INTRATROPICAL MIGRATION IN THE YELLOW-GREEN VIREO AND PIRATIC FLYCATCHER

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ABSTRACT.—The causes of intratropical migration in the Yellow-green Vireo and Piratic Flycatcher are discussed. Data on migration arrival and departure, breeding seasons, and food are presented and used to support the hypothesis that migration has been selected because of seasonal changes in fruit abundance rather than insect abundance. A removal experiment showed that floating populations exist on the breeding grounds in both species.—*National Zoological Park, Smithsonian Institution, Washington, D. C. 20009.* Accepted 14 July 1975.

THE Yellow-green Vireo (*Vireo flavoviridis*), often regarded as the Middle American population of the polytypic Red-eyed Vireo (*V. olivaceus*) (Mayr and Short 1970: 72; but cf. Eisenmann 1962), is common over its breeding range from northern Mexico to at least the Panama Canal Zone (Peters 1931). Another species, the Piratic Flycatcher (*Legatus leucophaius*) is less common, but conspicuous, as a breeding bird from southern Mexico through Middle America and South America to northern Argentina and Brazil (Wetmore 1972: 389). These two essentially lowland tropical species belonging to different families, Vireonidae and Tyrannidae, are considered together here because both are migratory, and all or nearly all of the populations leave their Middle American breeding grounds to spend the nonbreeding season in the upper Amazon basin. Few Panama breeding populations of birds are known to migrate out of the country (Eisenmann 1963).

Orians (1969) suggested that the presence of these species as breeders in parts of Costa Rica with well-marked dry seasons is related to the relatively greater flush of insects in these places when the rains return and plants grow new leaves. Eisenmann (1962) proposed a somewhat similar idea for the Yellow-green Vireo. Other than these references, no studies have tried to analyze the selective factors that promote intratropical migration in these species. With this in mind, I undertook studies, primarily on the vireo, on their migration and breeding biology.

STUDY AREA AND METHODS

All work was performed in the Panama Canal Zone from January 1970 through June 1971, thus encompassing two breeding seasons. I surveyed vireo arrival times across the Zone (see Fig. 1), but intensive work was restricted to the Pacific slope from Summit Gardens, near the continental divide, to Fort Kobbe. The region has well-marked dry and wet seasons, with the Pacific slope dry season usually beginning before and lasting longer than it does on the Atlantic slope (Fig. 2).

Food habits were determined by stomach content analysis and by watching foraging birds.

From 13 January through 14 May 1971 a removal experiment was conducted in a 4-ha plot surrounding the bayonet practice field in Fort Kobbe on the Pacific slope. All or most vireos were removed on 17 collecting days during the period. They were weighed in the field and then preserved after gonadal measurement. The purpose of this experiment was to collect stomach content information, to gain an index to possible migration patterns and, in a more general sense, to see if a "floating population" existed in this tropical species similar to that found for many temperate zone species (Stewart and Aldrich 1951). A removal experiment was also conducted at a nest occupied by a Piratic Flycatcher near the bayonet practice field.
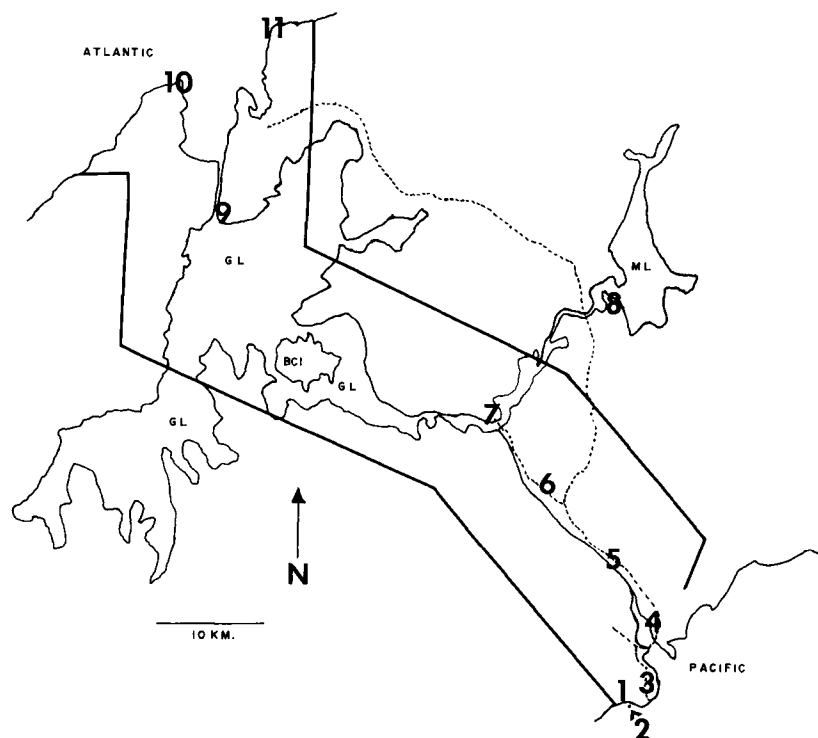
Fig. 1.—A map of the Panama Canal Zone and adjacent Panama showing *Vireo flavoviridis* study sites. 1, Fort Kobbe; 2, Fort Kobbe beach mangroves; 3, Farfan Road; 4, Balboa-Ancon; 5, Morgan's Gardens; 6, Summit Gardens; 7, Gamboa; 8, Madden Boy Scout Camp; 9, Gatun; 10, Fort Sherman; 11, Galeta. BCI = Barro Colorado Island, GL = Gatun Lake, ML = Madden Lake. The dashed line indicates portions of major roads, the Canal Zone boundary is marked by two solid lines.

YELLOW-GREEN VIREO

Sequence of vireo migration in the Canal Zone.—The arrival of males was a conspicuous event because of their persistent singing, which decreased after pair bonds were formed, then increased slightly in June and July during postbreeding molt and erratically through the breeding season as pairs started new nests. Males with females, although not singing persistently, frequently gave rapid, short, songlike phrases when moving toward the females. The females responded to this male approach with a harsh chatter, allowing one to census and document their arrival.

Arrival dates between the wetter Atlantic side of the Canal Zone and the drier Pacific slope differ distinctly. Upon my arrival in the Canal Zone on 13 January 1970, vireos were common in Balboa on the Pacific slope but absent from the Atlantic side of the Isthmus. In 1971 I made a more thorough survey of arrival times. Table 1 shows the earliest arrival dates, the dates populations peaked, and the dates when nesting activities were first noted for 1971 at several localities.

Vireos began returning to the immediate region of the Pacific coast in late December and by mid-January were at peak numbers. A few kilometers inland from the coast vireos returned later, on 29 December at Ancon, Morgan's Gardens, and Summit Gardens. On the Atlantic side, at Gatun, in coastal mangroves near Galeta
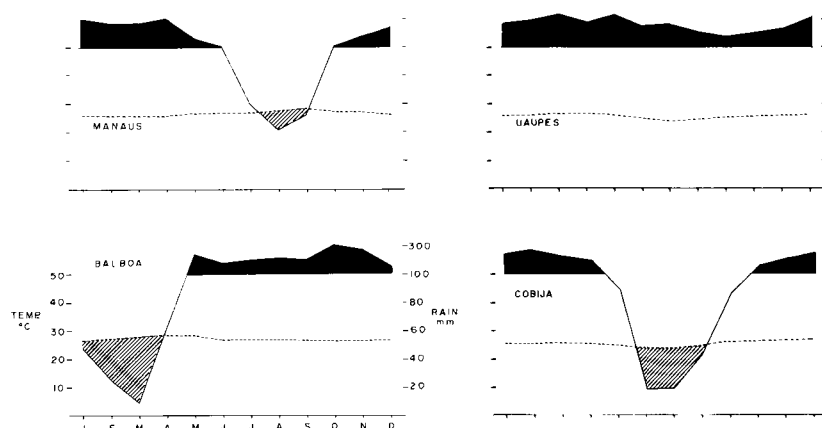
Fig. 2.—Climate diagrams of a *Vireo flavoviridis* breeding ground, Balboa, Canal Zone (08°57′N, 79°33′W) and areas near the nonbreeding range (no rainfall data were available from within the center of the nonbreeding range, but the data provided are probably indicative of the range of conditions there) Manaus, Brazil (03°09′S, 60°01′W); Uaupes, Brazil (00°08′S, 67°05′W); and Cobija, Bolivia (11°04′S, 68°44′W), showing this species' preference for relatively drier conditions (see text). Months are indicated on the horizontal axis; temperature and rainfall (10-year monthly averages, Anon. 1966) on the left and right vertical axes, respectively. The dashed line represents temperature; the solid line, rainfall. Temperature and rainfall axes are aligned such that a drought period (oblique lines) occurs whenever the rainfall curve drops below the temperature curve, monthly rainfall in excess of 100 mm (solid area) occurs as runoff, indicating extreme wet conditions (after Mueller-Dombois 1969).

Island, and at Fort Sherman, no vireos were seen or heard on 1 March, but they had begun to return by mid-March. As discussed below, the Pacific coast vireo populations were fledging young before any birds appeared on the Atlantic coast, a distance of only about 54 km. Although the dates of the first vireo sighting vary from year to year, in the 2 years of the study breeding birds consistently returned to the Pacific coast about 2 months before they reached the Atlantic coast.

Female arrival on male territories showed two divergent trends. The first males recorded at Fort Kobbe 20 through 29 December were already paired, but from 1 January through 13 January many newly arriving males were not paired. Thus little evidence supports the hypothesis that males arrive before females.

During late June and July, male vireos remained on the breeding grounds but showed no association with females. Males collected at this time were singing

TABLE 1

Dates of Arrival, Population Stability, and Breeding Initiation for the
Yellow-green Vireo in the Canal Zone, 1971

Location[1]	First arrival	Population stable	Egg-laying
Fort Kobbe	20 Dec.	13 Jan.	15 Jan.
Farfan Road	27 Dec.	21 Jan.	1 Feb.
Ancon	29 Dec.	21 Jan.	7 Feb.
Morgan's Gardens	29 Dec.	30 Jan.	3 Apr.
Summit Gardens	29 Dec.	30 Jan.	20 Apr.
Madden Boy Scout Camp	6 Jan.	No data	No data
Atlantic side[2]	1–10 Mar.	Early Apr.	No data

[1] Locations are arranged from Pacific to Atlantic slope sites, see Fig. 1.
[2] Includes sites 9, 10, 11 in Fig. 1.

and molting. The singing suggests that they may be exerting dominance now in superior breeding habitat, parhaps to lessen aggressive competition for it the next year.

The time of departure for South America is not known for individual birds, but the Yellow-green Vireo was rare at Fort Kobbe by the end of August, shortly before migrant Red-eyed Vireos arrived.

Removal study.—From 13 January to 14 May 1971, I conducted a removal experiment in a part of Fort Kobbe (see Fig. 1) known as the bayonet practice field. I tried to shoot all Yellow-green Vireos from this tract on 17 days during this time period, after observations showed a steady population of 8 singing males.

Vireo habitat surrounded the grassy practice field, which measured approximately 100 by 200 m, was roughly rectangular, and was situated about 300 m from the Kobbe beach. It was bounded by grassland uninhabited by vireos on one side, tall forest, also without vireos, on another, and by second-growth forest and brushy edge up to 14 m tall with scattered tall *Ficus insipida* trees about 30 m tall. This was dry second growth typical of Yellow-green Vireo breeding habitat on the Pacific coast.

During each vireo removal day between 0900 and 1000, I walked around the edge of the bayonet field and censused singing males. I sometimes used a playback of male song to elicit a vocal response or movement from quiet males. I then tried to collect all male vireos in the study area and any females that I saw but made no determined effort to remove females. The initial census on 13 January showed eight males occupying the study tract. The last day on which vireos were removed was 18 April, and by then I had collected 36 male vireos there. On 14 May, after 26 days without shooting, I censused 7 singing males in the tract. Thus new birds were entering the tract throughout the period from 13 January to late April when I stopped removing birds. In contrast, the mangrove breeding census area (Fig. 1, site 2), less than 0.5 km away (where I did no collecting), maintained a stable population after mid-January.

To determine whether the incoming males were perhaps physically different from birds that occupied the territories early in the breeding season, I collected birds from a place about 3 km away along Farfan Road to compare with the birds from the study tracts. I compared 11 adult male vireos collected on 9 and 11 March at Farfan with 10 from the removal area collected on 2 and 26 March (Table 2). The time of collection averaged about 30 min later in the morning for the removal area birds than for the Farfan birds. Even so, the birds from the removal area were significantly lower in weight than the sample from Farfan, from where I had not removed birds (Student's t-test $= 2.918$, 18 df, $P < 0.005$). The weights of adult male vireos collected in January at the removal site were significantly greater than March birds removed from the same place, but they were not significantly higher than the March Farfan sample. Thus the vireos moving into the removal area were lighter than birds taking up territories in January. Winglengths (flat) of the March removal area birds were slightly smaller but not significantly different from the Farfan sample (77.8 vs. 78.5 mm).

Testis size, as indicated by the length of the left testis measured in fresh specimens, remained small in the removal area males throughout the removal period. The March bird testes collected in the removal area averaged 4.1 mm while the Farfan control sample averaged 7.5 mm. In January the birds collected in the removal area

TABLE 2

MEAN WEIGHT AND TESTIS LENGTH OF *VIREO FLAVOVIRIDIS* IN THE REMOVAL AREA
AND FARFAN, JANUARY AND MARCH 1971

		Removal area			Farfan	
	N	Weight (g)	Testis length (mm)	N	Weight (g)	Testis length (mm)
Jan.	8	18.3 ± 0.95 SD 16.6–19.5 Range	3.2 ± 0.67 2.3–4.7	5	17.6 ± 0.86 16.0–18.6	2.5 ± 0.48 1.9–3.1
Mar.	10	17.1 ± 0.71 16.3–18.4	4.2 ± 1.38 1.6–6.1	10	18.4 ± 1.14 16.9–21.1	7.1 ± 0.53 6.3–7.7

averaged 2.9 mm. Oddly, the first male collected at Fort Kobbe, near but not on the removal area, had a testis length of 5 mm while all other January collected vireos had testes less than 4 mm in length (had that male ever moved from its breeding territory?).

The male vireos replacing those removed were, therefore, lower in weight and testis size than vireos that had been on the breeding grounds since late December. The birds that replaced those removed appear to have been a floating population that was near at hand and ready to breed but prevented from doing so by birds already occupying the suitable breeding habitat. This is indicated by the fact that birds replacing those removed did so rapidly but that the rate slowed with time. If only 3 days elapsed between 2 removal days, the rate of replacement, as indicated by the number of new birds divided by the number of days between 2 successive removal days, was between 0.67 and 1.33 birds per day, but if 8 or 9 days elapsed between removals, the recruitment rate was from 0.22 to 0.33 birds per day.

Vireo food habits.—I collected 119 specimens from 5 February 1970 to 14 May 1971, in all months except August to December 1970. Of these, 98 stomachs contained material for analysis (70 males, 28 females). Data are from the Pacific slope of the Canal Zone, mainly from Fort Kobbe, Farfan Road, and Chiva Chiva Road.

The stomach contents from freshly killed birds were examined to determine the relative proportions of fruit and insect food they contained and how full they were; 45 stomachs (46%) contained at least 90% fruit (by volume), 42 (43%) contained 90% insects, and 11 (11%) contained equal proportions of both insect and fruit food. Differences between males and females was not significant. Those stomachs containing mostly or totally insects tended to be emptier than stomachs containing mostly fruit. Of the mostly insect stomachs, 56% were "nearly empty," while stomachs containing fruit were 85% "full."

The stomach contents clearly showed a dichotomy in fruit or insects eaten, indicating that the birds tend not to mix their diets during a feeding period prior to collection. This is supported by observations suggesting that vireos learn the location of and return to specific fruiting trees, which may be some distance away from their breeding territory. Field study of vireos shows that most of their foraging time is consumed by insect foraging even though less than 50% of their food volume is insect food. This is due to the much greater amount of time needed to find insects than to fill up on fruit (Snow 1971, Morton 1973).

The fruit the vireos took varied considerably in size and color. The maximum fruit size taken was about 8 by 6 mm (*Connarus*) and the minimum was from the grass *Lasiacis* (2 mm long) that produces fruit attractive to fruit-eating but not granivorous

TABLE 3

STOMACH CONTENTS OF MOLTING AND NONMOLTING YELLOW-GREEN VIREOS,
16 APRIL–26 JULY 1970

	Fruit[1]	Insects[2]	Both
Molting (nonbreeding)	1	17	5
Nonmolting (breeding)	9	5	6

[1] 90% or more fruit in stomach.
[2] Most insects were winged termites that are abundant for a short time after rains. They are a short-term food that disappears by mid-June.

birds (Davidse and Morton 1973). In some cases arils or flesh surrounding seeds were taken: *Pithecolobium rufescens* (pea podlike curled fruit, which turns bright red and contains black seeds embedded in a white aril; birds eat the white aril, carrying away the seed in the process); *Tetracera* sp. (a woody vine, very common, whose fruit contains a black seed surrounded by an orange-red aril); *Xylopia* sp. (pagoda roof-shaped trees containing upright standing fruit, orange-red pulp surrounding reddish seeds that are eaten along with the pulp); *Connarus* sp. (large roundish black seeds with a whitish, milky pulp at one end).

Vireos took fruit at heights from 2 to 14 m above the ground. Plant species whose fruit could be identified from stomach contents included, in order of decreasing occurrence in stomachs: *Miconia* sp., *Pithecolobium rufescens*, *Didymopanax morototoni*, *Pittoniotus tricantha*, *Guazuma ulmifolia*, *Lasiacis sorghoidea*. Most of these fruit-producing plants characteristically have fruit ripening periods during the dry season, with a large overlap among the species.

In 1970 along the Canal Zone Pacific coast, vireos began to nest in late January and I noted evidence of breeding until 14 July (adults with dependent fledged young were last seen then). The time when most breeding (egg-laying) occurs here is during the height of the dry season (March), but continues into the early rainy season (early May), tapering off rapidly in mid-June.

In late May after the rains began, I tested the hypothesis that breeding birds might be using fruit more than nonbreeding birds, for by then both breeding and nonbreeding adults were present. After 20 May many adults were molting, but those that were still feeding young were not molting. On 8 June I collected three adults together with their dependent fledged young. In each case the adult's stomach contained largely or entirely fruit while the fledgling's stomach contained entirely insect food.

Table 3 shows the stomach content data from 43 adult vireos collected from 16 April through 26 July 1970 at three places on the Pacific slope of the Canal Zone. The molting birds were consuming significantly more insects than the nonmolting birds ($P < 0.01$).

PIRATIC FLYCATCHER

The Piratic Flycatcher usurps a nest from species that build covered or hanging nests (see Skutch 1960). It is highly aggressive toward conspecifics so that only one pair occupy an oropendola or cacique colony containing many suitable nests. The male spends ca. 90% of its time above the nest singing.

Piratic Flycatcher removal data.—At one end of the bayonet practice field stood a 30-m tall Panama tree (*Sterculia apetala*) containing active colonies of the Chestnut-headed Oropendola (*Zarhynchus wagleri*) and the Yellow-rumped Cacique (*Cacicus cela*). In mid-January a pair of Piratic Flycatchers usurped a cacique nest. I collected

the male on 19 January, but I did not try to collect *Legatus* systematically from this colony every time I visited the vireo removal site.

In both years I studied in Panama, the *Sterculia* tree containing the oropendola colony lost its leaves during the height of the dry season in March. Most of the oropendola and cacique nests were attached to the strong 8-inch leaf petioles of this tree and fell with the leaves, destroying the colony by mid-March, before any young fledged. The cacique nest that was usurped by the first *Legatus* in January never fell—it was one of an estimated 10% of nests that were attached to twigs as well as to leaf petioles and therefore remained in the tree after the leaves dropped. All of the 10 *Legatus* collected from this colony used the same nest occupied by the original pair, perhaps because it was somewhat isolated from the main part of the oropendola-cacique colony. This suggests that continued harassment of the host species after a nest is acquired is not behavior necessary for reproduction in *Legatus*. It is not even necessary for an active colony of birds to be near them, for *Legatus* occupied the cacique nest even after the icterids had abandoned their colony.

Like the vireos, *Legatus* replacement of removed birds was rapid and took place throughout the January to May removal experiment. Replacement also occurred within a day when a pair was removed from their nest at a second oropendola colony near Pedro Miguel, Canal Zone. At the *Sterculia* tree colony, on 27 February, 26 March, and 10 April, both male and female *Legatus* were removed and were replaced by another pair. On the four other days when *Legatus* was removed only the male was taken. The male was replaced, but it is not known whether the remaining female was joined by an unpaired male or whether another pair moved in.

Food of Piratic Flycatcher.—All 10 *Legatus* collected at the removal area, as well as 4 other specimens collected elsewhere from January to June, had only fruit in their stomachs. Not a single insect fragment was found. The fruit found in these stomachs was, in order of abundance, *Didymopanax morototoni*, palms (Royal palms, *Roysto-nea* sp., where they were planted), *Miconia argentea*, and the arils of *Tetracera* sp. vines. Two other fruits were unidentified. The stomach analysis showed two other important facts: some of the stomachs were gorged with fruit (26 *Miconia* and 12 *Didymopanax* in two examples), one packed stomach measuring 15 × 22 mm and many of the *Didymopanax*, *Miconia*, and palm fruits were unripe. In examining several other bird species that had eaten this fruit, I never found any unripe except *Miconia*. This indicates that *Legatus* is able to take large quantities of fruit at one time and that it can feed relatively fast because it does not have to choose ripened fruit.

It is known that they feed their newly hatched young insects (Skutch 1960), and I saw them foraging for insects only for this purpose and only at flowering trees. I watched one pair catching insects at the flowering spikes of *Coccoloba caracasana*, whose long spikes of small flowers attract large numbers of flies and stingless bees. The birds dropped awkwardly onto a flower cluster from above and pecked at the insects thus disturbed. They never ate any insects themselves, but flew off toward their nest with an insect in the bill, presumably to feed young. The hypothesis that *Legatus* is an obligatory fruit eater as an adult is further supported by its morphology: while placed in Tyrannidae, it has the wide gape and short bill typical of many totally frugivorous cotingas (Snow 1971). Its fruit diet allows *Legatus* an unusual time-energy budget, wherein the male spends nearly all of its time singing while perched near the nest site and little in foraging.

Perhaps *Legatus'* nest pirating behavior is tied evolutionarily to its fruit diet. Fruit provides energy that can be gathered quickly because little foraging or processing time is needed (Snow 1971). Because of this *Legatus* has the time needed for persistent harassment of the host while the host, in contrast, must eventually leave to search for food. Selection would favor those *Legatus* that pirated nests, once this was energetically feasible because of the fruit diet, as it should be advantageous to shorten the nesting cycle by skipping the nest building phase.

DISCUSSION

The Yellow-green Vireo and Piratic Flycatcher use a breeding strategy common to many tropical birds: the adults sustain themselves partially or entirely on fruit while breeding. The energy relationship between adults and their young that this produces is nearly unique to the tropics (Morton 1973). By nourishing themselves on easily found fruit breeding adults have more time to look for hard-to-get invertebrate food for young. This may explain why the vireo and flycatcher, along with many other species, breed during the dry season, for it is then that bird-eaten fruits are produced in greatest abundance.

This does not tell us why the vireo and flycatcher migrate while other species do not, even though they show the same breeding strategy. I hypothesize that they migrate because they depend on some fruit at many times during the year to maintain an adequate energy balance. Perhaps nonmigrant species can get sufficient energy for self-maintenance from invertebrate-searching strategies and depend on fruit-eating only when breeding increases the energy demand far above that needed for self-maintenance.

The data presented here support the fruit need hypothesis. The Yellow-green Vireo leaves the Canal Zone just before North American migrants become abundant, in the late rainy season when bird fruit is becoming scarce (Leck 1972), and probably go to regions that are then under dry conditions. (Compare the rainfall data for the Canal Zone and Amazonian Brazil in Fig. 2.) Bird-eaten fruit is generally more abundant in the dry season in all tropical habitats thus far studied (e.g. Janzen 1967 for Central America, Koelmeyer 1960 for Ceylon). Thus the vireo and flycatcher migration may be keyed to fruit abundance on both breeding and nonbreeding habitats. This hypothesis will be tested when data on the Yellow-green Vireo and Piratic Flycatcher food habits are available from their South American nonbreeding ranges.

Migration arrival time differences between the Pacific and Atlantic slopes of Panama support the theory that the return is based on fruit availability. Fruit ripens earlier and is more plentiful on the drier Pacific slope and the birds return there much earlier.

Vireos may not start breeding immediately after they return; the availability of fruit may stimulate nesting. During the 1970 breeding season at Summit Gardens, vireos first began laying on 2–6 March. In 1971, although males returned there in early January (first record 29 December) and sang persistently from then on, egg-laying was delayed until late April. W. John and Susan Smith, who studied vireos intensively at Summit in 1971, reported (pers. comm.) that not until 24 March did "pairs begin close association."

The only obvious difference between these 2 years in the environment of Summit Gardens was the availability of fruit. In 1971 one common fruit-producing species,

Didymopanax morototoni, failed to produce a fruit crop. The previous year the trees had borne ripe fruit from late January through mid-April. In 1971 the first fruit (*Miconia argentea*) became abundant during mid-March, and shortly thereafter the vireos began pairing. Perhaps males may be in breeding readiness upon arrival at the breeding grounds, but fruit abundance influences breeding readiness in females. The females, of course, need energy for egg production and, as no courtship feeding occurs in this species (pers. obs.), the females must feed themselves.

I hypothesize that selection has favored migration in the Yellow-green Vireo and Piratic Flycatcher because of seasonal changes in fruit abundance rather than insect abundance. Both species return to the Canal Zone shortly after the beginning of the dry season and the vireo favors habitats that contain a high proportion of deciduous trees and therefore fewer foliage insects (Eisenmann 1962) but abundant fruit supplies.

The Yellow-green Vireo probably leaves Middle America for the same reason that the northern Red-eyed Vireo population does not winter there—that natural selection favors a wintering ground with a greater abundance of fruit at that season. The Red-eyed Vireo is highly frugivorous while in fall migration in temperate North America and in Panama (Tyler *in* Bent 1950: 339–340). That the Red-eye is almost totally insectivorous during its breeding season (Southern 1958) is perhaps reflected in its size, which is smaller than the Yellow-green (16–17 g vs. 18–21 g nonfat weight), a reversal of Bergmann's rule. Selection in the Red-eye favors a size more in tune energetically with insect foraging strategies. But when fruit is always available to provide part of the individual's energy base, as it is in the Yellow-green populations, selection for intraspecific dominance competition or territoriality may result in a larger size.

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