

TEMPORAL DYNAMICS OF NEOTROPICAL BIRDS WITH SPECIAL REFERENCE TO FRUGIVORES IN SECOND-GROWTH WOODS

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ABSTRACT.—Birds were mist-netted and banded in a second-growth woodland in central Panama to examine temporal dynamics of capture rates and to examine if these dynamics reflected presence or absence of transient birds. Capture rates of frugivores fluctuated much more than insectivores; nectarivores were intermediate in their fluctuations. Consequently, insectivores were recaptured more frequently than frugivores, indicating greater spatial stability. Species within a guild differed in their recapture frequencies, but unstable species with low recapture frequencies were most often frugivores; stable species with high recapture frequencies generally were insectivores. Migrants exhibited the same patterns as nonmigrants of the same guild. Examination of two common nonmigrant frugivore species showed that fluctuations in capture rates were due mostly to movements by transient immatures or females. Capture rates of nonmigrant frugivores declined markedly during late March. The decline may be due to movements in response to an influx of migrants during spring migration, habitat switching, or microclimatic conditions. This study provides evidence that some tropical birds are highly dynamic and that such dynamics reflect transience in addition to other population processes. *Received 26 Apr. 1985, accepted 28 Aug. 1985.*

Evidence is accumulating that local abundances of a wide variety of tropical organisms, including plants (Hartshorn 1978, Brokaw 1982, Garwood 1983), insects (Janzen 1973; Willis 1976; Wolda 1977, 1978, 1980; Tanaka and Tanaka 1982), frogs (Toft 1980), and lizards (Sexton 1967, Sexton et al. 1971, Ruibal and Philibosian 1974, Schoener and Schoener 1980) vary markedly over time. Abundances of tropical forest birds also are temporally variable (Karr 1976a, 1981a, Karr et al. 1982, Faaborg 1982, Karr and Freemark 1983, Faaborg et al. 1984). Moreover, temporal variance may be greater for birds in young second-growth woods than in older forest and greater for tropical birds that rely on variable food types (Karr 1976a). With the exception of Karr (1976a), studies of tropical bird dynamics have focused on birds in older forests. Yet, young forest is an increasingly common habitat in the neotropics (Myers 1979, 1981). As many species of migrant birds from North America often concentrate in young forest, especially during migration (Willis 1966, Karr 1976b, Chipley 1977, Hutto 1980, Johnson 1980, Martin 1985a), young forest provides an opportunity to compare population fluctuations of both migrants and nonmigrants.

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Temporal variance in abundances can be caused by population recruitment and mortality. Short-term (e.g., <3 months) fluctuations in abundances, however, can be caused by movement of individuals into or out of a locality. Movements by individuals are thought to be an important cause of the variance in tropical bird abundances (e.g., Karr and Freemark 1983), but no one has tested directly whether fluctuations in bird abundances actually reflect occurrence of transients in a locality. A direct test can be made by banding birds and examining frequencies of recaptures; residents have a higher probability of recapture than transients. Consequently, if short-term fluctuations in abundances are caused by movement of transients, then recapture frequencies should be lower for those groups of birds that exhibit greater variation in abundances. Second, increases in abundances should be associated with greater numbers of transients and especially during seasonal periods when recruitment can not be a cause of population increase. Third, if fluctuations in abundances reflect movements due to variability of food resources, then birds that rely on more variable food types should show greater fluctuations in abundances and lower recapture frequencies. Furthermore, this prediction should hold for both migrants and nonmigrants with the same food habits.

We examined these predictions based on a study of birds in a young second-growth forest in Panama during which we captured over 1500 birds in nearly 6000 mist-net h. Variations in capture rates are compared among groups of birds of similar food habits (i.e., frugivores, insectivores, nectarivores) to examine dynamics as a function of resources. We emphasized frugivores because they represented the dominant portions of both migrant and nonmigrant populations. We compared recapture frequencies of banded birds to provide a direct test of whether variable capture rates reflect movements of birds. In addition, we examined recapture frequencies and capture rates of the transient and resident portions of the populations of the two most common nonmigrant species to determine if variation in capture rates reflected occurrence of transients.

METHODS

Bird sampling.—We used mist nets (12-m long, 4 shelves, 30-mm mesh) to sample birds within a 4.5-ha second-growth woodland in Parque Nacional Soberania, Panama. Abundances of birds were indexed based on capture rates (numbers of birds captured per 100 mist-net h). Relative abundances of birds represented in samples of standard number of captures were not used; relative abundances are dependent on representation of other birds in the sample and transients may be overrepresented (Van Remsen and Parker 1983). Capture rates are independent of the representation of other birds in the sample and, thus, more accurately reflect changes in actual abundances.

Birds were netted during the early (January) and late (March) dry seasons of 1980 and 1981. We used two lines of mist nets in 1980. One line included 6 nets and was operated

from 7 to 14 and from 20 to 23 January and from 16 to 27 March. A second line, approximately 30 m away, included 7 nets and was operated from 16 to 23 January and from 19 to 27 March. Both lines were operated from 9 to 22 January and 18 to 28 March 1981. Two additional lines, with 9 and 8 nets each, were operated from 23 January to 3 February and from 6 to 12 March 1981. Nets usually were operated from 06:15 to 17:30 h, when weather permitted, and checked every hour. Capture rates were calculated from the first 6 days of each netting period to standardize length of time each net was operated. Nets generally were operated longer than 6 days, however, to increase the number of captured and banded birds.

Paired net lines were operated in each sampling period as a check on adequacy of sample size. Temporal patterns should be the same for both lines of a pair if netting provides a reliable sample. As chi-square analyses showed no significant differences in species numbers or abundances between lines within a pair, data from paired lines were pooled. Two lines were added in 1981 to obtain additional data for different portions of the dry season (a later stage of early dry season and an earlier stage of the late dry season-premigration). New net lines were established because capture rates decline over time (Terborgh and Weske 1969, Karr 1979) and use of the same sites in late and early January could bias results.

All captured birds were banded with a numbered aluminum band except hummingbirds. For hummingbirds, we clipped the first primary to allow determination of recaptures within a sample period. Recaptures between sample periods could not be determined due to intervening molts.

Each net line was operated until at least 100 different individuals were captured during each sampling period. Birds recaptured during a single sampling period were not considered to be different individuals. Recaptures from previous periods were included in the 100-bird totals. Overall, 1518 birds were captured in 5994 net h.

We classified bird species into food habits groups based on Karr (1971), Wetmore (1965, 1968, 1972), and personal observations. Species that changed food habits, such as migrants, were classified based on the food category that constituted the major portion of their diet during the period they were present on the area. Comparisons of abundances or species richness among samples are based on Chi-square or Fisher's Exact Probability tests. Comparisons were made using the number of individuals or species captured and corrected by the sample effort (mist-net h).

Vegetation.—Vegetation was sampled using the point sampling method of Karr (1971). Points were sampled along two transects that ran parallel to each mist net; one transect was on each side and about 2 m from each net. Each transect included 20 points. Vegetation on lines 1 and 2 was similar (Fig. 1) with the canopy peaking mostly at 5 m, but with a few emergent *Didymopanax morototoni*. Vegetation was taller along lines 3 and 4 with the canopy peaking mostly at 7.5–10 m. Nevertheless, the vegetation was remarkably similar on each plot; below 5 m, foliage densities were similar for all lines.

Weather.—January through March are the driest months of the year in central Panama (Croat 1978). Total rainfall for these three months is generally around 11.4 cm (Table 1). The dry season (January–March) of 1980 was slightly wetter than average and the dry season of 1981 was much wetter than average, due especially to record rainfall in January; March also was slightly wetter than normal (Table 1).

RESULTS

Numbers of species.—We captured a total of 76 species in 1980 (52 species in January; 60 species in March) and 84 species in 1981 (57 in January; 69 in March). The two annual samples totaled 101 species. We

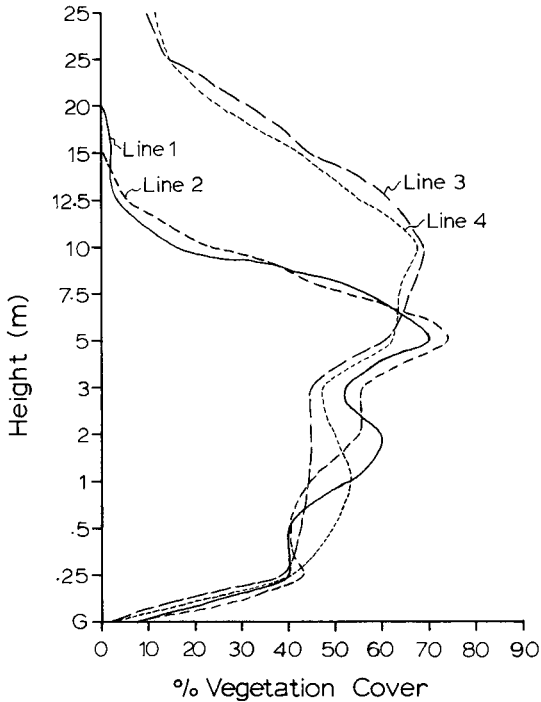


FIG. 1. Foliage profiles for the four net lines based on percent vegetation cover at increasing heights.

observed 136 species on the study area, overall, and considered 96 to be regular dry-season residents based on capture or observation of individuals in at least 3 periods of the study (Appendix 1). Additional species were not captured because their activities were restricted to the canopy. A higher ($P < 0.01$) percentage of species and individuals were migrants in late March than in January of both years (Fig. 2) due to spring migration.

Early January vs late March.—Capture rates of nonmigrant, migrant, and total insectivores did not change ($P > 0.10$) from January to late March in either year (Fig. 3). Nectarivores increased in March in 1980 ($P < 0.10$) and 1981 ($P < 0.01$). Nonmigrant frugivores decreased ($P < 0.001$) while migrants increased ($P < 0.001$), resulting in no difference ($P > 0.10$) in capture rate of all frugivores between months.

Late January vs early March.—Capture rates of migrant and nonmigrant insectivores did not change ($P > 0.10$) from late January to early March (Fig. 3). Nectarivores showed an increasing trend, but the increase was not significant ($P > 0.10$). Nonmigrant frugivores increased ($P <$

TABLE 1
MEAN RAINFALL (CM) FOR THE THREE DRY SEASON MONTHS FOR 1924–1962 (FROM CROAT 1978), 1964–1980 (FROM PANAMA CANAL COMMISSION CLIMATOLOGICAL CENTER), AND FOR THE TWO YEARS OF THIS STUDY

	January	February	March
1924–1962	5.6	3.3	3.1
1964–1980	6.4	2.5	2.5
1980	11.9 ^a	4.8 ^c	0.5 ^b
1981	39.9 ^c	2.0	6.1 ^c

^a Rainfall significantly different ($P < 0.05$) from the 1964–1980 mean.

^b Rainfall significantly different ($P < 0.01$) from the 1964–1980 mean.

^c Rainfall significantly different ($P < 0.001$) from the 1964–1980 mean.

0.05) from late January to early March. In fact, capture rates of nonmigrant frugivores were greater in early March than in early January ($P < 0.001$), late January ($P < 0.05$) or late March ($P < 0.001$) due to an increase from January through early March and a subsequent decline in the latter half of March (Fig. 3).

Between-years.—Capture rates of nonmigrant insectivores were less ($P < 0.05$) in 1981 than in 1980 in both months (Fig. 3). Nectarivores did not differ between years ($P > 0.10$) in either month, while capture rates of frugivores were markedly less ($P < 0.001$) in both months of 1981 than in 1980 for migrants and nonmigrants. In summary, frugivores exhibited greater within-season and between-year shifts in capture rates than other guilds.

Influence of common species.—Changes in importance of guilds were due, in part, to shifts in capture rates of the most common community members (Appendix 1). The frugivorous Red-capped Manakin, Golden-collared Manakin, and Ochre-bellied Flycatcher (scientific names are provided in Appendix 1) had the highest capture rates in January of both years and early March 1981. Capture rates of all three frugivores declined significantly in late March of both years (Table 2). They were replaced by Long-tailed Hermit, Swainson's Thrush, and Tennessee Warbler as the most abundant species (Table 2).

The increase in Swainson's Thrush and Tennessee Warbler reflected the increase in migrant frugivores in late March (Fig. 3). Capture rates of the three nonmigrant frugivore species did not reflect capture rates of all (migrant and nonmigrant) frugivores (Fig. 4) because these three species decreased in late March when the influx of migrants kept total frugivore capture rates constant (see above). Capture rates of each of these three frugivore species showed the same temporal trend as all nonmigrant fru-

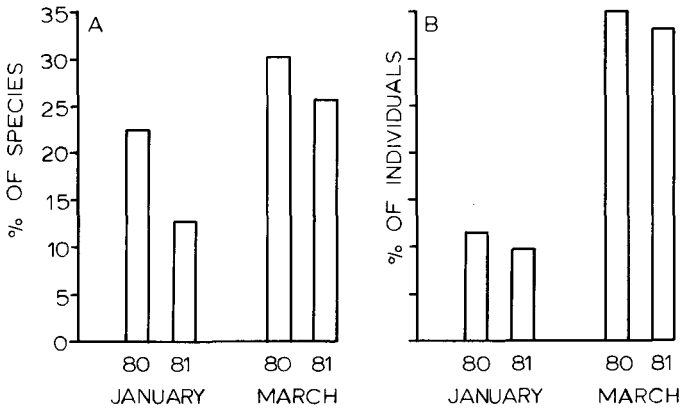


FIG. 2. Percent of species (A) and individuals (B) that were migrants in 200-bird samples in January and March of 1980 and 1981.

givores, increasing from January through early March, and decreasing in late March (Table 3) (Fig. 4). Furthermore, the decrease in nonmigrant frugivores in late March was not due simply to the three dominant species; abundances of all other nonmigrant frugivores also declined from January to late March (Table 2).

The increase in Long-tailed Hermits apparently was the primary cause

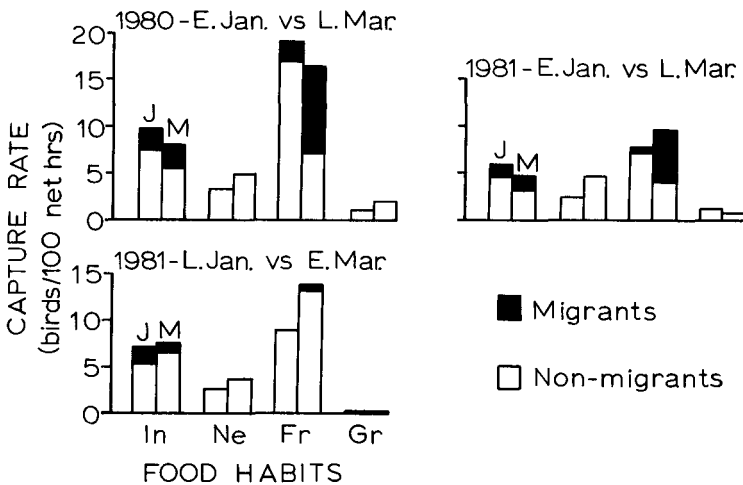


FIG. 3. Changes in capture rates of guilds in 200-bird samples from early January to late March (mist-net lines 1 and 2) in 1980 and 1981 and from late January and early March (mist-net lines 3 and 4) in 1981. Guilds include insectivores (In), nectarivores (Ne), frugivores (Fr), and granivores (Gr).

TABLE 2

CHANGES IN NUMBERS OF INDIVIDUALS CAPTURED FOR THE MOST COMMON SPECIES AND FOR NONMIGRANT FRUGIVORES AND NECTARIVORES WHEN THESE COMMON SPECIES ARE SUBTRACTED FROM 200-BIRD SAMPLES FROM JANUARY TO LATE MARCH OF 1980 AND 1981

	1980		1981	
	January	March	January	March
Red-capped Manakin	25	15 ^a	27	7 ^c
Golden-collared Manakin	38	17 ^c	23	14 ^a
Ochre-bellied Flycatcher	22	6 ^c	10	6
Long-tailed Hermit	2	9 ^a	10	24 ^b
Swainson's Thrush	1	8 ^b	3	18 ^c
Tennessee Warbler	—	23 ^c	—	24 ^c
Other nonmigrant frugivores	18	9 ^a	29	19 ^a
Other nectarivores	18	22	20	20

^a Significantly different ($P < 0.05$) using a binomial probability test and correcting for differences in numbers of net h.

^b Significantly different ($P < 0.01$) using a binomial probability test and correcting for differences in numbers of net h.

^c Significantly different ($P < 0.001$) using a binomial probability test and correcting for differences in numbers of net h.

of the increase in nectarivores; abundances of the other nectarivores changed little between months (Table 2). Finally, insectivore abundances were not influenced by any dominant species; no insectivore species contributed more than 6 individuals to any 200-bird sample (Appendix 1).

Spatial constancy.—If shifts in capture rates reflect transience, then insectivores should have higher recapture frequencies than frugivores because of the greater temporal variance of frugivores (see above). Recaptures between months and years were higher for insectivores than for frugivores (Fig. 5). Moreover, these trends hold when individual species are examined; more ($P < 0.013$) insectivore species (13 of 16) had recapture frequencies of 40% or greater between months than frugivore species (2 of 12) (Table 4). Also, more ($P = 0.039$) insectivore species (11 of 14) had recapture frequencies of 40% or greater between years than frugivore species (3 of 12). The low recapture frequency of frugivores suggests transience. Presence of transients was examined for the two manakin species.

Golden-collared Manakin.—A total of 164 Golden-collared Manakins was captured during this study (Table 5). Recapture rates between months and years were much higher for adult males than for immatures or females (IOFs) (Table 5). Also, a higher percentage of captures within a month were recaptures from previous months for males than for IOFs. All adult males that were banded in 1980 and recaptured in 1981 were recaptured on the same lines where originally banded. New lines were established in late January 1981, and any recaptures during this period are individuals

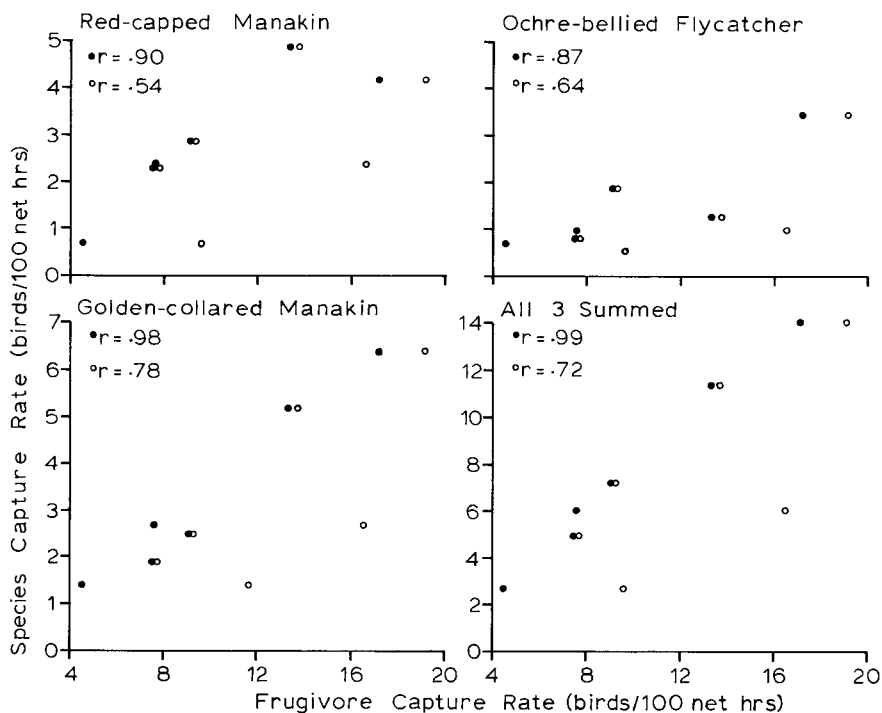


FIG. 4. Capture rate of the three most common frugivore species and the summed capture rate of all three species relative to the capture rate of all (migrants plus nonmigrants; open circles) and nonmigrant frugivores only (closed circles) for 200-bird samples. All comparisons with nonmigrant frugivores were significant and all comparisons with all frugivores were not significant.

that moved from the area of the original lines. Many IOFs, but no males, were recaptured on these new lines in late January (Table 5). This trend does not reflect net avoidance by IOFs because many (42%) IOFs were recaptured on these same lines in early March (Table 5). In general, however, IOFs had low recaptures. Thus, IOFs were much more transient than adult males.

The frequency of IOF Golden-collared Manakins (Table 5) tended to increase ($r = 0.83$, $P < 0.10$) with capture rates (Table 3) indicating that increased capture rates were the result of influxes of transient IOFs. Clearly, the increased capture rate in early March 1981 was due to influx of IOFs; 93% of the adult males captured in early March were recaptures, while only 42% of the IOFs were recaptures and 93% of the new (unbanded) individuals were IOFs (Table 5).

Finally, capture rates of adult males and IOFs showed males were less

TABLE 3
CAPTURE RATES (BIRDS/100 NET H) OF THE THREE MOST ABUNDANT FRUGIVORES

	1980		1981			
	Early January	Late March	Early January	Late January	Early March	Late March
Red-capped Manakin	4.2	2.4	2.3	2.9	4.9	0.7
Golden-collared Manakin	6.4	2.7	1.9	2.5	5.2	1.4
Ochre-bellied Flycatcher	3.5	1.0	0.8	1.9	1.3	0.6

transient than IOFs and that increased capture rates were due to the influx of IOFs. Capture rates for adult males in January 1980 (1.0 birds/100 net h), January 1981 (0.9) and early March 1981 (1.7) varied little. Capture rates for IOFs in January 1980 (5.4), January 1981 (1.0), and early March 1981 (3.5), however, varied by half an order of magnitude and paralleled changes in the overall capture rates of Golden-collared Manakins (Table 3).

Red-capped Manakin. — A total of 165 Red-capped Manakins was captured. Frequency of IOF Red-capped Manakins (Table 5) also increased ($r = 0.93$, $P < 0.01$) with capture rates (Table 3). Captures were generally skewed towards IOFs during all periods except early January 1981. The

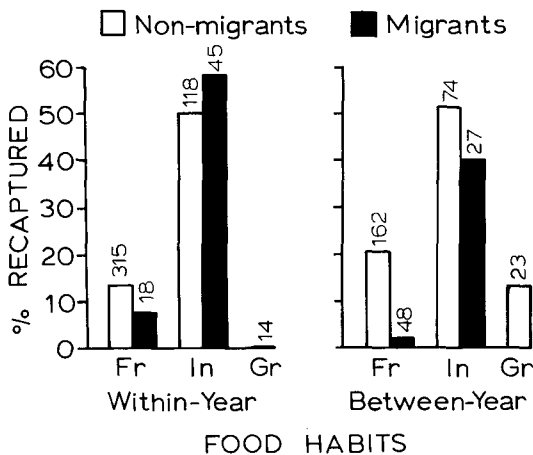


FIG. 5. Percent of individuals that were banded in January and recaptured in March (within-year) and banded in 1980 and recaptured in 1981 (between-year) for three guilds. Within-year recapture rates represent the average of 1980 and 1981. Numbers indicate the number of individuals originally banded. Guilds include frugivores (Fr), insectivores (In), and granivores (Gr).

TABLE 4
 PERCENTAGE OF BANDED INDIVIDUALS (NUMBER BANDED) THAT WERE RECAPTURED
 BETWEEN MONTHS WITHIN A YEAR FOR BOTH YEARS AND THE PERCENTAGE RECAPTURED
 BETWEEN YEARS

	Within years	Between years
Insectivores		
Gray-headed Tanager	0 (5)	40 (5)
Plain-brown Woodcreeper	0 (6)	50 (2)
Spotted Antbird	18 (11)	33 (3)
Northern Royal Flycatcher	40 (10)	100 (5)
Plain Xenops	42 (12)	40 (10)
Slaty Antshrike	42 (12)	38 (13)
Chestnut-sided Warbler	43 (7)	25 (4)
Ovenbird	44 (9)	50 (10)
Southern Bentbill	46 (13)	57 (7)
Checker-throated Antwren	50 (6)	—
White-flanked Antwren	50 (6)	—
Ruddy-tailed Flycatcher	50 (10)	50 (4)
Buff-throated Woodcreeper	73 (11)	60 (10)
Dusky Antbird	75 (16)	67 (15)
Kentucky Warbler	75 (24)	80 (10)
Magnolia Warbler	80 (5)	66 (3)
Frugivores		
Blue-crowned Manakin	0 (6)	50 (2)
Wood Thrush	0 (8)	13 (16)
Gray Catbird	0 (5)	0 (12)
Fulvous-vented Euphonia	0 (14)	0 (6)
Crimson-backed Tanager	0 (5)	50 (4)
Red-capped Manakin	9 (99)	6 (51)
Ochre-bellied Flycatcher	14 (66)	27 (26)
Swainson's Thrush	20 (5)	0 (21)
Red-throated Ant-tanager	27 (22)	50 (14)
Blue-black Grosbeak	33 (6)	0 (3)
Thrush-like Manakin	43 (7)	33 (3)
Golden-collared Manakin	46 (90)	38 (53)

increased incidence of males in January 1981 can be attributed to the reduced abundance of IOFs rather than to an actual increase in males. No Red-capped Manakin lek was present on our study area, and both males and IOFs were transient; few individuals of either class were recaptured (Table 5). The number of transient males, however, was low and did not vary with the overall capture rates of Red-capped Manakins (capture rates of adult males were 0.4, 0.9, 0.3 birds/100 net h for January 1980, January 1981, and early March 1981, respectively). On the other hand, presence

TABLE 5
NUMBER OF GOLDEN-COLLARED AND RED-CAPPED MANAKINS CAPTURED IN EACH NETTING PERIOD, PERCENT OF CAPTURES THAT WERE RECAPTURES, PERCENT OF JANUARY-BANDED BIRDS THAT WERE RECAPTURED IN MARCH, AND THE PERCENT OF BIRDS BANDED IN 1980 THAT WERE RECAPTURED IN 1981

	January						March						
	Early			Late			Early			Late			
	IOF ^a	Males		IOF	Males		IOF	Males		IOF	Males		
Golden-collared Manakins													
Number captured	33/11 ^b	7/7	-/18	-/18	-/14	-/15	-/26	-/15	-/10	18/10	3/2		
% captures that were recaptures	-/18	-/71	-/22	-/42	-/0	-/93	-/42	-/93	-/0	28/30	100/100		
% January recaptures										15/22	43/76		
% 1980 recaptures										33	71		
Red-capped Manakins													
Number captured	30/14	3/17	-/26	-/37	-/10	-/3	-/24	-/0	-/10	18/7	0/0		
% captures that were recaptures	-/0	-/0	-/4	-/24	-/0	-/0	-/24	-/0	-/0	0/14	0/0		
% January recaptures										0/6	0/0		
% 1980 recaptures										6	0		

^a Immature or female.

^b 1980/1981.

of IOFs was variable (capture rates of 3.8, 1.4, and 4.6 birds/100 net h in January 1980, January 1981, and early March 1981, respectively), paralleling changes in overall capture rates of Red-capped Manakins (Tables 3, 5). Thus, variation in capture rates of Manakins reflected presence or absence of transient IOFs and, in general, mirrored variation in capture rates of nonmigrant frugivores (Fig. 4).

DISCUSSION

Transience and fluctuations in capture rates.—Guild patterns may not necessarily apply to all species within a guild; species within a guild may differ in their transience (e.g., see Table 4, also Faaborg et al. 1984). An analysis of individual species is inappropriate with the present data due to the rarity of most of the species. Analyses of guilds, however, as performed here, identify central guild tendencies in spatial stability that provide a basis for more specific tests of individual species in future studies.

Insect foods are thought to be less patchy in space and time than nectar or fruits (Karr 1976a), so that spatial stability (territoriality) is most profitable for insectivores (Horn 1968). Indeed, insectivores exhibited the greatest recapture rates (Fig. 5) (Table 4). Spatial stability could not be directly analyzed for nectarivores because they were not banded.

Frugivores were the most variable of the guilds, and they provided evidence that such variability can be due, in part, to movements. The increase in frugivores during 1981 could not have been due to recruitment because the sampling periods were prior to the main nesting season and after the period of juvenile dispersal of manakins (Worthington 1982). Moreover, the decline in frugivores in late March was too rapid and too severe to represent mortality; frugivore capture rates in late March were only one-third of their capture rates in early March (Fig. 3). Finally, the manakins provided the clearest evidence that movements were an important influence on variation in capture rates. The results showed that IOF manakins tended to be highly transient, while adult males were stable spatially. These results follow from the fact that adult males retain courtship arenas, while females and immatures are not restricted to any particular site or individual during the nonbreeding season (Chapman 1935, Skutch 1949, Snow 1962a, b). The association between presence of transient IOF manakins and capture rates, plus the high frequency of recaptures between sets of lines document that movements by transients account in part for temporal changes in abundances of frugivores within a locality.

Such transience may reflect movements in response to lek locations or, alternatively, food availability. January 1981 was the wettest on record

(57 years of data); heavy rain in the early dry season delayed fruiting. In addition, the dry season of 1980 was wetter than average (Table 1), and a wet dry season tends to create fruit failure in the following year (Foster 1982). Capture rates of frugivores were indeed lower in January 1981 as compared to 1980. Even migrant frugivores such as Bay-breasted Warblers, Gray Catbirds, and Wood Thrushes that were commonly seen and netted in January 1980 were not seen or captured in January 1981 (Appendix 1). This decrease in January 1981 can not simply reflect mortality because abundances increased during the dry season in 1981 to the point where capture rates in early March 1981 equalled capture rates in January of 1980 (Fig. 3). In short, variable capture rates can be due to movement in addition to the normal population processes of recruitment and mortality.

Decline in frugivores in late March.—One possible explanation for the decrease in frugivore captures on our young forest site in late March is sampling artifact; birds may simply learn (from being captured in January) to avoid nets in March (Terborgh and Weske 1969; Karr 1977, 1979, 1981b). Several lines of evidence, however, argue against this possibility. First, capture rates of the three most common frugivore species in nearby old forest, which included Red-capped Manakins and Ochre-bellied Flycatchers, increased in late March relative to January (J. R. Karr, unpubl. data). Second, mist-net lines that were operated in late January and early March provided less time between sampling periods for birds to “forget” net locations than on the lines operated in early January and late March. Yet, capture rates of frugivores increased in early March relative to late January, while capture rates declined in late March of both years. Moreover, recapture rates of both manakin species were very high in early March (Table 5), which also indicates a lack of net avoidance. Third, all guilds did not show a decline from January to late March; nectarivores and insectivores increased or remained stable in both years. It is unlikely that frugivores decreased simply because frugivores were better at avoiding nets than the other groups. Fourth, birds did not move above net level in late March. The canopy was only 5 m high on the lines sampled in late March (Fig. 1), so birds had little space to move above nets. Furthermore, nonmigrant abundance at canopy fruits was extremely low in late March (Martin 1982, 1985a). Thus, net avoidance did not cause the seasonal patterns and the decrease in frugivores in late March.

The decrease in nonmigrant frugivores in late March could have been influenced by the influx of migrating frugivores; nonmigrants decreased in both years at a time when migrants appeared in large numbers and food was increasing (Smythe 1970, Croat 1978). Food sources of nectarivores also increase in the late dry season (Croat 1978), and nectarivores, which include few to no migrants, did not decrease in late March.

Alternatively, the temporal dynamics may reflect differential availability of food in different habitats. Frugivores should select and switch among habitats and patches as a function of fruit quality and abundance relative to other environmental influences such as predation risk or competition (Martin 1985b, Martin and Karr 1986). Bird-dispersed fruit plants are denser in young than old forest (Martin 1985a, unpubl. data) and fruit abundance appears to be lowest in December through February in older forest (Foster 1973, 1980, 1982). Some old forest frugivores may switch to young forest during this period and then switch back to old forest in the late dry season when fruits become more abundant. The increase in capture rates of Red-capped Manakins and Ochre-bellied Flycatchers in old forest in late March (J. R. Karr, unpubl. data) when they decline in young forest suggests possible habitat switching.

Some frugivores may move to our site from wetter or drier areas during the dry season; a marked moisture gradient exists over a short distance across the Isthmus of Panama (Rand and Rand 1982), and Karr and Freemark (1983) have provided evidence for the importance of macro- and microclimate for bird movements. The actual answer may lie in some combination of all these factors. Whatever the reason, transients apparently form a significant component of tropical bird communities, and the basis for their movements and their impact on residents needs investigation if we are ever to preserve the necessary habitats to sustain their populations.

ACKNOWLEDGMENTS

G. O. Batzli, J. G. Blake, N. Burley, G. W. Cox, J. Faaborg, L. L. Getz, J. R. Holomuzki, S. K. Robinson, and M. F. Willson provided helpful comments on earlier drafts of this paper. We thank The Smithsonian Tropical Research Institute for logistical support and the following agencies for financial support: Sigma Xi, Chapman Fund (American Museum of Natural History), Stewart Award (Wilson Ornithological Society), Wildlife Management Institute, Center for Field Research/Earthwatch, and the University of Illinois Research Board.

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APPENDIX 1
BIRD SPECIES CAPTURED IN 200-BIRD SAMPLES OR DETECTED IN A SECOND-GROWTH WOODLAND IN PANAMA

	1980			1981		
	Early Jan.	Late Mar.	Early Jan.	Late Jan.	Early Mar.	Late Mar.
Little Tinamou (<i>Crypturellus soui</i>) (G) ^a	+ ^b	1	+	+	+	1
Broad-winged Hawk (<i>Buteo platypterus</i>) ^c	-	+	-	-	-	1
Collared Forest-Falcon (<i>Microstur semitorquatus</i>)	-	+	-	-	-	-
Gray-headed Chachalaca (<i>Ortalis cinereiceps</i>)	+	+	+	+	+	+
Scalded Pigeon (<i>Columba speciosa</i>)	-	-	-	+	+	-
Blue Ground-Dove (<i>Claravis pretiosa</i>) (F)	-	3	+	+	+	1
White-tipped Dove (<i>Leptotila verreauxi</i>)	-	+	-	-	-	+
Gray-chested Dove (<i>L. cassinii</i>) (F)	-	+	1	2	-	4
Orange-chinned Parakeet (<i>Brotogeris jugularis</i>)	+	-	+	+	-	-
Blue-headed Parrot (<i>Pionus menstruus</i>)	+	-	+	+	-	-
Red-lore Parrot (<i>Amazona autumnalis</i>)	+	+	+	-	-	-
Squirrel Cuckoo (<i>Piaya cayana</i>)	-	+	-	-	+	+
Pheasant Cuckoo (<i>Dromococcyx phasianellus</i>) (I)	-	1	-	+	+	1
Common Pauraque (<i>Nyctidromus albicollis</i>) (I)	-	1	+	+	+	+
Rufous-breasted Hermit (<i>Glaucidis hirsuta</i>) (N)	1	+	-	1	-	+
Long-tailed Hermit (<i>Phaethornis superciliosus</i>) (N)	2	9	10	9	10	24
Little Hermit (<i>P. longuemareus</i>) (N)	5	2	5	2	1	1
White-necked Jacobin (<i>Florisuga mellivora</i>) (N)	1	2	1	-	1	+
Violet-bellied Hummingbird (<i>Damophila julie</i>) (N)	8	9	3	9	4	5
Blue-chested Hummingbird (<i>Amazilia amabilis</i>) (N)	1	3	7	7	2	13
Snowy-bellied Hummingbird (<i>A. edward</i>) (N)	1	-	-	-	-	-
Rufous-tailed Hummingbird (<i>A. tzacatl</i>) (N)	1	6	4	+	2	1
White-vented Plumeleteer (<i>Chalybura buffonii</i>) (N)	-	-	-	+	2	-
White-tailed Trogon (<i>Trogon viridis</i>)	+	+	+	-	+	-
Violaceous Trogon (<i>T. violaceus</i>) (F)	+	-	1	+	-	-
Slaty-tailed Trogon (<i>T. massena</i>) (F)	-	-	1	+	-	-

APPENDIX 1
CONTINUED

	1980				1981			
	Early Jan.	Late Mar.	Early Jan.	Late Mar.	Early Jan.	Late Jan.	Early Mar.	Late Mar.
	Blue-crowned Motmot (<i>Momotus momota</i>) (F)	+	1	2	1	1	1	1
Rufous Motmot (<i>Baryphthengus ruficapillus</i>) (F)	-	-	-	-	-	-	1	-
American Pygmy Kingfisher (<i>Chloroceryle aenea</i>) (F)	-	1	-	-	-	-	-	-
White-necked Puffbird (<i>Bucco macrorhynchus</i>)	-	-	+	+	-	+	-	-
Collared Aracari (<i>Pteroglossus torquatus</i>) (F)	+	+	+	+	+	+	+	2
Keel-billed Toucan (<i>Rhamphastos sulfuratus</i>)	+	+	+	+	+	+	+	+
Black-cheeked Woodpecker (<i>Melanerpes pucherani</i>)	-	+	-	-	+	+	+	+
Lineated Woodpecker (<i>Dryocopus lineatus</i>)	-	+	-	-	+	+	+	+
Buff-throated Foilage-gleaner (<i>Automolus ochrolaemus</i>) (I)	-	-	2	1	+	+	-	-
Plain Xenops (<i>Xenops minutus</i>) (I)	3	3	2	3	4	4	3	3
Scaly-throated Leaf-tosser (<i>Sclerurus guatemalensis</i>) (I)	-	-	2	2	1	1	-	-
Plain-brown Woodcreeper (<i>Dendrocincla fuliginosa</i>) (I)	2	-	1	3	-	-	-	1
Ruddy Woodcreeper (<i>D. homochroa</i>) (I)	-	-	1	-	-	-	-	-
Wedge-billed Woodcreeper (<i>Glyphorhynchus spirurus</i>) (I)	-	-	1	+	-	-	-	-
Buff-throated Woodcreeper (<i>Xiphorhynchus guttatus</i>) (I)	3	5	2	6	2	2	1	1
Fasciated Antshrike (<i>Cymbilaimus lineatus</i>) (I)	-	1	-	-	+	+	+	+
Slaty Antshrike (<i>Thamnophilus punctatus</i>) (I)	6	4	6	6	4	4	6	6
Checker-throated Antwren (<i>Myrmotherula fulviventris</i>) (I)	-	1	2	4	2	2	+	+
White-flanked Antwren (<i>M. axillaris</i>) (I)	-	+	5	-	4	4	+	+
Dot-winged Antwren (<i>Microrhopias quixensis</i>)	-	+	+	-	+	+	-	-
Dusky Antbird (<i>Cercomacra tyrannina</i>) (I)	4	6	5	2	3	3	4	4
White-bellied Antbird (<i>Myrmeciza longipes</i>) (I)	-	1	-	1	-	-	-	-
Chestnut-backed Antbird (<i>M. exsul</i>)	-	-	-	-	-	+	-	-
Spotted Antbird (<i>Hylophylax naevioides</i>) (I)	3	-	3	6	6	6	2	2
Bicolored Antbird (<i>Gymnopithys leucaspis</i>) (I)	-	+	3	3	2	2	+	+
Ocellated Antbird (<i>Phaenostictus mcleannani</i>) (I)	1	-	+	1	1	2	2	2

APPENDIX I
CONTINUED

	1980			1981		
	Early Jan.	Late Mar.	Early Jan.	Late Jan.	Early Mar.	Late Mar.
Black-faced Antthrush (<i>Formicarius analis</i>) (I)	-	-	+	1	+	-
Ochre-bellied Flycatcher (<i>Mionectes oleagineus</i>) (F)	22	6	10	20	11	6
Southern Bentbill (<i>Oncostoma olivaceum</i>) (I)	5	5	2	6	5	4
Brownish Flycatcher (<i>Cnipodectes subbrunneus</i>) (I)	-	-	1	3	1	1
Olivaceous Flatbill (<i>Rhynchocyclops olivaceus</i>) (I)	-	-	-	3	-	-
Golden-crowned Spadebill (<i>Platyrinchus coronatus</i>) (I)	-	1	-	-	3	+
Northern Royal Flycatcher (<i>Onychorhynchus mexicanus</i>) (I)	3	1	2	3	+	2
Ruddy-tailed Flycatcher (<i>Terentotriccus erythrorus</i>) (I)	5	1	4	2	3	1
Black-tailed Flycatcher (<i>Myiobius atricaudus</i>) (I)	1	2	-	-	+	-
Acadian Flycatcher (<i>Empidonax virescens</i>) [†] (I)	1	2	1	2	-	1
Willow Flycatcher (<i>E. traillii</i>) [†] (I)	-	2	-	-	-	-
Bright-rumped Attila (<i>Attila spadiceus</i>) (F)	-	-	1	3	1	+
Speckled Mourner (<i>Laniocera rufescens</i>) (F)	+	-	-	-	1	-
Rufous Mourner (<i>Rhytipterna holerythra</i>)	-	+	-	-	-	-
Dusky-capped Flycatcher (<i>Myiarchus tuberculifer</i>) (I)	+	3	-	-	1	3
Panama Flycatcher (<i>M. panamensis</i>) (F)	1	1	+	+	+	1
Great Crested Flycatcher (<i>M. crinitus</i>) [†] (F)	-	1	+	+	+	1
Boat-billed Flycatcher (<i>Megarhynchus pitangua</i>)	+	-	+	+	-	+
Social Flycatcher (<i>Myiozetetes similis</i>)	+	-	+	+	+	+
Streaked Flycatcher (<i>Myiodynamastes maculatus</i>)	+	+	+	+	+	+
Tropical Kingbird (<i>Tyrannus melancholicus</i>)	-	+	-	+	+	+
Eastern Kingbird (<i>T. tyrannus</i>) [†] (F)	-	1	-	+	+	+
Masked Tityra (<i>Tityra semifasciata</i>)	-	-	-	+	+	-
Black-crowned Tityra (<i>T. inquisitor</i>)	-	+	-	+	+	-
Blue Cotinga (<i>Cotinga nattererii</i>)	+	+	+	+	+	+
Purple-throated Fruitcrow (<i>Querula purpurata</i>)	-	+	-	+	+	-

APPENDIX 1
CONTINUED

	1980			1981		
	Early Jan.	Late Mar.	Early Mar.	Late Jan.	Early Mar.	Late Mar.
Thrushlike Manakin (<i>Schiffornis turdinus</i>) (F)	3	1	2	4	3	6
Golden-collared Manakin (<i>Manacus vittellinus</i>) (F)	38	17	23	26	43	14
Blue-crowned Manakin (<i>Pipra coronata</i>) (F)	1	-	3	2	2	-
Red-capped Manakin (<i>P. mentalis</i>) (F)	25	15	27	30	41	7
Black-bellied Wren (<i>Thryothorus fasciatoventris</i>) (I)	-	-	-	-	1	-
Bay Wren (<i>T. nigricapillus</i>) (I)	1	-	+	-	3	1
Plain Wren (<i>T. modestus</i>) (I)	-	-	1	-	-	-
White-breasted Wood-Wren (<i>Henichorina leucosticta</i>) (I)	2	-	-	1	1	-
Song Wren (<i>Cyphorhinus phaeocephalus</i>) (I)	2	-	3	3	2	1
Long-billed Gnatwren (<i>Ramphocaenus melanurus</i>) (I)	1	-	-	1	-	-
Tropical Gnatcatcher (<i>Poliopitila plumbea</i>)	+	-	-	+	-	-
Swainson's Thrush (<i>Catharus ustulatus</i>) ^c (F)	1	8	3	-	1	18
Wood Thrush (<i>Hylocichla mustelina</i>) ^c (F)	3	8	-	1	1	4
Clay-colored Robin (<i>Turdus grayi</i>) (F)	+	-	+	+	2	+
Gray Catbird (<i>Dumetella carolinensis</i>) ^c (F)	2	6	-	-	-	+
Yellow-throated Vireo (<i>Vireo flavifrons</i>) ^c	-	+	-	-	-	+
Red-eyed Vireo (<i>V. olivaceus</i>) ^c	-	-	-	-	-	+
Yellow-green Vireo (<i>V. flavoviridis</i>)	-	-	-	-	+	-
Blue-winged Warbler (<i>Vermivora pinus</i>) ^c (I)	-	+	-	-	-	1
Golden-winged Warbler (<i>V. chrysoptera</i>) ^c	-	+	-	-	-	-
Tennessee Warbler (<i>V. peregrina</i>) ^c (F)	+	23	-	-	-	24

APPENDIX 1
CONTINUED

	1980			1981		
	Early Jan.	Late Mar.	Early Jan.	Late Jan.	Early Mar.	Late Mar.
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>) ^c (I)	+	3	3	2	+	2
Magnolia Warbler (<i>D. magna</i>) ^c (I)	3	1	2	1	1	+
Bay-breasted Warbler (<i>D. castanea</i>) ^c (F)	3	6	-	-	+	1
Black-and-white Warbler (<i>Mniotilta varia</i>) ^c (I)	-	2	-	-	-	-
Prothonotary Warbler (<i>Protonotaria citrea</i>) ^c (I)	-	+	-	-	-	1
Ovenbird (<i>Seiurus aurocapillus</i>) ^c (I)	4	5	2	1	-	2
Northern Waterthrush (<i>S. noveboracensis</i>) ^c (I)	-	-	-	1	-	-
Kentucky Warbler (<i>Oporornis formosus</i>) ^c (I)	5	4	6	9	4	6
Mourning Warbler (<i>O. philadelphia</i>) ^c (I)	-	1	+	-	-	-
Plain-colored Tanager (<i>Tangara inornata</i>)	+	+	+	+	+	+
Golden-masked Tanager (<i>T. larvata</i>)	+	+	-	+	+	-
Scarlet-thighed Tanager (<i>Dacnis venusta</i>)	-	-	-	+	+	-
Blue Dacnis (<i>D. cayana</i>) (N)	-	+	+	+	+	1
Green Honeycreeper (<i>Chlorophanes spiza</i>)	+	-	-	+	-	+
Red-legged Honeycreeper (<i>Cyanerpes cyaneus</i>) (N)	1	1	-	1	+	1
Fulvous-vented Euphonia (<i>Euphonia fulvica</i>) (F)	3	+	8	+	+	-
Blue-gray Tanager (<i>Thraupis episcopus</i>)	+	-	+	+	+	+
Gray-headed Tanager (<i>Eucometis penicillata</i>) (I)	3	+	-	1	1	3
White-shouldered Tanager (<i>Tachyphonus luctuosus</i>) (I)	+	-	1	+	-	3
White-lined Tanager (<i>T. rufus</i>)	-	+	-	-	-	-
Red-throated Ant-tanager (<i>Habia fuscicauda</i>) (F)	8	3	8	5	6	6

APPENDIX 1
CONTINUED

	1980			1981		
	Early Jan.	Late Mar.	Early Jan.	Late Jan.	Early Mar.	Late Mar.
Summer Tanager (<i>Piranga rubra</i>) ^c (F)	-	4	-	-	1	1
Crimson-backed Tanager (<i>Ramphocelus dimidiatus</i>) (F)	1	2	3	+	1	1
Yellow-rumped Tanager (<i>R. icteronotus</i>)	-	+	+	+	+	+
Streaked Saltator (<i>Saltator albicollis</i>) (F)	+	2	-	-	-	1
Buff-throated Saltator (<i>S. maximus</i>) (F)	-	1	2	+	1	1
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>) ^c (F)	-	1	-	-	-	3
Blue-black Grosbeak (<i>Cyanococcyza cyanooides</i>) (F)	2	1	3	1	4	+
Indigo Bunting (<i>Passerina cyanea</i>) ^c (F)	3	-	-	-	-	-
Black-striped Sparrow (<i>Arremonops conirostris</i>)	+	-	+	+	+	+
Blue-black Grassquit (<i>Volatinia jacarina</i>) (G)	-	1	-	-	-	-
Variable Seedeater (<i>Sporophila aurita</i>) (G)	3	4	7	-	1	+
Thick-billed Seed-Finch (<i>Oryzoborus junereus</i>) (G)	2	5	1	-	+	+
Yellow-backed Oriole (<i>Icterus chrysater</i>)	+	-	+	+	-	-
Northern Oriole (<i>I. galbula</i>) ^c	+	+	-	+	-	+
Scarlet-rumped Cacique (<i>Cacicus uropygialis</i>)	-	+	+	+	+	+
Chestnut-headed Oropendola (<i>Psarocolius wagleri</i>)	-	-	+	-	+	-

^a Guild designations: I = insectivore, F = frugivore, N = nectarivore, G = granivore, P = piscivore. Guild designations are provided only for species captured in 200-bird samples.

^b Number of captures, detection (+), or lack of detection (-).

^c Migrants from North America.