

Seasonal shift in the foraging niche of a tropical avian resident: resource competition at work?

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Abstract: This study examined the foraging behaviour of a resident bird species, the rufous-capped warbler (RCWA, *Basileuterus rufifrons*), in a shaded-coffee farm in Chiapas, Mexico. Unlike many resident species that use shaded-coffee agroecosystems seasonally, RCWAs do not move to other habitats when migrants are present. RCWA foraging was compared when migrant birds were present (dry season) and absent (wet season). It was hypothesized that RCWAs would exhibit a seasonal foraging niche shift because of resource competition with migrants. Observations from both the canopy and coffee understorey show that RCWAs foraged almost equally in both vegetative layers during the wet season although they were more successful foraging in the canopy. In the dry season, migrants foraged primarily in the canopy and RCWAs shifted so that 80% of RCWA foraging manoeuvres were in the understorey. At that time RCWAs foraged less successfully in both vegetative layers. Avian predation in the dry season was found to reduce densities of arthropods by 47–79% in the canopy, as opposed to 4–5% in the understorey. In the canopy, availability of large (> 5 mm in length) arthropods decreased by 58% from the wet to dry season. Such resource reductions could have caused the RCWA foraging niche shift yet other alternative or additional hypotheses are discussed. Shifts in foraging niche may be a widespread mechanism for some small insectivorous residents to avoid seasonal competition with abundant migrant species.

Resumen: Este estudio examinó el comportamiento de forrajeo de un ave residente, *Basileuterus rufifrons* (RCWA), en una finca de café con sombra en Chiapas, México. A diferencia de muchas aves residentes que usan los agroecosistemas de café con sombra solamente durante una estación, RCWAs no se van a otros hábitats cuando los aves migrantes están presente. El forrajeo de RCWA fue comparado cuando las aves migrantes eran presente (la época seca) y ausente (la época de lluvia). La hipótesis fue que los RCWA exhibirían un cambio de forrajeo con los cambios de estaciones a causa de la competencia de recursos con los migrantes. Observaciones en el docel y el sotobosque en un cafetal muestran que durante la época de lluvia, los RCWAs forrajeaban igualmente en los dos niveles de vegetación, pero tienen más éxito forrajeando en el docel. Durante la época seca, los migrantes forrajeaban principalmente en el docel y los RCWAs se mueven al sotobosque donde efectúan 80% de las maniobras de forrajeo. Durante ese tiempo, los RCWAs tuvieron menos éxito forrajeando tanto en el docel como en el sotobosque. Durante la época seca el número de artrópodos bajó entre 47–79% en el docel y entre 4–5% en el sotobosque a causa de la depredación de las aves. En el docel, la disponibilidad de artrópodos grandes (> 5 mm en longitud) bajó en un 58% de la época de lluvia a la época seca. Tales reducciones de recursos podrían causar el cambio de lugar a forrajeo observado en RCWA, pero otras explicaciones e hipótesis son discutidas. Pueden ser que este cambio de forrajeo sea común en algunas aves residentes pequeñas que comen artrópodos para evitar la competencia con los migrantes durante la época seca.

Key Words: avian insectivory, birds, breeding demand, Chiapas, Mexico, coffee agroecosystem, direct interference, foraging, indirect competition, migrant–resident interaction, resource competition, rufous-capped warbler, sexual segregation, shaded coffee

INTRODUCTION

Each year millions of insectivorous birds arrive in tropical habitats during what is often the resource-poor time

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of year. Not surprisingly, avian ecologists have focused considerable effort on understanding the mechanisms by which migratory and resident populations are able to coexist (Greenberg 1995, Johnson *et al.* 2005, Rappole & Warner 1980, Ricklefs 1989). The interaction of the two avifaunas may be connected to the population dynamics of organisms at lower trophic levels in tropical areas. A large annual influx of insectivores with no detectable competitive effects would suggest that predator–prey populations are not tightly coupled. Studies examining the foraging behaviour of overwintering migrant birds in tropical habitats are common (see Greenberg 1986 for a review), yet surprisingly few have investigated how foraging behaviour of tropical residents is affected by migrant presence. Previous comparative studies showed that many resident birds were specialists and required more specific microhabitat conditions than did migrant species (for review see Greenberg 1986, Herrera 1978, Leisler 1990, Remsen & Parker 1983, Stotz *et al.* 1996). Accordingly, most migrants have been thought to avoid resource competition while in the tropics by foraging for resources underused by resident species and underrepresented in their foraging microhabitats (Herrera 1978, Lack 1986, for review see Leisler 1990, 1992; O'Connor 1981). However data from many studies fail to support these hypotheses (Johnson & Sherry 2001, Lack 1986, Post 1978, Strong 2000) and these hypotheses are now recognized as overly simplistic (Greenberg *pers. comm.*).

The four studies that examine how tropical residents forage before and after migrant arrival found that while a majority of resident species did not appear to change their foraging behaviour upon migrant arrival, a few generalist resident species exhibited seasonal shifts in foraging niche (Chiple 1976, Rabøl 1987, 1993; Waide 1981). In these cases, certain resident bird species were found to forage higher in the vegetative strata (in more favourable or preferred locations) when migrants were absent than when they were present. Contrary to conventional wisdom that resident birds out-compete migrants, these resident resource generalists may shift to under-exploited niches to avoid resource competition when migrants are very abundant.

The *resource competition hypothesis* is commonly offered as a possible explanation for this behavioural shift (Chiple 1976, for review see Leisler 1990, 1992; Rabøl 1987, Waide 1981). When migrants arrive they consume large numbers of arthropods in the canopy, and the resource competition hypothesis holds that this consumption results in such low densities of arthropods that it is no longer profitable for certain residents to forage in the canopy. In turn, residents forage lower in the vegetative strata. If this indirect competition with migrants is driving the displacement, the following predictions should be met: (1) shared food resources

should be reduced where migrants primarily forage and (2) resident birds should forage less successfully at those locations once migrants are present. One would expect that with time after arrival, migrants would also forage less successfully due to resource depletion, but testing this prediction is outside the realm of this study.

Shade-grown coffee farms in the Americas usually support a few resident bird species and a large number of insectivorous neotropical migrant species that arrive in high densities around the beginning of the wet season (Calvo & Blake 1998, Greenberg *et al.* 1994, 1997a,b; Johnson 2000, Johnson & Sherry 2001, Perfecto *et al.* 2003, Petit *et al.* 1993, Robbins *et al.* 1992, Vannini 1994, Willis 1966, Wunderle 1999, Wunderle & Latta 1996, Wunderle & Waide 1993). Because shaded-coffee farms support such large densities of migrants and because the vegetation is oftentimes heavily pruned, eliminating much of the vegetative complexity found in a tropical forest, it is a comparatively easier system to look for shifts in foraging niche. This study was conducted on a shaded-coffee farm where the rufous-capped warbler (RCWA, *Basileuterus rufifrons*) was the numerically dominant foliage-gleaning resident species. Additionally the RCWA was chosen for this study because it spends a considerable amount of time foraging in the coffee understorey. Unlike many resident species that use shaded-coffee agroecosystems seasonally, RCWAs maintain territories year-round and do not move to other habitats when migrants are present (Dietsch 2003). They breed during April–July when migrants are largely absent (Stiles & Skutch 1989). By observing both foraging behaviour and location of RCWA in the wet and dry season, this study tests the hypothesis that rufous-capped warblers exhibit a seasonal foraging niche shift. Also, by coupling these data with measurements of arthropod abundance and migrant presence, this study tests the hypothesis that the seasonal niche shift is caused by resource competition from migrants. Alternative hypotheses for this seasonal niche shift, such as climatic and seasonal effects, breeding demand, sexual segregation, predator avoidance and direct interference hypotheses are also examined in the discussion.

METHODS

Overview of study site

This research was conducted in Finca Irlanda (1040 m asl, 15°10'N, 92°20'W), a shade-grown, organic coffee farm located on the Pacific slope of the Sierra Madre del Sur, 40 km north-east of Tapachula in the Soconusco region of Chiapas, Mexico. In this region there is a pronounced wet season from March to October that receives approximately 4400 mm y^{-1} rainfall. The dry



Figure 1. Finca Irlanda photograph illustrating the two distinct vegetative layers.

season lasts from November to February and receives close to 60 mm of rain during the entire 4-mo period (Lin unpubl. data, Richter 2000). The study took place where the canopy consists of approximately seven tree species that are regularly pruned to a height of roughly 9 m, creating a consistent canopy cover of about 60% (Mas & Dietsch 2003, Perfecto *et al.* 2004) with scattered emergent trees. Approximately 60% of the canopy trees belong to the genus *Inga* (Fabaceae). The farm is classified as a commercial polyculture (*sensu* Moguel & Toledo 1999, Perfecto & Vandermeer 2002, Philpott *et al.* 2004), which means that coffee is grown under a planted canopy. The coffee understorey and canopy form two distinct strata of vegetation (Figure 1).

Foraging observations

In June 2002, 22 adult and hatch year rufous-capped warblers were banded with split plastic Avinet colour bands on a plot (approximately 275 × 250 m) flagged at 25 m intervals. Foraging observations were made on banded and unbanded RCWAs from 18 June 2002–17 July 2002, and from 18 December 2002–13 January 2003. No more than one foraging observation was made per banded individual per day. Two or more foraging observations were recorded on unbanded RCWA individuals on the same day only if the distance between observations was over 150 m, a distance assumed to minimize the probability of observing the same individual. This distance was chosen based on territory maps drawn from banded RCWAs in the area.

The foraging protocol used was adopted from Greenberg *et al.* (1999) and Dietsch (2003) based on Remsen & Robinson (1990). In order to reduce any

bias towards conspicuous individuals, RCWAs were located both aurally and visually. RCWAs were followed until a foraging manoeuvre was observed. Foraging manoeuvres were defined as actual foraging attacks, not merely searching for food. For each foraging manoeuvre recorded, the bird's height from the ground was estimated, the plant species (where the manoeuvre took place) identified, and RCWA colour bands were recorded. Because only male RCWAs sing to defend territories, it was noted whether the bird was singing. Attack manoeuvre was noted as either standing, aerial, or hanging. If the foraging attempt was 'clearly successful' the prey was identified, usually to insect order. If a bill wipe immediately followed the foraging manoeuvre it was recorded as 'successful not seen'. If prey capture or bill wipes were not visible, the manoeuvre was considered unsuccessful.

Arthropod sampling

In the same study site, two different bird exclusion experiments were carried out to determine the effects of birds on arthropods in the coffee understorey (Perfecto *et al.* 2004) and canopy (Philpott *et al.* 2004). In the coffee understorey, fishing gill nets (35 × 35-mm mesh) were used to form bird exclusion cages of approximately 10 × 5 × 3 m over at least 10 coffee plants in November 2000. Arthropods were collected from ten plants inside the enclosure and ten adjacent plants outside the enclosure (controls). Arthropods were vacuumed from two branches per plant in November 2001 and May 2002 into fine mesh bags with a 10-cm-diameter reversed leaf-blower (D-vac). Ethyl acetate was added to the bags to kill arthropods, which were later identified to order (or family) and measured in length (mm). Leaf biomass was estimated (as described by Perfecto *et al.* 2004) and arthropod data were standardized as number of individuals g⁻¹ of wet foliage.

Bird exclusions in the canopy were established in *Inga micheliana* trees in the dry season (12 December 2001 – 12 February 2002) and wet season (2 May 2002 – 15 July 2002; see Philpott *et al.* 2004). The exclusions were placed in 18 trees in the dry season and 20 in the wet season. Two branches that were 3–4 m above ground with 4–8 leaves were selected and randomly assigned to a control or exclusion treatment. Birds were excluded from foraging on *Inga* foliage by placing monofilament nylon fishing nets (35 × 35-mm mesh) over entire branches and tying nets to form a bag. Arthropods were collected in February and July 2002. Branches were covered with 60 × 90-mm plastic bags and cut. Cotton balls saturated with ethyl acetate were placed inside to kill all arthropods. The arthropods were then collected, identified to order (or family) and measured in length (mm). Foliage was dried and weighed and used to standardize all arthropod data

as number of individuals g^{-1} of dry foliage. To compare with coffee arthropod data, all arthropod data from *Inga* trees were converted to number of individuals g^{-1} of wet foliage with the following empirically derived, significant regression: wet leaf weight (g) = $2.29 \times$ dry leaf weight (g) $- 18.76$ ($R^2 = 0.861$, $P < 0.001$).

Analysis

Kolmogorov–Smirnov tests were performed on arthropod abundances. Some data were not distributed normally and were resistant to transformations so more conservative, non-parametric tests were used. Because arthropods in the understorey and canopy were sampled differently, we did not attempt a direct comparison between densities in the two vegetative layers. Instead we limit arthropod comparisons to (1) effect of season within each vegetative layer and (2) effect of bird enclosure. Seasonal differences in arthropod abundances (both total number of arthropods and the number of large arthropods > 5 mm in length) were tested using Mann-Whitney U-tests. Differences in enclosure and control arthropod abundances in the canopy and understorey were tested with paired Wilcoxon tests. RCWA foraging heights (total observations and male-female comparisons) were tested using Mann-Whitney U-tests. Chi-square contingency tests were used to compare all categorical variables: seasonal foraging layer, proportion of successful foraging attempts (by layer and season), and type of successful foraging manoeuvres. Bonferroni calculations were performed with a Texas Instruments TI-85 calculator and all other statistical tests were performed using SPSS 11.0 for Macintosh.

RESULTS

Seasonal foraging location

In the wet season, RCWAs were observed foraging equally as often in the canopy (47%, $n = 34$) and understorey (53%, $n = 39$), but in the dry season they foraged significantly more in the coffee understorey (81% of observations; $\chi^2 = 12.1$, $df = 1$, $P = 0.0005$, $n = 72$). The average foraging height of RCWAs significantly decreased from 4.6 m (SE = 0.5 m; median = 2 m) in the wet season to 2.0 m (SE = 0.2 m; median = 1.5 m) in the dry season (Mann-Whitney $U = 1753$, $P = 0.0005$, Figure 2). The average foraging height of male birds (sexed either by territorial singing or presence of a large cloacal protuberance while banding; mean = 4.0 m, SE = 0.5 m, $n = 52$) did not significantly differ from the average of female birds (sexed by the presence of a brood patch while banding; mean = 3.7 m, SE = 0.9 m, $n = 22$, $U = 485$, $P = 0.30$). Seasonal comparisons between male and

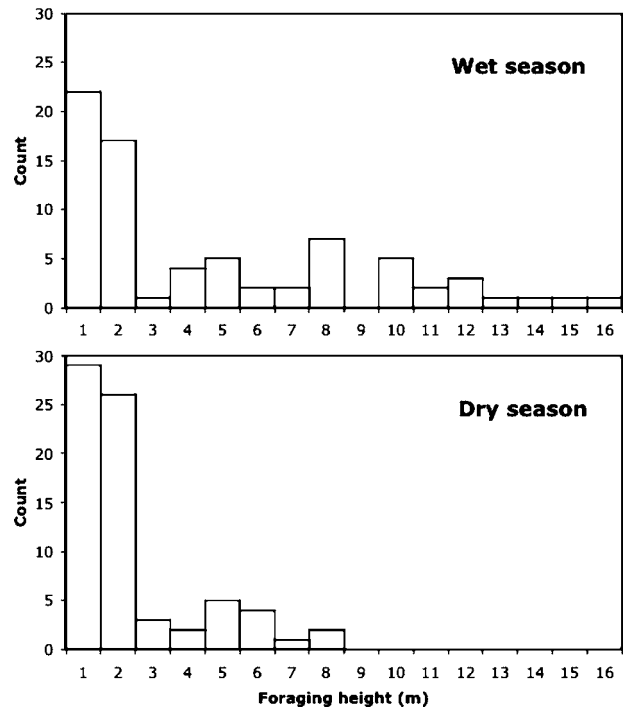


Figure 2. Histograms of rufous-capped warbler seasonal foraging heights. Each count represents separate foraging observations. With the exception of one observation in the wet season and two in the dry season, all foraging heights in the 0–1-m range were above the ground in low branches.

female average foraging heights were also not significant (dry season, male mean = 2.52 m, SE = 0.39 m, $n = 28$, female mean = 2.83 m, SE = 1.56 m, $n = 4$, $U = 51$, $P = 0.81$; wet season, male mean = 5.6 m, SE = 0.9 m, $n = 24$, female mean = 3.8 m, SE = 1.1 m, $n = 18$, $U = 156$, $P = 0.13$). Using the Bonferroni method to correct to the 0.05 level, the critical P -value for the above data on foraging height would be 0.017. For the 0.01 level, P would equal 0.003.

Successful foraging manoeuvres

When the seasons are pooled and success is defined as manoeuvres that were either clearly successful (CS) or successful not seen (SNS), RCWAs were proportionally more successful foraging in the canopy (44%, $n = 48$) than the understorey (27%, $n = 97$; $\chi^2 = 4.21$, $df = 1$, $P = 0.04$). Clearly successful manoeuvres were observed more in the canopy during the wet season than any other combination of season and vegetative layer, representing 38% of all documented foraging attempts ($\chi^2 = 4.34$, $df = 1$, $P = 0.04$, Figure 3). Additionally there was a higher proportion of successful manoeuvres (SNS and CS) in the wet season than in the dry season (Figure 3), but the differences were not statistically significant to the 0.05 level ($\chi^2 = 2.09$, $df = 1$, $P = 0.15$). Finally, successful

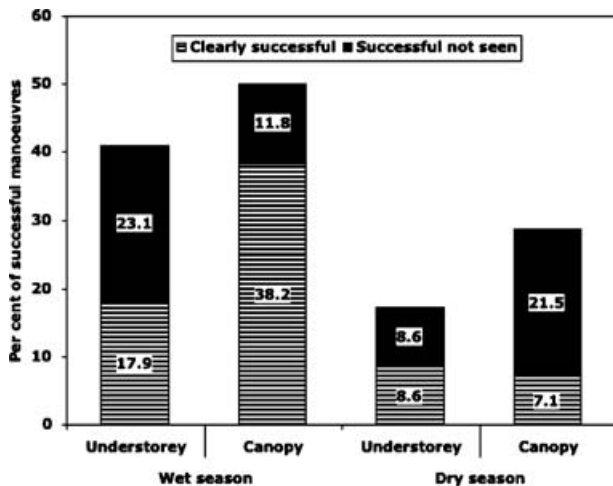


Figure 3. Per cent of successful manoeuvres out of total rufous-capped warbler foraging attempts in vegetative layers separated by season. The striped area below represents per cent of clearly successful manoeuvres and darker area above represents 'successful not seen' manoeuvres (manoeuvres followed by a bill wipe).

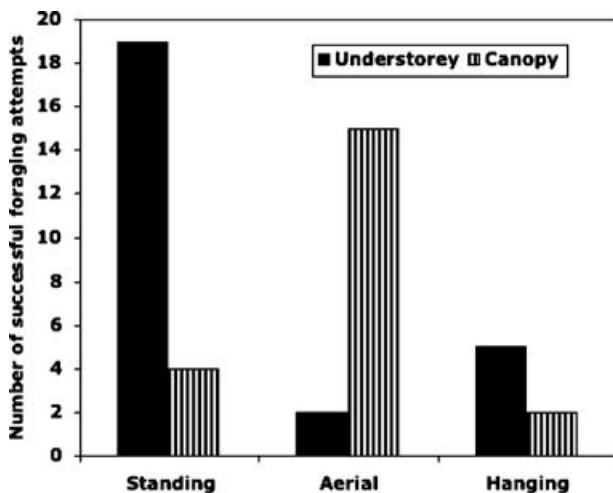


Figure 4. Foraging manoeuvre used to successfully capture prey in understorey and canopy. If the rufous-capped warbler was foraging while standing upright, the manoeuvre was classified as standing. If the bird foraged by either leaping or flying a short distance (striking) the manoeuvre was classified as aerial. If the bird was hanging on vegetation with the head positioned laterally or downwards, the manoeuvre was classified as hanging.

foraging events were more often performed with standing manoeuvres in the understorey and aerial manoeuvres in the canopy ($\chi^2 = 20.7$, $df = 2$, $P < 0.0001$, Figure 4). Using the Bonferroni method to correct to the 0.05 level, the critical P-value for the above data on successful foraging manoeuvres would be 0.012. For the 0.01 level, P would equal 0.002.

Arthropod abundance

Effects of season in the understorey and canopy. Total number of arthropods g^{-1} of leaf biomass in the coffee understorey ranged from 0.52 in the wet season to 0.43 in the dry season (Mann–Whitney $U = 4375$, $P = 0.13$, Figure 5). In the canopy, total number of arthropods varied from 0.30 g^{-1} in the wet season to 0.34 g^{-1} in the dry season (Mann–Whitney $U = 162$, $P = 0.60$).

Abundance of arthropods > 5 mm (large arthropods) did not significantly change seasonally in the understorey (0.023 g^{-1} in the dry season and 0.018 g^{-1} in the wet season, Mann–Whitney $U = 4325$, $P = 0.08$, Figure 5), however in the *Inga* canopy there were significantly fewer arthropods in the dry season (0.021 g^{-1}) than the wet season (0.049 g^{-1} , Mann–Whitney $U = 64$, $P = 0.001$).

Effect of bird exclosure in the understorey and canopy. In the canopy, total arthropod abundance was higher without bird predation (exclosure treatments) in both the wet season (Wilcoxon $Z = -3.55$, $P = 0.0004$, Figure 5) and dry season (Wilcoxon $Z = -2.37$, $P = 0.02$). In the understorey, arthropod abundance was not reduced by bird predation in the dry season (Wilcoxon $Z = -1.06$, $P = 0.29$), but in the wet season arthropod abundance was slightly lower without bird predation (Wilcoxon $Z = -2.08$, $P = 0.038$).

Large arthropod abundance was significantly higher on canopy trees without bird predation during the wet season (Wilcoxon $Z = -3.44$, $P = 0.0006$, Figure 5) and dry season (Wilcoxon $Z = -3.72$, $P = 0.0002$), but there was no exclosure-control difference in the understorey. Using the Bonferroni method to correct to the 0.05 level, the critical P-value for the above data on arthropod abundance would be 0.025. For the 0.01 level, P would equal 0.005.

DISCUSSION

RCWA seasonal niche shift

RCWAs clearly exhibited a seasonal foraging niche shift. In the wet season, RCWAs were observed foraging equally as often in the coffee understorey and canopy, but in the dry season they were observed foraging in the understorey 80% of the time. Similarly, Dietsch (2003) observed a significant decrease in the dry season foraging height of RCWAs during the 2 y prior to this study on the same farm. He also observed that during this time over 60% of foraging manoeuvres for migrant species were in the canopy and that most migrants were insectivorous.

The RCWA seasonal niche shift occurred despite the fact that total arthropod abundance in both vegetative layers did not change seasonally either on control

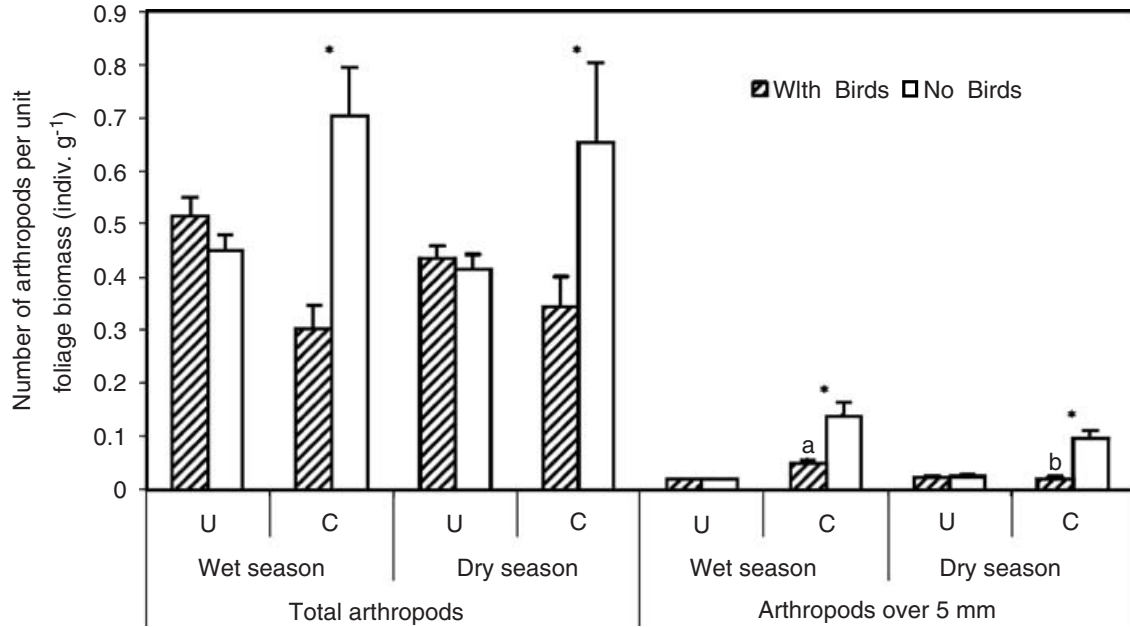


Figure 5. Number of arthropods g^{-1} of leaf biomass found seasonally in each vegetative layer (U = Understorey and C = Canopy). Total number of arthropods is represented by the left set of bars, and arthropods over 5 mm by the right set. Letters indicate significant seasonal differences in background arthropod abundance (control plants) and asterisks indicate statistical differences in arthropod abundance within season between paired control (with birds) and enclosure (no birds) plants due to bird predation ($\alpha = 0.05$).

branches or in experimental enclosures without foraging birds. However in the canopy, availability of large arthropods on control branches significantly decreased by 58% from wet season to dry season. Previous research in the same study location analysed arthropod data collected from stomach contents of all insectivorous birds sampled. The average length of consumed arthropods was estimated to be 3.24 mm (Greenberg *et al.* unpubl. data). Large arthropods (>5 mm) compose a very small proportion of the entire arthropod community, so a mean length of 3.24 mm may suggest that insectivorous birds are preferentially foraging on larger arthropods.

RCWAs were more successful when foraging in the canopy, perhaps due to the greater quantities of large arthropods found there. It is unlikely that this difference represents observer bias towards recording conspicuous manoeuvres in the canopy because RCWAs were most commonly observed foraging in the understorey. RCWAs primarily used aerial manoeuvres in canopy and standing manoeuvres in coffee for successful attacks further supporting the hypothesis that RCWAs were foraging on larger arthropods in the canopy. Larger prey are more likely to be targeted by aerial rather than standing manoeuvres simply because larger prey are more visible from farther away. Furthermore, birds are likely to incur a higher foraging cost (by using aerial manoeuvres) to obtain larger prey. Consequently, RCWAs were probably foraging on larger, more energetically favourable prey in the canopy.

Resource competition hypotheses

The resource competition hypothesis assumes that bird foraging behaviour will change as a result of lower resource availability. Some studies investigating the effect of ants on bird foraging have found evidence for this hypothesis. In separate studies Haemig (1992, 1994) found that number and duration of visits by insectivores and foliage-gleaners (but not by seed-eaters) to trees without ants was longer, presumably because there were fewer resources on trees with ants. Philpott *et al.* (2005) investigating the effects of aggressive ants on bird foraging in the same study site discussed here found that length of visits made by insectivorous birds, but not by other feeding guilds or overall, were reduced on trees with high ant densities, again suggesting that foraging was affected by a lower availability of shared resources, not because of direct interference or aggression which would be expected to affect all bird guilds equally.

In the context of the study presented here, the resource competition hypothesis would mean that because migrants lower arthropod abundance in the canopy, RCWAs forage elsewhere due to resource depletion. Large arthropods showed a four-fold decrease in abundance in the canopy due to avian predation when migrant birds were present. Moreover, abundance of large arthropods on control canopy branches significantly decreased by 58% from the wet to dry season. The observed foraging success rate of RCWAs in the canopy dropped from being

clearly successful 38% of the time in the wet season to only 7% in the dry season when migrants are present. It is likely that this is due to migrants preferentially foraging on large arthropods in the canopy and lowering their abundance and availability. This evidence supports the resource competition hypothesis.

Seasonal shifts in foraging niche and resource competition in other studies

RCWAs are not the only generalist avian residents found to exhibit a seasonal foraging niche shift. What is particularly striking is that each of the following empirical studies found that certain residents foraged at lower heights upon the arrival of migrants. For example, in the Colombian Andes, Chipley (1976) documented that three resident species (slate-throated redstart, *Myioborus miniatus*; brown-capped vireo, *Vireo leucophrys*; tropical parula, *Parula pitiayumi*) foraged at lower heights when migrant birds were present in dry season. Migrant competitors generally preferred the upper, more favourable vegetative strata where 90% of all clearly successful manoeuvres were observed. Chipley concluded that the shift to forage more in the canopy by slate-throated redstarts and tropical parulas in April/May was probably related to the corresponding migrant departure. Likewise, in August and early September, when there were no migrants present, both species had finished breeding and used the understorey the least. When migrants arrived in late September and October both species abruptly shifted back to using the understorey significantly more, supporting the resource competition hypothesis. Chipley finally concluded that migrant arrival probably had little to no effect on the majority of residents except for some small insectivorous species where competition with migrants may be important.

Waide (1981) studied a dry tropical forest in Campeche, Mexico and found that seasonal changes in the foraging behaviour of permanent resident species occurred. Six resident bird species foraged at lower heights in the dry season: tropical gnatcatcher (*Poliophtila plumbea*), grey-throated chat (*Granatellus sallaei*), white-bellied wren (*Uropsila leucogastra*), tropical kingbird (*Tyrannus melancholicus*), boat-billed flycatcher (*Megarynchus pitangua*), social flycatcher (*Myiozetetes similis*). However, by calculating the niche overlap between resident and migrant species, only the grey-throated chat significantly reduced its niche overlap with migrants by foraging at lower heights, foraging lower in the canopy crown, and changing foraging manoeuvres when migrants were present. Although he did not publish the data on prey abundance in this study, he noted that arthropods were scarcer in a drier wet season when compared with the

wetter following year. He concluded that there was not much evidence for resource competition between residents and migrants and suggested that perhaps competition is only noticeable later in the dry season (March–April) or in years with food shortages.

At Lake Naivasha, Kenya, Rabøl (1987) noted how the resident species black-breasted apalis (*Apalis flavida*) and grey-backed camaroptera (*Camaroptera brevicaudata*) foraged lower in less-preferred heights of the vegetation and that the black-breasted apalis clearly diverged in foraging behaviour from the migrant willow warbler (*Phylloscopus trochilus*) upon its arrival. Upon the arrival of willow warblers, Rabøl also reported decreased arthropod abundance, a diet switch by the black-breasted apalis, increased aggression among guild members, and a change in migrant foraging manoeuvres. Consequently Rabøl considered resource competition a likely explanation for the shifts in foraging niche.

In a follow-up study, however, Rabøl (1993) reconsidered resource competition as the primary explanation, because changes in brood rearing corresponded with the arrival of migrants and potentially explained the foraging shift (see below). His later study did not show as great a niche shift as his earlier research and arthropod abundances did not appear limiting. It is important to acknowledge that relative densities of willow warblers in two of the three habitats studied were 41% and 52% of their previous densities in the 1987 study, partly due to their late arrival. Even with the fewer competitors when compared with the resident black-breasted apalis in the woodlands, the migrant willow warbler was found significantly less in small trees and bushes, higher up in trees and their foraging height was much higher.

Analysis of alternative or additional hypotheses

Climatic and seasonal effects. As noted by Waide (1981) and Rabøl (1993), year to year variation in arthropod abundance may heighten competitive effects. In Chiapas, extended dry seasons occur periodically in association with El Niño that may exacerbate the effects observed in this study. Though the current study was not conducted during an El Niño event, Dietsch (2003) observed lower abundances of residence birds following a particularly harsh El Niño in 1997–8. Drought-induced resource limitations have been shown to induce rapid evolutionary response in birds (Grant & Grant 2002, Price *et al.* 1984). Consequently, climate-induced inter-annual variation in arthropod abundance may produce critical bottlenecks for RCWAs with important evolutionary implications. In fact, although RCWAs are considered generalist insectivores, the species may be specialized to forage in the understorey during the dry season. A more detailed study of RCWA diet and foraging behaviour may reveal

additional niche characteristics that indicate RCWAs exploit some resources more efficiently than migratory warblers.

It is possible that avian foraging shifts correspond to seasonal changes in rain or wind patterns or phenological changes in the environment. At the end of the dry season, *Inga* produces new leaves followed shortly by nectar-rich flowers which attract high densities of arthropods, especially Homoptera (Greenberg *et al.* 1997b, Johnson 2000, Koptur 1994). It is possible that larger arthropods respond strongly to these phenological changes while smaller arthropods may not, resulting in a different seasonal trend between the two controls. Increased densities of large arthropods in the canopy could influence avian insectivory. However, any climatic variation cannot account for the differences in enclosure and control arthropod densities demonstrating that avian insectivory strongly affects arthropod abundance. Additionally, Chipley (1976) noted that shifts in foraging niches of resident avian species corresponded with migrant presence during periods when the weather did not change.

Breeding demand hypothesis. In northern Latin America, most insectivorous residents breed primarily during the wet season, in the absence of migrants (Skutch 1950). Consequently, seasonal shifts in foraging niches may be partly a result of constraints imposed by reproductive activities (Chipley 1976, Leisler 1992, Lövei 1989, Rabøl 1987, 1993; Waide 1981). Adult birds may prefer different food sources than those they feed to their young, so they may forage in different locations depending on breeding status.

Chipley (1976) hypothesized that the shift to lower foraging heights in April/May for the slate-throated redstarts was related to changes in breeding demands because three slate-throated redstart nests were found in late May. Chipley also suggested that the shifts in foraging niche of the brown-capped vireo resulted from both breeding demands and migrant presence. Rabøl (1987) speculated as to whether a change in breeding demands contributed to the foraging niche shift for the grey-backed camaroptera and Waide (1981) noted that there was an abrupt decline in the number of resident species breeding upon migrant arrival.

The breeding demand hypothesis is compatible with the resource competition hypothesis. Although indirect competition may limit the foraging niche for RCWAs during the dry season, the absence of migrants may allow arthropods in the canopy to grow larger or to persist in the canopy during the breeding season. These arthropod resources would then be available if RCWAs need to expand their foraging niche to search for the necessary resources for feeding young. A more complete chronology

of foraging behaviour of the resident species through the breeding season, in particular during the periods when migrants arrive and depart, is needed to better document how readily RCWAs forage in the canopy. Additionally one should know the approximate date when adults stop feeding young. Although attempts were made in this study to document when fledglings were fed by adults, these data were too sparse to address the breeding demand hypothesis.

Regardless, in the case of the RCWA, it is unclear what the expected seasonal foraging pattern would be if breeding demands were a significant determining factor in their foraging location. During the breeding season RCWAs nest on the ground (*pers. obs.*, Stiles & Skutch 1989), and consequently may forage more in the coffee understorey as a way to remain closer to the nest and young. However, this may depend on how sub-optimal the coffee understorey is for arthropod abundance. Coffee plants contain alkaloid compounds that discourage herbivory. This is one possible explanation for the minimal impact of birds observed in the coffee understorey. Additionally, protection from avian predation within the enclosure may result in an osmotic effect of arthropods dispersing from enclosures to the point that control abundances are equal or even slightly greater than enclosure abundances. The canopy is very resource-rich with high densities of large arthropods and one may predict that RCWAs should forage there to increase their foraging effectiveness. Obviously future research in this area is warranted.

Direct interference hypothesis. This hypothesis assumes that migrants force residents to forage at lower, unfavourable levels due to agonistic interactions (Chipley 1976, Rabøl 1993). No aggressive behaviours between migrants and RCWAs were witnessed. Migrants were not observed to defend territories; rather, most were foraging in the canopy in large mixed species flocks. RCWAs did not join these flocks but foraged either alone, with one other RCWA, or in small intraspecific 'familial' groups (with their hatch years) in the coffee understorey during the dry season. Although it is possible that due to timing such agonistic interactions were missed, this study does not support the direct interference competition as a cause of the niche shift. Additionally, Chipley (1976) observed that agonistic encounters between residents and migrants were extremely uncommon (85% of the agonistic behaviours between individuals during the dry season were intraspecific interactions).

Sexual segregation hypothesis. Males of territorial avian species can often be found singing on high perches during the breeding season, claiming their territory. After singing, these males may stay and forage in

the higher vegetative strata (Waide 1981). When the breeding season is over and singing is softer and less constant, males may return to forage in lower vegetative strata. Consequently the territorial behaviour of singing males may be misinterpreted as a foraging niche shift of the species. Because Waide (1981) could not sex the individual birds he was observing, he could not test this hypothesis. In this study the differences in the wet season between average foraging height of males and females did not differ significantly although perhaps a larger sample size may be required to test this hypothesis.

Predator avoidance hypothesis. In order to avoid aerial predators, susceptible birds may concentrate their time foraging lower in the vegetative strata. During the dry season, the proportion of avian predators to potential prey is lower than during the wet season because passerine birds comprise the large majority of all migrants. Consequently foraging lower in the vegetative strata during the dry season is unlikely a result of increased predatory hawk and falcon abundance. However, in relation to other predators such as snakes it is unclear where RCWAs would be expected to forage to reduce risk of predation. Chipley (1976) ruled out this hypothesis because of the very low predator abundance during his study. More information would have to be known about the seasonal fluctuations of predator populations to address this hypothesis.

CONCLUSIONS

The results of this study support the claim of Chipley (1976) that migrants may be a significant competing force with small, generalist, insectivorous residents. Seasonal niche shifts, such as lower foraging heights, could be a relatively widespread mechanism for resident birds to reduce competition with migrant species, a subject that warrants further research. However, this interaction is rarely considered in migrant-resident studies, generally because these studies only include the dry season. Further studies should attempt to monitor any behaviour changes in residential species upon migrant arrival and consider the predatory effects this shift may have on the abundance of organisms at lower trophic levels. If resource competition with migrants is continually supported, this study among others will support the hypothesis that predator-prey populations are coupled.

Perhaps the best explanation for seasonal shifts in foraging niches of residents is the combined effects of indirect resource competition, the breeding demand hypothesis, and other alternative hypotheses acting in unison. If seasonal displacement is widespread in various tropical communities, these causal agents likely vary in

their contribution on a case-by-case basis and may be strong seasonal forces influencing community structure.

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