

September 2001

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# Niche Partitioning of Monteverde Warbler Species based on Differences in Microhabitat and Vertical Stratification

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## ABSTRACT

Two congeneric warbler species in Monteverde occupy similar niches and may be competing for resources. The Three-striped Warbler (*Basileuterus tristriatus*) and the Golden-crowned Warbler (*B. culicivorus*) are both forest interior species that glean and sally for insects within several meters of the ground. This study looks at foraging preferences in these two species in areas of overlap and non-overlap, which is particularly important in light of recent geographic shifts upslope by the Golden-crowned Warbler (Donnelly 1998; Pounds 1999). The results show that the Three-striped and the Golden-crowned Warbler significantly overlap in both altitude (between 1420 m and 1485 m) and in habitat. They each used different microhabitats with greater frequency - the Three-striped Warbler preferred to forage in leaves and among epiphytes while the Golden-crowned preferred to forage on branch interiors and on stems of bushes. When the species did not overlap, the Three-striped Warbler foraged at a mean height of 2.4 m and the Golden-crowned Warblers at a mean height of 2.8 m. They shifted these heights up and down respectively when they were found overlapping (Three-striped = 2.1 m, Golden-crowned = 3.3 m). When individuals were actually observed foraging in the same species flock, they continued to display these trends in mean foraging height (Three-striped = 2.8 m, Golden-crowned = 4.0 m). Therefore this study shows that based on microhabitat preferences and vertical stratification, these two species of warbler partition their niches.

## RESUMEN

Dos especies del género *Basileuterus* ocupan nichos parecidos y pueden competir por recursos. La Reinita cabecilistada (*B. tristriatus*) y La Reinita Coronidorada (*B. culicivorus*) son especies del interior del bosque que rebuscan activamente entre el follaje, metiendo el pico entre hojas y haciendo vuelos veloces tras insectos usualmente dentro del sotobosque. Este estudio investiga preferencias de forrajeo de estas especies, tanto en áreas donde se encuentran ambas especies como en áreas donde hay una sola especie, lo cual es relevante, especialmente en el contexto de reciente colonización por la Reinita Coronidorada de elevaciones altas (Donnelly 1998; Pounds 1999). Los resultados indican que las dos reinitas son encontrados en una franja altitudinal (1420 -1485 m), en

el mismo tipo de hábitat. Usan diferente micro hábitats: La Reinita Cabecilistada forrajea entre hojas y epifitas mientras La Reinita Coronidorada forrajea en los interiores de ramas y tallos. En áreas donde solo La Reinita Cabecilistada se encuentra, hace forrajeos a 2.4 m de alto y donde solo existe La Reinita Coronidorada, ella forrajea a 2.8 m. Ellos cambian de alturas preferidas a alturas de forrajeo cuando están juntos en el hábitat, con La Reinita Cabecilistada prefiriendo alturas de 2.1 m y La Reinita Coronidorada de 3.3 m. En las ocasiones cuando las dos especies forrajean en el mismo grupo de especies mixtas, La Reinita Cabecilistada se encuentra a los 2.8 m mientras La Reinita Coronidorada esta a los 4.0 m. Por eso, el estudio muestra que las dos especies reparten los nichos a través de diferencias en sus micro hábitats preferidos y alturas de forrajeo preferidas.

## INTRODUCTION

A niche is defined as the role an organism plays in a community based on the resources it uses to survive and reproduce (Krebs 1994). Some species experience overlaps in their niches by utilizing similar resources in similar ways, leading to potential competition (Shorrocks 2001). Over time, natural selection will inevitably cause one of these species to go extinct, an idea known as Hardin's Competitive Exclusion Principle (Ricklefs 1990). Or it is possible that these competitive pressures will lead to specialization by each species on different aspects the competing resources, in which case they partition their niches (Krebs 1994).

Many studies examining species interactions have shown that subtle differences in habitat, diet, nesting behavior, and/or other factors allow species to partition their niches (Shorrocks 2001). MacArthur (1958) examined five warbler species in pine forests of the Northeastern United States, showing how they niche partition through differences in foraging location, feeding behavior, and nesting preference. Others studies have shown that birds forage at different vertical heights within their habitat, enabling them to divide and partition their resources (Cronholm 1999; Pearson 1971; Terborgh 1980).

Changes in land use and climate can impact species' geographical ranges, throwing formerly separate species into direct competition. This may be the case with several closely related bird species in Monteverde, Costa Rica. Pounds et al. (1999) demonstrated that many low elevation birds have migrated upslope into Monteverde, into zones where they were not previously found. One aspect of the study showed that over the past three decades, higher elevation bird species maintained their altitude ranges, while lower montane species, including the Golden-crowned Warbler (*Basileuterus culicivorus*) which is studied in this experiment, showed a trend of upslope colonization. They demonstrated that these shifts in geographical ranges correlate with an overall drying effect in Monteverde, which he attributes to global climate change caused by increasing sea-surface temperatures (Pounds et al. 1999). A similar study by Lawton et al. (2001) attributes these same drying effects and geographic shifts in Monteverde to deforestation and conversion of Costa Rican lowlands to pasture and a rising cloudbank.

Here, I studied the effects of a reported recent upward expansion of the Golden-crowned Warbler into areas formerly occupied by the Three-striped Warbler (*B. tristriatus*). Both are common residents in Monteverde historically, only overlapping quantity (Fogden 1993). Fogden (1993) reports that the Golden-crowned Warbler's range

extends from 700 m up to 1500 m, and occasionally individuals are found up to 1600 m. This one hundred meter band between 1500 m and 1600 m defines the previous fatted of overlap between these species, as the Three-striped Warbler's range extends from 1500 m up to the Continental Divide (Fogden 1993). Furthermore, both species use the same habitats in the forest understory, gleaning and sallying for insects in both conspecific and mixed-species foraging flocks (Stiles and Skutch 1989). So the potential for competition and niche partitioning already exists between these two species. But recently it has been shown that the Golden-crowned Warbler is moving upslope and can be found up to the Continental Divide (Pounds et al. 1999; Donnelly 1998), which might suggest an increase in competitive pressures on the two species. Therefore, I hypothesized that the Three-striped and Golden-crowned Warbler will further partition their niches, as the Golden-crowned Warbler shifts more and more into the range of the Three-striped Warbler.

## **METHODS**

Data were collected between October 19 and November 15, 2001 at four different study sites of primary and secondary forest interior, as well as some edge habitats and some secondary scrub. The study sites used included the Monteverde Cloud Forest Reserve (~1500 - 1630 m), the Sendero Tranquilo Reserve (~1380 - 1535 m), the Bajo del Tigre Area of Bosque Eterno de los Niños (~1150 - 1360 m), and forest patches on the private Rockwell farm (~1300 - 1365 m). These four sites allowed fairly adequate forest ranges for the three warbler species studies based on altitudinal variation, but at lower altitudes, large stands of primary forest were largely absent. Proportionally I spent more days collecting data at the Sendero Tranquilo Reserve (~ 1380 - 1535m) because the Three-striped and Golden-crowned Warblers are found to overlap most frequently in forests at these altitude ranges.

Data collection involved bird watching at each of the four study sites, generally in the morning hours. I recorded visual observations of individuals, estimating foraging height and vegetational microhabitat preferences. I defined seven different microhabitats based on preliminary observations of all three species. These include foraging (1) on the ground, (2) in the exterior leafy portions of branches, (3) in the branch interiors, (4) along bush or tree stems/trunks, (5) in moss, (6) in or among epiphytes, and (7) and along vines. I also recorded the altitude for each individual and whether they foraged alone, in conspecific flocks, or in mixed-species flocks. Finally, I observed the foraging behavior of individuals - whether they were gleaning or sallying for insects

## **RESULTS**

### **Altitudinal Ranges**

I observed a total of 86 Three-striped Warblers and 125 Golden-crowned Warblers. Both of these warblers were seen in tracts of primary and secondary understory and congruent forest edges. Three-striped Warblers were observed ranging from 1420 m up to 1615 m, and the Golden-crowned Warblers ranging from 1275 m to 1485 m, leaving a 65 m zone of overlap. A One-way ANOVA Test showed these ranges to be different from one another ( $p < 0.0001$ ,  $F = 232.421$ ,  $df = 2, 218$ ). The mean altitude of the Three-striped

Warblers ( $1525 \pm 48$  m) was shown to be significantly higher than the Golden-crowned Warbler ( $1410 \pm 43$  m; Fisher PLSD Post hoc, significantly different; see Figure 1).

### **Microhabitat: Vegetational Preference**

Both the Three-striped and the Golden-crowned Warblers showed different locational preferences when foraging on different strata. A two-by-two contingency test revealed that Three-striped Warblers were observed foraging with greater frequency on the leafy branch tips (33% of observations), whereas Golden-crowned Warblers were observed more frequently on branch interiors (42% of observations; see Figure 2). Also, Three-stripes tended to forage in epiphytes twice as frequently as Golden-crowned (TS = 7% versus GC = 3%). Conversely, Golden-crowned individuals tended to forage almost twice as frequently on the trunks of small bushes than did Three-striped individuals (GC = 11% versus TS = 7%). Other than that, the two species spent nearly equal time foraging on the ground, in moss, and along vines.

### **Vertical Stratification at Non-overlapping Altitudes**

Both the Three-striped and the Golden-crowned Warbler were observed primarily in the forest understory. While the Three-striped Warblers were only seen foraging from the ground up to six meters in the understory, the Golden-crowned Warblers were seen foraging from the ground as far up as eight meters in the lower subcanopy. Furthermore, based on each species overall vertical height ranges, Three-striped Warblers were shown to forage significantly closer to the ground than the Golden-crowned Warblers. A two-by-eight contingency test revealed that Three-striped Warblers were sighted with the greatest frequency foraging between one and two meters (30 % of the time), while Golden-crowned Warblers were seen with the greatest frequency foraging between three and four meters above the ground (24 % of the time; see Figure 3). Otherwise there was a great deal of overlap in their foraging heights.

### **Vertical Stratification when Warblers Overlap**

By comparing data of individuals seen outside of overlapping altitudes (1420 - 1485 m; 77 GC individuals and 68 TS individuals), each species showed the same trends in vertical stratification. At these ranges, the Three-striped Warblers had a mean vertical height of  $2.4 \pm 1.3$  m, which an unpaired t-test revealed to be significantly different from that of the Golden-crowned Warblers; a mean height of  $2.8 \pm 1.3$  m (see Figure 4). Likewise, the 18 Three-striped and 48 Golden-crowned individuals observed where individuals of both species overlapped altitudinally (1420 m and 1485 m), demonstrated a slight shift in their preferred vertical heights: Three-stripes shift slightly down to a mean of  $2.1 \pm 1.1$  m, while the Golden-crowns shift slightly up to a mean of  $3.3 \pm 1.6$  m (see Figure 4). Shifts within each species were not statistically significant.

### **Stratification in Foraging Flocks**

Both species were observed foraging alone as well as in mixed-species and conspecific

flocks. When in conspecific flocks, Three-striped Warblers showed a lower mean height preference ( $2.2 \pm 0.1$  m) than the Golden-crowned Warblers ( $3.1 \pm 1.5$  m; significantly different; see Figure 5). This same trend was also shown when foraging alone (TS =  $2.2 \pm 0.8$  m; GC =  $3.7 \pm 1.7$  m), but the data were not significant because so few individuals of either species were observed foraging alone. When foraging in mixed-species flocks, both species tended to forage at very similar heights (TS =  $2.8 \pm 1.4$  m; GC =  $3.0 \pm 1.3$  m).

On two occasions, individuals of both species were observed foraging in the same mixed-species flocks. Unfortunately in one of these cases the two species were exhibiting atypical behavior, as they were foraging in the midst of an army ant colony. On that one unique occasion, both species were observed foraging on or within a meter of the ground. Though I recorded my observations, I did not include it in statistical analysis. On the other occasion when I observed both species foraging together, species' height preferences were shown to differ. The Three-striped Warblers had a mean height of 2.8 m while the Golden-crowned Warblers' mean height was 4.0 m. Since all of the individuals in each species had the same mean foraging height, no test could be done to compare these differences because of a lack of variance. These data are no more common than the data taken in the presence of army ants, but they did not have an extraneous variable altering the behavior patterns of both species (see Figure 5).

### **Further Observations**

Three-striped and Golden-crowned Warblers were both primarily observed gleaning for insects when foraging. But a two-by-two contingency test showed that Golden-crowned Warblers sallied for insects with a much greater frequency (30% of 125 individuals) than the Three-striped Warbler (8% of 86 individuals;  $X^2 = 14.13$ ,  $P < 0.05$ ,  $df = 1$ ). I also noted that Golden-crowned Warblers tended to glean on the undersides of leaves most often, while Three-striped Warblers did not seem to show a tendency to glean in any particular location on plant leaves.

## **DISCUSSION**

Data show that the Three-striped and the Golden-crowned Warblers overlap in elevation. These two overlap between 1420 m and 1485 m, where they both forage in the understory, gleaning for insects. Thus, there is the potential for competition in these areas of overlap. However potential competition is minimized because they tend to forage at different vertical heights: Three-striped forage at about 2.3 m and Golden-crowned forage at about 2.8 m. Furthermore, in their zone of overlap, the differences in preferred foraging height is enlarged, especially when they forage in the same mixed-species flock.

The Three-striped and the Golden-crowned Warblers reduce their potential for competition even further by foraging in separate microhabitats and by sallying for insects

The Three-striped and the Golden-crowned Warblers reduce their potential for competition even further by foraging in separate microhabitats and by sallying for insects in different frequencies. The microhabitats used most often by the Three-striped Warblers are leafy branch tips and epiphytes, whereas Golden-crowned Warblers use branch interiors and the bush stems more frequently. According to Terborgh (1980), vertical zones in the understory have denser and more diverse foliage, and therefore birds

can partition their niches based on slight differences in vertical height and microhabitat. The Three-striped Warblers' preferences for epiphytes and leafy branch tips and the Golden-crowned Warblers' for branch interiors and trunks may reflect differences in their altitudinal ranges - Three-striped in epiphyte-laden Elfin Forest and Golden-crowned in lower, drier habitat. Elfin Forests, unlike lower elevation forests, are characterized by shorter, more open canopies that facilitate dense, leafy understories, and also year-round precipitation which promotes epiphytic growth (Haber 2000).

I found no evidence that the Golden-crowned Warbler is moving into the Three-striped Warbler's range. Pounds (1999) and Donnelly (1998) found the Golden-crowned Warbler at higher elevations than observed here, possibly because they made their observations during the breeding season (April - June). Nevertheless, if Golden-crowned Warblers move into altitudes occupied by the Three-striped Warbler for even part of the year, competition could occur. Differences in vertical stratification and microhabitat preferences would lessen its effects, however. Should climate change continue at Monteverde, enabling birds to continue their upslope colonization (Pounds 1999), the Three-striped Warbler may lose its competitive advantage at higher elevations.

Interestingly, I found the Three-striped Warbler in a lower zone than I expected. Specifically I found individuals ranging as low as 1420 m in Zone 2, while Fogden (1993) recorded this species to only range as low as 1500 m in Zone 3. This may be related to anomalous weather experienced during the weeks of my data collection. In the middle of the study, a seven-day storm raged night and day in the tiny mountainous village of Monteverde, proceeded by the beginning of 'windy-misty' season. This could possibly have caused the Three-striped Warbler to move down in elevation to more hospitable conditions. This could also explain why I did not observe any Golden-crowned Warblers above 1600 m.

Based on this study, the Three-striped and the Golden-crowned Warblers show the potential for competitive interactions between the elevations of 1420 m and 1485 m. But competition is possibly avoided due to the fact that these two species forage at different heights in the understory, use separate microhabitats with greater frequency, and use varying methods of foraging. This study suggests that during the non-breeding season, Golden-crowned Warblers do not use the altitudinal ranges typically used by Three-striped Warblers. Future studies could include a repetition of this study either in the rainy season and/or the dry season, to see whether these same results are shown or whether the species do shift their ranges, increasing competition.

## **ACKNOWLEDGEMENTS**

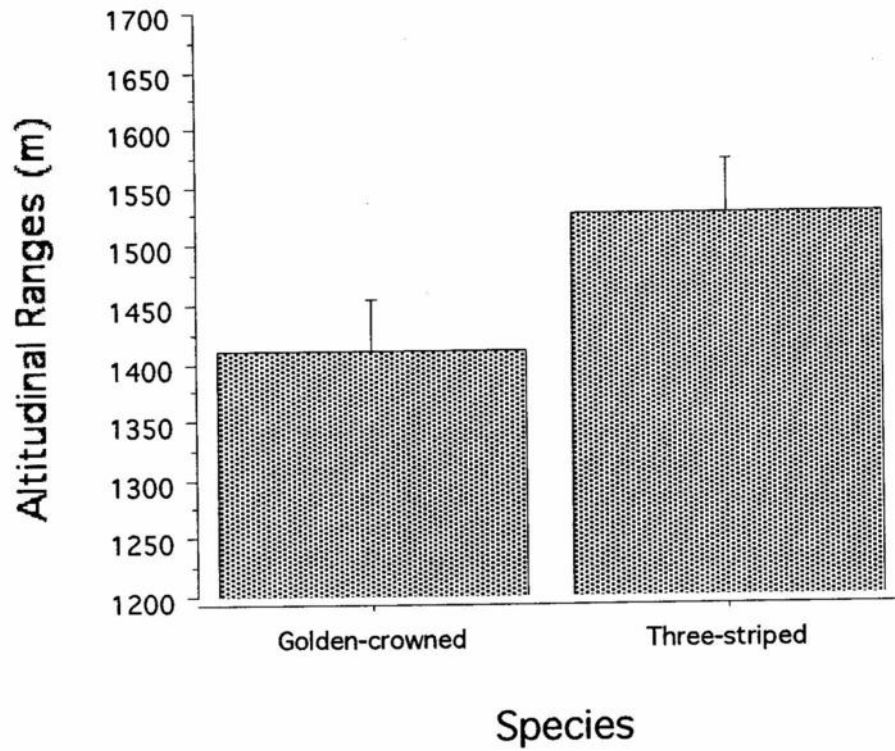
I would like to thank the people who allowed me to work at each of my four study sites: the Monteverde Cloud Forest Reserve, the Sendero Tranquilo Reserve, the Bajo del Tigre area of Bosque Eterno de los Niños, and the owners of the Rockwell farm. I would also like to thank Richard Laval who helped me devise my project, locate suitable study sites, initialize my preliminary data collections. Lastly I would like to thank my professors Alan and Karen Masters for guiding me through my study and for helping me overcome any and all obstacles I encountered.

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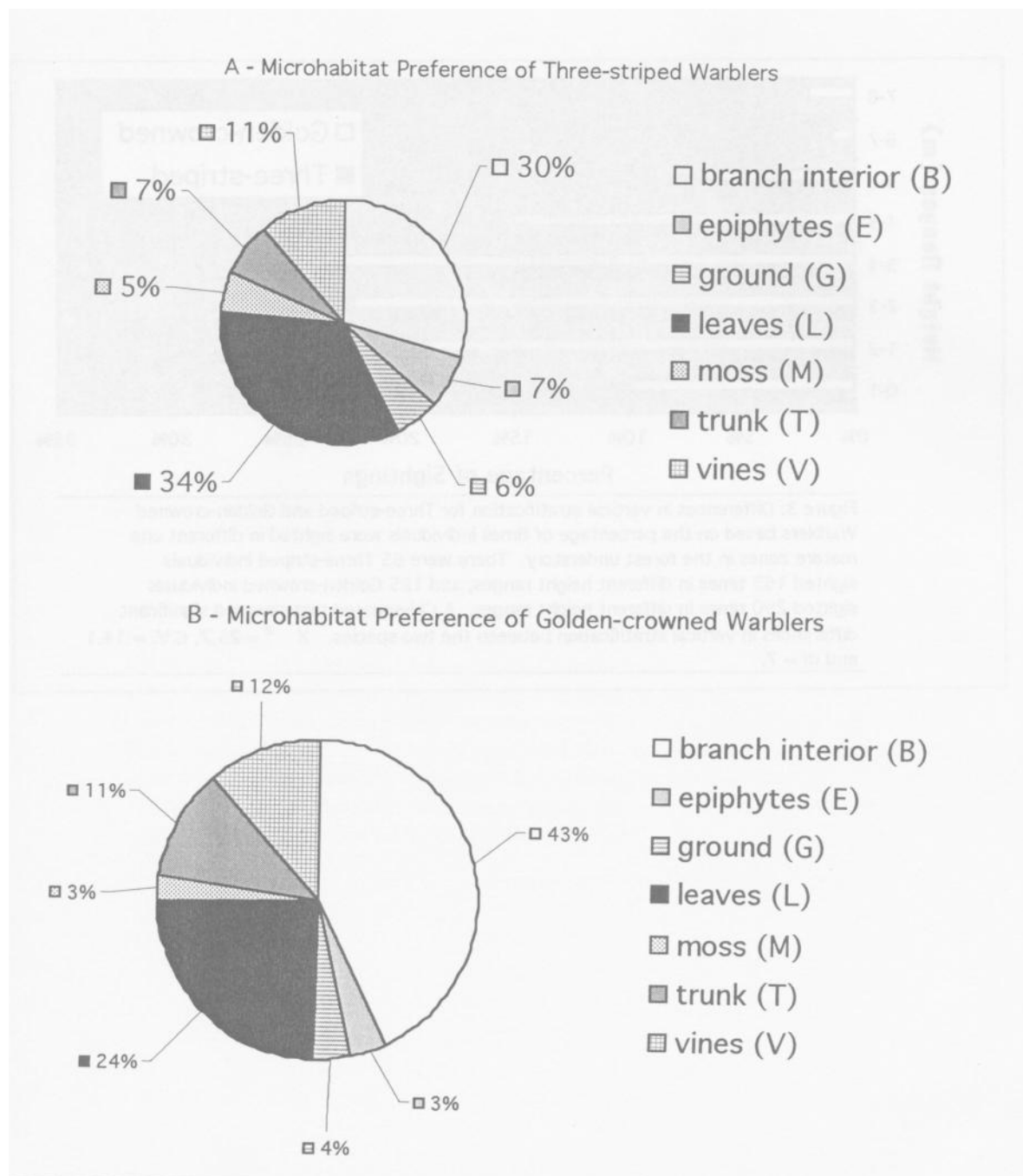




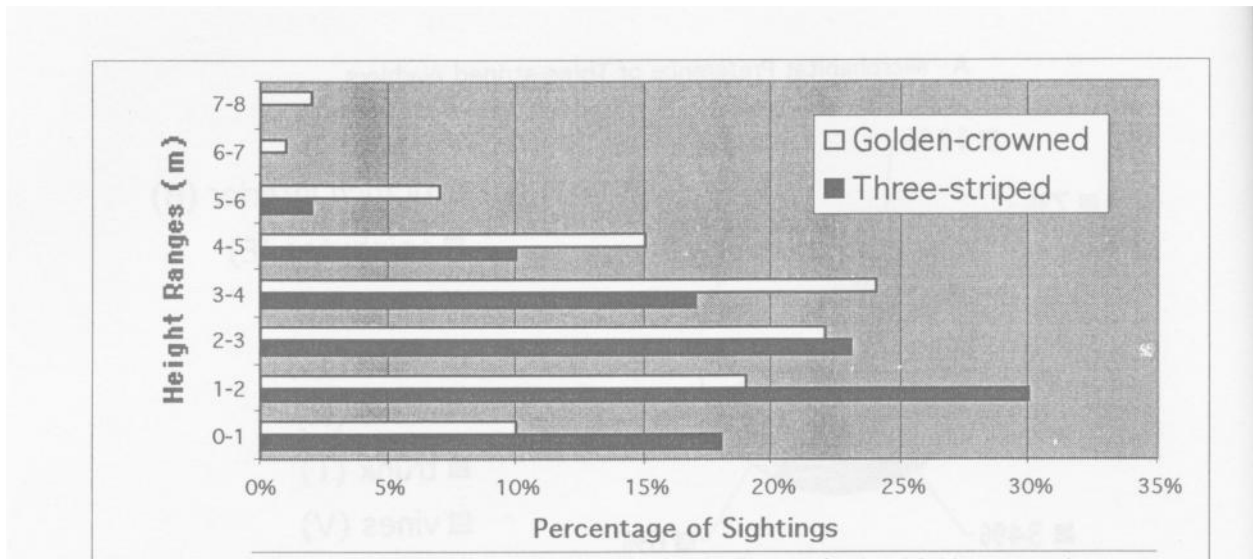
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Figure 1: Altitudinal means  $\pm$  1 SD for Golden-crowned and Three-striped Warblers. Golden-crowned have an altitudinal mean of  $1411 \pm 43$  m and Three-striped have a altitudinal mean of  $1525 \pm 48$  m. A Fisher's PLSD Post hoc test shows that they both have different mean altitudes. GC vs. TS:  $P < 0.0001$ , mean difference =  $-114.9$  m.

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**FIGURE 2:** Microhabitat preference of Three-striped and Golden-crowned Warblers, based on foraging in different types of vegetation. Numbers for Three-striped individuals in (A) are based on sighting 86 individuals in 230 different microhabitats. Numbers for Golden-crowned individuals in (B) are based on sighting 125 individuals in 268 different microhabitats. A two-by-two contingency test revealed that Three-striped Warblers prefer to forage in leafy edges more frequently than do Golden-crowned Warblers, while Golden-crowned Warblers prefer to forage among branch interiors more than do Three-striped Warblers.  $X^2 = 9.87$ ,  $p < 0.05$ ,  $df = 1$ .



**Figure 3:** Differences in vertical stratification for Three-striped and Golden-crowned Warblers based on the percentage of times individuals were sighted in different one meter zones in the forest understory. There were 85 Three-striped individuals sighted 163 times in different height ranges, and 125 Golden-crowned individuals sighted 290 times in different height ranges. A Chi-squared test revealed significant differences in vertical stratification between the two species.  $X^2 = 25.7$ , C.V. = 14.1 and  $df = 7$ .

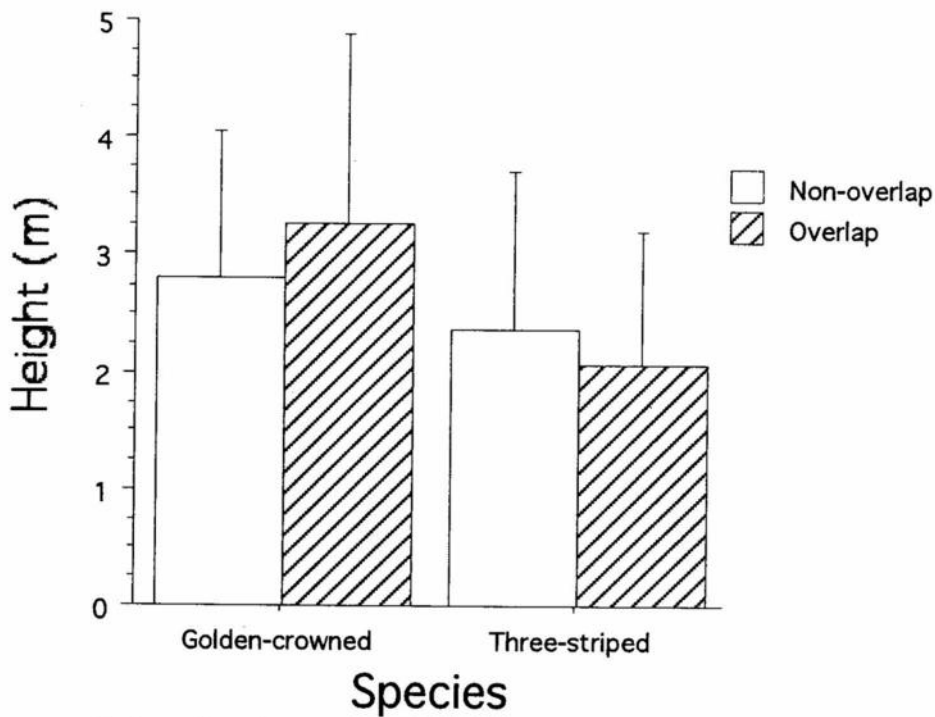


Figure 4: Vertical Stratification of Three-striped and Golden-crowned Warblers when observed foraging at altitudes which do and do not overlap. Non-overlap occurs below 1420 m and above 1485 m, including 77 Golden-crowned and 68 Three-striped Warblers. Overlap occurs at 1420 - 1485 m, including 48 Golden-crowned and 18 Three-striped Warblers. Difference when not overlapping statistically different (unpaired t-test,  $p = 0.0003$ ,  $F = 13.775$ ,  $df = 1$ ).