# The role of the white-eyed vireo in the dispersal of *Bursera* fruit on the Yucatan Peninsula

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ABSTRACT. White-eyed vireos (*Vireo griseus*) winter in the forests and secondary growth of the Yucatan Peninsula where *Bursera simaruba* (Burseraceae) is an abundant tree. Twenty-five per cent of all white-eyed vireos observed foraging visited *Bursera* trees. In addition, presence and abundance of territorial white-eyed vireos in small forest patches were correlated with the size of the *Bursera* crop. Vireos were the most reliable dispersers of *Bursera* seeds. These birds visited 32 of 35 trees observed for at least three hours. They accounted for approximately half of all bird visits, and two-thirds of the seeds dispersed. Most of the other species rarely visited (<5% of visits) or failed to remove seeds from the tree.

Peculiarities of phenology and fruit structure may contribute to the tendency of *Bursera* to be dispersed by relatively few species. The capsules of *Bursera* fruits do not open when the fruit ripens; birds apparently locate ripe fruit using visual cues, although these are few. In addition, only a small portion of the crop ripens daily over a 7- or 8-month period. The vireo–*Bursera simaruba* relationship, found regionally on the Yucatan Peninsula, may result from the prolonged fruit ripening period (October–March), the relatively depauperate frugivore community and the relatively high density of small *Bursera* trees in the hurricane-disturbed dry forests.

Small trees at all times, and all trees from October to February, depend upon territorial vireos for continuous, highly efficient local dispersal of a small number of fruits. In March and April residual fruits ripen rapidly and synchronously, attracting a greater variety of visitors for broad spectrum dispersal during a period of food scarcity. Thus, *Bursera* has an unusual two-phase phenological pattern, perhaps alternately to take advantage of both specialized and opportunistic dispersers.

KEY WORDS: avian energetics, *Bursera simaruba*, frugivory, migratory birds, mutualism, seed dispersal, *Vireo griseus*.

## INTRODUCTION

Although migratory birds disperse seeds of a large number of temperate zone shrubs and trees (Davidar & Morton 1986, Stiles 1980, Thompson & Willson 1979), migrants are generally less important to tropical plants than are resident frugivores. Tropical communities include a large number of frugivorous species,

so migratory birds are usually only a small component of a large set of potential dispersers (Greenberg 1981, Leck 1972). In addition, migratory birds tend to be small, and therefore unable to handle the large seeds characteristic of many tropical species, and few species of migrants show the dependence on fruit that is common among some tropical resident species (Levey & Stiles 1992). Nevertheless, a large portion of the species that make the long trip from North to South America are at least partially frugivorous (Terborgh 1989).

Migratory birds are disproportionately common at a small number of tropical tree species (Greenberg 1981, Howe & DeSteven 1979). Several authors (Howe & DeSteven 1979, Martin 1985, Morton 1973) have suggested that some plant species time their fruiting to coincide with periods of migration. During these periods, negative attributes of migrants as dispersers – such as their small size – may be outweighed by the sheer abundance of the birds. Furthermore, most trees with fruit dispersed by migrants display a particular phenological pattern, producing large crops over short periods, which attracts a large and diverse set of dispersal agents (McKey 1975). This contrasts with trees that ripen a few fruit per day over a long period and attract fewer, more specialized dispersers.

Because most trees used by migratory birds produce ephemeral fruit crops that attract many potential dispersers, and frugivorous migrants are rarely resident in a particular habitat patch, little opportunity exists for specialized relationships to develop between birds and plants. Recently, however, Bates (1992) suggested such a relationship for the territorial gray vireo (*Vireo vicinior* Coues) wintering in desert washes in Sonora, Mexico, and the Elephant Tree (*Bursera microphylla* A. Gray, Burseraceae). This shrub ripens a small number of fruit each day over the period that vireos remain resident on winter territories. During work on habitat use by migratory birds on the Yucatan Peninsula (Greenberg 1992, Greenberg *et al.* 1993), one of us noted a similar association between the white-eyed vireo (*Vireo griseus* Boddaert) and the gumbo-limbo tree (*B. simaruba* [L.] Sarg.; Pennington & Sarukhan 1968). We describe the association and discuss its possible evolution in this paper.

## SPECIES AND STUDY AREA

White-eyed vireos breed in eastern North America and northern Mexico (American Ornithologists' Union 1983). Those from breeding populations north of Florida and Mexico migrate, with a majority probably wintering in the dry forests of the Yucatan Peninsula. White-eyed vireos have been reported to be highly frugivorous (Barlow 1980, Chapin 1925), and both sexes are territorial in winter (Greenberg *et al.* 1993, Rappole & Warner 1980).

Gumbo-limbo is a widely distributed tropical tree, occurring from the subtropical zones of Mexico, southern Florida and the Caribbean islands to Central America and northern South America (Little & Wadsworth 1964). Its seeds

are dispersed by a variety of birds (Scott & Martin 1984, Trainer & Will 1984) and primates (Stevens 1983).

The research was conducted primarily on the road running northeast from Felipe Carrillo Puerto to Vigia Chico, Quintana Roo, Mexico. The area is generally referred to as 'Sian Ka'an', because of its proximity to the Sian Ka'an Biosphere Reserve. The vegetation is a mosaic of mature and regenerating tropical dry forest (approximately 1200 mm rainfall/y, Olmsted *et al.* 1983). The forests are of low stature and species diversity, perhaps in response to the limited and highly seasonal rainfall, well-drained limestone soils and frequent hurricanes (Jauregui *et al.* 1980, Rzedowski 1978).

The tropical dry forests of the Sian Ka'an area have two distinct phases: a low subdeciduous forest and a medium-canopy subperennial forest (Olmsted *et al.* 1983). The forest types differ in overall stature (Greenberg 1992) as well as in degree of leaf loss during the long dry season (January–June). There are also large areas of 2 m to 5 m tall 'acahual' (5- to 7-year-old secondary growth scrub regenerating in abandoned cattle pastures and burned areas).

Comparative research was conducted at Puerto Morelos, Quintana Roo (see Lynch 1989 for a description of the area), and the archaeological sites of Chichén Itzá and Uxmal, Yucatan. A survey of white-eyed vireos in forest fragments was conducted along Mexican Rte. 295, from the Yucatan–Quintana Roo border to a point 11 km north of Tizimin, Yucatan. Sites in the state of Yucatan are covered with secondary dry forest (low to medium subdeciduous forest; Rzedowski 1978).

METHODS

Gumbo-limbo is generally abundant in the study area, occurring at differing densities in a variety of habitats (Pennington & Sarukhan 1968). We estimated interhabitat variation in abundance in our study area, along four 1-km transects, one each in medium-canopy subperennial forest, low subdeciduous forest, ungrazed acahual and grazed acahual, between 6 and 8 March 1990. Five 0.1 ha circular plots (radius = 17.8 m) were sampled along each transect at 200 m intervals, beginning at metre 50 or 100. Each vertical stem was counted as a separate tree, although there was evidence of trees separated by up to 3 m sharing the same root system. In addition, branches arising from the upper surface of fallen tree trunks often gave rise to new and independent trees as the trunks rotted. Trees with bifurcating trunks (>28% of those sampled) were counted only once.

For all *Bursera* ⩾1 m tall, we recorded height (to the nearest 25 cm with a range finder), DBH (to the nearest mm with a DBH tape) and presence or absence of leaves. We also estimated crop size as the product of the average numbers of fruits on small branches, the average number of small branches per large branch and the total number of large branches.

*Fruit morphology and nutritional quality*

Fruits and their component parts were described, and whole fruits (length × diameter) and seeds (height, width and depth) were measured to the nearest 0.1 mm with calipers. Whole fruits, capsules (= exocarp), and seeds were weighed to the nearest mg in 17 lots of 1 to 28, and average mass per unit calculated. Because it was impossible to remove the aril (= mesocarp) intact from a seed, weights of mesocarps were determined by subtracting weights of the capsule and seed from the weight of the whole fruit.

Fruits were separated into component parts for nutritional analysis in the field, using forceps and a scalpel. Samples were weighed to the nearest mg and air dried. Parts from many fruits were combined to amass sufficient material for analysis. On return to the laboratory, samples were placed in a drying oven at 65°C until a constant mass was reached, and again weighed to the nearest mg to determine water content. Nutrient contents, as percentage dry weight, were analysed by the Palmer Research Center, Agricultural and Forestry Experiment Station, University of Alaska, Fairbanks, as noted below. Percentage nitrogen was determined colorimetrically (Orion Scientific Instrument Methods No. 116-S540-01 and 116-S540-02) and converted to protein by multiplying by 6.25. Percentage non-structural carbohydrate was also determined colorimetrically (Smith 1969; Technicon Industrial Systems Method No. 280-75A, 1976; G. B. Fermentation Industries Inc. Technical Data Sheet Myc-01-01/82.06), and percentage lipid was determined gravimetrically (Randall 1974). We calculated energy content using conversion factors (9.5 kcal g$^{-1}$ dry mass lipid, 5.65 kcal g$^{-1}$ dry mass protein and 4.1 kcal g$^{-1}$ dry mass carbohydrate) from Paine (1971). Because tissue for analysis was limited, we did not analyze ash content; thus nutrient values are calculated per gram dry mass rather than per ash-free dry mass.

Metabolizable energy content of the aril was estimated as in Foster (1977), on the basis of the presumed digestible fractions, i.e. lipid, soluble carbohydrate and protein (corrected for excretion of nitrogen in organic form, Ricklefs 1974). Digestive efficiency (assimilated energy/gross energy intake) of the digestible fraction was arbitrarily set at 90% (see Martin 1968, Fisher 1972).

*Phenology and other fruit characteristics*

Each month between November 1987 and August 1989, I. Olmsted (unpublished data) recorded the presence of fruits or flowers on 28 *Bursera* trees along four 1-km transects in subperennial and subdeciduous forests and grazed and ungrazed scrub habitats ('acahuales'). Fruits of *Bursera simaruba* can stay on the tree for more than 11 months (pers. obs.). However, the capsule typically remains closed when ripe, and capsule colour is not a reliable indicator of ripeness (pers. obs.). Thus, it is difficult to obtain reliable information on the timing of the availability of ripe fruit. We obtained information on crop ripening by monitoring fruit clusters enclosed in bags made of white nylon net, with a mesh size of less than 00 mm, to prevent removal by birds or other animals or

natural abcission. We monitored eight clusters on five trees at the Botanical Gardens of the Centro de Investigaciones de Quintana Roo, A.C. in Puerto Morelos were followed.

We have anecdotal evidence that the visitation rate of birds is a good indicator of the rate of fruit ripening. We bagged 360 fruits in a small *Bursera* in an acahual and examined those fruits and an additional 350 unbagged fruits on three afternoons over two weeks. We found a total of 11 bagged fruits that were ripe (but still on the pedicel) but no unbagged ripened fruits, suggesting that birds keep the standing crop of ripe fruit reduced to an unmeasurably low level.

*Energy requirements of vireos*

We netted four white-eyed vireos of undetermined sex at Sian Ka'an between 9 and 11 March. We weighed each to the nearest 0.1 g with a spring balance. Bill tip-gape – the distance on an open bill from the tip of the upper mandible to the tip of the lower mandible – was measured to the nearest 0.5 mm, as described in Foster (1987).

Basal metabolic rate (BMR) was calculated according to King (1974) as follows:

$$\text{BMR kcal d}^{-1} = 24 \times 4.78 \ W^{0.726}$$

where W is body mass in kg. Values were multiplied by 4.184 to convert them to kilojoules. Daily existence energy (DDE) requirements were calculated as 1.5 BMR; energy requirements for existence and the maintenance of social interactions (DSE) were calculated as 2.5 BMR (see discussion in King 1974).

*Bird visitation pattern*

We observed 35 different trees, with three observed in both October 1989 and March 1990, as follows: February 1989 – five trees at Sian Ka'an; October 1989 – six trees at Sian Ka'an, three at Puerto Morelos and three at Chichén Itzá; March 1990 – 15 trees at Sian Ka'an, three at Puerto Morelos (repeated) and three at Chichén Itza. All trees were at least 8 m tall and had 200–4000 fruits. We observed all study trees for a minimum of three hours, recording all visits and foraging attempts. All trees were watched in the early morning (between 06:00 and 09:30) because wind and heat depress bird activity in Yucatan forests (pers. obs.). For comparison, we watched eight (three in October and five in March) of the sample trees in the afternoon (15:00–18:00) at Sian Ka'an. We made a total of 133 h of observation in the morning and 28 h in the afternoon.

To examine the pattern of visitation to individual trees over time, we observed four focal trees (two in forest and two in shrubby secondary growth) for four to six consecutive mornings (06:00–09:30) in October 1989 and March 1990. We watched different trees in each season.

For each visitor species we recorded total number of visits, proportion of the seeds removed from a tree and proportion of trees at which the species was observed. To maximize the statistical independence of the data used in the analyses of visitor composition, we considered only the first three hours of morning observation for a particular tree (totalling 115 h). For other analyses all observation periods were used.

## Feeding methods

We recorded the length of each visit, the number of fruits tested and the number of arils consumed for most visiting individuals during tree watches. Handling time from first contact to consumption of aril was also recorded. Handling methods were categorized into one of five types (after Trainer and Will 1984): (1) Squeeze – bird grabs fruit in bill, causing the capsule to fall away, and swallows seed and attached aril; (2) Grab – bird flies by and plucks entire fruit or seed plus aril, returns to a perch, discards capsule and holds seed against branch with foot while pecking at aril; (3) Peck – bird pecks away part or all of the capsule of a fruit still attached to the tree and then pecks at aril; (4) Steal – one bird flies at a second at the exact moment the latter removes the capsule from a ripe fruit, displaces the second bird and pirates the exposed seeds plus aril; and (5) Ground – bird pecks aril from seeds on the ground.

We looked at the efficiency of foraging in *Bursera* trees in two ways. The first was the mean number of capsules per minute (i.e. capsules opened per visit divided by average length of visit). The second method examines the rate of fruit consumption as a function of overall energy demands. We estimated the energetic value of the arils consumed per minute, divided this by the estimated DEE requirements of the species and multiplied the quotient by 100 to convert the percentage of DEE consumed per minute.

## Small patch survey

White-eyed vireos often defend territories around patches of trees in secondary growth habitats (Greenberg *et al.* 1993). To examine the relationship between the distribution of white-eyed vireos and the abundance of *Bursera* fruit, we surveyed white-eyed vireos and estimated fruit crop size in small patches of trees isolated by pastures and agricultural fields, from 5 to 10 November and 10 to 15 March in the state of Yucatan. We visited 35 patches of trees ranging in area from 100 to 13,200 m² (mean = 1360 m²). Birds were surveyed between 06:00 and 09:30 by playing a 3-min tape of a white-eyed vireo song and then waiting an additional 5 min for a response. For patches greater than 1000 m², we did two playbacks. We also counted *Bursera* trees >4 m tall and estimated the number of *Bursera* fruits available in the patch, patch size (length × width), mean canopy height and understorey density. Understorey density was categorized to class (1 = no, 2 = sparse, 3 = moderate, and 4 = dense vegetation). From 5 to 10 November, we conducted playbacks at 10 points in pasture and 10 at points in acahual located a minimum of 200 m from a censused forest

patch. The purpose of surveys was to determine the degree to which activity was concentrated around forest patches.

## RESULTS

### Tree and fruit characteristics

*Bursera* trees were both more abundant and larger in subperennial forest and subdeciduous forest than in grazed and ungrazed acahuals (Table 1). Although ungrazed acahual had total numbers of *Bursera* comparable to the forest habitats, large trees (≥10 cm DBH) comprised more than 40 and 60%, respectively, of the *Bursera* in the forest habitats, and less than 3% of those in the ungrazed acahual. The grazed acahual had very low densities of *Bursera*, although a large portion (50%) were large, with a DBH of at least 10 cm (Table 1).

Table 1.   Abundance and characteristics of *Bursera simaruba* trees in four habitats around Sian Ka'an, Quintana Roo, Mexico.

| Habitat[1] | Density of trees[2] (ha$^{-1}$) | | | | DBH[3] (cm) | | Height[3] (m) | |
| | All | | ≥10 cm DBH | | | | | |
| | X̄ | (SD) | X̄ | (SD) | Range | Median | Range | Median |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| SPF | 142 | (83.5) | 62 | (68.7) | 3.2–30.4 | 9.1 | 3.2–17.5 | 10.5 |
| SDF | 160 | (48.5) | 98 | (22.8) | 1.9–35.2 | 11.4 | 3.0–20.0 | 14.0 |
| UGA | 184 | (192.6) | 4 | (8.9) | 0.5–19.0 | 3.1 | 1.3–10.0 | 3.0 |
| GA | 14 | (11.4) | 6 | (8.9) | 1.7–18.1 | 6.2 | 2.5–8.0 | 5.5 |

[1] SPF = subperennial forest; SDF = subdeciduous forest; UGA = ungrazed acahual; GA = grazed acahual.
[2] Trees ha$^{-1}$ = 10 × (mean number trees per 0.1 ha); N = five 0.1 ha plots for each habitat.
[3] DBH = diameter at breast height; N for DBH and height: SPF = 71, SDF = 80, UGA = 92, GA = 7.

*Phenology.* Leaf production, leaf loss and reproduction in *Bursera* are relatively synchronized at Sian Ka'an. Flowers are produced primarily in April and May. Capsules start appearing in April, and full crops are realized by June. Leaves are lost by most trees from February to March with new leaves appearing at the time of flowering in April. Fruits do not begin to disappear (marked by the presence of bare pedicels) until late September. Few fruits are lost early in the winter, but fruit loss is rapid in late February and March (Figure 1). This phenological pattern was found on a different set of trees during the 1993–1994 season as well. The period of fruit availability ends relatively abruptly. For example, 30% of 50 trees more than 10 m tall that we monitored still had some fruit in mid-March. By mid-April, however, only four retained fruit (totalling 150) from the previous season, and two trees had new fruit. Of those trees, 86% had new leaves and 66% had flowers.

*Crop size.* When trees were surveyed in March 1990 at Sian Ka'an, some trees in all habitats still carried fruits from the crop set the previous year (Table 2).
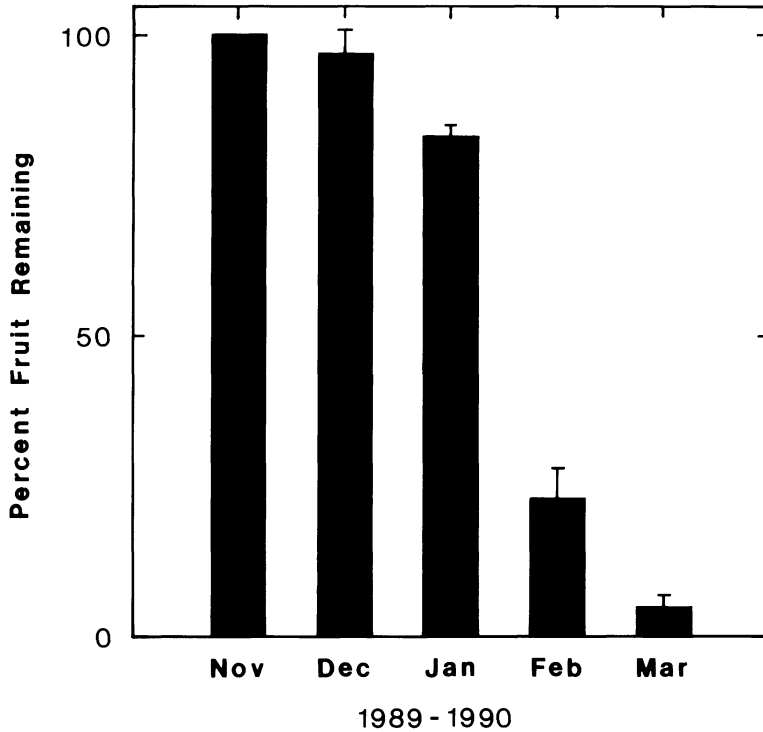
Figure 1. Mean percentage (±SE) of fruit remaining on bagged fruit clusters of *Bursera simaruba* at Puerto Morelos, Quintana Roo, Mexico. Initial sample sizes ranged from 20 to 150 fruit on 8 branches of 4 trees for a total of 522 fruits. Samples were standardized to a start value of 100%; thus there is no error value for the initial fruit census.

Table 2. Crop size and availability of *Bursera simaruba* fruits in four habitats around Sian Ka'an, Quintana Roo, Mexico, from 6 to 8 March 1990.

| Habitat[1] | Trees ha$^{-1}$ | | | Crop size range | Fruits[3] ha$^{-1}$ $\bar{X}$ |
|---|---|---|---|---|---|
| | with fruits No. (%)[2] | with ≥25 fruits No. (%)[2] | with ≥100 fruits No. (%)[2] | | |
| SPF | 26 (18.3) | 12 (8.5) | 8 (5.6) | 2–3000 | 7838 |
| SDF | 48 (30.0) | 24 (15.0) | 16 (10.0) | 2–400 | 4340 |
| UGA | 28 (15.2) | 2 (1.1) | 0 (0.0) | 1–30 | 246 |
| GA | 4 (28.6) | 2 (14.3) | 2 (14.3) | 15–143 | 316 |

[1] As Table 1.
[2] Percentage of mean number of all *Bursera* trees ha$^{-1}$ (see Table 1).
[3] Fruits ha$^{-1}$ = 10 × (mean number of fruits per 0.1 ha$^{-1}$); N = five 0.1 ha plots for each habitat.

However, trees with fruit were nearly twice as common in subdeciduous forest as they were in subperennial forest and ungrazed acahual, and 12 times as common as in grazed acahual. The size of the fruit crops also varied substantially, so that fruit availability (numbers/ha) differed among habitats in a pattern independent of numbers of fruiting trees (Table 2). Nevertheless, forest

habitats had more than an order of magnitude more fruits per ha than scrub habitats.

*Fruit characteristics.* The fruit of *Bursera simaruba* is a symmetrical, three-part capsule, somewhat longer than it is wide (Table 3). When cut, green capsules of unripe fruits release copious quantities of a strong-smelling, clear, sticky, astringent liquid. As fruits ripen, their capsules gradually become reddish, but unlike those of most arillate fruits, typically remain closed. The capsule valves fall away only when squeezed or, if the fruit is very ripe, when lightly tapped.

Each fruit contains a single seed covered by an aril. The cream-coloured aril of unripe fruits gradually turns bright red as it ripens. The aril is waxy in appearance, but when cut, is 'juicy', releasing a highly volatile liquid that dries quickly. The aril is oily and leaves a translucent grease spot on paper. The seed has an irregular, tear-drop shape and attaches by its base to the receptacle (Table 3). A thin layer of aril encloses the seed, forming three flat wings that run from its tip to its base and project outward for 1–2 mm. The aril is attached to the front distal surface of the seed.

*Nutrient content of fruits.* The high lipid content of the aril (Table 4) places *Bursera* among the richest species known (Foster & McDiarmid 1983). This lipid content is reflected in the high energy content of this tissue per unit dry mass, which is about 50% higher than that of either the capsule or the seed (Table 5). Even so, on a per fruit basis, the least energy is devoted to aril, followed by the seed and then the capsule – a reflection of the greater amounts of the latter tissues per fruit.

The metabolizable energy content of aril was even less because approximately half the aril consists of structural carbohydrate, which presumably is indigestible. We calculated metabolizable energy/aril/fruit as 0.556 kJ.

*Vireo morphology and energy requirements.* Tip-gapes of the bills of the four white-eyed vireos netted at Sian Ka'an averaged 12.4 mm (SD = 0.48, range = 12.0–13.0). This is 0.1 mm greater than the largest *Bursera* capsules measured (Table 3). The birds weighed an average of 12.9 g (SD = 0.80; range = 11.8–13.5).

Table 3. Dimensions (mm) of whole fruits and seeds of *Bursera simaruba* from Sian Ka'an, Quintana Roo, Mexico, March 1990.

|  | Fruit | | Seed | | |
|---|---|---|---|---|---|
|  | Length | Width | Length | Width | Depth |
| Mean | 10.5 | 9.0 | 6.8 | 5.3 | 3.9 |
| Range | 7.9–12.3 | 7.3–11.2 | 4.8–8.9 | 3.6–6.1 | 2.8–5.0 |
| SD | 1.26 | 0.72 | 0.90 | 0.55 | 0.46 |
| N | 100 | 100 | 132 | 132 | 132 |

Table 4.  Nutrient composition of fruit parts of *Bursera simaruba* from Sian Ka'an, Quintana Roo, Mexico, March 1990.[1]

| | Water (%) | Lipid (%) | Protein (%) | Carbohydrate | |
| --- | --- | --- | --- | --- | --- |
| | | | | Non-struc. | Structural[2] |
| **Capsule** | | | | | |
| Mean | 78.1 | 4.0 | 6.9 | 1.4 | 87.7 |
| Range | 76.2–80.0 | 3.8–4.3 | 6.1–7.7 | 1.4 | 87.1–88.2 |
| N | 2 | 2 | 2 | 2 | 2 |
| **Seed** | | | | | |
| Mean | 19.0 | — | 5.0 | trace | — |
| Range | 18.8–19.2 | 4.5 | 4.3–5.6 | — | 89.9 |
| N | 2 | 1 | 2 | 2 | 1 |
| **Aril** | | | | | |
| Mean | 10.3 | — | 2.7 | 1.2 | — |
| Range | 3.6–17.8 | 47.1 | 2.1–3.3 | 0.8–1.6 | 50.0 |
| N | 4 | 1 | 2 | 2 | 1 |

[1] Water content = percentage wet mass of tissue. All other nutrients = percentage dry mass of tissue.
[2] Determined by subtraction of other nutrients from 100%.

Table 5.  Average dry mass and energy values of fruit parts of *Bursera simaruba* from Sian Ka'an, Quintana Roo, Mexico, March 1990.

| Fruit part | X̄ Dry mass/ fruit (g) | X̄ Energy content (kJ) | | |
| --- | --- | --- | --- | --- |
| | | $g^{-1}$ dry mass | per fruit | % per fruit |
| Capsule | 0.102 | 18.506 | 1.888 | 47.5 |
| Seed | 0.069 | 18.535 | 1.279 | 32.1 |
| Aril | 0.029 | 27.937 | 0.810 | 20.4 |
| Whole fruit | 0.200 | 19.885 | 3.977 | 100.0 |

Their estimated daily BMR was 20.2 kJ; DEE was 30.3 kJ and DSE was 50.5 kJ. With a metabolizable energy of 0.556 kJ/aril/fruit, a white-eyed vireo would need to consume approximately 55 fruits per day to meet all of its existence energy needs and 91 fruits per day to meet its energy requirements for existence plus social interactions.

*Bird visitation*

White-eyed vireos were observed in all but two of the trees censused and accounted for more than half of the observed visits to *Bursera* and two-thirds of the seeds removed (Table 6). The next most common species (masked tityra, *Tityra semifasciata*, and Yucatan vireo, *Vireo magister*) were observed at only 15% and 12%, respectively, of the 35 trees observed. They and other species were far less frequent visitors to *Bursera* and removed far fewer seeds (Table 6). The three potential indicators of visitor importance presented in Table 6 are highly

Table 6. Frequency of visitation and seed removal by common bird visitors to *Bursera simaruba* at Sian Ka'an, Quintana Roo, Mexico.[1]

| Species | % watches[2] | % all visits[3] | % seeds removed |
|---|---|---|---|
| White-eyed vireo | 94 | 55 | 67 |
| Masked tityra | 12 | 12 | 13 |
| Yucatan vireo | 12 | 4 | 7 |
| Rose-throated tanager | 3 | 1 | 4 |
| Yellow-throated vireo | 15 | 9 | 3 |
| Gray-collared becard | 6 | 2 | 2 |
| Least flycatcher | 6 | 3 | 1 |
| Black-throated green warbler | 12 | 7 | 0.4 |

[1] Other visitors included: black-headed trogon (*Trogon melanocephalus*), rose-throated becard (*Pachyramphus aglaiae*), tropical kingbird (*Tyrannus melancholicus*), Yucatan flycatcher (*Myiarchus yucatanensis*), brown-crested flycatcher (*Myiarchus tyrannulus*), social flycatcher (*Myiozetetes similis*), Yucatan jay (*Cissilopha yucatanica*), lesser greenlet (*Hylophilus decurtatus*), mangrove vireo (*Vireo pallens*), black-cowled oriole (*Icterus prosthemelas*), hooded oriole (*Icterus cucullatus*), Altamira oriole (*Icterus gularis*).
[2] N = 35 trees (i.e. first 3 h of observation of each of 35 trees; total observation time = 115 h).
[3] N = 263 visits.

intercorrelated: percentage of watches with percentage of total visits, r = 0.99; and percentage of visits with percentage of seeds removed, r = 0.98).

*Seasonal variation.* Trees observed in October and February consistently had fewer visitors than those watched in March (Figure 2; Kruskal–Wallis, P < 0.01). In addition, no afternoon visits were observed in October. During paired morning and afternoon observations at three trees in October, we recorded 15 morning and zero afternoon visits. In contrast, equivalent observations at six trees in March resulted in a ratio of 75 morning to 49 afternoon visits ($\chi^2$, P < 0.01). White-eyed vireo visits tended to be relatively more common when overall visitation rates were low. The percentage visitation by white-eyed vireos was negatively correlated with the overall visitation rate (r = −0.68, N = 38, P < 0.01). For example, vireos made 83% of the visits during watches with fewer than two visits per hour, but only 20% of the visits during watches with rates of two or more visits per hour. Because of the seasonal increase in overall visitation rate, white-eyed vireos comprised 80% of the visitors in October and February and only 51% in March.

*Within-tree faithfulness of visitors.* Individual white-eyed vireos were the most faithful visitors to four *Bursera* that we watched for several days, visiting at least once a day during all of the census periods (Table 7): other visitors were more sporadic. The white-eyed vireo in whose territory a tree was located visited most frequently (76% of visits by all birds), but vireos from neighbouring territories also visited (mean = 5% visits).

*Search behaviour in trees.* Individuals of most bird species attempted to open only a few fruits per visit (Table 8). Such search behaviour suggests that most birds are
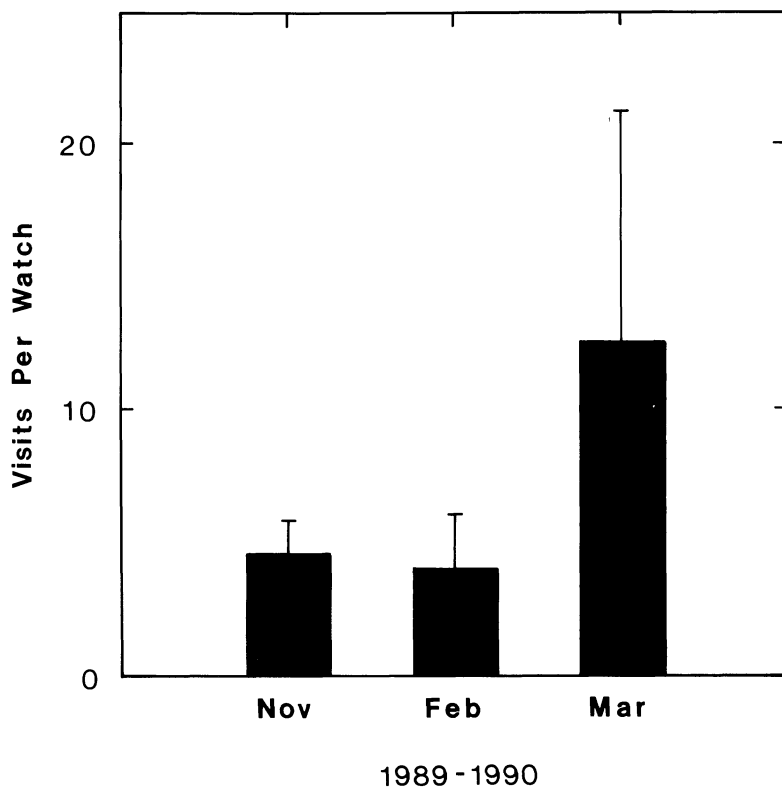
Figure 2. Mean number of visits per three-hour watch (±SE) during morning watches of *Bursera simaruba* on the Yucatan Peninsula, Mexico, February 1989–March 1990. Eight trees were observed in October for a total of 24 hours; 6 trees were observed in February for a total of 18 hours; and 24 trees were observed in March for a total of 72 hours.

able to discriminate potentially ripe fruits using visual cues. However, handling is required to select a ripe fruit with certainty. For most species, including the white-eyed vireo, the proportion of capsules opened averaged more than 50%. Our own observation of fruits showed no relationship between capsule redness and ripeness. However, lines present where the valves of the capsule join seem somewhat more pronounced in ripe or nearly ripe fruits. In ripe fruits, the connections between the valves become increasingly weak. This may explain the particularly high success of the least specialized foragers – the parulinae (wood warblers) – in opening capsules. These species peck at capsules and may only attempt to open fruits in which valves are obviously loosely connected.

A few species (primarily orioles, *Icterus* spp.; Yucatan jay; and *Melanerpes* woodpeckers) methodically squeezed large numbers of fruits in each fruit cluster and had low fruit opening rates (1–15%). These species appear unable to distinguish ripe fruits using visual cues.

Table 7.   Visitor constancy at four *Bursera simaruba* trees watched from 05:30 to 09:30 for four or six days at Sian Ka'an.

| Tree | Constancy (% days visited) | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | X̄ |
| Season | Autumn | Autumn | Spring | Spring | |
| Habitat | Scrub | Forest | Forest | Scrub | |
| Mornings watched | 6 | 4 | 5 | 5 | |
| Total fruits taken | 25 | 12 | 48 | 90 | |
| White-eyed vireo 1[1] | 100 | 100 | 100 | 100 | 100 (76%)[2] |
| 2 | 16 | 0 | 40 | 80 | 34 (5%) |
| 3 | 0 | 0 | 0 | 20 | 5 (0%) |
| Total | 100 | 100 | 100 | 100 | 100 (81%) |
| Mangrove vireo | 100 | 0 | 0 | 60 | 40 (1%) |
| Yellow-throated vireo | 16 | 25 | 0 | 60 | 25 (4%) |
| Social flycatcher | 0 | 0 | 0 | 80 | 20 (4%) |
| Rufous-browed peppershrike | 0 | 0 | 0 | 60 | 15 (3%) |
| Yucatan vireo | 33 | 0 | 0 | 20 | 13 (2%) |
| Masked tityra | 0 | 0 | 0 | 20 | 4 (1%) |
| Rose-throated becard | 0 | 0 | 0 | 20 | 4 (1%) |
| Yucatan woodpecker | 0 | 0 | 20 | 0 | 4 (1%) |

[1] Local territorial vireo; vireos 2 and 3 = trespassing neighbours.
[2] % total visits by all birds to all trees during both seasons; N = 167.

*Species-typical feeding behaviour and handling time.* Handling time for fruit varied significantly with feeding method (Kruskal–Wallis, comparing feeding types using species means as independent observations ($P < 0.01$, $N = 14$ species; Table 8). Species that swallowed the seed and aril (squeeze method) include vireos, tityras, becards and flycatchers. Their handling times were short, averaging from 1.6 to 5.3 seconds (Table 8). Yucatan jays, rufous-browed peppershrikes (*Cyclarhis gujanensis*), orioles (*Icterus* spp.) and woodpeckers (*Melanerpes* spp.) pecked the aril off the seed while they perched in a tree (grab method). These species had significantly longer handling times than the species that swallowed the seed and aril whole (Mann–Whitney $U = 0$, $df = 7,4$; $P < 0.05$; Table 8). Warblers, greenlets and small flycatchers dislodged the capsule and pecked the aril while the seed remained attached to the receptacle (peck method). These species had the longest handling times (Table 8). Stealing was observed only when visitation rates were high and was practised by Couch's kingbirds (*Tyrannus couchi*) and social flycatchers (*Myiozetetes similis*).

The aril of *Bursera* is thin and tightly attached to the seed. Casual observations suggest that birds that swallow the seed may remove the aril more completely than those that pick at the aril with their bills, which has been shown for Neotropical birds feeding on other species of fruit (Foster 1987). Traces of aril often remained on seeds that were pecked. Furthermore, species that pecked

Table 8. Feeding behaviour of common bird visitors to *Bursera simaruba* at Sian Ka'an, Quintana Roo, Mexico.[1]

| Feeding method Species (mass g)[1] | Length[2] of visit (sec) x̄ (N) | Success[3] x̄ (N) | Handling time (sec) x̄ (N, SE) | Fruits per visit[4] x̄ (SE) | Fruits min$^{-1}$ | % DEE[5] min$^{-1}$ |
|---|---|---|---|---|---|---|
| **Squeeze method** | | | | | | |
| White-eyed vireo (11) | 69 (144) | 53 (267) | 5.3 (60, 0.6) | 1.2 (0.2) | 1.0 | 1.9 |
| Masked tityra (79) | 197 (9) | 72 (12) | 1.6 (30, 0.3) | 4.5 (0.4) | 1.4 | 0.7 |
| Social flycatcher (28) | 171 (20) | 70 (34) | 5.3 (15, 1.3) | 2.3 (0.4) | 0.8 | 0.8 |
| Couch's kingbird (40) | 217 (13) | 81 (44) | 2.8 (17, 0.5) | 3.5 (0.5) | 1.0 | 0.8 |
| Yellow-throated vireo (18) | 95 (26) | 55 (60) | 5.0 (12, 0.9) | 1.6 (0.4) | 1.0 | 1.4 |
| Yucatan vireo (18) | 135 (9) | 73 (15) | — | 2.7 (0.7) | 1.2 | 1.7 |
| Rose-throated becard (30) | 57 (12) | 71 (14) | 2.3 (8, 0.7) | 1.5 (0.4) | 1.5 | 1.5 |
| Median | 135 | | 3.9 | 2.3 | 1.0 | 1.4 |
| **Grab method** | | | | | | |
| Yucatan jay (118) | — | 15 (67) | 30.1 | — | — | — |
| *Icterus* spp. (32–60) | 89 (19) | 1 (245) | 42.3 (10, 0.9) | 0.5 (0.8) | 0.3 | 0.3–5 |
| Rufous-browed peppershrike (29) | 165 (5) | 70 (20) | 32.3 (12, 1.3) | 2.0 (1.6) | 0.7 | 0.7 |
| *Melanerpes* sp. (63–85) | 100 (6) | 4 (123) | — | 0.7 (0.8) | 0.4 | 0.5 |
| Median | 100 | 9.5 | 32.3 | 0.7 | 0.4 | 0.5 |
| **Peck method** | | | | | | |
| Magnolia warbler (8.5) | 111 (19) | 90 (20) | 35.8 (19, 0.8) | 2.4 (0.8) | 1.3 | 3.1 |
| Northern parula (8.5) | 112 (12) | 83 (31) | 40.2 (12, 1.1) | 2.3 (0.7) | 1.2 | 3.0 |
| Black-throated green warbler (9) | 124 (9) | 84 (24) | 44.0 (9, 1.2) | 1.5 (0.5) | 0.7 | 1.7 |
| Median | 112 | 84 | 40.2 | 2.3 | 1.2 | 3.0 |

[1] Based on Dunning (1993) and personal notes.
[2] Time spent in tree.
[3] % tested fruit that were consumed.
[4] Fruit eaten.
[5] Estimated based on (number of fruits/min × 0.556 kJoule/fruit divided by estimated DEE) × 100; For estimation of DEE see Methods.

open the capsule often were flushed from the tree before they could consume the aril. When this happened, the exposed aril was never consumed. White-eyed vireos were commonly observed (away from *Bursera* trees) regurgitating seeds into their bills, manipulating the seeds and then reswallowing them. This behaviour suggests that seeds may be monitored until removal of the aril is complete.

Species using the squeeze method had a median harvesting rate of 1 fruit per minute – the value for the white-eyed vireo. Species using the grab method had a significantly lower harvesting efficiency (median = 0.4, Mann–Whitney U = 0, df = 4,7 P < 0.05). Species employing the peck method had a high rate ($1.2$ min$^{-1}$) comparable to the squeezers. White-eyed vireos consumed a greater percentage of their DDE per minute than any other species that fed by the squeeze or grab method. Overall, squeezers were significantly more efficient (median = 1.4%) than grabbers (0.5%). With this calculation, the wood warblers, which use the peck method, also consumed a large percentage of their DEE per minute.

*Species-typical feeding behaviour and seed dispersal.* The proportion of seeds dispersed (removed from a tree) by all species declined significantly with increasing visitation rate (visits h$^{-1}$, r = $-0.50$, N = 45, P < 0.01). Seeds of almost all (97%) fruits consumed when visits numbered fewer than 2 h$^{-1}$ were dispersed, whereas only 70% of those consumed when visits numbered two or more per hour were carried away.

*Abundance of white-eyed vireos and* Bursera *in forest patches.* During the November survey, white-eyed vireos were found in 32 of 34 patches with an overall average of 1.2 birds per patch. In contrast, white-eyed vireos responded to playbacks at only two of 10 and three of 10 points in pasture and scrub habitats, respectively. The distribution of vireos between patches was relatively even, so we made no attempt to identify correlates of abundance within patches.

In March, in contrast, vireos were found in only 15 patches. Of the five variables recorded for each of the patches, only fruit crop and number of fruiting trees were significantly correlated (Table 9) with the number of white-eyed

Table 9. Correlations between habitat variables associated with patches and the number of white-eyed vireos detected in patches during play-back censuses in March 1990 (N = 34).

| Variable | Range | Spearman | Number of birds per patch | |
| --- | --- | --- | --- | --- |
| | | | with vireo | without vireo |
| Patch size (m$^2$) | 100–13,362 | 0.06 | 1375 | 1355 |
| Height (m) | 6–12 | 0.21 | 9.1 | 9.5 |
| Vegetation density class | 1–4 | 0.14 | 3.1 | 3.4 |
| No. *Bursera* trees with fruit | 0–12 | 0.38* | 1.0 | 1.9 |
| No. of *Bursera* fruit | 0–3500 | 0.43* | 19 | 287 |

* P ≤ 0.05.

vireos detected per patch. None of the five variables was significantly intercorrelated. Patches with white-eyed vireos had 287 *Bursera* fruits on average, versus 19 for those without vireos.

## DISCUSSION

The white-eyed vireo is one of the few migrant species that is both highly frugivorous and defends long-term winter territories (Barlow 1980, Greenberg *et al.* 1993, Levey & Stiles 1992, but see Bates 1992). The proportion of foraging manœuvres directed towards fruits averaged 0.25, and the proportion of individuals visiting fruiting trees during foraging observation was even higher (Greenberg 1992). In our study area, 96% of all observations of frugivory involved the seeds and arils of *Bursera simaruba* (Greenberg 1992). Because of the high lipid content of the *Bursera* aril and the small size of the vireo, a moderate number of arils can supply the daily existence energy for a vireo. Although the number of ripe fruits available daily on each tree is small, a vireo territory generally includes several to many fruit-bearing trees.

White-eyed vireos defend territories of approximately 0.5–1 ha in dry forest (Greenberg *et al.* 1993) and therefore have on average 13–48 fruiting *Bursera* trees in their territories (Table 2). Even in March, at the end of the fruiting season, a randomly defended 0.5 ha territory should have 2000–4000 remaining *Bursera* fruit based on measures presented in Table 2. White-eyed vireos harvested an average of 1.1 fruits $h^{-1}$ at a single tree during our focal observations. This can conservatively be extrapolated to 4 fruits per day per tree, assuming vireos stopped visiting trees at 10:00. Based on our estimates of energy requirements, white-eyed vireos would only have to visit approximately 13 *Bursera* trees per day to acquire the DEE, which is equal to the minimum number of trees with fruit per 0.5 ha in forest habitat on our March surveys (Table 2). Because of its small size, a white-eyed vireo can probably meet a significant portion of its energy needs with *Bursera* fruits. Because the fruits are available throughout the winter, white-eyed vireos can be territorial and frugivorous, monitoring the crop and harvesting or defending ripe fruits as they appear.

For larger frugivores, territoriality and defence of the *Bursera* resource probably are not economically feasible because of the small absolute amount of aril per fruit. Other species of small birds that might profitably exploit *Bursera* fruits are either uncommon (yellow-throated and Yucatan vireos), are morphologically poorly adapted for opening the capsules (euphonias; lesser greenlets; northern parulas; magnolia and black-throated green warblers) or are socially subordinate to white-eyed vireos and therefore excluded from access to the fruits (mangrove vireo) (Greenberg *et al.* 1993).

*Bursera and the distribution of white-eyed vireos*

Previously, Greenberg *et al.* (1993) suggested that the higher density of white-eyed vireos in an ungrazed versus grazed area of shrubby second growth was

related to the higher density of *Bursera* in the preferred habitat (Table 1). The results of the survey of forest patches further support the hypothesis that the occupation of a habitat throughout the winter depends, in part, on the size of the available *Bursera* crop. On a larger scale, the greater density of white-eyed vireos in forest versus second growth habitats is a response to the higher density of *Bursera* fruit in forest (Table 2).

*White-eyed vireos as dispersers of* Bursera *seeds*

By all criteria white-eyed vireos were the most important dispersers of *Bursera simaruba* in our study area. They removed the largest number of seeds from the crown or the ground under the tree, and they were the species most universally present. Few tree species have been documented to depend so strongly upon a single species of avian disperser, particularly trees with such small fruit visited by such small birds (Bates 1992, Salomonson 1989).

Other workers have reported large numbers of species visiting *Bursera* (Scott & Martin 1984, Trainer & Will 1984). Scott & Martin (1984) argued that *Bursera* produces ripe fruits to coincide with the northward movement of migratory birds, providing a critical food source during the harsh dry season of the Yucatan Peninsula. Our observations suggest that either (i) the dispersal syndrome of *Bursera* in our study area is different from that in other localities or (ii) that the limited period and pool of trees sampled in the first two studies provided only an incomplete picture of the overall dispersal syndrome.

The first explanation has merit. We observed trees at Uxmal (the site of the Scott & Martin (1984) study) and at Chajul, Chiapas, and found that the diversity and volume of visitation was far greater than at any trees censused on the northern end of the Yucatan Peninsula. Furthermore, the most important visitors were tityras and other larger species.

We believe that the second explanation is also important. Infrequent but persistent feeding by vireos will yield a large proportion of their daily energy needs, but their activity in the tree is likely to be overlooked. This is particularly true prior to March, when ripening rates are low and the foliage of the tree crown is dense. Observers are much more likely to notice *Bursera* that, because of size or season, have large quantities of ripe fruit and great numbers of visitors.

*Has co-evolution occurred?*

Howe (1984), Herrera (1986) and Wheelwright & Orians (1982) argued that tight mutualistic relationships are unlikely to evolve between fruiting plants and their dispersers. They suggested that characteristics of one type of fruit are unlikely to influence the adaptations of a species that forages on many types of food. Similarly, a plant that supports a taxonomically diverse array of dispersers is unlikely to develop specializations to attract a single bird species. Both these factors would seem, at first, to apply particularly to migratory birds, because they are present in a community for only part of the annual cycle. However, if fruit is a critical resource during an otherwise food-poor time of the year and the presence

of the migratory species coincides completely with the fruiting season, then the possibility of co-adaptation may even be greater for migratory species.

*Possible adaptations of vireos for consuming* Bursera *fruits*

The digestive physiology of white-eyed vireos has not been studied. The only external morphological feature of these birds that could represent an adaptation for feeding on *Bursera* is the large bill tip-gape. The tip-gape of white-eyed vireos is the minimum size large enough to handle all *Bursera* capsules at Sian Ka'an. The relatively large tip-gape ensures that a white-eyed vireo can get its bill around a *Bursera* fruit and, therefore, employ the squeeze method of foraging, which involves the shortest handling time.

The tip-gape is large relative to the body size of the vireo, and the absolute efficiency of fruit removal by this species compares favourably with that of larger dispersers (e.g. species employing the squeeze method). Although white-eyed vireos opened a smaller proportion of tested fruit, had a longer handling time and ate fewer arils per visit, vireos showed a comparably high rate of aril consumption per minute in the tree (Table 8). Vireos have short visits which minimizes the time spent on exposed branches and danger from predators (Howe 1979). Furthermore, the white-eyed vireo is the smallest of the common visitors to the tree (Table 6, 8) and requires less total existence energy. If its foraging efficiency is comparable to those of larger visitors, it will harvest the *Bursera* arils it needs in a shorter time. In fact, the white-eyed vireo harvested the highest percentage of its DEE per unit time of all of the potential dispersers (squeeze method feeders). Only the wood warblers potentially consumed a higher proportion of their DEE per unit time. However, this assumes that they consumed the entire aril, which is unlikely, given their behaviour of pecking the fruit. Furthermore, wood warblers only foraged late in the season when a large number of ripe fruit was available.

*Fruit characteristics that promote specialized frugivory*

Several features of *Bursera simaruba* favour dispersal of its seeds by birds specialized to feed on its fruit. The indehiscent capsule, which releases a noxious liquid when cut, favours species that learn the subtle markings of a ripe fruit and that are able, when ripe fruits are scarce, to open fruits whose valves are relatively strongly joined. The capsules remain greenish or slightly rosy in coloration when ripe. The conspicuous bright red coloration of the ripe aril, generally thought to act as a long-distance signal for birds (Stiles 1982), remains unexposed until after the capsule is opened by a foraging bird. The lack of a long-distance cue for ripeness would favour a local disperser that continuously monitors the fruit crop. In addition, the limited amount of aril relative to seed selects for species better able to remove aril. The high lipid and, therefore, energy content of *Bursera* aril places it among the richest species known (Foster & McDiarmid 1983). However, because of its long fruiting period and

generally low rate of fruit ripening, *Bursera* provides limited returns in the short term, but a reliable source of a high energy food over the long term.

However, features that could be argued to be adaptations to promote dispersal by *Vireo* can also be viewed as responses to the dry conditions of the Yucatan Peninsula. For example, the unusual indehiscent capsule may prevent evaporation, which rapidly destroys the integrity of the aril–seed connection. The green coloration in the capsule is possibly a mechanism to increase the photosynthetic capabilities of *Bursera* during the period when most foliage is lost. The presence of chlorophyll in the bark suggests a tendency to use structures other than leaves for photosynthesis, as a way of minimizing water loss in a dry environment. Nevertheless, nearly half of the energy in each fruit is devoted to capsule. This level of investment, as well as the presence of noxious substances in the capsular tissue, suggests that protection of the seed from parasites or the aril from 'cheaters' (birds that consume the aril without dispersing the seed) is of high selective value to the plant.

### Community-level influences

Two community-level features probably interact to shape the specialized relationship between *Bursera* and the white-eyed vireo on the northern Yucatan Peninsula. First, the Yucatan forest has a lower overall abundance of both bird-dispersed fruits and avian frugivores than wetter tropical areas (R. Greenberg, unpublished data). Bates (1992) suggested that the specialized relationship between the gray vireo and *Bursera microphylla* might be a consequence of disperser scarcity in thorn scrub and desert habitats.

Second, *Bursera* trees occur at high densities in the Yucatan forest (Table 1) and have small crops (Table 2). *Bursera* at other sites are often larger and more widely dispersed, and produce larger crops. For example, trees at Chajul, in the Lacandon forest, are larger, occur at much lower densities than on the Yucatan Peninsula, have abundant crops (up to 50,000 or more) and attract more large frugivores (M. S. Foster, unpublished data). The differences parallel the findings of Howe & Vande Kerckhove (1979) at *Casearia corymbosa* in the Atlantic lowlands and Pacific dry forests of Costa Rica. Where trees are larger, more fecund and more widely dispersed, exploitation of the fruit crop is more profitable for larger birds. The small stature of the trees on the northern Yucatan Peninsula is probably a result of the low growth rates of trees in dry forests and the frequent hurricanes and tropical storms that uproot the trees (Jauregui *et al.* 1980).

### Bet-hedging and the dispersal syndrome of Yucatan Bursera

The timing of fruit production is the feature most likely shaped by *Vireo* visitation (see also Bates 1992). The long period of crop ripening is unrelated to flowering, which is synchronized over a short period. Furthermore, ripe fruits are available only for the period of winter residency of the vireo. Throughout most of the 7- to 8-month fruiting period, *Bursera* trees ripen fruit slowly and attract primarily a single species of disperser. However, large trees and trees in

mid- to late March apparently had large numbers of ripe fruit and attracted a larger, more diverse and more wasteful group of dispersers. Afternoon foraging became common, also suggesting a greater availability of ripe fruits during the course of the day. Rather than fitting either one of the phenological strategies outlined by McKey (1975), we suggest that *Bursera* depends upon a specialist species to remove a large portion of the crop. Ripening fruit slowly over the winter guarantees the daily visitation of a territorial white-eyed vireo. However, a single territorial bird is absolutely limited in the number of seeds it can remove. A more rapid ripening rate late in the season is a bet-hedging strategy to disperse that portion of the crop that exceeds the needs of the single dispersal agent. *Bursera* may be able to attract large, but unpredictable, numbers of transient migrants at this time (Scott & Martin 1984). In this way, a single tree receives the benefits of a reliable disperser while maintaining the ability to disperse a large crop, particularly when the tree becomes large.

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