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Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama

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ABSTRACT. Plants potentially compete for seed dispersal. Selection may favour temporally segregated fruiting phenologies to minimize this competition and also to maintain resident populations of dispersal agents. Alternatively, selection may favour temporally aggregated fruiting phenologies when the effectiveness of seed dispersal agents varies seasonally or when large, synchronous fruit displays enhance dispersal. These evolutionary scenarios assume that plants share seed dispersal agents. This assumption and temporal overlap in fruiting phenologies were evaluated for the *Miconia* and *Psychotria* of central Panama. These two genera accounted for 18 and 27%, respectively, of 1096 fleshy fruits found in regurgitation or faecal samples taken from 2054 birds of 103 species netted in the forest understorey. Two species of manakins accounted for 62% (123/200) of all *Miconia* fruit taken. Three species of manakins and three species of migratory thrushes accounted for 97% (282/292) of all *Psychotria* fruits taken. There is a high potential for intrageneric competition for seed dispersal for both plant genera. Null model analyses showed that the fruiting phenologies of *Miconia* (14 species) are segregated in time, while fruiting of *Psychotria* (21 species) is highly aggregated. The *Miconia* were found in up to 24% of the diet samples for the two manakin species, suggesting that *Miconia* may be a critical resource for both species. The *Psychotria* fruited when the diversity of understorey fruits was greatest, suggesting a high potential for both intra- and extrageneric competition. The abundance and nomadism of the six bird species that consumed most *Psychotria* fruit peaked when the *Psychotria* fruited, supporting the enhancement hypothesis.

KEY WORDS: competition, diet diversity, frugivorous birds, fruiting phenology, *Miconia*, Panama, *Psychotria*, seed dispersal

INTRODUCTION

Since Snow's (1965) seminal paper on *Miconia*, several studies have demonstrated segregated flowering or fruiting seasons among plants presumed to

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share a common pool of pollinators or seed dispersal agents (Ashton *et al.* 1988, Frankie 1975, Hilty 1980, Pleasants 1980, 1990, Smythe 1970, Stiles 1977, Wheelwright 1985). Such staggered or minimally overlapping phenologies have been interpreted as an evolutionary response to reduce interspecific competition for pollinators and dispersers (Foster 1973, Frankie 1975, Janzen 1971, Snow 1965). The overall effect is to provide a continuous food source to animal vectors, favouring their site attachment and potentially increasing their reliability as dispersal agents (Snow 1965).

Alternatively, congeneric plants fruiting synchronously may enhance each other's dispersal by mutually attracting more dispersers than each would alone (Rathcke & Lacey 1985, Sargent 1990). Temporally aggregated fruiting may also be favoured when few extra-generic species are fruiting or when the effectiveness of shared dispersal agents varies seasonally. Unlike aggregated flowering which is likely to decrease pollination success through stigma blocking and hybridization (Stiles 1975), aggregated fruiting could be beneficial to the plants by increasing the probability that seeds are dispersed away from conspecifics, potentially increasing seedling survival (Howe & Primack 1975, Janzen 1970, Ross & Harper 1972, Schupp 1993, Wheelwright & Orians 1982). Aggregated fruiting would not provide a constant food source to animal vectors, but the abundance of frugivores has been shown to vary temporally in many tropical habitats, presumably reflecting movements in response to variation in fruit availability (Levey 1988, Loiselle & Blake 1991, Van Schaik *et al.* 1993, Wheelwright & Orians 1982, Worthington 1982).

Although segregated fruiting phenologies have been documented in several tropical habitats and interpreted as reflecting adaptations to minimize competition for dispersal agents (Wheelwright 1985), no study has ever provided quantitative information on how food resources are shared among dispersers in conditions of aggregated or segregated fruiting patterns. These hypotheses can be tested by studying the abundance and diet of dispersal agents as they feed on sympatric plants exhibiting different fruiting phenologies. *Miconia* (Melastomataceae) and *Psychotria* (Rubiaceae) both produce small fleshy fruits commonly taken by opportunistic frugivorous birds (Charles-Dominique 1993, Snow 1981). Fruiting in *Miconia* spp. is well known to be segregated (Hilty 1980, Snow 1965), whereas fruiting of *Psychotria* spp. may be temporally aggregated (Wright 1991, Wright & Calderón 1995). We use null model analyses to evaluate fruiting phenologies of 14 *Miconia* and 21 *Psychotria* species from Barro Colorado Island, Panama. We further evaluate fruit intake by frugivores, as well as their abundance and diet diversity relative to the plant fruiting phenologies.

STUDY SITES

Information on plant phenology and frugivore diet are from two independent studies carried out respectively at Barro Colorado Island (BCI: 9°9′N, 79°51′W) and Soberanía National Park (9°10′N, 79°7′W) in central Panama. Descriptions of BCI can be found in Croat (1978), Leigh *et al.* (1982), and Windsor (1990). The study plot in Soberanía is a second-growth forest located along Pipeline Road, 10 km south-east of BCI. Both sites have a tropical monsoon climate under the Köppen system of climatic classification (Croat 1978) and support a semideciduous tropical forest with a mature canopy height of 35 m. Annual rainfall averages 2600 and 2133 mm, respectively. Mean monthly temperatures are 27 °C in April and 26 °C otherwise. A 4-mo dry season, during which 13% of annual rainfall occurs, begins in December, or rarely November, and ends in April, or rarely May.

METHODS

Fruiting phenologies

The null hypothesis that fruit maturation occurs independently among individuals was evaluated for *Miconia* and *Psychotria*. Timing of fruit maturation for virtually all sympatric congeners is provided by Croat (1978), as well as from phenological censuses of *Psychotria* conducted between December 1991 and December 1993.

Croat (1978) described the phenologies of 14 *Miconia* species and 23 *Psychotria* species by summarizing "observations made during more than three years in Panama and a survey of 50,000 herbarium specimens from BCI and adjacent areas." According to Croat (1978, p. 30), these data "represent what is thought to be the normal phenological variation for each species . . . In the better-known species, 95% or more of the flowering or fruiting probably falls within the timespan indicated." Analyses were performed for the monthly presence/absence of mature fruit.

The phenological census of *Psychotria* spp. included ten reproductively mature individuals of each species, with the exceptions of *P. brachybotrya* and *P. poeppigiana* for which just five and two mature individuals, respectively, were known from BCI. The presence/absence of mature fruit was recorded for each individual. Censuses were conducted monthly through December 1992 and once every second month thereafter. Analyses were performed for the monthly proportion of individuals with mature fruit.

Null model analyses were used to evaluate the hypothesis that congeners mature fruit independently in time. Null models developed to evaluate this hypothesis for flowering were recently reviewed by Ashton *et al.* (1988) and Pleasants (1990), and the appropriate models recommended by those investigators are used here.

Model 3 of Ashton *et al.* (1988) was used to evaluate temporal overlap for the presence/absence of mature fruit (data from Croat 1978). The simulation randomizes the date of the midpoint of the fruiting season of each species while preserving the length of the fruiting season observed for each species and also the overall length of the fruiting season observed for all congeners.

The number of months in which fruiting overlapped was calculated for each pairwise combination of congeners, and the sum of the observed values was compared with 99 summed simulated values.

The mean pairwise overlap model of Pleasants (1980, 1990) was used to evaluate temporal overlap for the proportion of *Psychotria* individuals with mature fruit. The simulation randomizes mean fruiting dates while preserving the observed distribution of the proportion of individuals fruiting for each species and the overall length of the fruiting season observed for all congeners. An overlap index (Pianka 1974) was calculated for each pairwise combination of congeners, and the mean observed value was compared with 99 mean simulated values. In both analyses, evidence consistent with temporally segregated (aggregated) fruiting occurred when the observed overlap metric was smaller (greater) than 95 simulated values.

Nomenclature follows Burger & Taylor (1993) for *Psychotria* and D'Arcy (1987) for *Miconia*.

Avian dispersal

Data on bird diets were collected twice monthly in Soberanía National Park through mist-netting sessions from September 1993 through November 1994. Thirty-six nets (3-m × 10-m, 32-mm mesh) were operated from sunrise to early afternoon under rainless condition for three days. The netting effort, which totalled 22 000 net-hours, was held constant during the whole sampling period to allow comparison of samples over time. Each bird captured was banded, weighed, forced to regurgitate, and released. Regurgitation samples were obtained by orally administering tartar emetic following the method of Poulin & Lefebvre (1995). Manakins (*Pipra* spp. and *Manacus*) suffer high stress from capture alone, and were not forced to regurgitate whenever a faecal sample was available. The mean number of food items identified for these birds did not differ between regurgitation and faecal samples (Kruskal-Wallis test, $H = 0.86$, $df = 1$, $P = 0.353$). Diet samples were preserved in 70% ethanol, and seeds were identified to species using a reference collection. Number of fruits taken was extrapolated from the number of seeds found in the diet samples. Fruit diversity (H) in a diet sample was calculated using the Shannon-Wiener index (Tramer 1969).

Community-wide fruiting

Passive fruit traps were used to evaluate seasonal variation in fruit availability. Two hundred traps are permanently located in mature forest on BCI, and all seeds and fruits captured have been identified to species weekly since 1 January 1987. Each trap has a surface area of 0.5 m^2 and is constructed from 1-mm mesh screen suspended from a PVC frame. Wright & Calderón (1995) provide further methodological details.

Only the fruit species identified in the diet samples of birds that fed on *Psychotria* fruit were considered to determine fruit abundance over time. Fruit

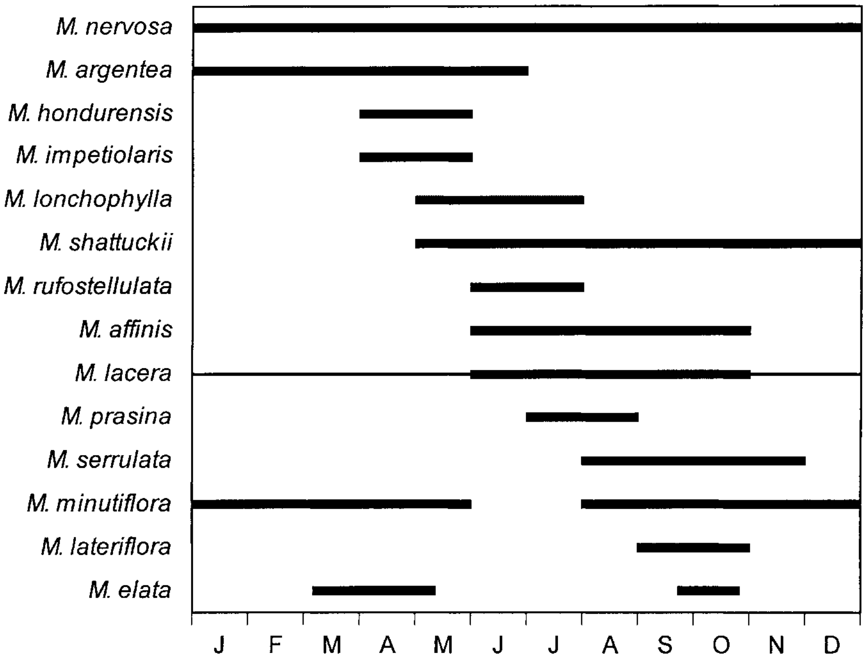

Figure 1. Fruiting phenologies of the 14 *Miconia* species from Barro Colorado Island, as reported by Croat (1978). *Miconia lacera* matures fruits year-round (thin line) but predominantly during July–October.

abundance was estimated for each species by summing the number of traps in which the species occurred in each census.

RESULTS

Fruiting phenologies

Fruiting phenologies of the 14 *Miconia* species reported by Croat (1978) are shown in Figure 1. The null model analysis indicates that fruit maturation tends to be temporally segregated ($P = 0.07$). The same analysis applied to published data from Trinidad (Snow 1965) and Colombia (Hilty 1980) indicates that *Miconia* fruiting phenologies are highly segregated in time ($P < 0.01$).

Three of the 23 *Psychotria* species reported by Croat (1978) have not been encountered on BCI in recent years (*P. carthagenensis, P. guapilensis* and *P. uliginosa*) and were not considered in our analyses. Croat (1978) overlooked *P. graciliflora*, which is locally abundant on BCI and was included in our analyses. The null model analysis indicates that fruit maturation is highly aggregated in time for these 21 *Psychotria* species ($P < 0.01$). Nineteen of the 21 *Psychotria* species were observed to mature fruit during the phenology censuses (Figure 2). The exceptions, *P. poeppigiana* and *P. pubescens*, flowered at the same time as most congeners but failed to set fruit (S. J. Wright, *pers. obs.*). The null model analysis indicates that fruiting is temporally aggregated for the 19 remaining

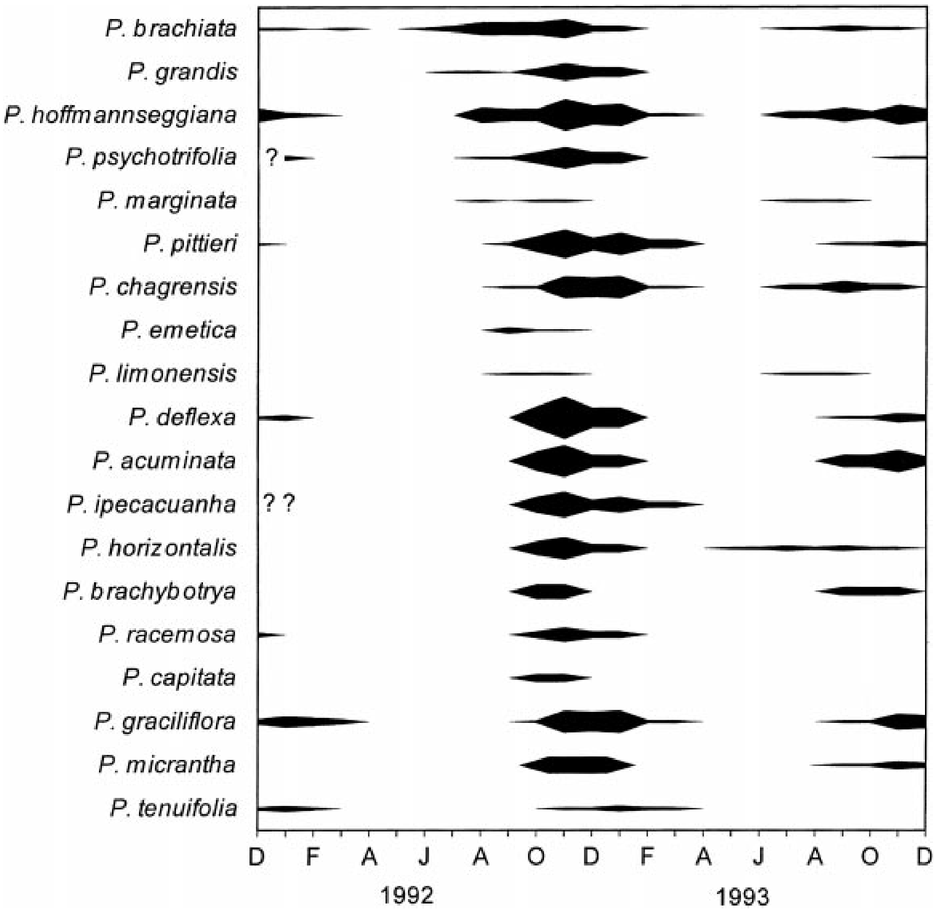

Figure 2. Fruiting phenologies of 19 *Psychotria* species from Barro Colorado Island based on the census carried out from December 1991 to December 1993. Band width represents the proportion of individual plants (n = 10) bearing mature fruits.

species. This result was robust for 1992 ($P < 0.01$), 1993 ($P < 0.05$) and the entire data set ($P < 0.01$ for December 1991 through December 1993).

Avian dispersal

A total of 2054 birds from 103 species was captured, from which 1417 regurgitation and 274 faecal samples were collected. Some 1096 fleshy fruits from 67 plant species were identified in the diet samples of 440 birds from 32 species (Table 1). *Miconia* and *Psychotria* accounted for 45% (492/1096) of all fleshy fruits taken by birds.

Nineteen bird species fed on 200 *Miconia* fruits (Table 2). However, only four *Miconia* species were found in the diet samples. We do not know whether the low number of *Miconia* species eaten is related to the scarcity of fruiting individuals at our study site or to the low sampling probability of mid-canopy birds

Table 1. Fruit intake by birds mist-netted in Soberanía National Park with sample size.

			Fruit intake	
Bird species[1]	Number of diet samples	Percentage of samples with fruit	Number of species	Number of fruits
Leptotila cassinii	3	100	10	19
Geotrygon montana	7	43	4	7
Phaethornis superciliosus	67	3	2	2
Trogon rufus	7	71	4	11
T. massena	2	50	1	3
Baryphthengus martii	6	17	1	3
Pteroglossus torquatus	1	100	2	8
Formicarius analis	15	7	1	1
Mionectes olivaceus	1	100	2	12
M. oleagineus	60	53	19	129
Oncostoma olivaceum	39	8	1	3
Empidonax virescens	20	10	3	3
Attila spadiceus	8	13	1	3
Schiffornis turdinus	26	42	10	34
Manacus vitellinus	25	96	18	47
Pipra coronata	83	88	26	168
P. mentalis	211	89	45	408
Catharus fuscescens	8	75	11	27
C. minimus	15	47	6	14
C. ustulatus	33	85	21	79
Hylocichla mustelina	4	25	1	4
Vireo olivaceus	1	100	1	2
Dendroica pensylvanica	1	100	1	2
D. striata	1	100	1	1
Seiurus aurocapillus	1	100	1	1
Euphonia fulvicrissa	6	100	3	8
Eucometis penicillata	16	25	4	13
Tachyphonus luctuosus	14	71	4	20
Habia fuscicauda	6	83	5	8
Ramphocelus dimidiatus	1	100	1	1
Cyanocompsa cyanoides	16	63	6	26
Oryzoborus angolensis	8	75	3	29
Total	712	62	67	1096

[1] Nomenclature follows Ridgely & Gwynne (1989).

that are likely to feed on *Miconia* fruits. Two species of manakins (*Pipra* spp.) fed on all four *Miconia* and accounted for 62% of *Miconia* fruit intake (Table 2). *Miconia* fruits were taken year-round, but predominantly in October–November (*M. lacera* and *M. minutiflora*), April (*M. argentea*) and June–July (*M. impetiolaris*) (Figure 3a). Each *Miconia* species was found in the diet samples over a period of 5–6 mo (Figure 3a).

Eleven bird species fed on 292 *Psychotria* fruits from 13 species (Table 3). Three species of manakins (*Pipra* spp. and *Manacus*) and three species of migrant thrushes (*Catharus*) together accounted for 97% of all *Psychotria* fruits found in the diet samples. These six bird species were responsible for at least 85% of all the fruits taken from any single *Psychotria* species. Overall, bird intake of *Psychotria* fruits peaked from October through December, a period during which all 13 *Psychotria* species were found in the diet samples (Figure 3b).

Table 2. Number of *Miconia* fruits taken by the bird species mist-netted in Soberanía National Park.

Bird species	*Miconia* species[1]			
	arg	*min*	*imp*	*lac*
Leptotila cassinii	1			
Mionectes oleagineus	1	2	1	
Empidonax virescens				1
Schiffornis turdinus			1	
Manacus vitellinus	2		2	2
Pipra coronata	5	16	16	17
P. mentalis	24	17	12	16
C. fuscescens				1
C. minimus		1		2
C. ustulatus	14	6		3
Dendroica pensylvanica	2			
D. striata	1			
Seiurus aurocapillus				1
Euphonia fulvicrissa				6
Eucometis penicillata	10		1	
Tachyphonus luctuosus	13			
Habia fuscicauda	1			
Ramphocelus dimidiatus	1			
Oryzoborus angolensis	1			
Total	76	42	33	49

[1] Miconia species are: *arg* = *argentea*, *min* = *minutiflora*, *imp* = *impetiolaris*, and *lac* = *lacera*.

Community-wide fruiting

Some 35 fruit species in addition to *Psychotria* were identified in the diet samples of *Psychotria*-fruit-eating birds. Abundance of these fruits in the BCI traps peaked in September–November (Figure 4a) when the number of species fruiting was maximum. Similarly, the number of *Psychotria* species maturing fruit was highest in September–December (Figure 4b).

Frugivore abundance

Of 2054 birds captured, 857 were from species that fed on fruits at least once during the sampling period. Monthly abundance of these birds was highly seasonal and ranged from 35 to 88 captures (Figure 5). Manakins and migrant thrushes accounted respectively for 50 and 6% of these captures. These birds were mainly responsible for the peak observed in the second part of the wet season, especially in October–December (Figure 5).

Frugivore diet

The number and diversity of fruits in a regurgitation or faecal sample can be used as an indicator of a bird's foraging mode, i.e., whether feeding bouts consisted of ingesting several fruits from a single plant species (possibly a single individual plant) or picking up single or few fruits from many plant species. Diet samples including more than one fruit species are suggestive of bird movements among different fleshy-fruited plants, which is a condition of the enhancement hypothesis. Overall, 46% (71/154) of the samples containing *Miconia* fruits included more than one fruit species, compared to 70%

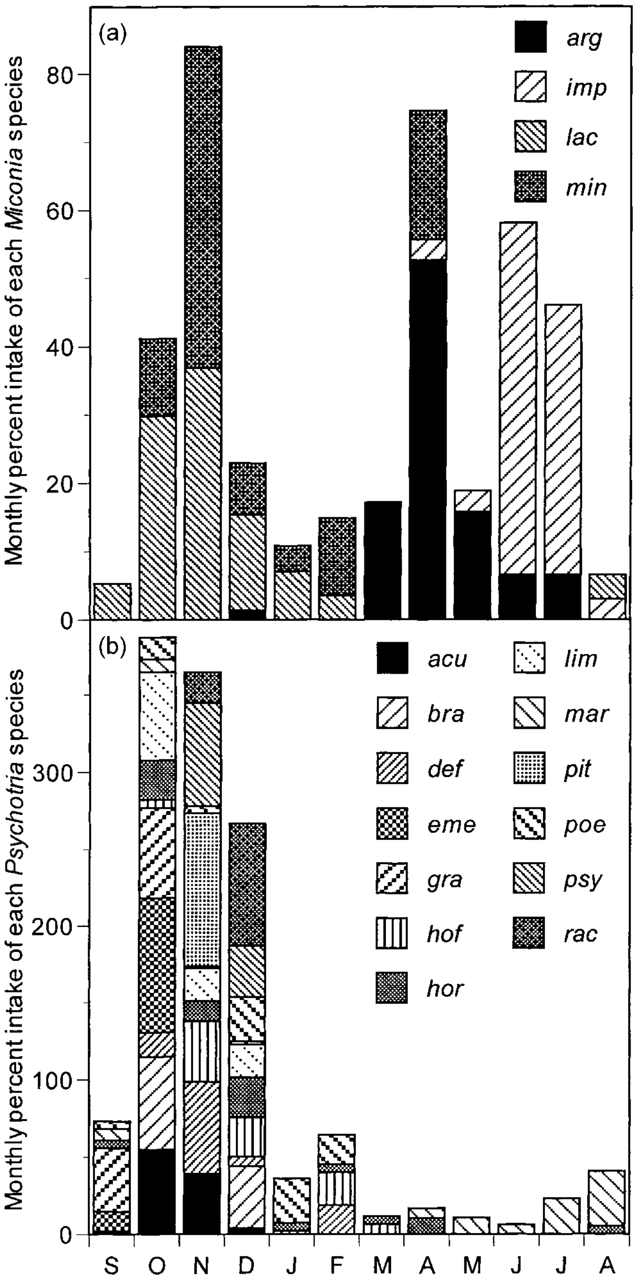

Figure 3. Monthly percentage of fruits taken from each (a) *Miconia* and (b) *Psychotria* species by birds mist-netted in Soberanía National Park. Species abbreviations are defined in Tables 1 & 2.

Table 3. Number of *Psychotria* fruits taken by the bird species mist-netted in Soberanía National Park.

Bird species	*Psychotria* species[1]												
	acu	*bra*	*def*	*eme*	*gra*	*hof*	*hor*	*lim*	*mar*	*pit*	*poe*	*psy*	*rac*
Trogon rufus									1				
Mionectes oleagineus							1						
Empidonax virescens							1						
Schiffornis turdinus						1			1				
Manacus vitellinus						1	2	1	10	2	1		1
Pipra coronata	7	2	11			7	2		16	1	3	2	1
P. mentalis	26	1	9		2	52	13	21	18		6	3	1
Catharus fuscescens	1					1	2	2	7				
C. minimus	3			4		3	1						
C. ustulatus	13	1	5	3		3	6	1	3		1		
Habia fuscicauda			3								2		
Total	50	4	28	7	2	68	28	25	56	3	13	5	3

[1] *Psychotria* species are: *acu* = *acuminata*, *bra* = *brachybotrya*, *def* = *deflexa*, *eme* = *emetica*, *gra* = *grandis*, *hof* = *hoffmannseggiana*, *hor* = *horizontalis*, *lim* = *limonensis*, *mar* = *marginata*, *pit* = *pittieri*, *poe* = *poeppigiana*, *psy* = *psychotrifolia* and *rac* = *racemosa*.

(135/192) for *Psychotria*. These two proportions were significantly different (χ^2 = 9.19, df = 1, P < 0.005). The monthly variation of fruit diversity in the birds' diet showed two peaks, one of which coincided with the *Psychotria* fruiting season (Figure 6). Moreover, diet samples including *Psychotria* had a fruit diversity significantly higher than the overall mean value (H = 0.48 *vs* 0.29; t = 4.85, df = 258, P < 0.0001).

DISCUSSION

The *Miconia* of central Panama fit the model of temporally segregated fruiting proposed originally by Snow (1965). Although only four *Miconia* species occurred in the diet of the bird species sampled, temporal segregation in fruiting allowed these birds to feed on *Miconia* year-round. Because fruits were produced over a longer period, more bird species fed on *Miconia* than on *Psychotria* fruit. The two most abundant frugivores locally, *Pipra mentalis* and *P. coronata*, ate fruits of all four *Miconia* species and accounted for 60% of fruit intake (123/200), suggesting a high potential for competition for dispersal agents among the *Miconia*.

The *Psychotria* were temporally aggregated in their fruiting phenologies. Fruit production was concentrated in the late wet season, a period of high fruit availability, especially among understorey fleshy-fruited plants (Foster 1982, Worthington 1982, this study). Such a pattern suggests a high potential for both intra- and extrageneric competition for dispersers. However, capture rates of understorey frugivorous birds also peaked during the *Psychotria* fruiting season. This increase in bird abundance was mostly related to the passage of migrant thrushes and to population recruitment and nomadism among the manakins.

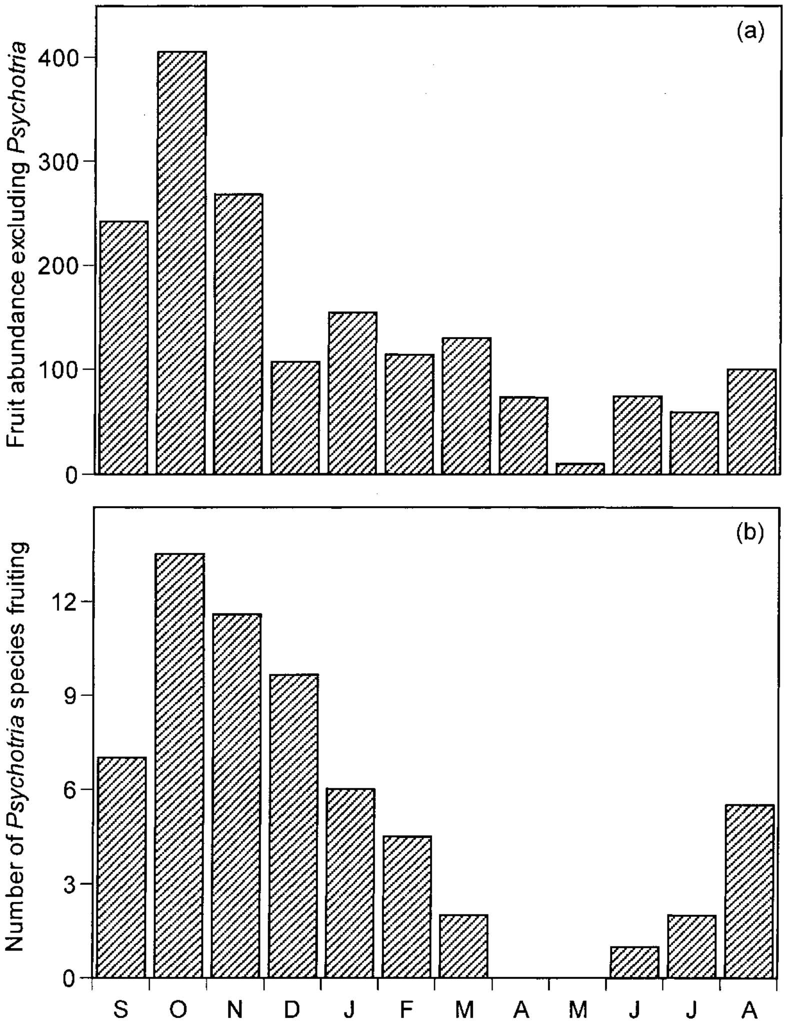

Figure 4. Monthly variation in abundance of fruits available to birds feeding on *Psychotria* fruit, excluding *Psychotria* (a). Fruit abundance for each species was estimated by summing the number of traps in which fruit occurred from January 1987 to December 1995. Mean number of *Psychotria* species fruiting on BCI for each calendar month (b).

Manakins ate 75% of all *Psychotria* fruits taken. Seasonal changes in the spatial behaviour in these year-round residents suggest that their ability to disperse seeds is highest during the *Psychotria* fruiting season. During the breeding season (February to July), manakins are sedentary and gather in leks (Foster 1977, Krijger *et al.* 1997, Worthington 1982) where seeds are often dropped under single display perches to the point of attracting seed predators (Krijger *et al.* 1997, Stiles *et al.* 1989). From August to December, adult and first-year individuals spend more time foraging and move longer distances to find fruit (Worthington 1982).

Catharus thrushes are transitory Nearctic migrants common during autumn

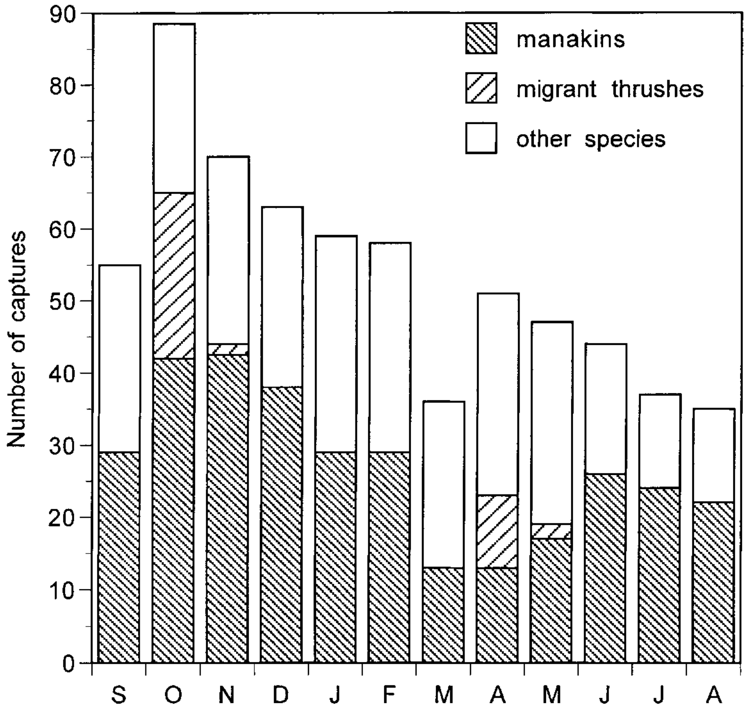

Figure 5. Monthly variation in the numbers of frugivorous birds mist-netted in Soberanía National Park.

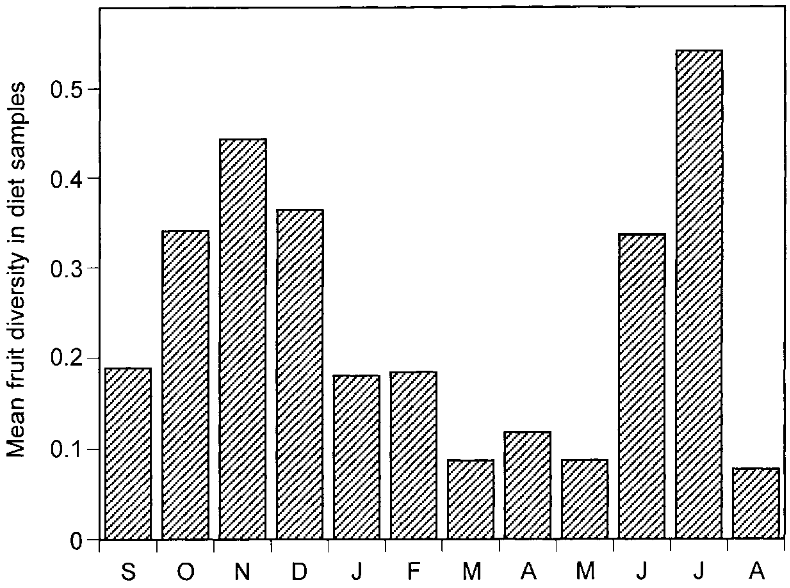

Figure 6. Monthly variation in the mean diversity (H) of fruit in diet samples of frugivorous birds mist-netted in Soberanía National Park.

migration in Panama (Martin 1985, Ridgely & Gwynne 1989). At our study site, 74% (32/43) of the regurgitations collected in October and November contained fruits, with an average of 1.5 *Psychotria*/sample. Recapture data suggest that these birds spend only a few days at our study site (Poulin & Lefebvre 1996). Although frugivory by these species is limited to a short period, it may have important consequences for seed dispersal because migrating birds exhibit a higher degree of transience than wintering individuals (Blake & Loiselle 1992).

Dispersal agents could respond to aggregated fruiting patterns by specializing on different fruit species. Examination of diet samples, however, suggests that birds feed on a greater diversity of fruit when more fruit species become available, such as during the *Psychotria* fruiting season.

Long-term advantages of producing fruits sequentially or synchronously among congeneric plants will probably depend on the individual and species' relative contribution to total fruit availability in relation to the foraging behaviour and abundance of frugivores. Understorey shrubs bearing small fruit crops such as most *Psychotria* will benefit more from an aggregated fruiting pattern than species with large fruit crop, especially if fruits are produced during periods of high nomadism and abundance of frugivores (Sargent 1990, Stapanian 1982). In contrast, segregated fruiting will be most beneficial to plants producing large fruit crops that are taken by sedentary dispersers, especially those exhibiting territoriality (Stapanian 1982).

Dispersal agents are not the only selective force acting on plant phenology, and aggregated fruiting in *Psychotria* could simply result from a common physiological response of closely related species to similar environmental conditions. However, because *Psychotria* spp. are asynchronous in both their flowering (Croat 1978) and seed germination patterns (Gardwood 1983), it is tempting to hypothesize that the temporary high abundance and nomadism of avian dispersers in the late wet season may have selected for aggregated fruiting of *Psychotria* at that period.

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