

## Revising the convergence hypothesis of avian use of honeydew: evidence from Dominican subtropical dry forest

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A honeydew-producing scale insect (family Margarodidae, tribe Xylococcini, genus *Stigmacoccus*) was found associated with the tree *Bursera simaruba* in subtropical dry forests at elevations of 100–400 m on the south side of the Sierra de Bahoruco, Pedernales Province, Dominican Republic. At two study sites, 91% of *Bursera* trees supported locally dense populations of Margarodidae. Fifteen species of birds were observed foraging on the honeydew, but most observations were of the winter resident Cape May warbler (*Dendroica tigrina*) and black-throated blue warbler (*D. caerulescens*), and the permanent resident bananaquit (*Coereba flaveola*) and black-crowned palm tanager (*Phaenicophilus palmarum*). The Cape May warbler actively defended the honeydew resource but frequency of use of honeydew was influenced by the close presence of flowering agave and scale insect density. Data suggest that honeydew may be a critical component of the diet of this species especially during the late winter dry-season. Hymenopteran insects also were observed feeding on honeydew, but rates of consumption did not approach that of avian species. The occurrence of this phenomenon in Dominican dry forest is discussed in light of the convergence hypothesis of bird use and defense of homopteran honeydew in which it is proposed that birds are able to maintain relationships with scale insects in moist, warm temperate forests because it is in these climates where ant abundance is low. We suggest that our observation of a well-developed bird–homopteran system in classic subtropical dry forest supports the proposed mechanism of reduced competition with ants allowing bird use of honeydew, but we suggest that a broader array of especially insular habitats which may be relatively depauperate in terms of ants also can be expected to support bird–homopteran systems.

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Honeydew is a carbohydrate solution produced and secreted by individuals from six families of homopteran scale insects (superfamily Coccoidea) that feed on the phloem of host plants. Phloem-feeders remove soluble nitrogen compounds for protein building but dispose of the honeydew waste which can contaminate the individual scale or serve as a medium for the growth of harmful sooty moulds (Mibey 1997). Many Coccoidea secrete, spray, or release wax-encapsulated drops of the honeydew. Members of the coccoid family Margarodi-

dae are unique in possessing a long filamentous anal tube to deliver the honeydew at a distance from the scale itself. Even though the honeydew which the insects secrete has passed through their digestive system, it still has high sugar concentrations and is a rich food source.

Well-developed ant–homopteran mutualisms that are based on this type of honeydew have been described from many locations (Way 1963, Bach 1991, Gullan 1997). Though less frequently reported than ant–

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homopteran mutualisms, several examples of bird use of margarodid honeydew have been described (summarized in Greenberg et al. 1993). The use of honeydew by birds has been most often reported from Australia (Paton 1980, Loyn et al. 1983, Woinarski 1984), but has also been described in New Zealand (Gaze and Clout 1983, Moller and Tilley 1989), Costa Rica (Jiron and Salas 1975), Colombia (Koster and Stoewesand 1973), Brazil (Reichholf and Reichholf 1973), and Mexico (Edwards 1982, Greenberg et al. 1993). In most of these areas, honeydew is used by permanent residents, but honeydew has been reportedly used in migratory stopover (Kunkel 1997), and in Mexico the resource is used by winter resident migratory birds, especially the yellow-rumped warbler (*Dendroica coronata*).

Greenberg et al. (1993) postulated a 'convergence hypothesis' to explain the spotty geographical distribution of the phenomenon of bird use of honeydew. They rejected unique evolutionary histories as an explanation for this ecological pattern, and suggested that common regional climatic conditions have resulted in ecological convergence; the conditions found in moist, warm, temperate, evergreen forests have resulted in the few cases known of birds feeding on honeydew, perhaps because the cool, relatively aseasonal habitats in these environments contributes to a lack of honeydew-consuming ants and thereby promotes bird use of honeydew. Greenberg et al. (1993) predicted that future reports of bird use of homopteran honeydew would come from similar moist, equable, and cool sites.

Here we describe bird use of homopteran honeydew from a relatively low elevation, subtropical dry forest site on the Caribbean island of Hispaniola. We quantify the distribution of the resource at the landscape, site, and within-tree level, and we quantify honeydew use by both winter resident migratory birds and permanent residents. We also describe the conditions under which this resource is defended. Finally, we use these data to evaluate the convergence hypothesis as a means of describing the distribution of bird-homopteran systems.

## Study site and methods

### Study site

We studied bird use of honeydew in subtropical dry forest (Holdridge 1964) in the Sierra de Bahoruco National Park, Dominican Republic as part of a larger study of wintering neotropical migratory birds and avian communities across an elevational gradient. Latta (SCL) was present in the Bahoruco from 1 October to 1 April 1996–1997 and 1997–1998, and all authors were present in the same area from 8 January to 15 February 1999. We selected two principal study sites in the Aceitillar sector of the park (18°0' N, 71°38' W) in

Pedernales Province. These sites were situated at elevations of 300 m and 365 m. Similar dry forest has been studied at a site at 245 m elevation <2 km away by Fisher-Meerow and Judd (1989). At that site trees of the Malvaceae, Euphorbiaceae and Fabaceae are most abundant. Common trees include *Capparis ferruginea*, *Zizyphus rignoni*, *Bursera simaruba*, *Cameraria angustifolia*, *Cordia buchii*, and *Plumeria obtusa*; in disturbed areas *Acacia macracantha*, *Prosopis juliflora*, *Cassia atomaria* may be found. Mean temperatures are approximately 28.5°C in August and 25.0°C in January; rainfall is estimated at 750–1000 mm per year with two pronounced dry seasons annually from December to March and July to August (Fisher-Meerow and Judd 1989).

### The scale insect

We quantified homopteran scale insect presence at three levels: landscape, site, and within-trees. At the landscape level we conducted a census across two altitudinal gradients along the south-facing Aceitillar road and the north-facing Puerto Escondido – Aguacate road of the Sierra de Bahoruco National Park. We searched *Bursera* trees throughout their elevational range for signs of homopteran patches. These were most readily identified by the presence of black sooty moulds (Mibey 1997) and anal tubes of individual scale insects bearing drops of honeydew.

At the site level, we quantified homopteran presence by censusing *Bursera* trees along two 1 km × 30 m wide transects and recording the presence or absence of homopterans on each tree. These transects were our principal study sites (described above) and were located where densities of scales appeared highest.

We quantified homopteran presence at the level of the individual tree by randomly selecting 22 *Bursera* trees for intensive study. For each of these focal trees we recorded tree height (as measured with a viewfinder) and diameter at breast height. We quantified scale insect distribution by estimating the relative number of tubules in each of three zones of the tree (1 = inner third, including the trunk; 2 = middle third; 3 = outer third) based on a 6-point scale (0 = no tubules; 1 = 0–20% of branches bearing tubules; 2 = 21–40% of branches bearing tubules; 3 = 41–60% of branches bearing tubules; 4 = 61–80% of branches bearing tubules; 5 = 81–100% of branches bearing tubules), as well as estimating one score for scale insect density for the tree as a whole. All estimates of tubule densities were made by the same person (JRT) on the same day to reduce error. We also estimated the maximum density of tubules on each of these trees by counting the number of tubules visible in the most densely occupied 1-ft section of branch or trunk, estimating the branch diameter, and then calculating the number of tubules

per square meter. In addition, we calculated a mean tube length from the measurement of 100 randomly selected tubules.

### The birds

To quantify bird use of honeydew we made observations on our 22 randomly selected focal trees. We completed observation periods of 1 h each from 0700 to 1000 (67 h of observation) and from 1600 to 1900 (38 h of observation) when birds were most active. During each 1-h observation period we recorded the species and number of birds visiting the tree; the total time spent in the tree by each individual on each visit; and the total time spent feeding on honeydew. We also used intermittent time-activity sampling (Bart et al. 1998) to record the activity of each bird present in the tree at 5-min intervals: feeding on honeydew, feeding on other resource, resting, preening, or intraspecific interactions. To identify which individual defended the honeydew resource as part of its territory we also recorded all interspecific or intraspecific aggressive interactions. In approximately 30% of cases at least one individual among interacting pairs could be recognized because many parulid warblers had been color-banded as part of a larger study. In other cases, plumage differences (often associated with age and sex differences) could be used to identify individuals, or territorial birds especially could be followed visually into and out of focal trees.

We compared the proportionate abundances of species using honeydew to proportionate abundances derived from point count data. A total of 12, 10 min  $\times$  25 m fixed-radius point counts (Hutto et al. 1986) were conducted from 19 to 30 January 1999 at these sites. Each point was at least 100 m from all others. Counts were initiated at sunrise and terminated by 1000, and all counts were made by the same observer. We calculated the mean number of detections for each species per point count circle.

Using the most common consumer of honeydew, the Cape May warbler (*Dendroica tigrina*), we tested for temporal differences in honeydew use at two scales: within day and within season. To test for within-day differences in foraging activity we compared the number of visits and the accumulated time of visits to 13 of the 22 focal trees where observations were made during both morning and evening hours. To test for seasonal variation in bird use of honeydew, we used foraging observations of Cape May warblers made from October to April 1996–1997 and 1997–1998 at these same sites. These were made while walking slowly along transects through the sites. For each Cape May warbler encountered we recorded the first foraging event 5 s after a bird was detected to avoid a bias toward more conspicuous feeding techniques. We sought to record only a

single foraging event from an individual each day to reduce the problem of autocorrelation inherent in sequence data (Wagner 1981). Using these data we calculated the percent of all foraging observations in which the Cape May warbler gleaned a food item from the bark of the trunk or limb of a *Bursera* tree. Winters were divided into early (October–November), middle (December–January), and late (February–March) periods. Although in these earlier observations we did not record the food items collected, we believe these gleanings were almost exclusively for honeydew.

We calculated feeding rates of birds on honeydew by counting the number of honeydew tubules visited in a single feeding bout. Rates were calculated during focal tree observations and opportunistically. In all measures of feeding rates, we excluded individuals who did not visit a minimum of four tubules. Because we could not monitor or measure droplet size, we assumed in all feeding rate calculations that droplet size did not vary significantly between tubules.

Finally, we attempted to identify the factors that affected bird visitation rates to trees containing honeydew-producing scale insects. In addition to the focal tree-specific data gathered to quantify homopteran presence and within-tree distribution patterns (described above), we also recorded the number of other *Bursera* trees and flowering agave (*Agave antillana*) within 15 m of the focal tree, with the assumption that both may serve as alternate food sources for territorial birds (SCL pers. obs.).

### Hymenopterans

To quantify insect use of honeydew we made 1-h observations on 1-m segments of 15 trees where densities of tubules were high. Observations were made during mid-afternoon in sunny weather when insect activity was expected to be highest. At each 5-min interval we recorded the presence and activity (feeding on honeydew; other activity) of ants, and bees and wasps, present at the tree.

We calculated feeding rates of hymenopterans as we did for birds by counting the number of honeydew tubules visited and dividing by elapsed time. Rates were calculated during focal tree observations and opportunistically. In all measures of feeding rates, we excluded individuals who did not visit a minimum of four tubules.

### Statistical analyses

The software package SYSTAT Version 5.2 (Wilkinson 1992) was used to perform various statistical tests described in Sokal and Rohlf (1981). A probability of Type I error of 0.05 or less was accepted as significant,

but greater values are shown for descriptive purposes. Data presented are means  $\pm$  1 SE. We used an independent samples *t*-test to test for temporal differences in foraging behavior. We used a  $2 \times 2$  Test of Independence with a  $\chi^2$ -statistic or a Row  $\times$  Column Test of Independence with a *G*-statistic to compare the use of honeydew by species groups with relative abundance from point count data, to compare the distribution of tubules within a tree, and to analyze seasonal changes in honeydew use. Regression was used to relate the occurrence of a species at a honeydew source to log transformed relative abundance from point counts.

A stepwise regression was used to determine which of six vegetation and resource variables (height of focal *Bursera* tree, DBH of focal tree, number of *Bursera* in 15-m-radius circle, number of flowering *Agave* in 15-m-radius circle, score of abundance of homopteran tubules, maximum tubule density) accounted for the greatest amount of variation in number of visits to honeydew sources by the Cape May warbler. Stepwise multiple regression identifies which variables explain the greatest amount of variation in number of visits; the first variable to enter the stepwise model accounts for the greatest variability. Only variables that made significant contributions to the overall model were kept ( $p < 0.05$ ). After first employing the stepwise procedure to identify significant variables, we analyzed the overall model again using multiple regression.

## Results

### The scale insect

Honeydew-producing homopteran insects were found only on the south-facing slope of the Sierra de Bahuco at elevations of 100–400 m; they were most common above 250 m. Scale insects were always associated with the tree *Bursera simaruba* and were identified as the larval stage of what is likely a new species of scale insect (family Margarodidae, tribe Xylococcini, genus *Stigmacoccus*; D. Miller in litt.). Because new species are identified from adult male insects which we were unable to collect, the species has not been formally described. There are only two other species currently recognized in the genus: one from Chiapas, Mexico (Greenberg et al. 1993), and the other from Brazil (D. Miller in litt.).

Locally dense populations of scale insects were found on 91% of *Bursera* trees at our two study sites. Distribution of the tubes across three zones of  $n = 22$  trees was not normal ( $\chi^2 = 130.4$ ,  $p < 0.001$ ). Relative tube density increased from the inner third (mean score = 0.59) to the middle third (mean score = 2.09) and the outer third (mean score = 2.23) of the tree. Maximum tube density was calculated as  $3200.2 + 552.7$  tubes/m<sup>2</sup>. Mean length of  $n = 100$  anal tubes was  $11.75 \pm 0.76$  mm.

### The birds

We recorded 15 species of birds making 437 trips to forage on homopteran honeydew (Table 1). Seven species were winter resident migratory birds and they made 63.8% of all foraging trips to the honeydew; eight species were permanent residents. Four nectarivorous species made 67.7% of all foraging trips, while ten insectivores (30.4% of all trips) and one omnivore (1.9% of all trips) also consumed honeydew. The most frequent visitor to the scale insect honeydew was the Cape May warbler ( $n = 202$  trips), followed by the bananaquit (*Coereba flaveola*,  $n = 82$ ), black-throated blue warbler (*Dendroica caerulescens*,  $n = 57$ ), and black-crowned palm tanager (*Phaenicophilus palmarum*,  $n = 50$ ). Among Cape May warblers, males were significantly more frequent visitors than females to honeydew sources ( $\chi^2 = 9.760$ ,  $df = 1$ ,  $p = 0.002$ ).

The probability of occurrence of a species at a honeydew source could not be predicted from log transformed point count abundance data ( $r = 0.22$ ,  $df = 1$ ,  $p = 0.287$ ). In comparing the use of honeydew by winter resident migratory birds and permanent residents, we found that the proportionate abundance of migratory individuals consuming honeydew was significantly higher than the proportionate abundances derived from point count data ( $\chi^2 = 83.27$ ,  $df = 1$ ,  $p < 0.001$ ). When analyzed by diet type, the proportionate abundances of individual insectivores did not differ significantly from that derived from point count data ( $\chi^2 = 2.50$ ,  $df = 1$ ,  $p = 0.114$ ). In contrast, the proportionate abundance of individual nectarivores consuming honeydew was greater than proportionate abundances derived from point count data ( $\chi^2 = 37.22$ ,  $df = 1$ ,  $p < 0.001$ ), while the proportionate abundances of individual omnivores consuming honeydew was significantly less than that derived from point count data ( $\chi^2 = 60.43$ ,  $df = 1$ ,  $p < 0.001$ ).

Temporal differences (within-day) in honeydew use were calculated only for the most active forager – the Cape May warbler. We found no significant difference in the number of foraging trips ( $t = -0.095$ ,  $p = 0.926$ ) or the total time spent foraging on honeydew ( $t = -1.012$ ,  $p = 0.333$ ) by Cape May warblers between morning and afternoon observation periods, so foraging data from all observation periods were combined for all analyses for each species.

Cape May warblers recorded the highest number of visits to homopteran honeydew (Table 1). Among the most active foragers, the black-throated blue warbler, the bananaquit, and the Cape May warbler had the highest proportion of visits in which honeydew was consumed (Table 1); each fed on honeydew on  $> 85\%$  of their visits. The mean length of stay in focal trees while consuming honeydew was longest for the black-crowned palm tanager, followed by the black-throated blue warbler and the Cape May warbler (Table 1).

Results from our intermittent time-activity sampling for the four most abundant species showed similar results and indicated that the Cape May warbler dominated honeydew sites (Fig. 1) as they were recorded feeding on honeydew in a mean of 11.8% of sample periods.

The fastest foragers on honeydew were the Cape May warbler and the bananaquit. Mean feeding rates for the most abundant species were: Cape May warbler ( $n = 50$ ),  $36.8 \pm 2.1$  drops harvested/min; bananaquit ( $n = 12$ ),  $34.8 \pm 4.9$  drops harvested/min; and black-crowned palm tanager ( $n = 6$ ),  $26.2 \pm 3.9$  drops harvested/min. There was no significant difference in feeding rates of Cape May warbler and bananaquit ( $t = 0.367$ ,  $p = 0.719$ ), the two most abundant consumers of honeydew.

In 105 h of observation at focal trees, 50 acts of intra- or interspecific aggression were observed (Table 2). Honeydew was most actively defended by the Cape May warbler (58.0% of aggressive acts), but the bananaquit (28.0%), American redstart (8.0%), black-crowned palm tanager (4.0%), and black-throated blue warbler (2.0%) were all observed attempting to exclude other individuals from *Bursera* trees containing scale insects. Among the most active consumers of honeydew, the Cape May warbler was the most aggressive

and dominant species and was never excluded by any other bird except other Cape May warblers (Table 2). Male individuals were dominant and significantly more aggressive than female Cape May's ( $\chi^2 = 156.2$ ,  $df = 1$ ,  $p < 0.001$ ); males were involved in 91% of the acts of aggression by this species. The bananaquit was the second most dominant species, followed by the black-throated blue warbler.

Foraging observations beyond those made at focal trees also suggest that honeydew is an important season-long component of the diet of the Cape May warbler. We collected 388 individual observations of Cape May warblers foraging at our two principal sites between October and April. Foraging by the Cape May warbler on honeydew increased significantly over the winter ( $\chi^2 = 8.869$ ,  $df = 2$ ,  $p = 0.012$ ), so that by mid-winter (December–January) and late-winter (February–March) > 55% of Cape May warbler foraging observations were on honeydew.

Our broader analysis of factors that influence Cape May warbler use of *Bursera* trees containing homopteran honeydew suggest that the presence of other food sources also influence honeydew use. Stepwise regression indicated that the number of visits made by Cape May warblers to *Bursera* trees was affected most

Table 1. The resident status, diet, number of visits to focal trees, propensity for honeydew consumption, mean length of honeydew foraging visits, and abundance of each of 26 species of birds observed in subtropical dry forest in the Sierra de Bahoruco, Dominican Republic.

Species	Res <sup>1</sup>	Diet <sup>2</sup>	No. <sup>3</sup>	% <sup>4</sup>	Lgth <sup>5</sup>	Abd <sup>6</sup>
Cape May warbler ( <i>Dendroica tigrina</i> )	M	N	233	0.87	103.7 (5.6)	50.0
Bananaquit ( <i>Coereba flaveola</i> )	R	N	92	0.89	70.8 (6.9)	150.0
Black-crowned palm tanager ( <i>Phaenicophilus palmarum</i> )	R	I	68	0.74	154.3 (21.4)	100.0
Black-throated blue warbler ( <i>D. caerulescens</i> )	M	I	58	0.98	119.4 (15.7)	25.0
Greater Antillean bullfinch ( <i>Loxigilla violacea</i> )	R	O	43	0.19	142.2 (31.9)	100.0
Stolid flycatcher ( <i>Myiarchus stolidus</i> )	R	I	36	0.0		33.3
Gray kingbird ( <i>Tyrannus dominicensis</i> )	R	I	23	0.0		16.7
Broad-billed tody ( <i>Todus subulatus</i> )	R	I	17	0.0		58.3
American redstart ( <i>Setophaga ruticilla</i> )	M	I	16	0.94	64.8 (18.0)	8.3
Vervain hummingbird ( <i>Mellisuga minima</i> )	R	N	14	0.71	86.1 (26.2)	33.3
Antillean mango ( <i>Anthracothonax dominicus</i> )	R	N	8	0.25	13.5 (1.5)	33.3
Green-tailed ground warbler ( <i>Microligea palustris</i> )	R	I	5	0.80		8.3
White-crowned pigeon ( <i>Columba leucocephala</i> )	R	O	2	0.0		16.7
Antillean piculet ( <i>Nesocittes micromegas</i> )	R	I	1	1.00		0.0
Hispaniolan woodpecker ( <i>Melanerpes striatus</i> )	R	I	1	1.00		33.3
Red-legged thrush ( <i>Mimocichla plumbea</i> )	R	O	1	0.0		25.0
Palmchat ( <i>Dulus dominicus</i> )	R	O	1	0.0		25.0
Black-whiskered vireo ( <i>Vireo altiloquus</i> )	M	I	1	1.00		8.3
Northern parula ( <i>Parula americana</i> )	M	I	1	1.00		8.3
Prairie warbler ( <i>D. discolor</i> )	M	I	1	1.00		8.3
Black-and-white warbler ( <i>Mniotilta varia</i> )	M	I	1	1.00		0.0
Rose-breasted grosbeak ( <i>Pheucticus ludovicianus</i> )	M	O	1	0.0		8.3
Key West quail dove ( <i>Geotrygon chrysis</i> )	R	O	0	0.0		8.3
Hispaniolan parrot ( <i>Amazona ventralis</i> )	R	O	0	0.0		33.3
Hispaniolan lizard cuckoo ( <i>Saurothera longirostris</i> )	R	I	0	0.0		8.3
Hispaniolan emerald ( <i>Chlorostilbon swainsonii</i> )	R	N	0	0.0		8.3

<sup>1</sup> Resident status: R = permanent resident, M = migratory winter resident.

<sup>2</sup> Diet based on Wunderle and Latta (1996): I = insectivore, N = nectarivore, O = omnivore.

<sup>3</sup> Total number of visits to focal trees.

<sup>4</sup> Proportion of visits by a species to focal trees during which the individual was observed foraging on honeydew.

<sup>5</sup> Mean (SE) length (s) of honeydew foraging visit.

<sup>6</sup> Mean number of birds per point count ( $\times 100$ ).

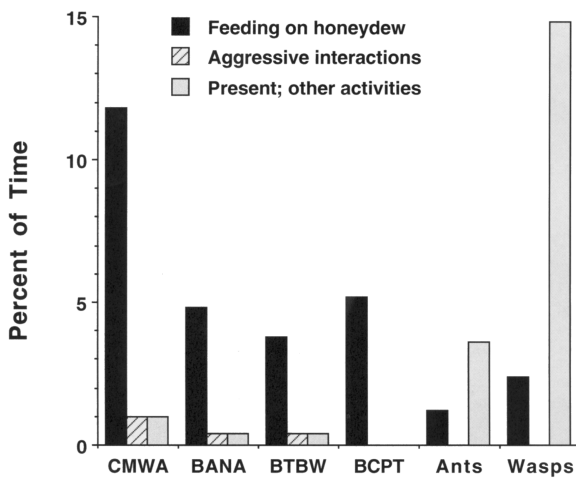


Fig. 1. The mean percent of time in which Cape May warbler (CMWA), bananaquit (BANA), black-throated blue warbler (BTBW), black-crowned palm tanager (BCPT), ants, and bees and wasps were feeding on honeydew, engaged in aggressive interactions, or present but involved in other activities, during intermittent time-activity samples at focal trees bearing honeydew-producing scale insects in the Sierra de Bahoruco, Dominican Republic.

by the number of flowering *Agave* sp. (an alternative food source;  $T = 1.856$ ,  $p = 0.080$ ) nearby and the relative abundance of homopteran tubules on the tree ( $T = 3.251$ ,  $p = 0.004$ ). Cape May warblers significantly increased their visitation rate at trees where more agave were nearby and with relatively higher densities of tubules ( $F_{2,18} = 9.285$ ,  $R^2 = 0.51$ ,  $p = 0.002$ ).

### Hymenopterans

Insects were uncommonly recorded feeding on homopteran honeydew. The only ant species observed foraging on honeydew was identified as *Cephalotes unimaculatus* (R. Snelling in litt.). Two species of native wasps were also found foraging on honeydew. These included a species of *Polistes* (family Vespidae) and a sphecid wasp (family Sphecidae). Results from our intermittent time-activity sampling show ants, and bees and wasps, present at only 4.8% and 17.2%, respectively, of sampling intervals (Fig. 1). However, only

1.2% of sampling intervals showed ants foraging; only 2.4% of sampling intervals recorded bees and wasps foraging. Ants were able to remove drops of honeydew from the ends of anal tubes that were either short in length or lay flush to the tree. Mean foraging rates for  $n = 21$  ants was  $2.4 \pm 0.2$  drops harvested/min; for  $n = 24$  wasps the foraging rate was  $5.1 \pm 0.6$  drops/min. Wasps and ants fed significantly slower than the most active avian forager (Cape May warbler;  $t = -14.61$ ,  $p < 0.001$  and  $t = 4.212$ ,  $p < 0.001$ , respectively).

Birds also may be attracted to the trees to forage on insects which are feeding on the honeydew. Sit and wait insectivores such as the broad-billed tody (*Todus subulatus*), gray kingbird (*Tyrannus dominicensis*), and stolid flycatcher (*Myiarchus stolidus*) were frequently recorded foraging from perches in *Bursera* trees, and the black-crowned palm tanager was seen to consume wasps feeding on honeydew on at least four occasions.

## Discussion

### The avian-homopteran honeydew system

In this dry broadleaf forest, scale insect honeydew appears to be an important resource supporting both winter resident and permanent resident bird populations. Honeydew was used by a large number of species, including insectivores and omnivores, but use by nectarivores predominated. Winter resident migratory birds played an important role in this bird-homopteran system. While permanent resident hummingbirds and bananaquits foraged on honeydew, the Cape May warbler was the most active forager and defended the resource most aggressively. The importance of the resource to the Cape May warbler is seen not only in the direct measures of honeydew consumption, but also in its aggressive defense of the resource; similar aggressiveness by this species has been noted in other situations by previous observers (Baltz and Latta 1997). While the proportion of visits to focal trees in which honeydew was consumed, and the mean length of honeydew foraging bouts are lower for the Cape May warbler than those recorded for some of the other species, this is likely the result of repeated visits by the Cape May

Table 2. Number of aggressive interactions between each of five species of birds which most actively consumed homopteran honeydew in the Sierra de Bahoruco, Dominican Republic. CMWA = Cape May warbler, BANA = bananaquit, BTBW = black-throated blue warbler, BCPT = black-crowned palm tanager, AMRE = American redstart.

	CMWA	BANA	BTBW	BCPT	AMRE
Aggressor					
CMWA	8	13	5	1	2
BANA	0	3	10	0	1
BTBW	0	1	0	0	0
BCPT	0	2	0	0	0
AMRE	0	0	0	0	4

warblers to defend a territory rather than visits only to consume honeydew.

Avian use of Dominican honeydew can be compared with the bird–homopteran honeydew system described by Greenberg et al. (1993) in Mexican highlands. Males tend to dominate the resource in both systems. In Mexico, most yellow-rumped warblers were males, and among the Townsend warblers (*Dendroica townsendi*) which also utilized the honeydew males were dominant over females. In the Dominican example, male Cape May warblers visited the honeydew more frequently than females and were more aggressive in its defense, despite female Cape May warblers being more frequent in mist-net captures in this same site (Latta 2000). Rates of aggression were much higher at Mexican sites (12.2 chases/h) than in the present study, but tubule density may have been lower in Mexico (3–5000 scale insects/bird territory) than in some of the Dominican sites (maximum tubule density of 3200 tubules/m<sup>2</sup>). Finally, local abundance of the dominant species utilizing honeydew is dramatically higher (> 22 times) around scale insect patches than in randomly selected patches in Mexico; in this study the abundance of the dominant Cape May warbler is only twice as high in habitat with scale insects as it is in adjacent habitat (Latta 2000).

These differences between bird–homopteran honeydew systems may be better understood if put into a landscape perspective. In a concurrent study, Latta (2000) showed that the distribution of Cape May warblers across the Dominican landscape is consistent with the ideal despotic model of Fretwell (1972) where males and adult birds are expected to dominate females and juvenile birds for access to optimal winter habitats. Dominican dry forest was shown to be suboptimal habitat for wintering Cape May warblers relative to adjoining pine forest, so it is not surprising that male Cape May warblers dominate the apparently preferred food resource (honeydew) in a female-dominated habitat, and concentrations of birds around the resource are not as dramatic as that seen in Mexico. Differences between Mexican and Dominican systems in rates of aggression may reflect this demographic structure in that males in a female dominated habitat may be able to defend the resource without overt chasing. Alternatively, differences in tubule density, droplet size or honeydew quality (which we did not measure), or the presence of other food resources within the habitat or the landscape may influence levels of aggressiveness between sites.

Studies of avian–homopteran honeydew systems involving migratory birds (Greenberg et al. 1993, this study) have suggested that honeydew is of less importance to permanent resident species than to migratory species. Greenberg et al. (1993) argued that because of the temporal nature of the resource, defending a particular food source in the non-breeding season may not be

advantageous for permanent residents if it negatively effects the individuals “ability to compete for reproductive openings that may become available during the non-breeding season”. The temporal nature of the resource may make honeydew less attractive to permanent residents who must balance breeding and non-breeding season demands and intermittent resources in judging territorial quality.

Temporality of the honeydew resource may also be an issue even within the non-breeding season as Cape May warblers in this system did not use honeydew consistently throughout the winter. This seasonality of honeydew use may be the result of periodicity in the abundance of larval instars of scale insects that produce honeydew (Greenberg et al. 1993, Kunkel 1997). However, while we did not quantify scale insect abundance across the year, we did find scales producing honeydew throughout the winter months and even into early August (SCL, pers. obs.), suggesting that there may be reasons other than homopteran periodicity behind trends in warbler use of honeydew. An alternative explanation for the increase in Cape May warbler use of honeydew is that warblers may have ready access to preferred or alternate foods early in the winter when we found less use of homopteran honeydew. Seasonality and changes in the relative abundance of different food sources is suggested by the pronounced dry season that these sites experience which effects the availability of flowers, fruit, and insects (SCL unpubl.). The effect of alternate food sources on warbler use of honeydew is also suggested by our finding that the number of foraging trips made by Cape May warblers to homopteran colonies was influenced most by the number of flowering agave in sample plots.

### The convergence hypothesis

Greenberg et al. (1993) first went beyond a simple description of bird–honeydew interactions to attempt to explain under what conditions this unusual phenomenon occurs. They recognized an association between the geographic distribution of the then-described bird–homopteran systems and the occurrence of moist, warm temperate forests (Walter 1973), and suggested that in these climates where ant abundance is low, birds are able to maintain relationships with honeydew-producing scale insects.

The occurrence of a well-developed bird–homopteran system in classic subtropical dry forest in the Dominican Republic clearly does not fit this pattern. Climatic conditions in this dry forest are more equable than in the moist, warm, temperate forests which characterize other sites where bird use of honeydew has been reported, but a distinct annual temperature cycle is still evident. More important in defining these sites is the presence of two pronounced dry seasons when very

little rain falls. These are the “dry deciduous tropical forests” or “semievergreen forests” of Walter (1973).

### Revising the convergence hypothesis

We suggest that our observation of a well-developed bird–homopteran system in classic subtropical dry forest, as opposed to moist, warm temperate forests, supports the proposed mechanism of reduced competition with ants allowing bird use of honeydew, but we suggest that a broader array of especially insular habitats which may be relatively depauperate in terms of ants also can be expected to support bird–homopteran systems. Both evolutionary history and regional climatic conditions have effected the development of this phenomenon and contribute to this analysis. Evolutionary history is invoked by considering the phylogenetic history of scale insects, the current distribution of the Margarodidae, and the zoogeography of ants. Regional climatic conditions must be considered in analyses of the effects of climate and environmental factors on zoogeographic distributions of homopterans and ants. By including both evolutionary history and local climatic conditions in our analysis we can elucidate a broader pattern of bird use of homopteran honeydew than that described by Greenberg et al. (1993).

Consideration of evolutionary history in the development of bird–homopteran interactions must begin with an analysis of the phylogenetic history of the Margarodidae. Among the Coccoidea, the members of the family Margarodidae are unique in secreting a long wax tube to deliver honeydew. The presence of long anal tubes appears to be the primitive condition among the Coccoidea (Hodgson 1997); it is in the more advanced families that one sees reduction of the tube or the production of showers of small droplets of honeydew and the concurrent evolution of close relationships with ants. Honeydew produced by the Margarodidae may be particularly suitable for avian consumption because the anal tube produces relatively large droplets, and because the long tube does not allow ants to harvest the honeydew thereby reducing competition for the resource. The few ants observed to forage on honeydew in this system avoided the longer anal tubes and foraged only on shorter tubes which they could easily reach. Similarly, Greenberg (pers. comm.) observed that in the mountains of Veracruz, Mexico, ants foraged on honeydew produced by scale insects with short tubes in early winter, but that by mid-winter, when tubes were longer, migratory birds dominated this resource.

Evolutionary history is also considered in analyzing biogeographic patterns of the Margarodidae. While most members of the Margarodidae have a tropical or subtropical distribution, the family is distributed worldwide in all of the major zoogeographic regions and

nearly all climatic subregions (Morrison 1928, Jakubski 1965), so there is little a priori reason to expect bird–homopteran relationships to develop in a single, narrow ecological region. No studies have looked at margarodid distributions at a finer scale to relate historical, climatic, or environmental factors to scale distributions, and in fact studies of biogeographic patterns of any scale insects are rare because of insufficient distributional data and the estimated large number of as yet unidentified species (Kozár and Ben-Dov 1997). Scales have not been found on *Bursera* from mainland sites where it is a common tree (R. Greenberg pers. comm.), nor do we know if scale presence on *Bursera* is a general phenomenon on Caribbean islands. However, Kozár (1992) analyzed the distribution of scale insects on six host plant genera world-wide, including *Quercus*, the genus of the host-plant of the margarodid studied by Greenberg et al. (1993). Kozár found that the partitioning of host plants by scale insects on a geographic scale must be based on evolutionary patterns and biogeography, including historical events, plate tectonics, glaciation, climatic zonation, and isolation. Furthermore, Kozár concluded that ecologically-based theories and hypotheses like ecological age, heterogeneity, competition, plant chemistry and even co-evolution could not explain the observed species richness of these insects on plants in different regions.

In contrast, Greenberg et al. (1993) suggest that the biogeographic patterns of ants, and thereby the development of bird–homopteran interactions, may be explained by regional climatic conditions. The greatest diversity and abundance of ants is found in tropical rainforests, and then decreases with increasing latitude, elevation, and aridity (Kusnezov 1957); but relatively large and diverse populations of ants are still present in the hottest and driest habitats in the tropics and warm temperate zones (Hölldobler and Wilson 1990). While the scarcity of ants in moist, warm temperate forests may allow birds to better compete for the valuable honeydew resource (Greenberg et al. 1993), and we concur that low densities of ants may be needed to promote bird–homopteran interactions, evolutionary history has resulted in more complex patterns of ant distribution which do not always follow strict regional climate models. In the present case, while subtropical dry forest may be expected to have relatively high abundance and diversity of ants (Hölldobler and Wilson 1990), geological and dispersal events dictate otherwise. Oceanic islands are relatively depauperate in terms of insects (Janzen 1973), including ants, and so may be expected to more often develop bird–homopteran relationships if honeydew-producing scale insects are present. In fact, many of the most well-known bird–homopteran systems that have been described have come from islands, including the North Island of New Zealand (Gaze and Clout 1983), South Island of New Zealand (Gaze and Clout 1983, Moller and Tilley

1989), Tasmania (Woinarski 1984), Kangaroo Island (Australia; Paton 1980) and now Hispaniola (this study).

Finally, we suggest that there may be ecological and behavioral considerations in the development of bird-homopteran interactions as well that are worth investigating. For example, for ants as well as birds not all honeydews are alike. The constituents of phloem and hence honeydew may differ among plant species, on different parts of the same plant, with plant age, or seasonally (Way 1963). These differences in the chemistry of the honeydew can effect the ants which attend them (Gullan 1997) and presumably the birds, especially when the honeydew is produced by a scale living on a tree such as *Bursera* in which secondary compounds such as terpenes could potentially be present in the phloem as it is in the leaves and branches (Janzen 1983). Even if the honeydew is an appropriate resource for birds, there are further questions concerning the conditions under which bird-homopteran systems develop. For example, homopterans would presumably need to be distributed densely enough to be worth defending. The birds making use of this resource must also be capable of nectarivory and flexible enough to utilize and defend a temporal resource. Finally, experimental studies (sensu Greenberg et al. 1993) are needed to address the question as to whether birds have the same symbiotic function as ants have in ant-homopteran interactions (Way 1963, Bach 1991, Gullan 1997) in which ants serve roles in enhancing scale insect growth and survival, deterring natural enemies, and dispersal of scale insects.

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