

SHORT COMMUNICATION

Bird predation on insects reduces damage to the foliage of cocoa trees (*Theobroma cacao*) in western Panama

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(Accepted 13 July 2007)

Key Words: agroforestry, enclosure experiment, insectivory, multi-trophic interactions, *Theobroma cacao*

In the Neotropics, crops that are grown in agroforestry systems with shade trees support high levels of bird diversity compared with crops grown without shade (Estrada & Coates-Estrada 2005, Faria *et al.* 2006). Several experiments in shaded coffee farms have explored how insectivorous birds reduce herbivore numbers and their damage to plants and have simultaneously approached ecological questions that are applied (e.g. biological control) and basic (e.g. tri-trophic interactions) (Borkhataria *et al.* 2006, Greenberg *et al.* 2000, Perfecto *et al.* 2004). Here we used enclosures to test whether birds lower the densities of herbivorous insects and reduce insect damage to cocoa (*Theobroma cacao* L., Sterculiaceae) foliage in shaded farms of western Panama. Although bird predation has been shown to reduce insect damage to crops in other systems (Mols & Visser 2002), we provide the first test for shade-grown cocoa.

We maintained bird enclosures on cocoa trees at two focal farms, in the communities of La Gloria (9°20'N, 82°28'W, altitude 45 m) and Charagre (9°23'N, 82°33'W, altitude 25 m). The study farms were within 2 km of 10–20-ha primary forest fragments. Both study farms were in the flood plains of large creeks, in locations which were chosen for their accessibility and flat ground. No chemical inputs (i.e. insecticides, fungicides) were applied to foliage in these farms. The mean canopy cover from shade trees was 54% (measured with a concave densiometer for 20 plots per farm, Van Bael, unpubl. data) and the farms shared the same predominant shade-tree species, *Cordia alliodora* (Ruiz & Pavón) Cham. (Boraginaceae). Throughout western Panama, 102 shade-tree morphospecies were counted in

cocoa farms, with *C. alliodora* accounting for 42% of all stems (Van Bael *et al.* 2007). We counted 188 bird species in cocoa farms throughout this region and 27 species were observed foraging in the foliage of cocoa trees (Van Bael *et al.* 2007).

At the two farms, we surveyed the effects of birds on 10 enclosure trees (–birds) and 10 control trees (+birds) per farm, for a total 20 enclosure and 20 control trees. The experiment began in January 2004 when we placed monofilament gill netting (mesh openings were 3 cm) over the 20 enclosure trees. The enclosures were in place for 13 mo. The netting was attached to nearby trees with rope and it did not touch foliage of the cocoa tree. This type of netting does not reduce light or change microclimatic conditions (Marquis & Whelan 1994) but does allow arthropods to move freely on and off the trees while excluding birds from the foliage.

We assessed arthropod density (the number of arthropods m⁻² leaf area) on the 40 experimental trees in April, June and October 2004. During each assessment, we bagged and clipped two haphazardly chosen branches (Johnson 2000) per experimental tree. We separated arthropods from leaves and branches for identification to order and for classification into two size groups, <3 mm and ≥3 mm. Leaf area was estimated by measuring the length of each leaf in the sample and inserting leaf measurements into the allometric equation for leaf area; $\log(\text{area}) = 1.99\log(\text{length}) - 0.55$ ($n = 280$ leaves, $r^2 = 0.98$, $P < 0.001$, Van Bael unpubl. data).

We estimated leaf damage by insect herbivores and new leaf production on four branches per tree in February, April, June, October 2004 and January 2005. The branches were chosen haphazardly before the experiment started, and we returned to the same branches and

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Table 1. Arthropod density, leaf damage and new leaf area produced on trees in the presence (+ birds) and absence (– birds) of bird foraging.

Independent variable fixed effects ¹	+ birds (mean ± SE)	– birds (mean ± SE)	df	F	P
Large-arthropod density (no. m ⁻² leaf area)					
Bird enclosure treatment	8.3 ± 1.7	15.3 ± 4.0	1, 110	5.5	0.020
Time			2, 110	1.95	0.147
Site			1, 110	0.16	0.691
Small-arthropod density (no. m ⁻² leaf area)					
Bird enclosure treatment	33.3 ± 3.1	35.1 ± 3.2	1, 110	1.99	0.161
Time			2, 110	6.26	0.003
Site			1, 110	2.88	0.093
Leaf damage (% leaf area removed)					
Bird enclosure treatment	7.6 ± 0.6	9.7 ± 0.7	1, 181	5.6	0.019
Time			4, 181	3.1	0.017
Site			1, 181	0.1	0.731
New leaf area produced since previous census (cm ²)					
Bird enclosure treatment	593 ± 70	503 ± 54	1, 150	2.1	0.158
Time			4, 150	14.8	<0.001
Site			1, 150	2.7	0.100

1. Models for all variables included site × treatment and time × treatment interactions; all were non-significant (P > 0.05).

leaves at each census period for measurements. We numbered each new leaf and used a plastic grid to estimate foliar area (1-cm² grid) and area damaged by insects (0.25-cm² grid). We recorded the foliar area of newly expanded leaves and counted abscised leaves on these same branches. Ten branches per tree were chosen and marked in January 2004 to measure branch extension growth. Branch extension growth was assessed once at the end of the experiment (January 2005). In February 2004, four trees had not produced new leaf area, so herbivory measurements were not available. In September 2004, one enclosure tree was destroyed by a treefall, reducing the sample size by one for subsequent arthropod and herbivory censuses. A huge storm and flooding in the region destroyed most of the crop and our bird enclosures, so we could not do a final assessment of harvest yield and damage to fruits at peak harvest time (January 2005).

The arthropod density (sum of two branches), mean leaf damage and mean new leaf production (average of four branches) variables for each experimental tree were log-transformed and subjected to repeated-measures analyses using mixed models in SAS (SAS Institute, Cary NC, USA). In each of four models, (1) large-arthropod density (≥ 3 mm), (2) small-arthropod density (< 3 mm), (3) % leaf area with herbivore damage and (4) new leaf area produced were modelled as a function of bird enclosure treatment, time, site, site × treatment, and time × treatment (Table 1). To assess the effect of bird enclosure treatment on different arthropod orders, we calculated the number of arthropods m⁻² leaf area in each order for each tree at each census period. There were many zeroes for most orders throughout the dataset. We removed orders that rarely appeared in our collection, the combined total of which represented <2% of all

individuals captured. Next, we averaged the arthropod densities for each order over all census periods and then proceeded with non-parametric analyses. We compared the effect of bird enclosures on different arthropod orders using Wilcoxon–Mann–Whitney (WMW) tests (non-parametric analogue of t-test, StatXact, Cytel Software, Cambridge MA). We used study site as a stratum variable in WMW test, so that scores were ranked within sites first (i.e. trees nested within sites). We also used the WMW test with study site as a stratum variable to compare branch extension growth.

Bird predation significantly reduced densities of large arthropods and damage by foliage-chewing insects. We found approximately twice as many large arthropods (≥ 3 mm) on trees without birds relative to trees with birds (Table 1, Figure 1a). This pattern was consistent at both farms (no site effect, Table 1). We did not observe significant treatment differences for smaller arthropods (< 3 mm) (Table 1). Spiders and caterpillars increased significantly in the absence of bird foraging (Table 2). We observed 14 caterpillar morphospecies of seven Lepidoptera families (Apatelodidae, Arctiidae, Geometridae, Noctuidae, Notodontidae, Crambidae and Saturniidae) feeding on cocoa leaves.

Bird foraging produced significant reductions of leaf damage on cocoa foliage, small increases in new leaf area production, and no effect on leaf abscission rates or branch extension growth. Leaf damage to cocoa plants by insects was significantly greater where birds could not forage (Table 1, Figure 1b). New leaf area production was not affected by bird removal over the course of the experiment at either site, although production of new leaf area decreased where birds could not forage in the October census (Table 1, time effect). Despite greater herbivory on trees where birds did not forage, we did not find a

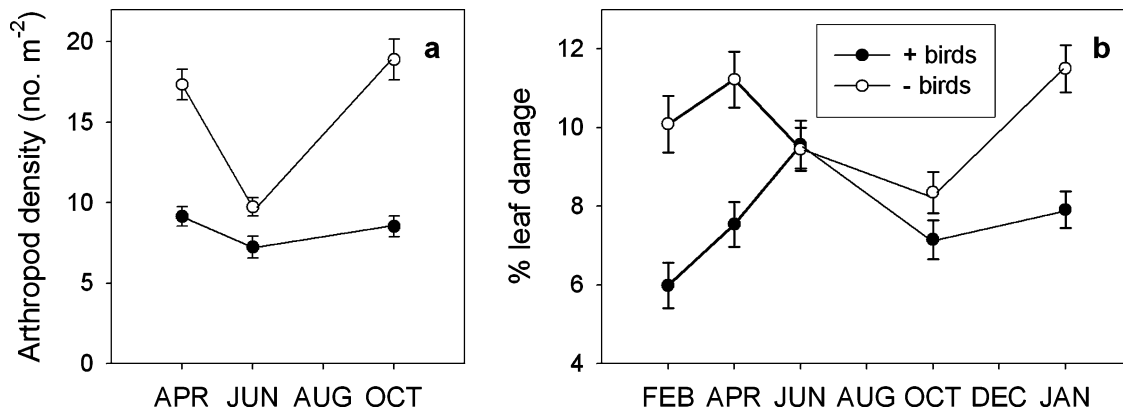


Figure 1. Impacts of bird foraging on cocoa crops in Bocas del Toro, Panama. Mean \pm SE density of large (≥ 3 mm) arthropods on cocoa trees with and without bird foraging in April, June and October of 2004 (a). Mean \pm SE per cent leaf area removed by insect herbivores on cocoa trees with (+ birds) and without (– birds) bird foraging (b).

difference in the percentage of immature leaves that were abscised throughout the experiment (– birds, $54\% \pm 2\%$, + birds, $56\% \pm 2\%$ leaves abscised). At the end of the experiment, we did not observe significant differences in branch extension growth on the experimental trees (– birds, 113 ± 11 cm, + birds, 106 ± 10 cm, WMW $T = 199$, $P = 0.33$).

Insectivorous birds reduced herbivore abundances and their damage to plants in some, but not all studies where predation by birds has been assessed (Mols & Visser 2002, Van Bael & Brawn 2005). Variation in top-down effects by birds may be due to characteristics such as plant age (Boege & Marquis 2006), plant quality (Sipura 1999), and intraguild predation (Mooney & Linhart 2006). Here we observed a temporal shift in bird predation. Birds were less effective at reducing arthropods and their damage to leaves during the June census period (Figure 1). One interpretation is that the insectivory pressure of migrants, relative to resident birds, was particularly intense in cocoa farms: the June census period was also when migratory

birds were completely absent in the farms. We observed particularly high levels of insectivory by the chestnut-sided warbler, *Dendroica pensylvanica*, a migrant that was frequently foraging in the cocoa layer for extended periods (Van Bael & Bichier, pers.obs.).

What are the implications of bird predation on arthropods for cocoa crops? A potential effect is a lower crop yield because (1) losing photosynthetic material reduces fruit production and/or (2) insects or insect-vectored pathogens directly damage fruits. First, in this experiment, bird insectivory reduced large-arthropod densities by an average of 46%. This reduced the loss of photosynthetic material by an average of 21% over the year (Table 1). While we were unable to collect reliable data on fruit production for this study, leaf area loss has been shown to reduce fruit production in other tropical plant species (Marquis 1984, Rockwood 1973). Cultivated cocoa trees, however, have high levels of early leaf abscission and the trees are also trimmed regularly by farmers, so we suggest it is unlikely that the

Table 2. Mean density of arthropods (no. m^{-2} leaf area) by order in the presence (+ birds) and absence (– birds) of bird foraging. Mean differences were compared using the Wilcoxon–Mann–Whitney test. Effect sizes and their confidence intervals (CI) were calculated using Hodges Lehman estimates of population shift.

Order	+ birds (mean \pm SE)	– birds (mean \pm SE)	P	Effect size	95% CI
Aranae	2.6 ± 0.35	8.3 ± 2.6	0.001	–3.01	(–4.8, –1.03)
Blattidae	0.35 ± 0.16	0.57 ± 0.18	0.12		
Coleoptera	2.7 ± 0.52	2.8 ± 0.38	0.29		
Diptera	1.2 ± 0.24	1.7 ± 0.31	0.18		
Hemiptera	0.69 ± 0.27	1.5 ± 0.51	0.14		
Homoptera	6.4 ± 1.6	10.2 ± 3.1	0.35		
Hymenoptera ants	17.5 ± 4.0	13.3 ± 3.6	0.11		
Hymenoptera wasps	1.4 ± 0.59	1.9 ± 1.1	0.47		
Lepidoptera	1.3 ± 0.29	3.3 ± 0.70	0.01	–1.3	(–2.3, –0.06)
Orthoptera	0.57 ± 0.15	0.79 ± 0.15	0.13		
Thysanoptera	1.5 ± 0.61	1.9 ± 0.77	0.45		

small differences in leaf area lost observed here would affect fruit production. Second, pathogen damage occurs more frequently than insect damage on cocoa pods in western Panama (Van Bael, pers. obs.). Transmission of the two major fungal diseases in this area, frosty pod disease (*Moniliophthora roreri* (Cif.) Evans *et al.*) and black pod disease (*Phytophthora* sp.), has yet to be linked to any insect or vertebrate vectors, and fungal spores appear to be entirely wind-dispersed (Fulton 1989). Because most pod loss is due to pathogens that are not insect-vectored, bird predation on insects is not likely to have economically significant effects on yields over the short-term in this region. Over the long-term, however, there is still the potential that a reduction in bird-predator activity could lead to a compounded increase in insect abundance and damage, pest outbreaks, and lower crop production (Mols & Visser 2002, Perfecto *et al.* 2004).

In other cocoa-growing regions around the world, such as Africa and Asia, there are direct relationships between insect feeding and large crop losses to disease; capsid (Heteroptera: Miridae) feeding increases pod loss and increases risk of fungal disease (Wills 1962), while mealybug (Hemiptera: Pseudococcidae) feeding spreads the cocoa swollen shoot virus (CSSV, Hughes & Ollennu 1994). Moreover, in Asia, insect pests such as the cocoa pod borer (Lepidoptera, Gracillariidae) and others cause tremendous amounts of crop damage (Wood 2002). In these cases, management intensity is usually high, often with greater levels of chemical input and less use of natural shade (Wood 2002). Management of shade to promote bird insectivory of these important pests could have large economic impacts in Africa and Asia, where the majority of cocoa is currently grown.

In summary, bird predation is a potential 'ecosystem service' that benefits farmers by limiting pests in the cocoa agroforestry system. While birds aid farmers with pest control, the presence of shade crops in the region provides important habitat for a wide diversity of resident birds and migratory birds from North America (Van Bael *et al.* 2007). Further studies should address whether crop yields are affected by bird predation on insects, and how agroforestry systems can be managed at local and landscape scales in order to increase habitat quality for important insectivores.

ACKNOWLEDGEMENTS

The authors thank E. Herre, D. Janzen, S. Philpott, W. Laurance, M. Libsch and H. Shapiro for comments on the manuscript. For assistance in the field and laboratory

we thank M. Morazon, I. Ochoa, M. Libsch, V. Aguilar, O. Morales, E. Rojas, L. Mejia, D. Alvarez, L. Ramirez, V. Castillo, R. Vargas, S. Philpott, J. diTrani and E. Herre. For logistical support and permission we thank the Lozado family in Charagre, the Aguilar family in La Gloria, the Smithsonian Tropical Research Institute, COCABO and ANAM of Panama. All financial support came from the sale of Smithsonian Migratory Bird Center 'Bird Friendly Coffee', a certification and labelling programme in which coffee companies dedicate \$0.25 per pound of coffee sales to research in shaded tropical agroforest systems.

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