SEASONAL CHANGES IN FEEDING PRESSURES OF FRUIT- AND NECTAR-EATING BIRDS IN PANAMÁ

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It is only recently that the seasonal fluctuations of fruit and nectar abundance have become well documented in the botanical literature for the New World tropics (Janzen 1967; Croat 1969). Much work now remains for the zoologists, however, to correlate these fluctuations with the seasonal aspects of the life histories of animals. In this study, the feeding behavior and ecology of fruit- and nectar-eating birds were examined in the Panama Canal Zone to determine how they were affected by seasonal changes of food supply.

METHODS

Records of the birds exploiting common species of fruiting and flowering plants were obtained in the wet (September–December 1968) and dry (January–April 1969) seasons. Data collected included total numbers of feeding visits per avian species, aggressive interactions, and foraging behaviors. One of the most abundant plants chosen for this analysis was a mistletoe (*Oryctanthus* sp.). In the wet season, one tree with this parasite was observed for five 20-hr periods, each of which took from five days to a week to complete. The 20-hr period was a composite of two full sets of each of the following periods: 06:30–07:00, 07:30–12:00, and 12:30–17:30. In the dry season, the feeding visitation rates were so significantly decreased that to demonstrate the seasonal differences it was only necessary to collect data for three additional 20-hr periods at the same plant.

Other important study plants included those species which fruited in both seasons, albeit different individuals were involved. For example, a *Cecropia* sp. tree was watched on the same wet season schedule as the *Oryctanthus* described above, and others were observed on similar schedules in the dry season.

Hamelia nodosa, a common introduced shrub throughout the tropics, also provided data on seasonal differences in the exploitation of individual fruit species. The time I spent at such individual plants, including those mentioned above, totaled more than 800 hr. Also included were many species which bore fruits or flowers in one season only, as such seasonality is apparently more common than continuous reproduction.

Although no formal indexing of avian populations was attempted, 40 individuals of 18 common species in the study area were color-banded. All recaptures or sightings of these birds were recorded, and these records made possible some estimates of the small populations.

Finally, in an attempt *experimentally* to measure seasonal changes in feeding pressures, birds in the study area were tested for their exploitation of an artificial food source in both seasons. In the tests, free-living birds were offered a continual supply of live crickets on laboratory window screens for a series of mornings (06:00–07:00) with all feeding visits recorded.

THE STUDY AREA

Field work was conducted at Barro Colorado Island, Canal Zone, September 1968–April 1969. The 3884-acre island bears essentially mature lowland rain-forest with a small clearing about the field station of the Smithsonian Tropical Research Institute. The general ecology of the island, including the clearing study area, is treated in numerous papers (e.g., Kenoyer 1929; Standley 1933; Eisenmann 1952; Kaufmann 1962). About the study area are many plants associated with second-year succession (e.g., *Heliconia* and *Piper*), while pioneer forest species invade the edges (e.g., *Ochroma* and *Tetracera*). Introduced plants are also important (e.g., *Hibiscus*). Thus, in many ways the clearing is representative of man-disturbed areas throughout Latin America.

As a whole, the climatic pattern falls into Holdridge's (1964) classification of Humid Lower Tropical Zones. And although the annual temperature variation on the island is slight (Allee 1926), there are considerable seasonal differences in rainfall, with a dry season extending from January through April, and a wet season from May through December.

Fruit and flower (nectar) production is apparently well synchronized with the seasons. Fruiting is highest towards the end of the dry season and the beginning of the wet season (Kaufmann 1962; Croat 1969; Smythe 1970; and others), while peak flowering is about two months earlier, during the first half of the dry season.

RESULTS

FEEDING PRESSURES AT FRUIT SOURCES

Strictly comparable data on feeding pressures between the two seasons require *individual* plants that are continually fruiting. While thus limited, the main *Oryctanthus* permitted such a comparison. The visitation rates of the

TABLE 1. Summary of exploitation, by species, of four of the more important food plants in the Barro Colorado Island study area.

	Food source and frequency of use[a]											
	Cecropia spp.[b] (Family Moraceae)			*Hamelia nodosa*[c] (Family Rubiaceae)			*Lantana camara*[d] (Family Verbenaceae)			*Oryctanthus occidentalis*[e] (Family Loranthaceae)		
Bird species	irreg.	reg.	freq.	irreg.	reg.	freq.	irreg.	reg.	freq.	irreg.	reg.	freq.
Columba nigrirostris												F
Brotogeris jugularis	F											
Thalurania furcata				N								
Damophila julie				N			N					
Amazilia tzacatl				N			N					
Pteroglossus torquatus		F		F								
Ramphastos swainsonii	F											
Centurus pucherani		F										
Manacus vitellinus					F		F			F		
Tyrannus melancholicus				F			F					
Megarynchus pitangua				F								
Myiodynastes maculatus							F					
Myiozetetes similis				F								F
Tyranniscus vilissimus												F
Tyrannulus elatus												F
Ornithion brunneicapillum											X(ants)	
Pipromorpha oleaginea												F
Hylocichla ustulata				F								
Vireo olivaceus										F		
Vireo flavoviridis										F		
Dendroica petechia	X(mullerian bodies)											
Dendroica pensylvanica				F								
Coereba flaveola				N								
Chlorophanes spiza				F			F					
Dacnis cayana								F				
Euphonia fulvicrissa	F			F					F			
Tangara inornata			F		F			F				
Tangara larvata	F											F
Thraupis episcopus		F			F							
Thraupis palmarum			F		F							
Piranga rubra	F										F	
Tachyphonus luctuosus											F	
Heterospingus rubrifron	F			F								F
Sporophila aurita	F											F

[a] F = fruits or berries; N = nectar; X = others; irreg. = irregularly visited (usually fewer than five records); reg. = regularly visited (usually several records per week); freq. = frequently visited (usually daily, often eaten in considerable quantities).

[b] Common medium-sized tree of the clearing and forest edge; fruit in the form of a catkin. Although fruiting all year, the number of individuals in fruit was highest during the dry season. This is a widespread genus in Central America and is often abundant in second-growth areas. Avian feeding is important for its dispersal; seed viability is outstanding after passing through the digestive system. Monkeys (*Ateles geoffroyi*) also fed on the fruits and leaves. Eisenmann (1961) added a number of species feeding on *Cecropia* fruits in the same locality during a summer (early wet season).

[c] In the clearing, several shrubs larger than 10 ft as well as a number of smaller plants. Orange tubular flowers, and small berries that are first red, and then, when fully ripe, purple. In addition, two lizards (*Iguana* and *Basiliscus*) ate berries.

[d] A very common shrub of the clearing and widespread in the tropics. Orange and red flowers, yielding small blue-black berries in clusters. On the mainland a number of open country species (e.g., *Crotophaga ani*) feed on this plant.

[e] Probably the most common mistle-toe on the island; frequently abundant in tree tops; parasitic, as with all members of the family. The very small green berries are produced in both seasons. Throughout the tropics of the world, mistletoes are closely associated with birds as dispersal agents. In feeding, the tanagers peeled the edible pericarp and dropped the seed. The pigeon and flycatchers swallowed fruits whole, the pigeon excreting the seeds and the flycatchers regurgitating them later.

birds feeding on the berries ranged from 162–180 visits per 20-hr census period (average, 169) in the wet season to 50–89 visits per census period (average, 76) in the dry season. As the birds were residents (see table 1) and present in the study area in equal numbers in both seasons, the data (fig. 1) indicate reduced feeding pressures in the dry season.

Similarly the wet season exploitation of the berries of ten *Hamelia nodosa* shrubs was sufficiently heavy that berries were eaten before they were ripe (often while they were "hard") but in the dry season, with reduced feeding pressures, many berries were able to mature and remain uneaten on these same shrubs. By considering further the total diets

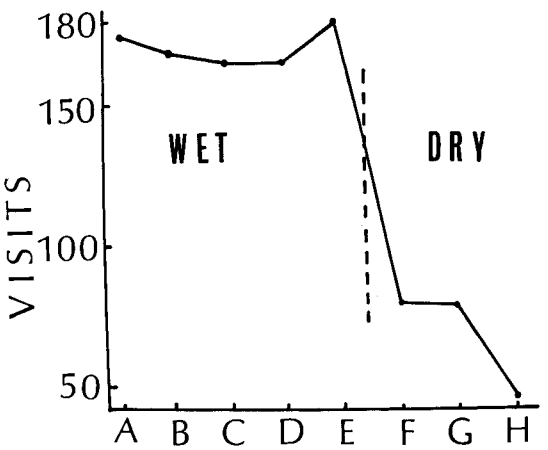

FIGURE 1. Total numbers of visits to *Oryctanthus* plants in wet and dry seasons. Each period (A–H) represents 20 hr of observation (see text): A = 26 Sept.–7 Oct., B = 7–15 Oct., C = 17–24 Oct., D = 25 Oct.–1 Nov., E = 6–12 Nov., F = 16–28 Jan., G = 11–18 Feb., and H = 19–28 Mar. (Included are nine species of common visitors and a lesser number of irregular or rare visitors which fed at the plants. All but one of the common species were present in both seasons).

of the birds that fed at *Hamelia*, it is possible to see that the dry season reduction in visits resulted from an increased availability and exploitation of alternate foods (table 2). These data (obtained through general daily censuses) indicate that 8 of the 15 species of alternate fruits utilized are restricted to, or are more abundant in, the dry season, and that only 2 species limit their fruiting to the wet season. Thus, there was a general trend for the frugivorous birds to reduce their exploitation of *Hamelia* in the spring. The dry season switch to alternate food plants was verified for individuals, as well as for the 11 species, through color-banding.

Another example of dry season reduction in feeding pressures is provided by one of the more common shrubs of the clearing, *Lantana camara*. In the fall the heavily exploited berries were *always* taken before they were ripe, by two species of honeycreepers, two species of tanagers, and a manakin (see table 1). In the dry season, however, both honeycreepers switched to new alternate sources (for nectar) as they appeared (*Ochroma*, *Trichlospermum*, *Cordia*, *Macrocnemum*, and *Tabebuia*), and the other bird species, as well as one of the honeycreepers, added the berries of several other dry season species to their diets. With the released feeding pressures, the *Lantana* then had many ripe berries available.

For both the *Hamelia* and *Lantana*, the dry season berry superabundance led to opportunistic exploitation by species which had not fed at the plants in the wet season. These new species included three flycatchers and a migrant warbler at *Hamelia*, and two flycatchers and a migrant mimid at *Lantana*. At the island each of these birds was generally insectivorous, and apparently became frugivor-

TABLE 2. Alternate foods in the diets of birds which fed on the berries of *Hamelia nodosa*.

Alternate food source	Season(s) of primary availability	Species of birds using the alternate food
Isertia	both	*Tangara inornata*
Piper (sp. 1)	both	*Manacus vitellinus, Tangara inornata, Euphonia fulvicrissa*
Piper (sp. 2)	both	*Euphonia fulvicrissa, Thraupis episcopus, T. palmarum*
Phoradendron	both	*Euphonia fulvicrissa, Tangara inornata*
Pothomorphe	both	*Euphonia fulvicrissa, Tangara inornata*
Cecropia	dry	*Pteroglossus torquatus, Chlorophanes spiza, Euphonia fulvicrissa, Tangara inornata, Thraupis episcopus, T. palmarum, Heterospingus rubrifrons*
Citrus	dry	*Pteroglossus torquatus*
Lantana	dry	*Manacus vitellinus, Tyrannus melancholicus, Chlorophanes spiza, Euphonia fulvicrissa, Tangara inornata*
Oryctanthus	dry	*Manacus vitellinus, Myiozetes similis, Tangara inornata, Heterospingus rubrifrons*
Didymopanax	dry	*Pteroglossus torquatus, Tyrannus melancholicus, Megarynchus pitangua, Tangara inornata, Thraupis episcopus, T. palmarum*
Ochroma	dry	*Chlorophanes spiza*
Tabebuia	dry	*Thraupis palmarum*
Tetracera	dry	*Tangara inornata*
Trichlospermum	wet	*Chlorophanes spiza*
Psychotria	wet	*Chlorophanes spiza*

TABLE 3. Intra- and interspecific supplanting attacks during the wet and dry seasons.

Bird complex	Attacks	Wet season (101 hr)	Dry season (112 hr)
Frugivorous Flycatchers[a]			
	Intraspecific	41	4
	Interspecific	7	4
	Totals	48	8
Tanagers[b]			
	Intraspecific	17	5
	Interspecific	49	4
	Totals	66	9
Nectivorous Honeycreepers[c]			
	Intraspecific	1	3
	Interspecific	1	9
	Totals	2	12
Hummingbirds[d]			
	Intraspecific	5	11
	Interspecific	1	15
	Totals	6	26

[a] Flycatchers: *Myiozetetes similis, Tyranniscus vilissimus, Tyrannulus elatus, Microtriccus brunneicapillus,* and *Pipromorpha oleaginea.*
[b] Tanagers: *Euphonia fulvicrissa, Tangara inornata, T. larvata, Thraupis episcopus, T. palmarum, Piranga rubra,* and *Heterospingus rubrifrons.*
[c] Honeycreepers: *Coereba flaveola, Dacnis cayana, Cyanerpes cyaneus, Chlorophanes spiza.*
[d] Hummingbirds: *Phaethornis superciliosus, Florisuga mellivora, Anthracothorax nigricollis, Thalurania furcata, Damophila julie,* and *Amazilia edward.*

ous only when berries were sufficiently ripe and available (i.e., when feeding pressures by obligate fruit feeders were reduced). These species are thus considered "opportunistic frugivores." There are probably distinct diet dichotomies between opportunistic and obligate species at most fruit resources, with migrants particularly inclined toward opportunism.

AGGRESSIVE BEHAVIOR OF FRUGIVORES

Aggressive behavior, particularly at food sources, might also be affected by seasonal changes in food availabilities. Supplanting attacks, in which displacement of one individual is caused by the arrival of another, were an easily identified and quantified element of aggressive behavior, but were relatively infrequent among the frugivorous birds. Nevertheless, sufficient numbers of encounters were recorded in the study area to compare the two seasons (table 3) which showed significant differences (Chi-square tests, $P < 0.001$). Thus, for both the tanagers and frugivorous flycatchers the numbers of supplanting attacks were much reduced in the dry season, with the increased food availabilities and concomitant decline of feeding pressures. It is important to realize that the bird population numbers showed no observable changes with the seasons. The residents were common species which did not exhibit seasonal movements or breeding recruitment in the period, September–early April, and thus they were being reduced in numbers only by adult mortality (low). The few migrant species involved in supplanting attack records were usually color-banded winter residents that similarly showed no decline between the two seasons. Hence, because of crowding at fewer resources in the wet season, on an individual basis birds had their feeding interrupted more frequently than in the dry season. The "disturbance factor" resulting from the crowding may or may not also have involved heightened aggressiveness per se with the approach of the breeding season. Territoriality at food sources was not evident for the frugivores.

TABLE 4. Seasonal changes in abundance[a] of honeycreepers and hummingbirds at Barro Colorado Island.

Species	Wet season (November 1968)	Dry season (February 1969)
Cyanerpes cyaneus	once	common
Chlorophanes spiza	none	regular
Dacnis cayana	few	abundant
Coereba flaveola	common	common
Phaethornis superciliosus	none	regular
Florisuga mellivora	once	regular
Lophornis delattrei	none	once
Thalurania furcata	regular	regular
Damophila julie	common	common
Amazilia tzacatl	few	regular
Heliothrix barroti	none	irregular

[a] Glossary: once = only record for the month; few = 2 or 3 records for the month; irregular = 4–10 for the month; regular = more than 10 but less than 30; common = daily records; several individuals; abundant = daily records; small flocks.

NECTAR FEEDERS

Another possible effect of food shortages is the emigration of those animals that depend on the limited foods in their diets. A comparison of the abundances of nectar-feeding species (honeycreepers and hummingbirds) during the wet and dry seasons at Barro Colorado Island revealed that most species in these groups were much less common in the rainy season than in the dry season (table 4). These population differences were due apparently to the return of many birds near the beginning of the dry season, at the time of maximum flowering activity, or greatest nectar availability. Similarly, Sick (1968) has described local migrations in response to seasonal changes in food abundance for a number of South American nectar-feeding species. At present it is unclear where the populations of

honeycreepers and hummingbirds spend the end of the rainy season, for they apparently departed from adjacent areas of the Canal Zone as well. Presumably they move to some areas along the more arid Pacfic Coast, where flowering continues later through the fall months (Standley 1928).

Another measure of seasonal changes in feeding pressures was possible with those honeycreepers (spp.?) which regularly made small holes in the calyx of various flowers when feeding. This habit permitted a direct measure of the level of exploitation, as the percentage of flowers having such coerebid holes could be quickly determined by inspection. Unfortunately very few flowers were available during the wet season, but a sample of 75 *Quassia amara* blossoms from several shrubs in the forest revealed a utilization of 89 per cent in December. And while *Quassia* was unavailable for a dry season comparison, the recorded levels of exploitation of other plant species (indetermined) in the forest were always below the wet season estimate. Further, two *Jacaranda copaia* trees permitted a comparison of the dry season exploitation levels of one in the forest, where 19 per cent of the fallen blossoms ($n = 400$) were pierced, with one at the edge of the clearing, where 49 per cent ($n = 400$) had been visited. This difference is probably a consequence of the habitat preferences of coerebids, which are essentially "edge" species (Moynihan 1968). These limited data suggest that honeycreepers' feeding pressures would be highest at forest edges and during the wet season, the period of less food abundance. As the situation parallels that of the frugivorous species it is apparent that the aforementioned wet-season emigrations from the island do not completely reduce the effects of the seasonal changes in flower availabilities for the individuals remaining on the island.

The aggressive behavior of honeycreepers and hummingbirds at food plants was highest during the dry season (table 3), contrary to the results for flycatchers and tanagers. In the wet season, with few plants in flower, the populations of most species were reduced by emigration and it appeared that the remaining individuals seldom had inter-specific encounters. In the dry season, with many more species and individuals present (as described earlier; table 4), feeding overlap was frequent and aggressive encounters resulted, although there appeared to be a superabundance of nectar sources. The basis of these supplanting attacks thus appears not to be essential food competition, but rather a simple byproduct of the greatly increased numbers and thus density of nectar-feeding birds in the study area. (Recall that frugivores exhibited seasonal changes in the numbers of supplanting attacks with relatively constant populations.)

TABLE 5. Numbers of feeding visits at experimental cricket food supply in the clearing at Barro Colorado Island.

Species	Wet season 16 mornings 24 Oct.– 8 Nov.	Dry season 22 mornings 13 Mar.– 5 Apr.
Thamnophilus punctatus	184	77
Tyrannus melancholicus	79	54
Myiodynastes maculatus	159	136
Total	422	267
Mean visits/morning[a]	26	12

[a] Comparisons of seasons by number of feeding visits per morning, using Kolmogorov-Smirnov two-sample two-tailed test, gave the following P values: *Thamnophilus punctatus*, < 0.001; *Tyrannus melancholicus*, $= 0.05$; *Myiodynastes maculatus*, < 0.05.

RESULTS OF EXPERIMENT WITH ARTIFICIAL FOOD SOURCE

Attempts to measure seasonal changes in the exploitation of an artificial fruit supply were unsuccessful because of continual monkey raids. Experiments with insects (crickets) as a food source were practical however, and their exploitation by three common bird species proved significantly higher in the wet season than in the dry season (table 5). As color-banding showed that equal numbers of birds (several individuals of each species) were present at the artificial food source in both seasons, it is again suggested that natural feeding pressures were more intense in the wet season. Thus, in the dry season, with more alternate foods available (e.g., various berries for the frugivorous flycatchers), the demand for the experimental food supply declined.

DISCUSSION

The seasonal variations in feeding pressures, measured by the various methods described above, are reflections of conspicuous changes in food availabilities that are now being quantified by Robin Foster and other tropical botanists. These annual changes in food abundances also contribute to the temporal limitations of breeding seasons throughout Central America. Thus, most nectar feeders begin breeding immediately at the start of the dry season with the burst of flowering (Skutch 1950), while the courtship and breeding periods of fruit-eating birds are generally centered within or at the end of the dry sea-

son (from the Canal Zone data of Eisenmann 1952). Clearly, the reproductive periods for such frugivorous species are adaptively synchronized within the periods of maximum plant food availabilities, although flushes of insect life at the beginning of the wet season may also be important in limiting the breeding season (Lack 1966). Other manifestations of the food fluctuations should be expected, such as changes in diet quality with increased fruit abundance or with the nesting period, as noted in Trinidad with *Steatornis caripensis* (Snow 1962). Also it appears that some birds may expand their foraging areas (vertically) with the decreased fruit availability of the wet season, much as frugivorous mammals show expanded foraging during unfavorable periods (Enders 1935). For example, the foraging range of *Thraupis episcopus* came much closer to the ground in the wet season than in the dry season.

Reviewing briefly, the following characteristics of the wet season are indicated in this study: consumption of unripe fruits, availability of few alternate foods, high rates of fruit resource visitation, increased aggressive encounters (fruit eaters), and emigration (nectar feeders). Might we expect these changes in feeding pressures for birds in other areas of the tropics? The wet season shortage of fruit (and nectar) considered for Barro Colorado Island may be typical of most of Central America, as such distinct seasonality is found in large areas throughout the neotropics (Harrower 1936; Skutch 1954, 1960). Most tropical areas in South America (Snow and Snow 1964), Africa (Moreau 1950), and Malaysia (Koeppe and Long 1958) also have significant seasonal patterns of rainfall, and hence probably have seasonal changes in food availabilities. It should be emphasized, however, that the dry season may become the period of food shortage even for nectar and fruit feeders if that season is sufficiently long (e.g., six months), as is found in some parts of Africa. In such cases, the severity of the dry months selects against fruit production at that season. Also, in recent years an hypothesis has developed regarding the possibility of continued fruit superabundances in some of the more climatically stable areas of the tropics (Snow 1965), although regions of constant food supply have not yet been rigorously demonstrated. If such regions do exist, they are probably quite limited, for world rainfall data (Koeppe and Long 1958, and Rumney 1968) suggest that only relatively small areas of the tropics are sufficiently unvarying in rainfall to permit similar levels of fruiting throughout the year. And even in one of the most constant areas (Singapore, Malaysia) it has been shown that fruit availability and avian reproduction are significantly seasonal (Ward 1969).

Note, however, that in recent times the differences of the wet and dry season are reduced in man-disturbed areas, where a variety of cultivated shrubs and trees produces a continual supply of fruits (Leck 1969, 1970).

Finally, it is suggested that emigration in response to reduced flower availability is characteristic of nectar feeders throughout the world (e.g., hummingbirds in Central America, Wolf 1970; meliphagids in Australia, Keast 1968, and others). Why is emigration so frequently associated with nectar feeders but not with frugivores, when the latter experience similar changes in food abundances? Perhaps the difference developed from a need to be responsive to sudden changes in nectar availabilities, as flowers are more ephemeral than fruits. The nomadic habits of coerebids may be an indication of such responsiveness, as well as a result of their own destructiveness of food resources (through corolla holes). Further research on the adaptive strategies of birds during food shortages should be sensitive to such differences between groups with different diets, as an indicator of resource dependability.

SUMMARY

A study of the feeding pressures of fruit- and nectar-eating birds revealed significant seasonality at Barro Colorado Island in the Canal Zone. The feeding pressures, as measured by a number of natural parameters, were significantly higher during the wet season when production of flowers and fruit were much reduced. These parameters included rates of visitation per resource, quality of fruits, numbers of "alternate" foods in the diets, and amounts of aggressive behavior. The reduced pressures of the dry season are correlated with increased flower (early) and fruit (later) production. Comparisons with other areas indicate that such seasonality is probably common to most of the tropics.

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