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Frugivory in Some Migrant Tropical Forest Wood Warblers

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ABSTRACT

Three species of wood warblers (Parulidae), the bay-breasted, chestnut-sided, and tennessee warblers, eat fruit in the winter on Barro Colorado Island, Panama. A seasonal pattern of frugivory was observed for the two congeners (bay-breasted and chestnut-sided), both species displaying a strong peak in frugivory in the late dry season. They also were highly frugivorous earlier in the winter, during a general fruiting low, in response to the fruit crops of *Lindackeria laurina* and *Casearia* spp. Chestnut-sided and bay-breasted warblers occur commonly at only a few species of fruiting trees, mainly *Miconia argentea* and *Lindackeria laurina.* These trees were visited by warblers far out of proportion to the relative abundance of warblers among small omnivorous forest birds. *Lindackeria* was visited almost exclusively by warblers. While the mechanisms are not clear, *Lindackeria* appeared to be specialized for dispersal by warblers to a degree not reported for any other migrant-dispersed fruits in the tropics. Warblers were more frugivorous in 1978-1979 than 1977-1978. This situation may be a result of the lack of overlap in fruit production in *Miconia* and *Lindackeria* in 1978-1979. The bay-breasted warbler was more frugivorous than the chestnut-sided warbler during both winters. The spacing system of the two species may play a prominent role in this difference. Chestnut-sided warblers defend small territories, a circumstance which makes preferred fruiting trees an undependable food supply. Bay-breasted warblers aggregate from a large area to feed on preferred trees, so fruit supply is more predictable. Bay-breasted and tennessee warblers (and other migrants such as red-eyed vireo) are far more intraspecifically gregarious than are most tropical forest residents. It is possibly the tendency to visit fruiting trees in large flocks that makes migrants potentially good dispersers for some plants.

MIGRANT WOOD WARBLERS (Parulidae), like many other primarily insectivorous birds, are often observed visiting fruiting trees in tropical areas (Leck 1972, Howe and De Steven 1979, Morton 1980). Fruit is such an energy-rich and easily procured food that some opportunistic frugivory should be expected by many bird species. The importance, however, of warbler frugivory to warbler populations or to the plants that warblers visit is poorly understood.

Few data have been gathered on use of fruit by warblers through entire winters, though observers in the Panama Canal Zone generally have found migrant warblers to be frugivorous during the late dry season (March-April), during a period of general fruit abundance, a seasonal pattern shared by a number of small, omnivorous tropical birds (Morton 1973). Leck (1972) found thar warblers, as other opportunistic frugivores, visited *Hamelia patens* Jacq. (Rubiaceae) on Barro Colorado Island (BCI) only in the late dry season despite the fact that fruit was also produced in the late wet season. Competition for *Hamelia* berries was intense in the late wet season, and Leck hypothesized that only more specialized frugivores can forage on the scarce fruit. These findings suggest that the degree of frugivory in warblers is determined by the general abundance of fruit rather than by the availability of any particular species. Morton (1980), however, found that most warblers frugivorous in the Canal Zone during the late dry season fed on *Miconia argentea* (Sw.)DC. (Melastomaraceae). Howe and De Steven (1979) working on BCI found that tennessee warblers (*Vermivora peregrina*) and other migrants were the most frequent visitors to *Guarea glabra* Vahl. (Meliaceae), a small understory tree, during the late dry season.

The importance of warbler frugivory to the plants they visit is even less clear. Leck (1972), basing his conclusions on observations of plants in the BCI laboratory clearing, believed that migrants were uncommon at fruiting trees in lowland tropical areas. Howe and De Steven (1979), however, found that migrants, by virtue of their sheer abundance, were important in dispersing seeds of *Guarea glabra.* They suggested that fruit production by *Guarea* may be timed to attract migrants that are drifting north from South America. Morton (1971) suggested that *Didymopanax morototoni* (Aubl.) Dec. and Planch (Araliaceae) may time fruit production to coincide with the passage of eastern kingbirds (*Tyrannus tyrannus*). More observations are needed to generalize further from these two views.

In this paper I examine the frugivorous behavior of migrant warblers both from the viewpoint of the various warbler species populations and of the trees visited by warblers. I will consider the seasonal and year-to-year variation in frugivory of warblers, the breadth of the fruit diet of warblers, interspecific differences in use of fruit, and relative abundance of warblers at their favorite fruiting trees.

The species I studied, the bay-breasted and chestnut-sided warblers, are characteristic of woodlands and forests of Central Panama (Eisenmann 1957). The bay-breasted warbler, the more common species during the study, breeds in the boreal forests of North America and winters mainly from central Panama eastward to northern South America. The chestnut-sided warbler breeds in deciduous second growth of eastern North America and winters from central Panama westward to Honduras. While data presented in this paper are generally restricted to these two species, the tennessee warbler will be discussed since it may be an important frugivore in the BCI forest.

METHODS

Data for this paper were gathered during two winters: from 20 October 1977 to 20 March 1978 (winter 1) and 30 October 1978 to 30 April 1979 (winter 2). Most of the observations were made on BCI (9°09'N, 79°51'W) with some data gathered from forests of the adjacent mainland near the towns of Gamboa and Frijoles. With the exception of observations made in the small laboratory clearing on BCI, all study sites were covered with moist forest. The area receives 2500 mm rainfall (Leigh and Smythe 1978); little rain falls in a dry season usually lasting from December through April.

These observations of frugivory were made as part of a larger study on the behavior and ecology of the two species of *Dendroica.* I will detail here only those techniques I used for quantifying frugivorous behavior. General methods for studying spacing behavior and general abundance of warblers will be published elsewhere.

FRUGIVORY INDEX (FI).—I kept a record of all warblers I observed while walking the trails of BCI. I determined the general foraging mode (i.e., insectivory or frugivory) based on 1311 sightings of bay-breasted and 410 sightings of chestnut-sided warblers. An individual was considered frugivorous if at any time during my observations it ate at least a portion of a fruit. To index the degree of frugivory per month I divided the number of sightings of frugivorous birds by the total number of sightings for which the foraging mode was determined. Because repeated observations were often taken from known fruiting trees, the index would be biased if it included all observations of frugivory. To eliminate repeated observations I considered only the maximum number of birds seen in or around the tree at any one time, at any particular tree each month.

FRUITING TREE CENSUS.—Two tree species, *Lindackeria laurina* Presl. (Flacourtiaceae) and *Miconia argentea,* were identified as particularly important to warblers. Trees of these species were censused for 60 hours in 1978-1979 to assess the relative abundance of warblers among visitors. I used two census techniques: 1) I stopped at a tree for 5 min and counted the number of individuals of each bird species present (spot surveys); 2) I censused for longer periods (up to 2 hours) and summed the counts for each 5-min period (censuses). Maximum counts per 5-min period were used, rather than the number of visits, because often too many (15-20) individuals were in these trees to be recorded. Trees were selected for censusing before I knew which species were visiting the tree, and censuses were discontinued if in 10 minutes I observed no visitation. I visited the forest trees between 0630 and 1200 hrs and spaced my visits to cover the entire fruiting season of each species. Ten *Lindackeria* trees were censused for 16 hours (20 December-3 February) including 19 spot surveys at all trees and nine censuses (14.5 hrs) at five trees. The trees censused were in the BCI old forest (6), BCI young forest (2), and Pipeline Road (2). For forest *Miconia,* 16 trees were censused for 16 hours (2 March-30 April) including 19 spot surveys and 11.25 hrs of censusing at five trees. Twelve of the censused *Miconia* were in the BCI young forest, and four were in the old forest. In addition, a *Miconia* in the BCI clearing was censused, in periods throughout the day, for 10 hours 11-20 March 1978 and for 18 hours from 15 March to 15 April 1979. I censused this one tree so extensively because it was visited by a partially marked population of warblers.

RESULTS

SPECIES DIFFERENCES.—Bay-breasted warblers were consistently more frugivorous than chestnut-sided warblers (fig. 1). The FI value was greater (sign test $p < 0.05$) for bay-breasted warbler in 10 of 11 months. The overall monthly average (November-March) was 20 percent in winter 1 and 24 percent in winter 2. Chestnut-sided warbler had average FI values of 6 percent each year. The overall proportion of frugivorous bay-breasted warblers was significantly higher ($X^2 = 42$, d.f. $= 1$, $p < 0.001$).

SEASONAL PATTERN OF FRUGIVORY.—Both species showed a dramatic peak in frugivory in the late dry season (March). In both years a smaller peak in frugivory occurred earlier in the winter. Winter 2 had a peak in December and January with FI values of 21 percent and 26 percent in bay-breasted warb-

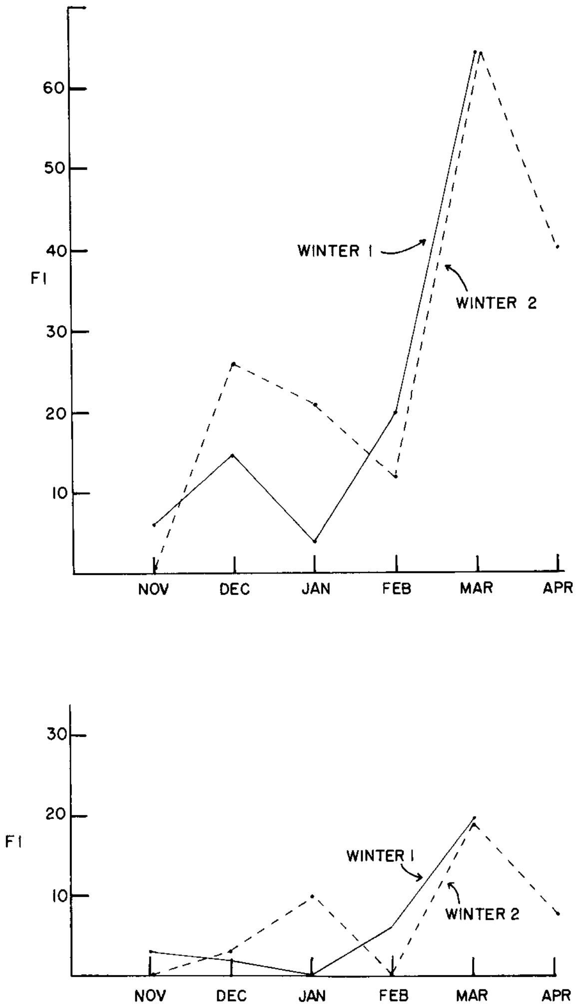

FIGURE 1. Monthly Frugivory Index (FI) values (see methods) for (upper) bay-breasted and (lower) chestnut-sided warbler in BCI forest for winters of 1977-1978 (winter 1) and 1978-1979 (winter 2). Monthly sample sizes for the bay-breasted warbler are: (winter 1) 144, 132, 82, 63, 40; (winter 2) 190, 137, 131, 172, 146, 75. Monthly sample sizes for chestnut-sided warbler are: (winter 1) 38, 45, 38, 32, 18; (winter 2) 59, 37, 29, 28, 55, 38.

lers; winter 1 had a smaller December peak. Despite the fact that December is generally a month of low fruit abundance (Foster 1974, Leigh and Smythe 1979), both species consumed a considerable amount of fruit in this month.

FRUIT SPECIES EATEN BY *Dendroica*.—I have observed the bay-breasted warbler feed on 21 species of fruit on BCI (table 1). The list for the chestnut-sided warbler is smaller (7 species) and wholly contained within the bay-breasted warbler list. Despite the apparent diversity of fruit taken, bay-breasted warbler concentrated on only three fruit types during the two winters: *Miconia argentea, Lindackeria laurina*, and *Casearia* spp. Flacourtiaceae (*C. arborea* [L. C. Rich] Urban and *C. sylvestris* Sw.) (75-85% of all observations in both years).

ANNUAL VARIATION IN FRUGIVORY.—The various peaks of frugivory described above were comprised of visits to primarily one species of tree. The March peaks for the bay-breasted warbler consisted of 90 percent observations at *Miconia argentea* and 40 percent to *Miconia* by the chestnut-sided warbler. The smaller December peak in winter 1 for bay-breasted warbler in winter 2 (24% monthly average November-March) versus winter 1 (20%) probably resulted from a shift in the fruiting season of *Lindackeria* (see fig. 2). Bay-breasted warbler showed comparably high peaks in March of both years. However, the proportion of frugivorous birds in December ($X^2 = 5.0$, d.f. $= 1$, $p < 0.05$) and January ($X^2 = 13.0$, d.f. $= 1$, $p < 0.01$) was greater in winter 2 than in winter 1. This larger peak in winter 2 was comprised of birds visiting *Lindackeria. Lindackeria* produced fruit during December and January of winter 2, but during February and

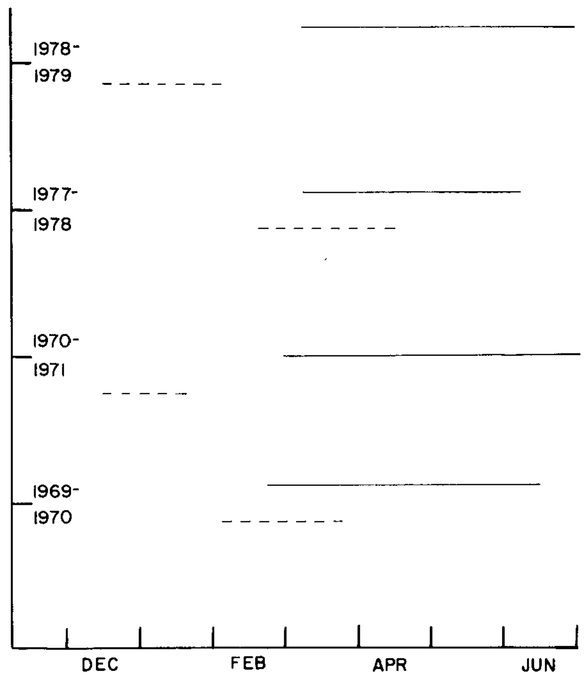

FIGURE 2. Season of fruit production in *Miconia argentea* (solid line) and *Lindackeria laurina* (dashed line). Range for 1977-1978 and 1978-1979 based on 10 *Miconia*. Range for *Lindackeria* based on three trees in 1977-1978 and 10 trees in 1978-1979. Range for 1969-1970 and 1970-1971 based on food-trap data (R. Foster unpubl.).

TABLE 1. *Relative use of different fruit by bay-breasted warbler. (Percent of total frugivorous observations.)*

Tree species	Winter 1 (n = 81)	Winter 2[a] (n = 164)	$\overline{X}$
Miconia argentea (Sw.) DC. Melastomataceae	45	45	45
Lindackeria laurina Presl. Flacourtiaceae	13	31	22
Casearia sp. (*arborea* [L. C. Rich] Urban and *sylvestris* Sw.) Flacourtiaceae	19	8	13.5
Ficus costaricana (Liebm.) Miq. Moraceae	9	2	5.5
Hyeronima laxiflora (Tul.) Müll. Arg. Euphorbiaceae	4	4	4
Coussarea curvigemmia Dwyer Rubiaceae	1	3	2
Alchornea costaricicensis Pax and Hoffm. Euphorbiaceae	0	2	1
Faramea occidentalis (L.) A. Rich. Rubiaceae	2	0	1
Myrcia fosteri Croat Myrtaceae	2	0	1
Psychotria horizontalis Sw. Rubiaceae	2	0	1
Quassia amara L. Simbaroubaceae	2	0	1
Zanthoxylum sp. Rutaceae	2	0	1
Zuelania guidonia (Sw.) Britt. and Millsp. Flacourtiaceae	0	2	1
Davilla nitida (Vahl) Kub. Dilleniaceae	+[b]	+	+
Eugenia sp. Myrtaceae	0	1	—
Hamelia patens Jacq. Rubiaceae	+[b]	+	+
Hasseltia floribunda H. B. K. Flacourtiaceae	0	1	—
Scrocea affinis Hemsl. Moraceae	1	0	—
Didymopanax morototoni (Aubl.) Dec. and Planch Araliaceae	1	0	—
Tetracera sp. Dilleniaceae	0	1	—

[a]Winter 2 excludes April observations (to make data comparable to Winter 1). Observations for April include: 24 *Miconia argentea*, 3 *Casearia sylvestris*, 2 *Coussapoa panamensis* Pitt. Moraceae, 1 *Miconia impetiolaris* (Sw.) D. Don ex DC. Melastomataceae.

[b]Observed to be eaten, but not in BCI Forest.

TABLE 2. *Percentage of census observations for visitors to* Miconia argentea *and* Lindackeria laurina.

Visitor	Clearing *Miconia* 1978 10 (308)[a]	Clearing *Miconia* 1979 18 (1396)	Forest *Miconia* 1979 16 (968)	*Lindackeria* 1979 16 (918)
Bay-breasted warbler	53	35	65	56
Chestnut-sided warbler	6	7	2	4
Tennessee warbler	4	7	2	24
(Total parulids)	(65)	(54)	(71)	(84)
White-shouldered tanager	6	5	3	5
(Total resident Thraupidae)[b]	(25)	(27)	(19)	(1)
Bananaquit	3	9	1	1
Pipridae	1	2	1	<1
Tyrannidae	6	5	1	3
Species total	24	46	36	23

[a]Hours observed (numbers observed).

[b]Including *Dacnis, Chlorophanes,* and *Cyanerpes* (Storer 1970).

March of winter 1 overlapping the fruiting of *Miconia.* The separation of the fruiting peaks of the two preferred trees may account for the overall greater degree of frugivory seen in winter 2.

Based on seed-trap data (Foster unpubl.), *Miconia* produced fruit from late February through May in 1970 and 1971. *Lindackeria,* however, produced fruit in December 1969 and February 1971. Variable timing in fruiting may be typical of *Lindackeria* (Fig. 2).

RELATIVE ABUNDANCE OF WARBLERS AT FRUITING TREES.—Warblers were the most common visitors to both *Lindackeria* and *Miconia* (and probably *Casearia sylvestris*) (see table 2). However, the relative abundances of visiting species will be discussed separately. Census numbers give no indication of the numbers of fruits consumed or dislodged by different species.

Lindackeria produces red (0.08g wet/0.04g dry) arils surrounding large (0.02g) seeds and contained in green soft-spiny capsules that droop from branch ends (A. Worthington unpub.). Few bird species ate *Lindackeria* arils in any quantity. Although 24 species were observed to take fruit, most did so rarely, and only six species accounted for more than 1 percent of the total census observations. Fifty-four percent of the 908 observations were for bay-breasted warblers; in fact, I never found a *Lindackeria* with visiting birds that did not include bay-breasted warblers. An additional 24 percent of the sightings were of tennessee warblers. Other common omnivorous birds were notably absent. The only tanagers observed were the white-shouldered (*Tachyphonus luctuosus*) and, in the Pipeline Road area, carmiol's (*Chlorothrapis carmioli*). Species of honeycreepers and other tanagers were never observed in *Lindackeria*, although they were common on BCI at this time. Most of these small tanagers, particularly plain-colored tanager (*Tangara inornata*) and blue dacnis (*Dacnis cayana*), were observed frequently at other fruiting plants such as *Hyeronima laxiflora* (Tul.) Mull. Arg. Euphorbiaceae, *Tetracera* sp. Dilleniaceae, and *Ficus costaricana* (Liebm.) Miq. Moraceae during December and January.

A comparative census helped to establish the selective use of *Lindackeria* by warblers. I quantified differential bird use of a large *Lindackeria* (20m) and an *Alchornea costaricensis* Pax and Hoffm. Euphorbiaceae (25m) 20 m apart and visible from each other. Both trees were censused in alternate 15-minute periods during two mornings (after one hour of initial censusing at *Lindackeria*). The relative abundance of species visiting the *Lindackeria* was quite distinct from that of *Alchornea* (table 3). *Lindackeria* was almost completely dominated by bay-breasted and tennessee warblers. The neighboring *Alchornea* received visits from many different, small, omnivorous birds. I observed no behavioral interference at either tree.

Miconia argentea produces an abundance of small (3-8mm, 0.10g wet/0.02g dry) berries. A tree may produce several hundred clusters of 50-200 green fruits with a few purple (ripe) fruits. Forest *Miconia* visits were dominated (65%) by bay-breasted warblers. Tennessee warblers, in contrast, accounted for only 5 percent of the observations. Unlike *Lindackeria*, a large (23.5%) proportion of the observations were of resident tanagers. All local species of honeycreepers were observed, including the uncommon scarlet-thighed dacnis (*Dacnis venustus*). Overall, a larger number of species (36 vs. 24) were observed at forest *Miconia* than *Lindackeria*. Twelve species comprised more than 1 percent of the total visits.

During the censuses in winter 2, I observed

TABLE 3. *Percentage of census observations of visitors to neighboring* Lindackeria *and* Alchornea.

Species	*Lindackeria* (342 obs.—225 min.)	*Alchornea* (127 obs.—165 min.)
PARULIDEA		
Bay-breasted warbler *Dendroica castanea*	43	17
Chestnut-sided warbler *D. pensylvanica*	5	0
Tennessee warbler *Vermivora peregrina*	37	13
THRAUPIDAE		
Green honeycreeper *Chlorophanes spiza*	0	6
Shining honeycreeper *Cyanerpes lucidus*	0	5
Blue dacnis *Dacnis cayana*	0	7
Scarlet-thighed dacnis *D. venustus*	0	2
Fulvous-vented euphonia *Euphonia fulvicrissa*	<1	0
Sulphur-rumped tanager *Heterospingus rubrifrons*	1	2
Summer tanager *Piranga rubra*	4	+
Plain-colored tanager *Tanager inornata*	0	8
White-shouldered tanager *Tachyphonus luctuosus*	2	0
COERIBIDAE		
Bananaquit *Coereba flaveola*	<1	0
VIREONIDAE		
Lesser greenlet *Hylophilus decurtatus*	0	8
Yellow-throated vireo *Vireo flavifrons*	<1	6
Philadelphia vireo *V. philadelphicus*	0	4
TYRANNIDAE		
Ochre-bellied flycatcher *Pipramorpha oleaginea*	<1	10
Great crested flycatcher *Myiarchus crinitus*	<1	0
Dusky-capped flycatcher *M. tuberculifer*	<1	2
Yellow-margined flycatcher *Tolmomyias assimilis*	0	3
OTHER SPECIES		
Red-capped manakin *Pipra mentalis*	0	3
Purple-throated fruitcrow *Querula purpurata*	1	2
Slaty-tailed trogon *Trogon massena*	<1	0
Black-cheeked woodpecker *Melanerpes pucherani*	<1	0
Mealy parrot *Amazona farinosa*	4	0

more species at the clearing *Miconia* than the forest *Miconia* in similar sample periods (45 vs. 36). Warblers comprised a smaller portion of total birds observed (54%), but tennessee warbler was relatively more common. The BCI clearing, particularly in the late dry season, has a tremendous local abundance of small omnivores which may explain their greater abundance at the *Miconia.* Censuses at the clearing *Miconia* during winter 1 were conducted during the first 10 days of ripe fruit availability, and visitation rates were low. Still, similar values for abundance of warblers and other groups of visitors were obtained. The low relative abundance of tennessee warblers may reflect their general scarcity on BCI during winter 1.

RELATIVE ABUNDANCE OF WARBLERS AWAY FROM FRUITING TREES.—In both *Lindackeria* and *Miconia,* bay-breasted warbler occurred out of proportion to its relative abundance among small (< 50g) omnivores on transects. Based on two 1-km transects, the first through primarily young and the second through primarily old forest, I estimated bay-breasted warblers to comprise 35 ± 2 percent (S.E. based on arcsine transformation, n = 21 censuses) and 32 ± 0.5 percent (n = 21) of small omnivores, respectively. These transects probably underestimated small, omnivorous birds, many of which are high-canopy species (Greenberg, in press). I censused canopy birds from a tower in the BCI young forest and found bay-breasted warbler to comprise 18.8 ± 1.7 percent (n = 32) of the small-canopy omnivores. A correct estimate for the proportion of bay-breasted warblers among small omnivores is probably 25-30 percent. This figure is considerably lower than the 55 to 65 percent relative frequency of bay-breasted warbler observations at *Lindackeria* and *Miconia.* Tennessee warbler is quite uncommon in the BCI forest (3 ± 0.2 percent transects; 5 ± 0.3 percent canopy), and the 24 percent relative frequency at *Lindackeria* is probably close to an order of magnitude greater than its relative abundance among small omnivores away from fruiting trees.

SOCIAL BEHAVIOR OF *Dendroica* AT FRUITING TREES.—Bay-breasted warblers often form aggregations of 10-20 individuals that move back and forth between fruiting trees and the adjacent trees. These aggregations may persist for long periods; flocks were seen for at least one month at two *Lindackeria* and four *Miconia.* The composition of these groups may be stable as indicated by the observation of six color-banded birds visiting the *Miconia* in the BCI clearing 11-20 March 1978.

Bay-breasted warblers show little intraspecific aggression when foraging at forest *Miconia* (0 chases in 16 h) or *Lindackeria* (10 chases in 16 h). One color-banded individual attempted to defend the clearing *Miconia* for 10 days during winter 1. While nine others entered the tree silently, this bay-breasted warbler flew in chipping loudly and chased all conspecifics out before feeding; it chased other bay-breasted warblers 40 times in 10 hours. Its visits comprised 53 percent of all 106 bay-breasted warbler visits, indicating some success at discouraging interlopers.

Chestnut-sided warblers are territorial in the BCI Forest (Greenberg 1979) and generally occur solitarily at fruiting trees. In the forest I observed two individuals at only one *Lindackeria* and three *Miconia,* and each of these were near known territory borders. Four different chestnut-sided warblers (one banded) visited the clearing *Miconia* in winter 1, and four (2 banded) in winter 2. The small territories in the clearing probably contributed to this joint use. The laboratory-clearing *Miconia* was at the boundary of three territories. An individual foraging in the tree generally greeted another chestnut-sided warbler with the entire array of winter territorial maintenance behavior: rapid chipping, zeeting, and chasing.

DISCUSSION

The overall picture of frugivory in warblers on BCI is one of specialization. During the two years of study I observed a concentration of frugivory in all three warbler species on only a few types of fruits. The little data available indicate that resident omnivores are more generalized in the range of fruit they eat. Snow (1962a), for example, found that white-bearded manakins (*Manacus manacus*) ate over 60 species of fruit, including over 40 species in one dry-season month. The smaller golden-headed manakin (*Pipra erythrocephalus*) had a less diverse fruit diet; 23 species of fruit were consumed in the winter months (October-April) (Snow 1962b). In contrast to bay-breasted warblers, no single fruit species dominated the diet of golden-headed manakin; three species of *Miconia* comprised 50 percent of the fruit diet, *Didymopanex morototoni* comprised 18 percent, and *Alchornea triplinervia* (Spr.) Mull. Euphorbiaceae, 5 percent. Although Snow and Snow (1971) did not present complete lists of fruit taken by tanagers and honeycreepers in Trinidad, it is clear that no species of fruit dominated the tanager diets to the degree *Miconia argentea* and *Lindackeria* dominated warbler diets on BCI. Within the specialization that characterizes warbler frugivory, frugivorous behavior exhibits inter-seasonal inter-annual and inter-specific variation.

INTER-SEASONAL VARIATION.—The view of seasonal patterns of frugivory that emerges from this study is somewhat more complicated than that of previous workers in Panama. While I observed the expected late dry-season peak, there was also a smaller, earlier peak. The seasonal distribution of frugivory in warblers can be correlated with the phenology of a few preferred species rather than with any abstract notion of seasonal superabundance of animal-dispersed fruit. None of the three warblers occurred mainly as migrants or were frugivorous primarily during migration. Indeed from 15 March to 5 April, during the peak of frugivory, over 60 percent of the bay-breasted warblers were in visible body molt (Greenberg, pers. obs.; Morton 1980).

INTER-ANNUAL VARIATION.—Year-to-year differences in the timing and degree of frugivory noted in this short-term study also appear to relate to variation in fruiting of the few preferred species. One species, *Miconia argentea*, appears to have little annual variation in the onset of fruiting. Based on four years of phenological record, *Lindackeria laurina* showed considerable variation in fruiting period.

SPECIES-SPECIFIC VARIATION.—The different degree of frugivory found in the two species of *Dendroica* is probably in part related to the divergent spacing behavior of the two species. Chestnut-sided warblers defend small (0.5-1.5 ha) territories throughout the winter. These territories coincide with antwren territories (Gradwohl and Greenberg, in press) and are established in October or November, long before *Lindackeria* or *Miconia* are in fruit. The probability of one of the preferred species being represented on the territory may be good, but the probability of both species present is low. During winter 2, I tabulated the number of these trees on five territories on the BCI plateau: Territory 1—3 *Miconia*; territory 2—1 *Lindackeria*; territory 3—2 *Miconia*; territory 4—1 *Lindackeria*; territory 5—neither species. While four of five territories had one species, no territory had both species.

Bay-breasted warblers have a more fluid spacing system. Aggregation of up to 20 birds can occur at fruiting trees that represent (at 1.5 warblers/hectare; Greenberg, pers. ob.) 13 hectares of dispersed insectivorous warblers. As evidence for the attraction that *Miconia* holds for bay-breasted warblers, I observed five marked birds visiting the clearing tree in March 1978 that I had not seen in the clearing area for three to five months and three in March 1979 that had not been seen since March 1978. Because bay-breasted warblers can aggregate from a large area at fruiting trees, preferred fruit is a more predictable resource for them than for the more sedentary chestnut-sided warbler.

WARBLER-ATTRACTING TREES.—Fruit dispersed by small birds, with the exception of the understory shrubs, generally attracts a diverse array of bird species. The high proportion of visits by bay-breasted and tennessee warblers to *Miconia* and *Lindackeria* is unusual. It cannot be explained by the high relative abundance of these species among small forest omnivores. The tennessee warbler, in particular, is a rare bird away from fruiting trees in the BCI forest. In the case of *Miconia*, the bay-breasted warbler occurred out of proportion to its abundance among the array of small, omnivorous, forest birds. This situation could result from their greater restriction to *Miconia*. Other species of small frugivorous birds are mostly larger and less restricted to small fruit, and may be feeding on other species of fruit besides *Miconia*. A number of the honeycreepers probably are also visiting large canopy trees which flower during this period.

The dominance of warblers at *Lindackeria* from which a number of common omnivorous species are absent is more puzzling. In this case *Lindackeria* appears to be highly attractive to warblers, but somehow discouraging to small tanagers and flycatchers. In part, fruit structure and digestibility may be responsible. The capsule generally opens downward from the end of a long branch. Most birds employ a hover-gleaning or leaping attack movement to grab or pick at the aril. Only rarely have I observed small tanagers employing these movements while foraging. However, they may be relatively inefficient at such acrobatics. This explanation would not account for the low rate of visitation of small, hover-gleaning birds, such as manakins or flycatchers. In addition, the aril has a distinctly waxy texture and odor. A high wax content may interfere with the digestion of the more nutritive portions.

That *Lindackeria* may specialize on warbler dispersal is supported by the following observation. During the course of feeding experiments, we searched under eight different trees in peak fruit production and never found open capsules with uneaten arils on the ground. The presence of rotting fruit on the forest floor is often considered part of the syndrome of "superabundance" which is found in trees that attract large numbers of small omnivorous birds (McKey 1972, Howe and Estabrook 1977).

WARBLERS AS DISPERSERS.—Warblers are distinctive in several features which would affect their performance as seed dispersers. Mosr obvious is their small size; only a few residenr omnivores are in the 8-11 gram size range of warblers. In most cases small size would probably reduce the importance of warblers, on an individual basis, in the removal of seeds. Howe and De Steven (1979) found that while tennessee warblers made 30 percent of the visits to *Guarea*, they removed only 19 percent of the seeds.

Warblers show a distinctive pattern of visiting fruiting trees. Whereas most residents and migrants move rapidly into a tree from some distance, warblers tend to remain in the vicinity of the tree or even in it when not actively feeding. Feeding observations of bay-breasted warblers in one *Miconia* include 10 percent (5/50) individuals that did not feed in five minutes of observation. Such birds, observed in nearly all *Miconia*, often preened. This tendency of warblers to remain in the vicinity of the fruiting tree would result in a large portion of the seeds eaten landing in a small area around the tree.

A third unique feature of tennessee and bay-breasted warblers is probably their primary attribute as dispersal agents: they are more inrraspecifically gregarious than any small resident omnivore (alrhough other migranrs during migration are highly gregarious—red-eyed vireo *Vireo olivaceus*, swainson's thrush *Catharus ustulatus*, eastern kingbird). Most tanagers and honeycreepers occur in pairs or small family groups (Moyhnihan 1962). But even the uncommon tennessee warbler may occur in groups of 10-15 individuals, outnumbering all resident omnivores in a mixed-species flock. While bay-breasred warblers on BCI show only a hint of the gregariousness displayed in other parts of their range (Greenberg, pers. obs.), they commonly occur in small flocks or aggregations. The fluid spacing system in bay-breasted and tennessee warblers and their tendency to aggregate would guarantee that a plant that attracts warblers would be attracting a large number of potential dispersers. The gregariousness of these migrant warblers and perhaps other migrants, such as eastern kingbird (Morton 1971) and red-eyed vireo, may make them important dispersal agents.

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NOTE

Giant Neotropical Ant Paraponera clavata Visits Heliconia pogonantha Flower Bracts in Premontane Tropical Rain Forest

Although most ponerine ants are believed to be chiefly predaceous, the giant neotropical ponerine *Paraponera clavata* is known to take exudates from at least one understory shrub in premontane tropical rain forest in northeastern Costa Rica (Young 1976). The markedly broad range of potential food items harvested from the canopy of the forest by these ants (Young and Hermann 1980) suggests that the species requires a variety of food-types.

Over a two-day period (4-5 February 1981) between 1000 and 1100 hrs several workers of *P. clavata* visited open inflorescences on two adjacent flowering and fruiting bracts of a single plant of the pendulant *H. pogonantha* situated at the edge of a mixed primary-secondary forest adjoining a cacao plantation, "Finca La Tigra," near La Virgen, Heredia Province, Costa Rica.

Six workers of *P. clavata* were seen at one time on one of the bracts; of these two were seen scraping with their mandibles at the creamy-yellow basal area of the conspicuous perianth. Each ant was engrossed in this behavior for several minutes, sometimes one ant replacing the other more or less alternately. There was only one inflorescence with an intact perianth as the other flowers on the bract had already fruited. A variety of other insects were seen on the bracts, most attracted to the fruits, but only *P. clavata* was attracted to the sleek basal area of the perianth. On the second bract, two *P. clavata* were seen, of which one was observed to exhibit the same behavior. The ants did not carry off any noticeable droplets of fluid or dislodged plant tissue after finishing the scraping motions. When a scraping ant was deliberately disturbed, it exhibited an aggressive posture, scurried away, but invariably returned to the same spot and resumed the scraping behavior, all within a few minutes.

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