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THE IMPACT OF AVIAN INSECTIVORY ON ARTHROPODS AND LEAF DAMAGE IN SOME GUATEMALAN COFFEE PLANTATIONS

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Abstract. Experimental work has established that vertebrates can have a large impact on the abundance of arthropods in temperate forest and grasslands, as well as on tropical islands. The importance of vertebrate insectivory has only rarely been evaluated for mainland tropical ecosystems. In this study, we used exclosures to measure the impact of birds on arthropods in Guatemalan coffee plantations. Variation in shade management on coffee farms provides a gradient of similar habitats that vary in the complexity of vegetative structure and floristics. We hypothesized that shaded coffee plantations, which support a higher abundance of insectivorous birds, would experience relatively greater levels of predation than would the sun coffee farms. We found a reduction (64–80%) in the number of large ($>$ 5 mm in length) but not small arthropods in both coffee types which was consistent across most taxonomic groups and ecological guilds. We also found a small but significant increase in the frequency of herbivore damage on leaves in the exclosures. This level of predation suggests that birds may help in reducing herbivore numbers and is also consistent with food limitation for birds in coffee agroecosystems. However, the presence of shade did not have an effect on levels of insectivory.

Key words: antiherbivore defenses; Coffea arabica; *exclosure experiment; food limitation; leaf damage; migratory birds.*

Introduction

In recent decades, a number of studies have measured the effect of vertebrate insectivory through the use of netting exclosures (birds) or removals (lizards). Such experiments have shown a measurable and often large decline of arthropods due to the foraging activity of the target predators (Holmes et al. 1979, Atlegrim 1989, Bock et al. 1992, Marquis and Whelan 1994, Spiller and Schoener 1994, Gunnarsson 1996). Furthermore, several of these experiments have further demonstrated a reduction in herbivore-caused plant damage in the presence of vertebrate insectivores (Atlegrim 1989, Spiller and Schoener 1990, Marquis and Whelan 1994, Dial and Roughgarden 1995, Spiller and Schoener 1997). To date, exclosure and removal experiments have focused on temperate forest and grassland habitats and tropical islands. Few such experiments have been conducted in continental tropical ecosystems (but see Gradwohl and Greenberg 1982).

In the northern Neotropics of Mexico and the Caribbean, shaded coffee (*Coffea arabica)* plantations support among the highest densities and species richness of birds of both natural and anthropogenic habitats (Aguilar-Ortiz 1982, Waide and Wunderle 1993, Greenberg et al. 1997*b*). Migratory birds are particularly abundant and can comprise up to 70% of the foliage-gleaning insectivores (Greenberg et al. 1997*a*). Largely because of this influx from the North, the abundance of foliage insectivores is high, and the impact of birds on arthropods of coffee agroecosystems is potentially great, but it has not yet been measured.

Most studies of the impact of bird predation on arthropods in agroecosystems have focused on particular pest species (Kirk et al. 1997). With the exception of the seed-boring *broca* (*Hypothenemus hampeii*) and coffee leaf miner (*Leucoptera coffeela*), coffee in the northern Neotropics has relatively few insect pests (LePelley 1973). The lack of pests, however, still leaves the possibility that bird predation affects herbivorous arthropods that fail to reach outbreak population levels. Therefore, unlike most studies of insectivorous birds in agroecosystems (Kirk et al. 1997), we focused on

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the impact of bird predation on populations of all foliage arthropods. We modeled this study of the impact of avian insectivory after exclosure studies conducted in natural woodland or second-growth habitats (Holmes et al. 1979, Gradwohl and Greenberg 1982, Moore and Yong 1991, Marquis and Whelan 1994). In addition to censusing arthropod populations, we estimated the levels of insect-caused leaf damage in and out of exclosures.

On a more theoretical level, the coffee system allows us to test the influence of increasing structural and floristic diversity on levels of insectivory within a habitat. Coffee is cultivated in systems that range from monocultural (sun coffee) to complex polycultures with a diversity of shade trees (Rice 1990). The ''natural enemies hypothesis'' (Root 1973) explains the generally lower abundance of herbivorous insects on plants in polycultural agroecosystems by positing that alternate food resources support generally higher populations of arthropod predators and parasitoids. The hypothesis, however, has been tested primarily in arthropods (Russell 1989). Despite the fact that both increased structural and floristic diversity of plant communities often leads to increases in avian diversity and abundance (Wiens 1989), the effect of increased vegetative diversity on avian insectivory has not been measured.

The presence of shade trees often increases avian abundance and diversity by offering enhanced structural diversity and more food (Wunderle and Latta 1996). In the Guatemalan farms used in this study, we found an ~30% increase in bird abundance and 15% more species in shaded vs. sun coffee plantations (Greenberg et al. 1997*a*), and we found even greater increases in these values in plantations in Mexico, where shade tree canopies were more structurally and floristically diverse and less well pruned (Greenberg et al. 1997*b*).

A shade canopy may act as a natural buffer zone (e.g., Altieri and Smith 1986) and support predators that would otherwise not live in a coffee field; the overall increase in bird activity supported by the canopy trees should increase the predation levels of birds in the coffee. However, it is also possible that the greater bird abundance is proportional to the increase in canopy resources, and results in no net increase in predation pressure in the coffee shrubs. The resolution of these scenarios has important implications for the general role of structural diversity of ecosystems on predation levels as well as for the management of coffee farms. Therefore, in addition to assessing the overall impact of avian insectivory on the standing crop of arthropods, we designed the experiment to compare the effects for coffee with and without shade.

Methods

Study sites

The study was conducted in Tucurú (15°16′45″ N, 90°6′30″ W) at 701–1036 m elevation in the foothills of the Sierra de las Minas above the Polochic Valley (Departamento de Alta Verapaz, Guatemala), on Finca Dulce Nombre (study site a), Finca Constancia (study site b), and Finca Esperanza (study site c). Coffee on these farms was grown in a manner typical of the Polochic Valley, using cultivation systems ranging from no shade to a low diversity; low-stature shade was dominated (60% by individuals) by three species of *Inga* (Greenberg et al. 1997*b*). The coffee cover was dense and high, consisting primarily of modern dwarf hybrids of *Coffea arabica* (e.g., *caturra*). The experiments were conducted between 4 January and 18 May 1995, a period that corresponds to the dry season in this generally wet locality (rainfall is ~3000 mm/yr). All three fincas were sprayed once or twice annually with insecticides, primarily endosulfan (Thiodan, FMC corporation, Philadelphia, Pennsylvania), at a rate of 0.4–2.0 L/ha, as well as herbicides and foliage fertilizers. However, these treatments did not occur <4 mo prior to the initiation of this experiment.

Techniques

The experiment consisted of setting up exclosures of netting around individual coffee plants. Experiments of this kind may be biased by the small volume of habitat enclosed if the target arthropods are highly mobile (Moore and Yong 1991). If arthropods move freely between coffee plants, then the effect of predation will not be detected. In general, this biases the results of this experiment toward incorrectly accepting the null hypothesis of no predation effect.

We assume in this study that birds are the primary foliage-gleaning vertebrates excluded by the netting. However, it is possible that bats, lizards, and other animals may contribute to the estimated predation levels. In particular the effect of lizards on arthropod populations has been shown to be great in studies in the Caribbean Islands (Spiller and Schoener 1994, Dial and Roughgarden 1995), a region known for its high lizard abundances compared with the mainland tropics (Andrews 1979). During our many hours of fieldwork in Guatemalan coffee plantations, however, we found an extremely low abundance of lizards, and no lizards associated with coffee plants. Those we found were small, terrestrial species that could easily pass through or under the netting cages.

To determine the impact of birds on arthropods of coffee plants, pairs of adjacent coffee shrubs of similar stature were located within 10-m intervals; one was randomly selected to be the experimental plant. The entire experimental coffee plant was enclosed using a frame of steel rods (2.75 m × 6.4 mm) covered with transparent monofilament nylon gill netting (58-mm diagonal mesh). The four steel rods were bound together at the top to form a pyramid, and the netting was draped and then wired to the rods and loosely sewn shut with string.

Two successive insect samples were collected at monthly intervals from each coffee plant. To collect a sample, a transparent 226-L plastic bag was placed over four to six coffee branches (∼150 g, or 170 leaves) and quickly closed. This sampling removed ∼15% of the foliage of the coffee plants. The bases of the branches were clipped, and the bag sprayed with insecticide. The bagged samples were transported to the Universidad del Valle (UVG) within four hours of collection and placed immediately into a freezer until sorting, weighing, and identification took place. At UVG, foliage was weighed, arthropods were sorted by taxonomy (family) and ecological guild, and body length was measured. In addition, the number of leaves with insect-caused damage, and the total number of leaves, were determined.

Originally, the experiment was to be conducted within adjacent parts of coffee plantation at sites a and b that were in full sun or under shade. The design called for a balanced distribution of sun and shade coffee at each site (five of each). However, we had a problem with theft of the experimental materials. In the end we had five shade coffee exclosures at site a, and 4 at site b; one sun coffee exclosure at site a and 5 at site b with an additional five constructed at site c.

Statistical analyses

We first tested the difference in density (number/100 g foliage) between control and experimental exclosures for the small (<5 mm) and large (>5 mm) arthropods on a per sample basis. We based our analyses on the pairwise comparison of control and experimental exclosures (Sokal and Rohlf 1995: 655). We assumed that we had dampened the environmental variation (soil type, exposure, chemical applications, etc.) by selecting adjacent plants of comparable morphology. In cases where we tested the hypothesis that arthropod densities and leaf damage would be lower in the control (with birds) than in the experimental exclosures (birds excluded), we used one-tailed tests for significance. We relied upon a two-tailed test when we compared different coffee types, because there was no a priori hypothesis. We restricted our analysis to cages for which two collections were made. An ANOVA was conducted using control and exclosure as one repeated factor, and collecting date (one month vs. two months) as a second repeated factor. Because the variance of arthropod abundance was much greater in shade than sun coffee samples, a difference that was not eliminated by standard transformations, we conducted the analyses separately for sun and shade coffee. Once we determined an overall effect for bird predation on large arthropods, ANOVAs were conducted for each of the major ecological guilds (sapsucker, leaf chewer, and predator) and taxonomic orders (using the systematics of Arnett [1997]) of large arthropods where >10 individuals were detected. The ANOVAs used a repeated-measures model (exclosure vs. control, dates), but unlike the analysis for overall abundance, we analyzed shade and sun coffee together.

After an effect of exclosures on arthropod numbers was detected, we compared the level of reduction by pooling all data and calculating the proportional change in abundance between exclosure and control samples (exclosure abundance − control abundance)/(exclosure abundance + 0.0001). The constant was added to avoid a zero denominator. Because the rare negative values can be very large and greatly affect the variance estimates, we tested the median standardized reduction between sun and shade coffee using a Kruskal-Wallis test.

Finally, the percentage of leaves showing any type of insect damage was used to calculate a Leaf Damage Index (LDI). We tested the difference between exclosure and control with a repeated-measures ANOVA using the arcsine-transformed LDI in and out of exclosure as the repeated factor, and coffee type as an independent grouping factor. In this case, we conducted the ANOVA with both coffee types in the same model, because the variance in LDI was not significantly different between them. As leaf damage is a cumulative effect, we restricted our analysis to the LDI for the second sampling period.

RESULTS

We found significantly more large arthropods (standardized to 100 g of foliage) inside exclosures than outside, in both sun coffee ($F_{1,10} = 8.29$, $P = 0.008$) and shade coffee ($F_{1,7} = 6.19$, $P = 0.02$) (Fig. 1). We found no significant effect for date of collection (shade coffee $F_{1,7} = 4.64$ and sun coffee $F_{1,11} = 0.51$) nor for the interaction between exclosure by date ($F_{1,7} = 0.40$; $F_{1,11} = 0$). We found no significant exclosure effect for small arthropods (shade coffee $F_{1,7} = 1.75$; sun coffee $F_{1,11} = 1.45$).

Large arthropods were much more abundant in the shade than in the sun coffee foliage (Fig. 1, within exclosures, Student's *t* with separate variance estimates = 2.91, $n = 38$, $P = 0.006$). Therefore, we tested the relative impact of birds on large arthropods using a Kruskal-Wallis test on the ranking of the standardized reduction values. The median value of the standardized reduction in large arthropods was higher (87% vs.

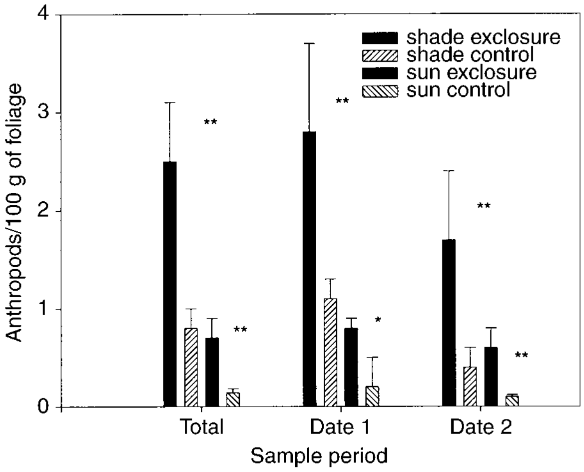

FIG. 1. Mean (+ SE) of the number of large arthropods per 100 g of foliage for exclosure and control samples in sun and shade. Data are presented for 1-mo (''Date 1'') and 2-mo (''Date 2'') collections and for the pooled (''Total'') sample. $*P < 0.05$, $**P < 0.01$.

61%), but not significantly so, for sun vs. shade coffee (Kruskal-Wallis $H = 1.07$, $n = 38$, $P = 0.29$).

The Leaf Damage Index (LDI) showed a significant effect of coffee type ($F_{1,17} = 16.79$, $P = 0.0007$) and exclosure effect ($F_{1,17} = 6.887$, $P = 0.009$). Using planned comparisons, we found a significant effect for exclosure within sun coffee ($F_{1,10} = 3.07$, $P = 0.048$) and shade coffee ($F_{1,7} = 3.77$, $P = 0.069$). Mean LDI ($\pm$1 SD)for shade coffee was 43.7 $\pm$ 14.5 and 37.0 $\pm$ 14.8 for exclosure and control, respectively, and was 23.4 $\pm$ 10.0 vs. 18.3 $\pm$ 7.1 for sun coffee.

All taxonomic and ecological guilds of arthropods (Fig. 2) were more abundant inside than outside the exclosures. This result is significant for the taxonomic orders based on a sign test ($P < 0.05$). We tested the difference in abundance of each group with a repeated-measures ANOVA and found that in three of the taxonomic groups (orthopterans, spiders, and dictyopterans) and two of the ecological guilds (leaf chewers and predators) the difference between exclosure and control was significant ($P < 0.05$).

DISCUSSION

The impact of birds on arthropods in coffee compared with other systems

Birds reduced the abundance of large arthropods by at least 64–80%, depending on coffee type. This high level of predation is consistent with other bird exclosure studies (Holmes et al. 1979, Gradwohl and Greenberg 1982, Moore and Yong 1991, Greenberg and Salgado Ortiz 1994). The fact that the effect was only detected for larger arthropods is most likely explained by the general preference of birds for larger arthropods. Within the large arthropods we found that birds consistently reduced numbers from all taxonomic classes. This result is in contrast to other studies that found birds have a detectable effect on only certain groups, such as Lepidoptera larvae and Orthoptera (Holmes et al. 1979, Gradwohl and Greenberg 1982, Moore and Yong 1991).

The implication for migratory bird distribution

Food limitation remains an important hypothesis for patterns of intra- and interspecific habitat use patterns by migratory birds (see Sherry and Holmes 1996 for a recent review). Greenberg (1995) proposed that large arthropods were particularly limiting. Although a number of studies have correlated the distribution of migratory birds with the abundance of arthropods (for coffee plantations see Johnson, *in press*), few have measured the degree of standing crop reduction by bird populations. We found extremely high levels of reduction for larger arthropods in coffee. Furthermore, despite the 10-fold greater abundance of arthropods in *Inga* foliage than in shade coffee, we found a 65% reduction of arthropods in *Inga* as well (R. Greenberg et al., *unpublished data*). This suggests that the level of arthropod prey reduction was similar throughout the plantation habitat. This study and that of Greenberg and Salgado Ortiz (1994) demonstrate that avian insectivory in the nonbreeding season in a tropical habitat where migratory birds are abundant, can be substantial (50–87%). Such high levels of insect predation are consistent with the concepts of food limitation and exploitative competition. Where birds show no detectable

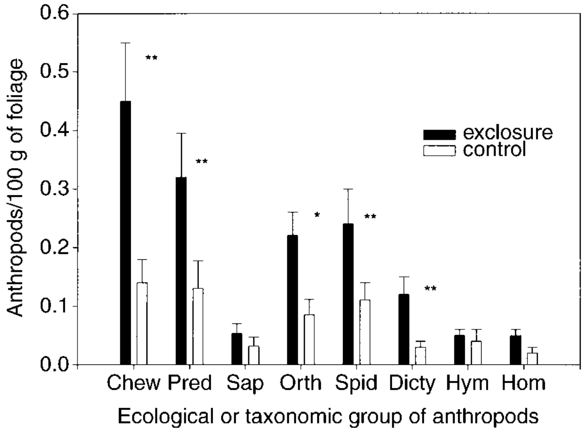

FIG. 2. Mean (+ SE) of the number of large arthropods (per 100 g of foliage) in specific taxonomic or ecological groups. Abbreviations are as follows: Chew = leaf chewers; Pred = predators; Sap = sap feeders; Orth = Orthoptera; Spid = spiders; Dicty = Dictyoptera; Hym = Hymenoptera; Hom = Homoptera.

effect on arthropod abundance, such as the shrubsteppe of western North America during the summer months, it has been argued that there is no reason to expect food competition to be important in influencing foraging behavior (Wiens 1989).

The relative impact of birds and arthropods in the coffee agroecosystem

We demonstrated a lower abundance of large, predatory arthropods outside of the exclosures (Fig. 1). The proportional reduction is similar for other guilds of large herbivores. Still, if birds substantially deplete large predatory or parasitic arthropods, and these arthropods, as a group, have a different prey base than birds, then bird insectivory will have an additional indirect impact on arthropod assemblages (Spiller and Schoener 1994. Although arthropod predators (particularly ants and spiders) are relatively abundant in coffee plantations (Robinson and Robinson 1974, Ibarra-Nuñez 1990, Perfecto et al. 1996), we do not have data on the quantity or types of arthropods they consume. It seems likely, however, that ants and spiders, as a whole, primarily consume smaller prey. Therefore, if birds reduce the population of arthropod predators, this would provide an additional reason why we found no experimental effect for smaller arthropods. What is needed is an integrated research program on the impact of different predator taxa in coffee plantations; such analysis of the ecological relationship between vertebrate and invertebrate predators has only rarely been undertaken (Spiller and Schoener 1994).

The impact of bird insectivory on leaf damage

Although we have not demonstrated that birds control the populations of specific coffee pests in a density-dependent manner, the high levels of predation can be expected to (1) reduce endemic levels of herbivory (Marquis and Whelan 1994), which may act in the long run to limit the need for plants to synthesize higher concentrations of alkaloids and produce tougher leaves (Frischnecht et al. 1986), which impose considerable cost on the plant (Coley et al. 1985); (2) lower the populations of a large number of herbivorous insect species, perhaps preventing some from ever attaining pest status; and (3) act as an agent of natural selection on the morphology, presence of chemical defenses and behavior of herbivorous arthropods that would reduce their efficiency (Heinrich 1979, Holmes et al. 1979).

The higher leaf damage in the exclosures supports the possible importance of the reduction of herbivory. This study joins several other studies of vertebrate insectivores in demonstrating an impact of their insectivorous behavior on levels of herbivore damage to plants (Atlegrim 1989, Spiller and Schoener 1990, 1997, Marquis and Whelan 1994, Dial and Roughgarden 1995). We have demonstrated a difference in the rate of leaf damage over a short period of time, but how this damage accumulates is unknown. Furthermore, coffee plants might compensate for low levels of herbivore damage ($<$10% of leaf area) detected in this short-term study (Cannell 1987). After all, leaf area loss is miniscule compared to what is lost through pruning by farmers (R. Greenberg et al., *personal observation*). However, pruning is generally directed toward older branches and shoots, whereas herbivores probably concentrate on newer foliage. Bird predation may differentially protect the most palatable and productive leaves. Furthermore, cutting has a qualitatively different impact on plant photosynthesis than does herbivory (Meyer 1993). Clearly, the biological and agronomic significance of the small effect on the leaf damage measured in this experiment is difficult to assess without more long-term study.

Vegetation diversity and insectivory

The results of this experiment provide no support for the hypothesis that increased vegetative diversity increased the impact of bird predation on prey populations, as would be predicted if the enemies hypothesis applied to this system. Despite the higher density and diversity of birds found in shaded plantations, we found no increase in the proportional reduction of arthropod standing crop abundance in the coffee shrubs of the shaded plantations. Furthermore, data gathered in similar exclosures of seven coffee plants under diverse tropical forest canopy cover in Ocosingo, Mexico (R. Greenberg et al., *unpublished data*) produced a significant overall impact of 65% on large arthropods, a value very similar to the levels found in both sun and managed-shade sites in this study.

Where the effects of avian predation have been removed, arthropod abundance is higher in shade than in sun exclosures. This suggests that factors other than predation are important in determining the difference in arthropod numbers between the coffee types. These additional factors might include greater abundance of alternate resources and greater climatic buffering offered by the addition of a shade canopy, physiological changes in coffee plants grown in full sun.

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