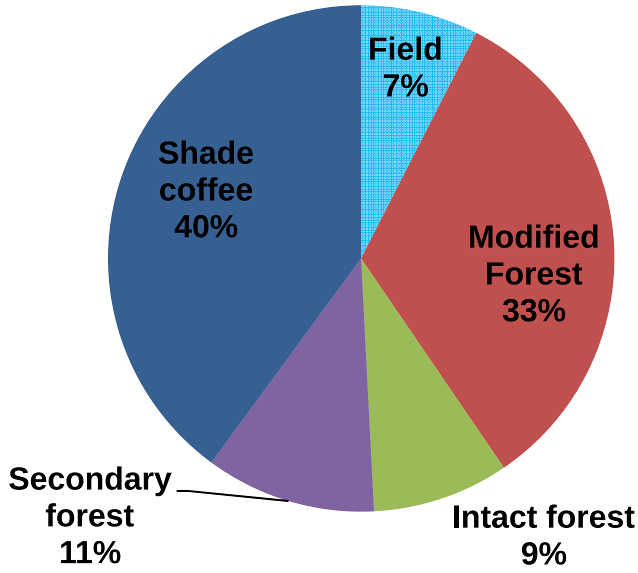


Figure 8a. Mean habitat composition of territories of *T. modestus* that produced no chicks

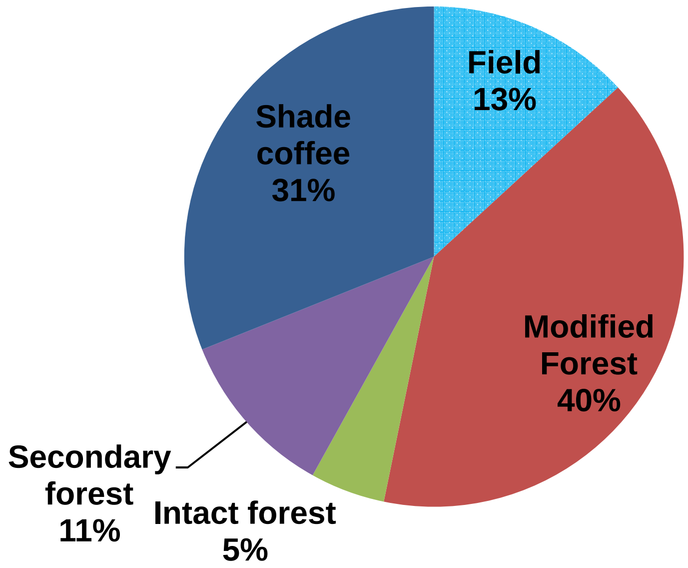


Figure 8b. Mean habitat composition of territories of *T. modestus* that produced at least one trick

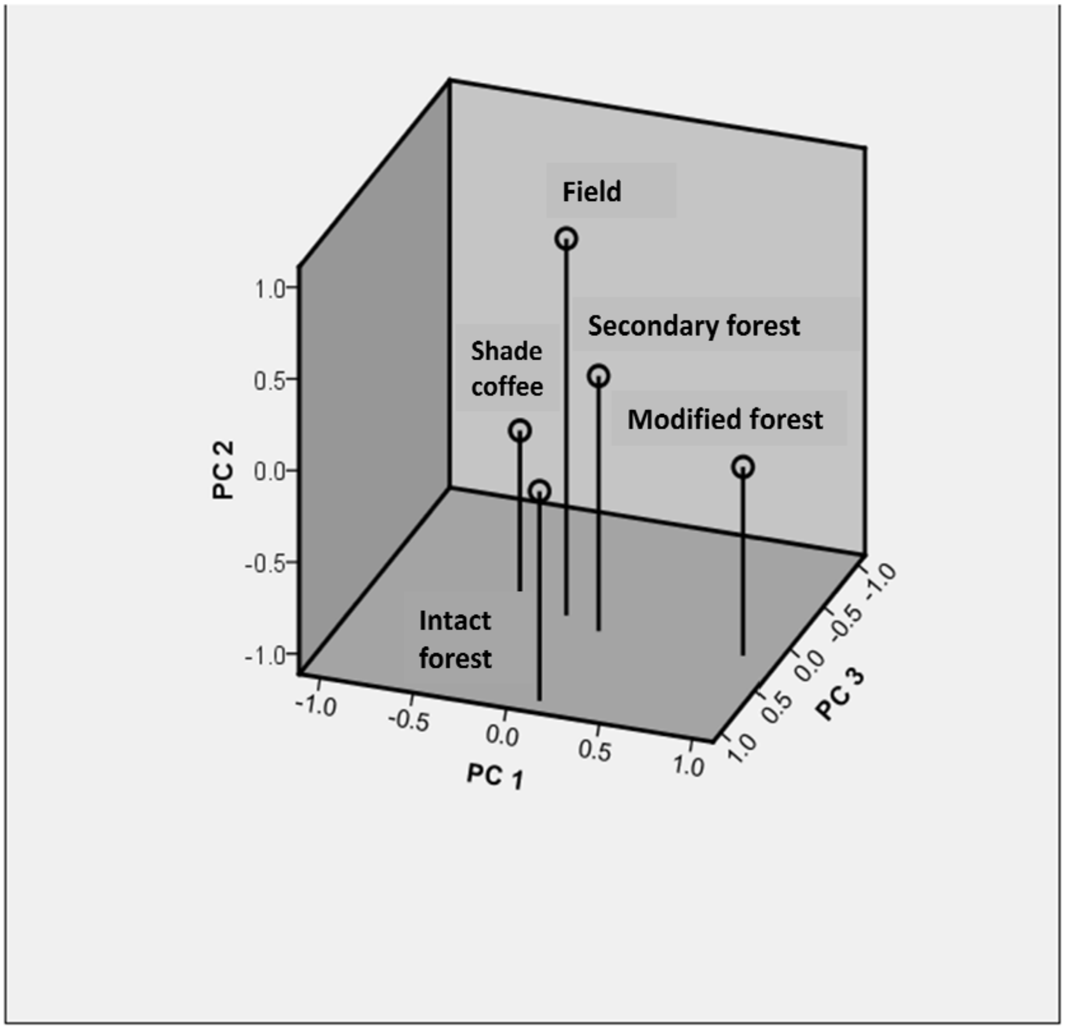


Figure 9. Each principal component captured the variation between one habitat type and all other habitat types in the territories of *T. modestus*. PC 1 captured variation between territories attributable to the proportion of modified forest. PC 2 captured the variation attributable to the proportion of fields. PC 3 captured the variation between territories attributable to the proportion of intact forest.

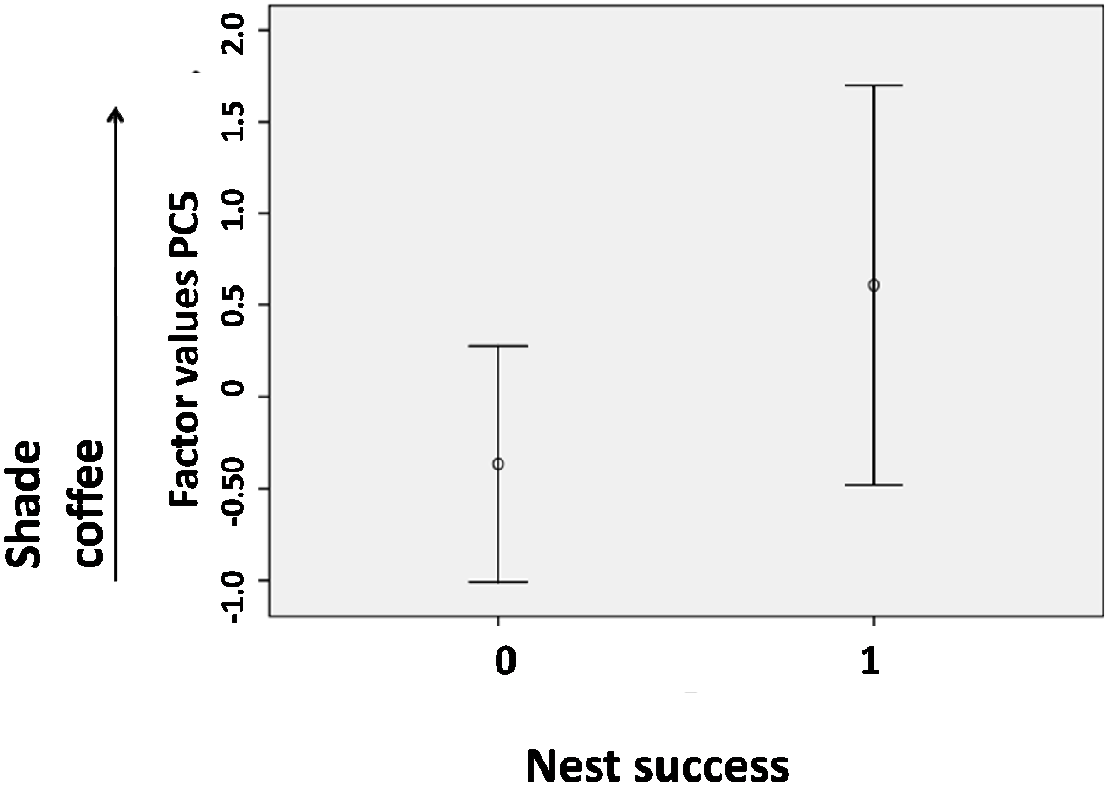


Figure 10. The mean factor values from PC 5 for territories containing nests that fledged no chicks (nest success=0), and nests that fledged at least one chick (nest success=1). The proportion of shade coffee in the territory had no effect on nest success. There was no relationship between the proportion of any habitat in the territory and nest success.

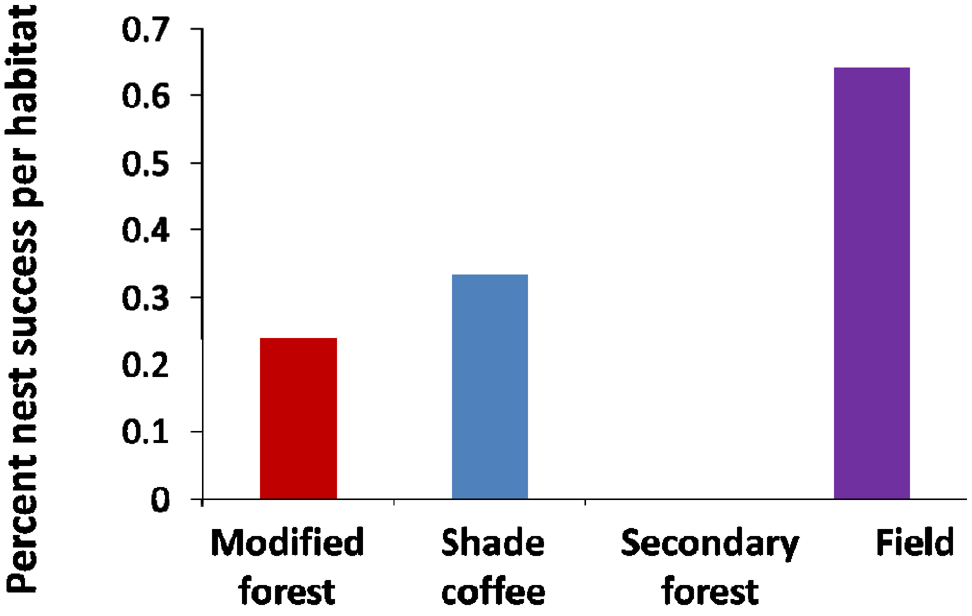


Figure 11a. Percent of successful nests in each habitat. There were 25 nests in modified forest, 21 nests in shade coffee, 13 nests in secondary forest, and 14 nests in field.

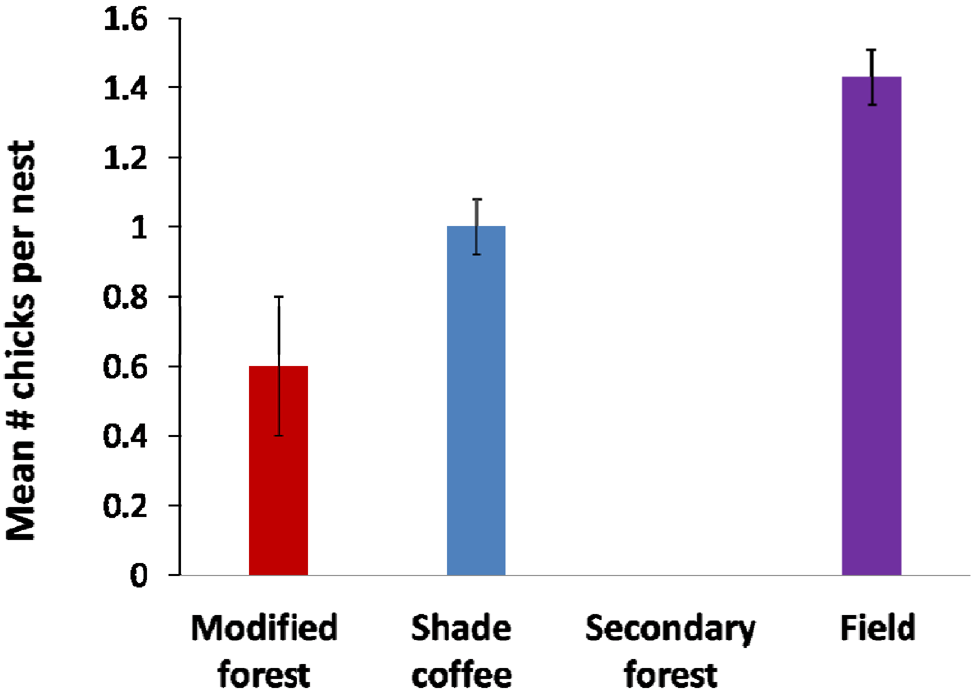
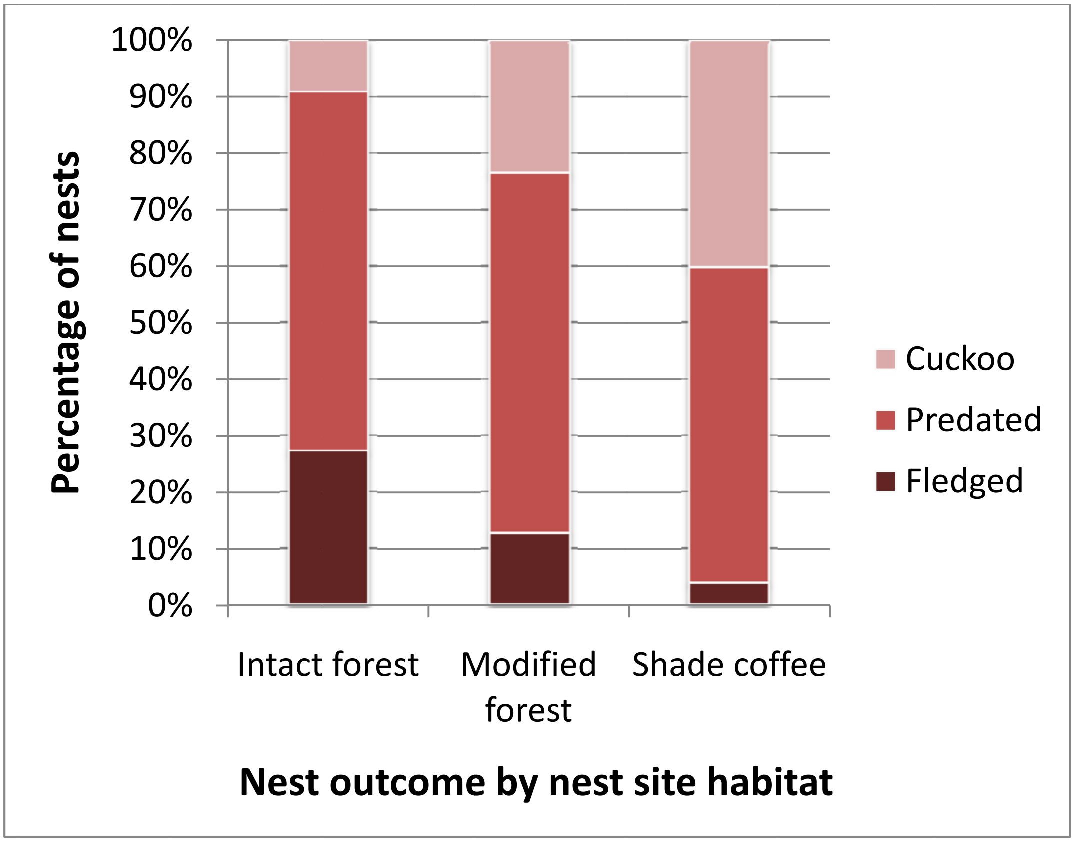


Figure 11b. The mean number of chicks of *T. modestus* fledged for nest sites in different habitats. There was only a significant difference in the number of chicks fledged for nest sites in secondary forest



	Shade coffee	Modified forest	Intact forest
Fledged	3	6	6
Predation	43	30	14
Cuckoo	31	11	2
Disturbance	4	0	0

Figure 12. The percentage f nests that fledged, were lost to predation, or lost to nest parasitism in each nest site habitat. There was a significant relationship between the fraction of failed nests lost to cuckoos vs. predators and the habitat where the nest was located, G-test, Chi-square = 6.85, df = 2, P = 0.033.

Figure 13. The cause of nest loss was not predicted by the habitat composition of the territory, as represented by factor values from principal components analysis. As the regression factor increases so does the proportion of modified forest to shade coffee.

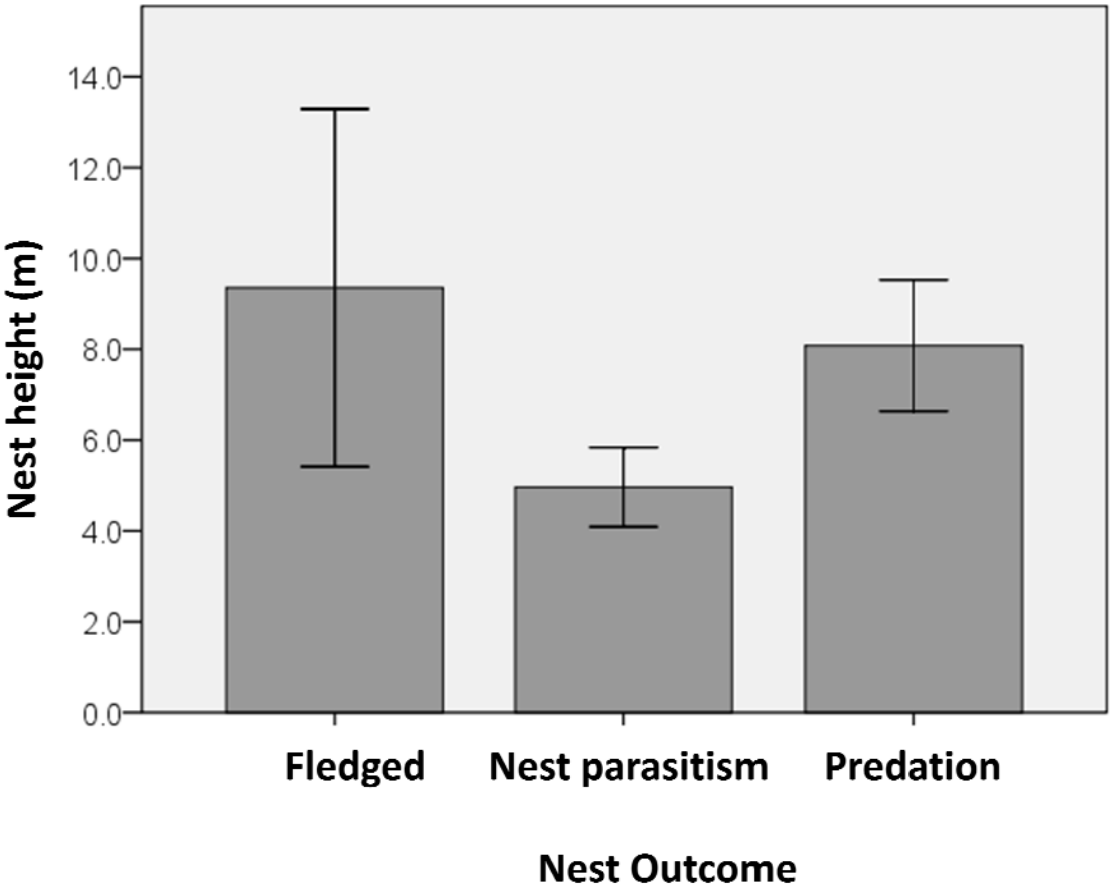


Figure 14. The cause of nest loss was influenced by nest height. Higher nests was more likely to be parasitized by *T. n. excellens* than predated.

	Field	Modified forest	Intact forest	Secondary forest	Shade coffee
PC 1	-0.142	0.981	0.424	0.009	-0.962
PC 2	0.044	-0.162	0.205	0.939	-0.268
PC 3	-0.048	0.053	0.971	-0.019	-0.349

Table. 1 Table of rescaled loading values for each habitat**.** The rescaled loading values for each habitat on the components is below the plot. Principal component 1 captured the relationship between modified forest and coffee, and accounted for 86% of the variation. Principal component 2 captured the variation between territories attributable to secondary forest and accounted for 15% of the variation. Principal component 3 captured the variation between territories attributable to intact forest and accounted for 5% of the variation

	Field	Modified forest	Intact forest	Secondary forest	Shade coffee
PC 1	-0.069	0.923	0.131	0.144	-0.373
PC 2	0.945	-0.081	0.034	0.282	-0.221
PC 3	0.034	0.152	0.979	0.143	-0.116
PC 4	0.264	0.138	0.123	0.925	-0.174
PC 5	-0.174	-0.314	-0.091	-0.154	0.877

Table. 2 Table of rescaled loading values for each habitat**.** Principal component 1 captured variation between territories attributable to modified forest and accounted for 47% of the variation. Principal component 2 captured the variation between territories attributable to fields and accounted for 23% of the variation. Principal component 3 captured the variation between territories attributable to intact forest and accounted for 16% of the variation. Principal component 4 captured the variation between territories attributable to secondary forest and accounted for 9% of the variation. Principal component 5 captured the variation between territories attributable to shade coffee and accounted for 4% of the variation.

Chapert 4: Host specific parasitism in the Central American striped cuckoo (*Tapera naevia excellens*)

ABSTRACT

Old World cuckoos and their brood hosts are one of the oldest model systems used to study coevolution. Many theories on the evolution of brood parasite strategy and host defense have been formulated from research on egg color matching and host egg recognition capabilities. However, no studies have been conducted on host parasite dynamics in the New World cuckoos. I conducted an egg rejection experiment on two hosts of the New World cuckoo *Tapera naevia excellens* to investigate if this brood parasite exhibits host specific egg color matching that increases acceptance rates by the reported hosts *Thryothorus rufalbus* and *Thryothorus modestus*. I found that *T.n.excellens* lays highly mimetic eggs for *T. rufalbus*, in both color and brightness. *T. rufalbus* displayed a high acceptance rate of mimetic experimental eggs and high rejection rates of non-mimetic experimental eggs. *T. modestus* exhibited low rejection rates for both mimetic and non-mimetic experimental eggs, and suffered zero natural parasitism. This indicates that *T.n.excellens* specifies on a single host, *T. rufalbus*, at the study site in northern Nicaragua.

4.1 INTRODUCTION

Scientists use model systems to investigate complex biological phenomena, with the expectation that findings from these studies can be applied to other organisms. One model system for the study of coevolution between hosts and parasites is that of the Old World cuckoos (Family Cuculidae) and their host species. Brood parasitism by the common cuckoo (*Cuculus canorus*) has captivated naturalists since Aristotle, and Darwin used his theory of natural selection to explain the evolution of this unusual breeding strategy (Davies 2000). Over 200 years of research on Old World cuckoos have produced many theories and experimental evidence on the coevolution of parasite strategies and host defenses, many of which focus on egg mimicry and foreign egg recognition. However, virtually nothing is known about parasite and host strategies in the American ground cuckoos (Family Neomorphidae), and it is unclear if the mechanisms identified in European cuckoos are broadly applicable to all cuckoos. In this paper, I present the results of the first experimental study on host specific egg mimicry by a member of the Neomorphidae, the striped cuckoo, *Tapera naevia excellens*.

Brood parasites employ different strategies to avoid rejection of their eggs by a host. One such strategy is a specialist one where they lay highly mimetic eggs to avoid rejection by a single host that is able to discriminate even small variations in egg color, pattern, and size (Davies and Brooke 1989; Johnsgard 1997). However, some species of Old World cuckoos exhibit another strategy, egg color polymorphism that enables different individual parasites to successfully mimic the eggs of multiple host species. Species-specific egg polymorphism is the result of host-specific races , whereby females specialize on a single host for which their eggs are mimetic (Payne 2005). Egg color is likely controlled by female sex-linked W chromosome in Old World cuckoos, and so host specific races can exist in sympatry and are not disrupted by a lack of assortative mating (Gibbs, Sorenson et al. 2000). Host-specific races have been documented for *Cuculus canorus*, *C. pallidis*, *Molothrus rufoaxillari*, and *Chalcites basilis*, and a genetic basis for these races has been shown in *C. canorus* and implicated in *M. rufoaxillaris* (Moksnes and Roskaft 1995; Davies 2000; Gibbs, Sorenson et al. 2000; Langmore, Kilner et al. 2005; Starling, Heinsohn et al. 2006; Mahler, Adamson et al. 2009). Currently, the maintenance of egg polymorphism in a single species of brood parasite is thought to be maintained by host-specific races. Host specificity can be the result of host preference, or from preference for habitat structures near which certain species are found (Honza, Moksnes et al. 2001; Roskaft, Moksnes et al. 2002).

One species of the New World cuckoos, *T. naevia*, lays variable egg morphs, and in this study we examine if host-specific races are present in this species. *T. naevia* is divided into three non-overlapping subspecies that utilize more than 20 host species and vary in egg morphology (Payne 2005). *T.n. chochi*, which ranges from Argentina to southern Brazil, lays only plain white eggs that match the egg color of the 10 hosts found within its range (Friedmann 1933). *T.n. naevia* inhabits northern South America, and has been documented to lay blue-green, bluish-white, or white eggs, although all parasitism events have only been recorded for host species that lay plain white eggs. Most records come from Haverschmidt (1955) and Haverschmidt (1961). In 13 nest parasitism events he found 3 instances of egg color mismatch as perceived by a human observer, with blue-green cuckoo eggs amongst all white clutches of host eggs. *T. n. excellens*, for which there is the least host information, ranges from Panama to Mexico and lays exclusively blue-green eggs. In Nicaragua, the only host record for *T.n.excellen*s is *Thryothorus rufalbus*, which lays blue-green eggs. Two isolated reports from Costa Rica in 1977 document the use of another host *Thryothrus modestus*, which lays plain white eggs (Kiff and Williams 1978). At my study site in Nicaragua, both potential host species are present, yet *T.n. excellens* only parasitize *T. rufalbus*. One explanation for this behavior is that the study site consists of a single host specific race of *T.n. excellens.*

If the study population of *T.n. excellens* is a host race specific for *T. rufalbus*, certain predictions can be made about egg mimicry and host recognition: (i) The degree of egg mimicry exhibited by a host race should reflect the degree of egg discrimination by the preferred host, and (ii) species that are not used as hosts would not display strong egg discrimination. In order to test these predictions, I firstquantified the egg color matching of *T. n. excellens* for *T. rufalbus* using spectrophotometry, as the visual spectra of birds and humans differ. Observations of similarities or differences between host and parasites eggs are not sufficient to identify mimicry, and the identification of host races assessed by human perception of egg color matching may not coincide with the host perception of matching. Secondly, I conducted an egg rejection experiment both *T. rufalbus* and *T. modestus*. The goal of this study was to test whether *T.n.excellens* lays mimetic eggs for *T. rufalbus*, and if color matching increases host acceptance of parasite eggs, indicating a genetically differentiated host race of *T. n. excellens*.

4.2 STUDY SITE AND SPECIES

I conducted this study in Reserva Miraflor (UTM WGS 84 1467524N 165751289E) in the Pacific Slope of Nicaragua, at an altitude of 1100-1280m. This area is a mixture of semi-deciduous montane forest fragments and shade coffee plantations interspersed with pasture and agricultural areas. At the study site, both *T. rufalbus* and *T. modestus* are common and while their territories often overlap, there are some habitat use difference between the species. *T. modestus* prefers dense scrub along the borders of forest or shade coffee and open areas, while *T. rufalbus* nest most commonly along streams, in secondary forest, and in shade coffee plantations. *T. rufalbus*, like most reported host species for *T. n. excellens*, constructs closed retort-shaped nests at 1.5-15m from the ground, while *T. modestus*, constructs domed nests low to the ground. *T. modestus* lays plain white eggs, and *T. rufalbus* lays plain blue-green eggs. Parasitized nests were easily identified, since *T.. n. excellens* eggs are larger and slightly paler in color than T. rufalbus eggs, and parasite chick vocalizations are distinct from host chick. .From 2005-2007, I monitored the nest outcome of 230 *T. rufalbus* nests and 97 *T. modestus* nests and found parasitism rates of the nests of *T. rufalbus* of 29%, with no brood parasitism of *T. modestus* recorded.

4.3 METHODS

4.3.1 Egg Color Mimicry

Egg color similarity between *T. n. excellens*, *T. rufalbus* and *T. modestus* was tested using spectrophotometry of eggs collected from the field site. Spectrophotometry assesses egg coloration, information in the near ultraviolet-ultraviolet range, which is visible to passerine birds (Aviles and Moller 2003). Measurements of ca. 2mm diameter of the eggshell's surface were taken at 0.48nm intervals in the range of 300 – 700nm (the visible spectra for passerines; (Hart and Hunt 2007)) at three random locations on the egg. This was done using an Ocean Optics USB2000 Miniature Fiber Optic Spectrometer, connected to a portable computer, illuminated by a DT mini-lamp and OOIBase32TM operating 136 software (Ocean Optics, Inc. Dunedin, FL, USA). All measurements were taken using a probe maintained at a 90^{o} angle. White and dark standard reflection calibration measurements were taken every 3-6 measurements using an Ocean Optics WS-1 diffuse reflectance standard and a miniature cardboard box, respectively (Cassey, Honza et al. 2008).

Spectrophotometry samples were taken from four *T. n. excellens* and eight *T. rufalbus* eggs from three parasitized nests, and additional samples of *T. rufalbus* eggs were collected from two non-parasitized nests. Four egg samples were taken from three non-parasitized nests of *T. modestus*. Reflectance measurements were taken at 880 wavelengths within the visual spectrum of birds, and I calculated the covariances between these values. Principal components analysis (PCA) was conducted on the covariances of reflectance data for *T. n. excellens* and *T. rufalbus* to summarize color variation into a few orthogonal variables (Aviles, Stokke et al. 2006). The covariance data were used to enable identification of variation in reflectance values representing differences in both color and brightness between the two species.

4.3.2 Host egg discrimination

I conducted an egg rejection study from April to September 2006-2007. I used both plain white and plain blue-green eggs which mimic (verified by spectrophotometry) the color of the eggs laid by *T. modestus* and *T. rufalbus,* respectively. The experimental eggs were made of plaster of paris using a mold measuring 23.3 by 17.9 mm. Experimental cuckoo egg size was based on size records from South America, which turned out to be larger than the average size of collected *T. n. excellens* eggs at the study site, 15.8 by 12.8mm. The larger size of the experimental eggs could trigger a higher rejection rate for both blue-green and white false eggs, but should not alter predictions of egg discrimination by the hosts since all experimental eggs were equal in size. The mass of experimental eggs were similar to host eggs. Both blue-green and white eggs were painted with acrylic paint and sealed with a matte glaze. The reflectance values for false eggs and eggshell samples of *T. n. excellens* were measured along the avian visual spectrum to confirm that the blue-green false eggs accurately matched of the brood parasite eggs. This was done using an Analytical Spectral Devices (ASD) Fieldspec Pro JR spectroradiometer (M. Keuhn, pers. comm.).

For both host species, eggs were placed in the nest within three days of the first egg laying event, and I did not remove a host egg. Eggs were placed in the nests during the late morning, which is when *T. n. excellens* lays (pers. obs.). Because experience with foreign eggs can influence subsequent recognition behaviors, the egg color order was randomized, with an equal number of nests receiving blue-green or white experimental eggs first . The nest was monitored for three days after egg placement. On the third day, the contents of the nest were reviewed, and the first experimental egg was removed if still present, and a different colored egg was placed in the nest. We monitored the nest for another three days after placement of the second egg. In addition, the adults at each nest were the subjects of focal observations at two days and four days after egg placement. Birds were considered to reject eggs when eggs were physically removed from the nest, or if false eggs remained in the nest but displayed evidence of having been pecked. There is no evidence that female *T.n. excellens* remove eggs from the nest before laying their own. Egg rejection results were analyzed using a Kruskal Wallis ANOVA with rejection as a grouping variable, and egg color and order of placement as test variables.

4.4 RESULTS

4.4.1 Egg Color Mimicry

The average reflectance spectra of *T. n. excellens* and *T. rufalbus* both have peak reflectance in the range of 470-530 nm, which corresponds to the blue-green color as seen by humans (Fig. 1). The reflectance for *T. modestus* was flat across most of the spectra, which corresponds to its uniform white appearance. The reflectance data for *T. n.*

excellens closely mimics that of the host *T. rufalbus*, but with lower reflectance values, so that the parasite egg would appear darker than *T. rufalbus* eggs, especially under low light conditions, when achromatic variation between objects is more visible.

The PCA of reflectance values as different wavelengths resulted in three components that explained 99.6% of the data. PC1 explained 96.92% of the data and shows that the majority of the variation between host and parasite eggs is achromatic. It was expected that a large portion of the variation would be explained by achromatic differences, since the eggs of *T. rufalbus* have higher reflectance values than the eggs of *T. n. excellens* (Fig.1). PC1 was nearly spectrally flat, but showed high and negative values at 300-325nm (ultraviolet range) and high and positive values at 650-700nm (infrared range), so that differences in brightness are strongest under high and very low light conditions. PC2 and PC3 combined account for 2.7% of the variance, showing high positive and high negative values at the edge of the bird's visual range in the UV, 350-380nm as well as at 470-510nm, along a green-blue gradient (Fig. 2).

4.4.2 Similarity of experimental egg to *T. n. excellens* egg

The eggshell of *T. n. excellens* had a higher reflectance than either of the false eggs, but reflectance for all eggs was very similar at 380nm (Fig 3). Passerine birds that are ultra violet sensitive have sensitivity maxima between 350-380nm, 450-480nm, 510-540nm, and 570-580nm (Chen, Collins et al. 1984; Rajchard 2009). At the second sensitivity maximum, 450-480nm, reflectance for the false blue-green egg and the true *T. n. excellens* egg were similar. At the third maximum, 570-580nm, the reflectance of the false blue-green egg was slightly higher. The white false egg had a higher reflectance at all wavelengths over 400nm. Thus, the false blue-green eggs were relatively similar to the eggs of *T. n. excellens*, and were a much closer match than the plain white false eggs

4.4.3 Host egg discrimination

In the course of our three year field study, *T. rufalbus* was never documented to reject the eggs of *T. n. excellens*, and we have never found the eggs of *T. n. excellens* in the nests of *T. modestus*. *T. rufalbus* accepted mimetic eggs and rejected non-mimetic eggs, while *T. modestus* accepted both mimetic and non-mimetic eggs (Fig. 4). *T. rufalbus* was more likely to reject non-mimetic experimental eggs than *T. modestus* (Table 1; p=0.005, df=1). *T. modestus* did not exhibit significant levels of rejection of either color false egg (Table 1; Chi-square test: p>0.5, df=1). *T. rufalbus* was more likely to reject a white false egg than a blue-green false egg (Table 1; Chi-square test: p=0.002, df=1). The order of the placement of eggs in the nest did not affect rejection rates (Kruskal-Wallis H test: p=0.367). All cases of egg rejection by *T. rufalbus* were through nest abandonment.

4.5 DISCUSSION

At the study site, *T. n. excellens,* lays highly mimetic eggs for a single host, indicating that the study population may be a host race specializing on *T. rufalbus*. I made two predictions that would support the contention of a host specific race for *T. rufalbus*: (i) The degree of egg mimicry exhibited a host race should reflect the degree of egg discrimination by the preferred host, and (ii) species that are not used as hosts would not display strong egg discrimination. The results of this study found that rates of non-mimetic egg rejection by *T. rufalbus* were consistent with foreign egg discrimination but that the non-host species *T. modestus* did not exhibit egg rejection had has low discrimination capabilities.

My first prediction was that the degree of egg mimicry in a host-specific race should reflect the degree of egg discrimination by the host. Spectral analysis demonstrates that *T. n. excellens* eggs are chromatically mimetic for the host *T. rufalbus*, but not for the non-host species, *T. modestus*. Although there is no data on the color sensitivity of *Thryothorus* wrens, many passerine birds are violet or ultraviolet sensitive, with sensitivity peaks at 450-480nm and 565-620nm. At these wavelengths, the reflectance values were closely matched between host and parasite eggs (Fig. 2). Many species of insectivorous birds use chromatic cues to find prey, and it is likely *Thryothorus* wrens experience violet sensitivity (Stobbe, Dimitrova et al. 2009).

The most frequently documented form of egg mimicry is chromatic, but there is strong evidence that achromatic reflectance plays a role in rejection-avoidance strategies employed by nest parasites. Studies of the common cuckoo have shown that brighter parasite eggs result in higher rates of rejection in nests with low light conditions (Aviles 2008). Bronze cuckoos (*Chalcites spp.*) lay dark colored eggs in the enclosed nests of the superb fairy wrens (*Malurus cyaneus*), and avoid egg rejection through crypsis rather than mimicry (Langmore and Kilner 2009; Langmore, Stevens et al. 2009). *T. n.*

excellens may attempt to decrease rejection rates by laying eggs that are both color matched and that have a lower reflectance, making them less visible in low light conditions. In this study, the majority of variation in reflectance between host and parasite eggs was in the achromatic range, with the most variation at high wavelengths, which would be the most predominant form of light in the enclosed nests of *T. rufalbus*. The results demonstrate that the eggs of *T. n. excellens* are highly mimetic for the eggs of *T. rufalbus* in color and may also rely on reduced reflectance to evade detection in the closed nests of the host.

Having shown that the eggs of *T. n. excellens* are mimetic, I predicted that *T. rufalbus* would exhibit a high degree of egg discrimination, and reject experimental non-mimetic white eggs. I found that *T. rufalbus* displayed levels of egg rejection (47%) that are consistent with the theory that the host is able to discriminate between its own eggs and non-mimetic foreign eggs (Robert and Sorci 1999; Langmore, Kilner et al. 2005; Cassey, Honza et al. 2008). *T. rufalbus* and was significantly more likely to accept blue-green over white eggs experimental eggs, supporting the hypothesis that egg color matching by *T. n. excellens* is a host-specific strategy to avoid egg rejection (Fig. 4).

My second prediction, that passerine species not used as hosts should not display strong egg discrimination, is supported by the lack of egg discrimination in the *T. modestus* for both mimetic and non-mimetic eggs (Fig. 4). At the study site, the *T. naevia* has only been observed to parasitize *T. rufalbus,* and parasite eggs have only been found in their nests. In three years of study, we never observed *T. naevia* to visit the nests of the *T. modestus,* nor did we ever find parasite eggs in their nests. The lack of parasitism did not appear to be the result of host specific habitat use, host density, or host population variance (Vogl, Taborsky et al. 2002; Brown and Lawes 2007; Stokke, Hafstad et al. 2007; Soler, Vivaldi et al. 2009). Although *T. rufalbus* has a larger population size than *T. modestus* at the study site, both species have high local densities, frequently overlap territories, and maintained stable population sizes over the course of the study (M. Mark, unpub. data). In other host-parasite systems, the size of the nest and/or the placement of the nest in the habitat influences rates of parasitism (Soler, Martinez et al. 1999; Hauber 2001). The most plausible explanation for the lack of parasitism on *T. modestus* is that *T. n. excellens* prefers the nest type and location of *T. rufalbus* over that of *T. modestus*. All other reported hosts of *T. naevia* construct closed or retort shaped nests at least 1m high, while *T. modestus* constructs dome shaped nests often close to the ground. In addition, only one report exists for *T. modestus* a host species for *T. naevia*, indicating it may be a rarely used or unsuitable host (Kiff and Williams 1978).

The evidence presented here suggests that the study population of *T. n. excellens* is a host-specific race for *T. rufalbus*, but the origin of this specificity in unknown. The observed 47% rate of rejection of non-mimetic eggs and natural parasitism rates of 30% should provide theoretically sufficient directional selection to lead to the predominance of a single egg color, blue-green, in *T. n. excellens* (Oien, Moksnes et al. 1995; Langmore, Kilner et al. 2005; Aviles, Stokke et al. 2006). Robert and Sorci (1999) found that rates of egg rejection from a novel nest parasite increased nearly three-fold in a sixteen year period when foreign eggs were non-mimetic. Nest parasitism by *T. n. excellens* is associated with a high cost, and parasitism defense behaviors would be expected to evolve rapidly. However, it is unclear why *T.n. excellens* would evolve mimetic eggs for a host with dark enclosed nests, unless these eggs are rejected less frequently than cryptic eggs. Although there was almost complete acceptance of color-matched eggs, I did not tests if the host was unable to discriminate between its own and the experimental eggs due to the blue-green color or the reduced reflectance in a dark nest. *T. rufalbus* is the only reported host species with blue-green eggs, and further studies on host discrimination abilities would increase our understanding on the coevolution of host-parasite strategies in this system (Sorenson, Sefc et al. 2003; Payne 2005). Ahumada (2001) found that in a population of *T. n. naevia* in northeastern Colombia that *T. rufalbus* was used as a host, while the congener *Thryothorus leucotis* was not, indicating that perhaps *T. naevia* subspecies are composed of host-specifc races throughout its range. The confirmation of a host-specific races in *T. n. excellens* would be possible through studies of population genetics and host preferences and egg color for different populations within each subspecies.

4.6 CONCLUSIONS

The coevolutionary dynamics of brood parasites, although an active area of research, are still not well understood, and the most detailed work has come from studies of European and Australian cuckoos (Oien, Moksnes et al. 1995; Gibbs, Brooke et al. 1996; Langmore, Kilner et al. 2005; Aviles, Stokke et al. 2007; Kruger 2007; Broom, Ruxton et al. 2008; Davies and Welbergen 2009; Soler, Vivaldi et al. 2009). Host specialization and egg mimicry are key components of existing theories on the origins of brood parasitism, and any information regarding these strategies in the poorly-studied

New World ground cuckoos can further our development of these theories. This study represents the first experimental evidence of egg discrimination by hosts of the striped cuckoo *T. n. excellens.* Egg mimicry by *T. n. excellens* and lack of egg discrimination for mimetic eggs by *T. rufalbus* provide evidence for host specificity at the study site. To fully understand the role of egg mimicry in host-parasite dynamics in *T. n. excellens,* more information is needed on the genetic relationship between populations of *T. n. excellens* and interactions between the brood parasite and other reported and potential host species throughout its range.

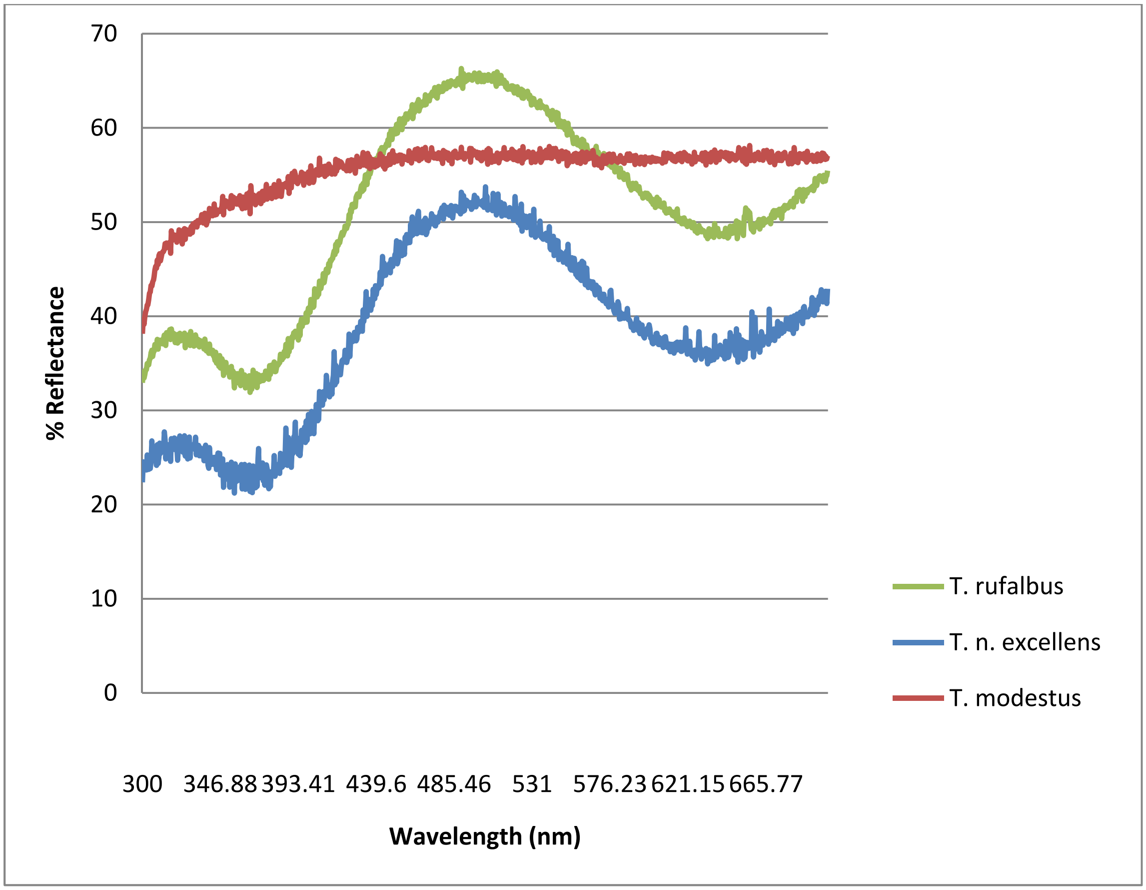


Figure 1. Average reflectance spectra of the brood parasite *T.n. excellens* and two reported hosts, *T. rufalbus* and *T. modestus*.

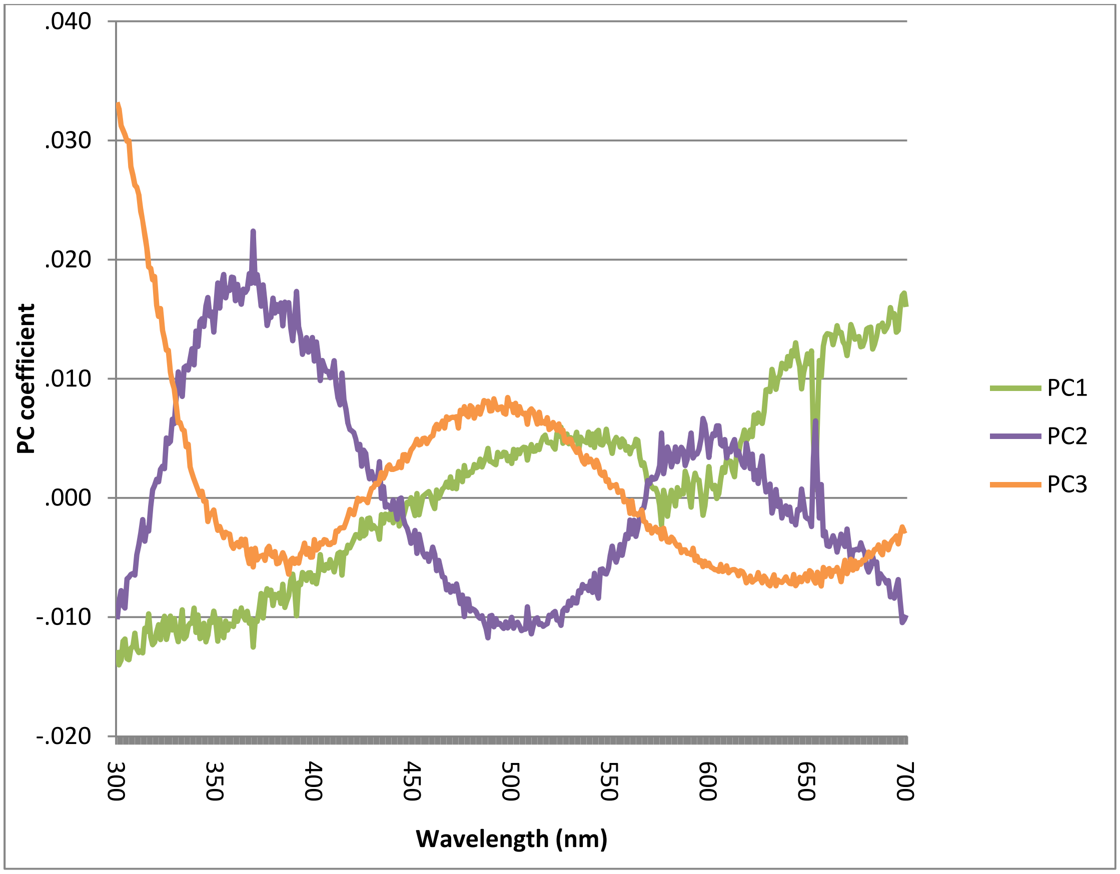


Figure 2. Principal components derived from reflectance spectra of *T.n. excellens* and *T. rufalbus* eggs. PC1 is principal component 1 and describes achromatic variation (96.9% of variation). PC2 and PC3 are principal components 2 and 3 respectively and describe chromatic variation (2.71% of variation).

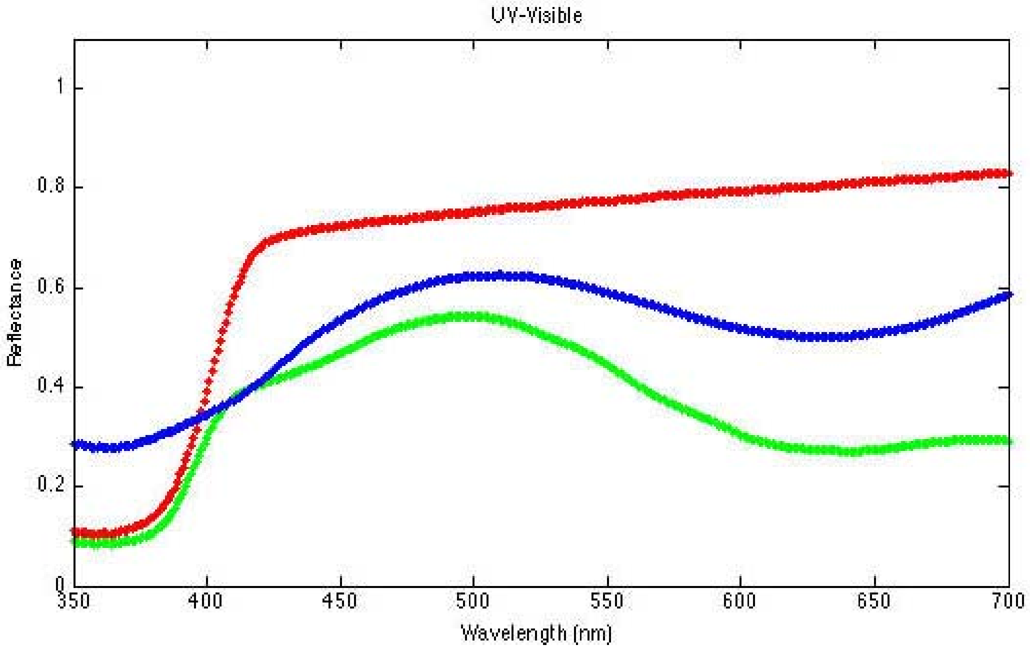


Figure 3. Reflectance spectra of *Tapera naevia* egg (blue), false blue egg (green), and false white egg (red) in the ultraviolet (<400nm) and visible (400nm-700nm) spectra.

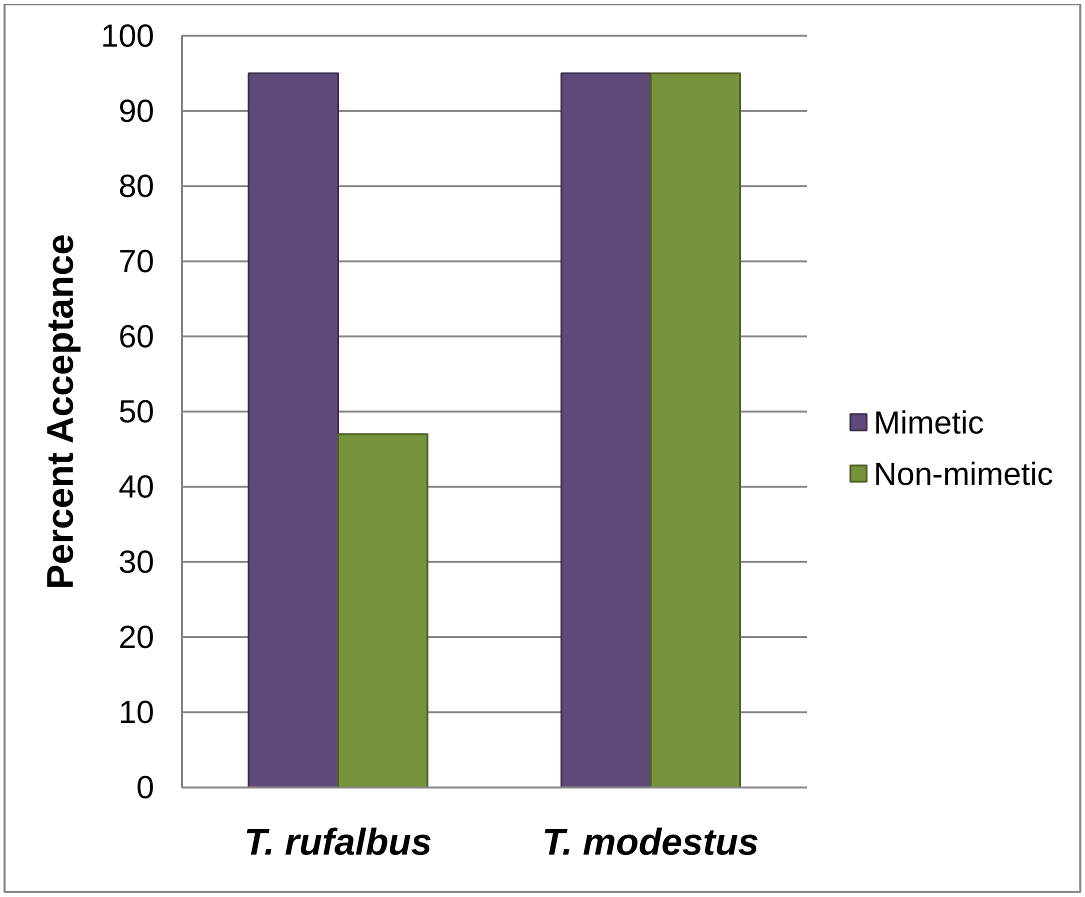


Figure. 4 Percent acceptance of mimetic and non-mimetic eggs of two potential host species.

SPECIES	**Accepted blue-green**	**Rejected blue-green**	**Accepted white**	**Rejected white**
Thryothorus rufalbus	18	1	8	11
Thryothorus modestus	20	1	20	1

Table 1. Egg discrimination by *T. rufalbus* and *T. modestus* for mimetic and non mimetic experimental eggs.

Chapter 5. Discussion and conclusions

5.1 DISCUSSION

Habitat loss is the largest threat to avian biodiversity in Mesoamerica. Agroforestry systems can contribute to preservation of biodiversity in rural Mesoamerican landscapes by facilitating dispersal between forest fragments and maintaining metapopulation dynamics (Vandermeer 2007). For birds, this claim is based on numerous studies that have measured high abundances of generalist forest species in floristically and structurally diverse coffee farms. High abundance is purported to be an appropriate proxy for demography, but this is approach is questionable in human modified landscapes where novel conditions can disrupt the link between indicators of habitat quality and individual response to those cues (Battin 2004; Bock and Jones 2004). Habitat selection models can be used to evaluate the capacity of coffee agroecosystems to protect avian biodiversity by providing a habitat alternative to native forests.

Habitat ecology is the interplay between habitat choices and the consequences of those choices (Jones 2001). Scale has been shown to influence habitat choices of birds in modified rural landscapes in temperate areas (Chalfoun and Martin 2007). However, little is known about how territorial Neotropical birds exhibit habitat choice in modified landscapes. In this study, I investigated the habitat ecology of two wren species in an agroecosystem. First, I examined the influence of scale on habitat selection in two species of wren frequently found in shade coffee, *Thryothorus rufalbus* and *Thryothorus* *modestus.* Second, I focused on the consequences of habitat selection on reproductive success in *T. rufalbus*. Lastly, I studied how brood parasitism by the striped cuckoo, *Tapera naevia excellens,* is a limiting factor to reproductive success in *T. rufalbus* but not *T. modestus.*

Both wren species displayed habitat preferences at the level of the territory and the nest. At the level of the territory, both species showed a preference for shade coffee, although this preference was much stronger in *T. rufalbus*. Non-breeding *T. rufalbus* preferred shade coffee more than their breeding counterparts, while the opposite was true for *T. modestus. Thryothorus modestus* placed equal importance on shade coffee and modified forest in the territory. At the nest level, only *T. rufalbus* exhibited a strong preference for placing nests in shade coffee, while *T. modestus* exhibited a weak preference. *T. rufalbus* prefers nests sites with low understory vegetation and high canopy cover, while the opposite is true of *T. modestus*. Each species placed their nests in different locations in shade coffee in order to maximize the preferred vegetation around the nest.

Habitat choice by these birds highlights the important of evaluating habitat quality of coffee agroecosystems on a species-specific basis. Rettie and Missier (2000) suggest that habitat selection made at broader scales may be more relevant to studies of habitat choice, as these decisions occur more slowly and constrain lower-level processes. For *T. rufalbus,* habitat selection at the scale of the territory constrained nest site selection by reducing the availability of appropriate nest sites. However, it was selection of the preferred nest site vegetation that determined in which habitat the nests were placed, so that the study of higher level selection alone is not sufficient to understand the consequences of habitat choice. And for *T. modestus*, nest site selection was not constrained by higher level selection at the scale of the territory. Because of this, *T. modestus* was able to place its nests in almost any habitat, *T. rufalbus* exhibited strong preference for nest site characteristics that were most common in intact forest and shade coffee.

In the second part of this study, I examined how habitat choices made at different scales affected reproductive success in *T. rufalbus*, the species that exhibited the strongest habitat preferences,. At the scale of the nest site, preference for certain nest site variables did not reduce the risk of nest loss; conversely, these preferences may contribute to an ecological trap. The primary factor limiting nest success in all habitats was nest predation. An additional threat, brood parasitism by *Tapera naevia excellens*, only occurred in territories with shade coffee, and disproportionately at nests in shade coffee sites. *Thryothorus rufalbus* exhibited preference for nest site variables commonly found in shade coffee and intact forest. These habitats confer the lowest and highest reproductive success, respectively. Nest sites were placed in the more abundant of the two habitats and the proportion of shade coffee in the habitat was negatively correlated to forest habitat. Thus, habitat choice at the level of the territory constrained the ability to make adaptive habitat choice decisions at the scale of the nest, resulting in high variation in nest success. The only vegetation variable around the nest that had a positive influence on nest success was also correlated with intact forest habitat, where nest parasitism rarely occurred. *Thryothorus rufalbus* also exhibited a high propensity to place territories near waterways, and anecdotal evidence suggests that waterways provide a movement corridor for *T. n. excellens* in agroforestry landscapes. This provides further evidence for the

Rettie-Meisser hypothesis that habitat selection at broader scales is most relevant when evaluating demographic effects. In this case, preference for shade coffee at broader scales does not help individuals to overcome the population-limiting factor of nest parasitism, but instead increases susceptibility to it.

In the third part of this study, I focused on the high rate of nest parasitism by *T. n. excellens* on *T. rufalbus*, and the lack of parasitism on *T. modestus*. *Tapera n. excellens* is a little studied New World cuckoo, and host-parasite dynamics in this species are not well understood. *Tapera n. excellens* lays eggs that are similar in color to those of *T. rufalbus*, and I hypothesized that host specificity explained the lack of parasitism on the other reported host, *T. modestus*. From an egg rejection experiment, I found that *T. modestus* did not exhibit any foreign egg recognition, and accepted all eggs into its nest. *T. rufalbus* accepted color matched eggs, and exhibited mixed acceptance of non-color matched eggs. *Tapera n. excellens* is host specific for *T. rufalbus* at the study site, and this specificity may be explained by rejection behavior for non-mimetic eggs in *T. rufalbus*. *Tapera n. excellens* prefers open areas and scrubland as foraging sites and typically parasitizes nests on forest edges. While this species generally avoids forest interiors, is commonly found moving and foraging in shade coffee moving through shade coffee, and has been seen foraging in shade coffee areas (pers. obsv.Haverschmidt 1955; Haverschmidt 1961). *T. modestus* is also an edge species, and *T. n. excellens* should encounter an equal number, if not more, nests of *T. modestus* than *T. rufalbus* in agroforestry landscapes, yet remains host specific for *T. rufalbus*. Land use conversion of forests to shade coffee may have increased the contact between *T. n. excellens* and *T.*

rufalbus, as shade coffee has provided an additional habitat for the former and an alternative for the latter.

Harvey et al. (2007) proposed six strategies to combine biodiversity conservation and sustainable rural livelihoods in Mesoamerica. The first strategy is to identify and prioritize rural hotspots, and coffee production overlaps with many biodiversity hotspots in the region. The second strategy identified by Harvey et al. (2007) is to identify and mitigate key threats to biodiversity. The evidence from this study suggests that shade coffee itself can be a threat to some species of birds, and that management of shade coffee that benefits one species may be detrimental to another. However, if preference to shade coffee is maladaptive, steps can be taken to either reduce preference or reduce the risks associated with preference. In the specific case of *T. rufalbus*, the development of forest borders around shade coffee may discourage *T. n. excellens* from moving into coffee areas. Another possible management tool would be to encourage shade coffee to be planted further from streams, which may reduce the amount of shade coffee included in the territory.

The results of this study, although focused on two species of *Thryothorus* wren, have broader implications for the conservation of common birds in human modified landscapes. Conservation efforts for common species have lagged behind those of threatened species with good reason: a limited amount of time and money necessitates focusing efforts on species on the brink of extinction. However, this approach can be more costly and less effective than preventative measures ensuring that common and abundant species do not become rare. Common species that are able to survive in modified landscapes have received the least attention, due to their apparent ability to survive in areas where more sensitive species cannot. But, as the results of this study show, high abundances do not always indicate stable populations. Agroforestry landscapes with a high diversity of bird species provide an opportunity to work towards the preservation of biodiversity and the promotion of sustainable development, while also providing an experimental landscape for the study of common species.

Shade grown coffee has been the focus of development efforts in Nicaragua as a fair trade product that can improve the lives of local small-holding farmers. As part of this development process, coffee cooperatives actively manage farms to meet certification criteria that ensure a higher price for their product. Differing management regimes have been shown to affect biological communities in shade coffee, and studies on the ecological processes taking place within coffee can inform management decisions. However, there have been few studies on how to effectively manage shade coffee to support stable populations of species so that agroforestry landscapes can contribute to the the long term preservation of biodiversity. In the case of birds (and many other species), long-term data on reproduction and survival in different habitats would be the first indicator of population health. I suggest that teams of locals could be established in agroforestry landscapes to provide this basic, but necessary, information. This information could then be used to direct future studies on management of shade coffee so that it is attractive to those species it benefits, but less accessible to species for which it may be an ecological trap or population sink. Conservation initiatives in agroforestry landscapes could be effective if they result in an economic benefit to impoverished farmers. I suggest that conservation biologists work closely with fair trade and organic certification bodies to encourage the requirement of population monitoring programs and possibly a price bonus for coffee produced from highly diverse farms.

5.2 CONCLUSIONS

True alternative habitats that contribute to conservation will promote the survival and reproductive success of individuals that choose those habitats. Shade coffee is an attractive idea as an alternative habitat because is offers a compromise between profitability and biodiversity preservation. Floristically and structurally diverse shade coffee farms create habitat for many species of birds (Tejeda-Cruz and Sutherland 2004; Hernandez-Martinez, Manson et al. 2009). However, the results of this study suggest that shade coffee cannot be considered an alternative high quality habitat for all species that are found in high abundances. In fact, preference for shade coffee that results in high abundance may be detrimental to the population, as is demonstrated for *T. rufalbus*. The costs and benefits of residence in shade coffee should be evaluated for individual species of interest. If coffee is to be considered an alternative habitat, it must be subject to the same critical analysis that ecologists have conducted on native forests habitats. Some researchers even advocate shade coffee as a model system for the study of forest ecosystem processes (Cruz-Angon, Sillett et al. 2008). The successful management of shade coffee production to maximize the long-term preservation of avian biodiversity depends upon having accurate information on habitat selection and its consequences for birds living in rural landscapes.

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