

TEMPORAL FEEDING PATTERNS OF
SOME TROPICAL FRUGIVORES

GAIL E. KANTAK

Differences in activity cycles among members of an animal community are generally thought to be less important than other differences as a means of sharing food and space (Schoener 1974a). Resource partitioning according to time is most common among groups of predators whose principal prey populations are active at different times of the day, resulting in the exploitation of different foods. For example, Pianka (1969) concluded that differences in activity time of two species of *Ctenotus* lizards were important in avoiding competition for food. In contrast, animals who feed on a food supply such as fruit, which is not replenished or replaced during the day, cannot reduce competition for food by feeding at different times. Once a fruit is removed, it is gone, and there is no apparent advantage for individuals to feed at different times. Nevertheless, I could find no data in the literature on feeding times of frugivores that could be used to test such hypotheses. The objectives of my study were to document the temporal feeding patterns of some tropical fruit-eating birds and examine the role of time in their feeding ecology.

STUDY SITE AND METHODS

I conducted field work from late May till early August 1975 near the Mayan ruins of Chicanná and Becán,

near the town of Xpujil in the state of Campeche, Mexico. The vegetation here is a diverse "semi-evergreen seasonal forest" (Beard 1955), with Leguminosae contributing 19.2% of the species in the flora, and most families contributing less than 1% (Shepherd 1975).

I watched birds for 320 h at 13 trees of five species: *Neea psychotrioides* (Nyctaginaceae), *Ficus padifolia* (Moraceae), *Ehretia tinifolia* (Boraginaceae), *Metopium browneii* (Anacardiaceae), and *Talista olivaeformis* (Sapindaceae). All the trees were in edges between forest and clearings, and no two trees were more than 2 km apart. Fruit size and color and other details on observational methods are given in Kantak (1979). Voucher specimens are on file at the University of Wisconsin Herbarium.

I recorded arrival and departure times of birds feeding in the fruit tree under study. I defined a "visit" as any period during which fruit was consumed or plucked and carried away by a bird. Observations at a given tree were made over a number of days but were scheduled so that each hour between approximately 05:30 and 18:00 was observed equally. Thus, the number of visits made by a bird species during each hour of the day could be tallied. Although the number of feeding visits may not reflect the actual amount of fruit consumed, it is nonetheless a baseline estimate of feeding activity, which is at the same time practical for use in large scale studies of frugivore communities (cf. Diamond and Terborgh 1967, Leck 1969, 1971, 1972, Snow and Snow 1971).

I compared the temporal patterns of visits to fruit trees by pairs of bird species with a chi-square test on the null hypothesis that the proportions of visits in each time period did not differ between bird species. In

TABLE 1. Total number of visits and percentage of visits made during the hour preceding the designated time. Nomenclature follows Paynter (1955).

	Number of visits	Percentage of visits before													
		06:00	07:00	08:00	09:00	10:00	11:00	12:00	13:00	14:00	15:00	16:00	17:00	18:00	
<i>Ortalis vetula</i>	31	32.3	6.4	0.0	0.0	0.0	0.0	3.2	16.1	16.1	9.7	9.7	0.0	6.4	
<i>Aratinga astec</i>	632	0.3	3.3	3.8	12.5	11.1	3.3	5.7	20.6	12.2	9.3	10.1	6.8	1.0	
<i>Amazona albifrons</i>	31	16.1	35.5	16.1	6.4	0.0	0.0	0.0	3.2	0.0	6.4	0.0	12.9	3.2	
<i>Trogon citreolus</i>	392	6.1	16.6	16.8	22.2	11.7	13.3	7.1	1.3	2.6	1.5	0.3	0.3	0.3	
<i>Pteroglossus torquatus</i>	148	14.9	10.8	12.8	11.5	5.4	6.1	8.8	2.7	5.4	6.8	6.8	3.4	4.7	
<i>Ramphastos sulfuratus</i>	404	14.8	16.6	15.3	2.9	6.7	5.9	4.0	3.0	3.0	4.0	3.7	5.4	4.7	
<i>Centurus aurifrons</i>	1,343	4.8	10.6	9.5	8.3	8.6	7.5	7.1	9.0	8.5	7.1	7.4	6.6	4.8	
<i>C. pygmaeus</i>	98	4.1	7.1	15.3	9.2	14.3	7.1	16.3	4.1	7.1	6.1	3.1	6.1	0.0	
<i>Cotinga amabilis</i>	27	7.4	33.3	11.1	7.4	3.7	3.7	18.5	0.0	3.7	3.7	7.4	0.0	0.0	
<i>Tityra semifasciata</i>	66	0.0	3.0	12.1	13.6	21.2	18.2	7.6	4.5	7.6	9.1	0.0	1.5	1.5	
<i>Tyrannus melancholicus</i>	82	2.4	15.8	14.6	9.8	8.5	4.9	7.3	15.8	12.2	4.9	3.6	0.0	0.0	
<i>Pitangus sulphuratus</i>	259	5.0	10.4	9.7	15.1	5.4	10.8	7.0	12.0	6.2	5.0	4.2	8.1	1.2	
<i>Myiozetetes similis</i>	116	6.0	6.0	5.2	10.3	10.3	7.8	9.5	12.1	12.9	7.8	7.8	1.7	2.6	
<i>Megarhynchus pitangua</i>	26	0.0	15.4	19.2	11.5	19.2	7.0	0.0	3.8	7.7	11.5	0.0	0.0	3.8	
<i>Psilorhinus morio</i>	179	7.8	2.8	11.7	11.7	7.3	11.7	11.7	8.4	8.9	5.0	2.8	7.3	2.8	
<i>Cyanocorax yncas</i>	47	2.1	10.6	6.4	10.6	12.8	4.3	6.4	21.3	17.0	6.4	0.0	2.1	0.0	
<i>Cissilopha yucatanica</i>	441	6.1	6.1	4.3	5.4	7.5	6.3	5.2	11.6	8.8	7.7	12.2	6.1	12.5	
<i>Turdus grayi</i>	179	4.5	10.6	11.2	15.1	11.7	5.6	7.3	11.7	3.9	5.6	2.8	6.1	3.9	
<i>Icterus gularis</i>	183	7.1	6.0	17.5	8.2	10.4	8.7	8.7	9.3	7.1	4.9	4.9	4.9	2.2	
<i>I. prothemelas</i>	33	0.0	0.0	6.1	12.1	27.3	21.2	15.2	3.0	6.1	3.0	0.0	3.0	3.0	
<i>I. auratus</i>	34	0.0	0.0	0.0	11.8	14.7	8.8	17.6	11.8	8.8	0.0	0.0	8.8	17.6	
<i>I. chrysater</i>	29	0.0	13.8	6.9	27.6	17.2	3.4	3.4	6.9	3.4	0.0	0.0	6.9	10.3	
<i>I. mesomelas</i>	28	3.6	7.1	25.0	10.7	10.7	10.7	7.1	7.1	0.0	7.1	10.7	0.0	0.0	
<i>Dives dives</i>	185	4.3	7.6	10.3	12.4	11.9	10.8	9.7	8.6	11.9	3.2	4.3	2.7	2.2	
<i>Euphonia affinis</i>	39	5.1	10.2	10.2	5.1	7.7	0.0	25.6	10.2	2.6	5.1	17.9	0.0	0.0	
<i>E. hirundinacea</i>	322	9.9	10.2	6.5	5.9	11.2	7.4	8.1	5.3	6.5	8.7	3.1	9.3	7.8	
<i>Saltator atriceps</i>	195	8.2	16.9	9.2	9.2	8.2	9.2	7.2	9.2	3.1	5.1	8.7	2.0	3.6	

TABLE 2. Comparison of the two most common avian feeders in each tree species.

	No. of visits	No. of time periods	χ^2
<i>Neea psychotrioides</i>			
<i>Pteroglossus torquatus</i>	18		
<i>Ramphastos sulfuratus</i>	29	2	6.81, $P < .01$
<i>Ficus padifolia</i>			
<i>Pitangus sulphuratus</i>	100		
<i>Euphonia hirundinacea</i>	319	13	38.99, $P < .001$
<i>Ehretia tinifolia</i>			
<i>Aratinga astec</i>	537		
<i>Centurus aurifrons</i>	1,110	13	192.60, $P < .001$
<i>Metopium brownei</i>			
<i>Aratinga astec</i>	82		
<i>Centurus aurifrons</i>	69	7	44.38, $P < .001$
<i>Talisia olivaeformis</i>			
<i>Centurus aurifrons</i>	91		
<i>Cissilopha yucatanica</i>	97	11	49.00, $P < .001$

cases where the number of visits was sufficient to attain the minimum expected values required for the test (in Conover 1971), time periods were one hour in duration. Where minimum expected values could not be attained with such periods, hours with few visits were lumped to the minimum extent necessary. Table 1 presents the data in percentages for comparative purposes, but the tests were applied to the raw data.

RESULTS

Table 1 lists the total number of visits made by each bird species and the percentage of visits in each one-hour period. These percentages are based on the total number of visits summed over all five tree species. Species with fewer than 25 total visits have not been included. In general, the species differ considerably in the timing of their visits.

Table 2 presents the results of the chi-square tests on the temporal feeding patterns of the two most common feeders in each kind of fruit tree. All five tests are highly significant, leading to rejection of the hypothesis that the two most common feeders fed at the same time.

I observed aggressive encounters among birds but recorded only those interspecific encounters which caused supplanted individuals to leave the fruit tree, as these were most obvious to me and could be accurately tallied. Hence this method conservatively estimates the total number of aggressive encounters that occurred. I list here the aggressor species, the supplanted species, and the number of my records for such encounters. Keel-billed Toucan (*Ramphastos sulfuratus*) supplanted Scrub Euphonia (*Euphonia affinis*)—2; Great Kiskadee (*Pitangus sulphuratus*) supplanted Keel-billed Toucan—1; Yucatan Jay (*Cissilopha yucatanica*) supplanted Orange Oriole (*Icterus auratus*)—1, and the Brown Jay (*Psilorhinus morio*)—6; Brown Jay supplanted Yucatan Jay—5, and the Aztec Parakeet (*Aratinga astec*)—2; Melodious Blackbird (*Dives dives*) supplanted Brown Jay—2, and the Altamira Oriole (*I. gularis*)—1.

DISCUSSION

Land (1963) and Leck (1969, 1971) reported that frugivorous birds feed most actively during the early morning. My data, however, show that 15 of 27 bird species made most of their feeding visits after 10:00

(Table 1). Because it is possible that birds are eating more fruits per visit during their early morning visits, my results do not necessarily contradict those of the earlier studies. Nevertheless, investigators who observe only during early morning hours may miss those species that make more visits later in the day.

Metabolic cost of activity is important in the optimal placement of feeding periods over the activity cycle (Schoener 1971). Although the pattern of feeding activity of these frugivores may be fixed in a broad sense by physiological constraints, local factors peculiar to each fruit tree could cause variations. Such factors may include proximity to nest, availability and quality of alternate food resources, and location and activity of predators or competitors.

Several studies have dismissed competition for fruit in the tropics as unimportant (e.g., Willis 1966, Leck and Hilty 1968, Leck 1972, Morton 1973), but trees in fruit are not always widespread in the tropics, and competition for this finite supply is possible (Terborgh and Diamond 1970). Earlier (Kantak 1979), I presented data which showed that the frugivores in this study made uneven use of the fruit trees, and I suggested possible factors underlying this partitioning. The question addressed now is whether birds might influence the temporal pattern of feeding visits of other birds to fruit trees. Aggressive interference among frugivores has been documented here and elsewhere (Leck 1969, 1972, Terborgh and Diamond 1970) and therefore one might predict that birds using these fruit trees may tend to do so at different times of day. Schoener (1974b) explained why feeding times rarely serve as a means of partitioning resources, but ecological reality may not be the all-or-none situation he modeled. A bird supplanted at one tree may simply move to another tree rather than abandon its feeding attempts altogether, and ideally it would go to a tree where it would not be supplanted or otherwise disturbed. Thus, some of the differences I found in temporal feeding patterns may be a result of interference competition, even though partitioning as modeled by Schoener (1974b) was not occurring. Interference may be less important than physiological or other factors in determining time of feeding but it should not be dismissed. Further work should be undertaken to ascertain its role in the competitive interactions among coexisting frugivores.

I thank Robert Waide, Edward Beals, Timothy Moer-

mond, Mark Stromberg and John Shepherd for assistance and encouragement during this work, and Eugene Morton and an anonymous reviewer for their comments on the manuscript.

LITERATURE CITED

- BEARD, J. S. 1955. The classification of tropical American vegetation types. *Ecology* 36:89-100.
- CONOVER, W. J. 1971. *Practical nonparametric statistics*. Wiley, New York.
- DIAMOND, J. M., AND J. W. TERBORGH. 1967. Observations on bird distribution and feeding assemblages along the Rio Callaria, Department of Loreto, Peru. *Wilson Bull.* 79:273-282.
- KANTAK, G. E. 1979. Observations on some fruit-eating birds in Mexico. *Auk* 96:183-186.
- LAND, H. C. 1963. A tropical feeding tree. *Wilson Bull.* 75:199-200.
- LECK, C. F. 1969. Observations of birds exploiting a Central American fruit tree. *Wilson Bull.* 81:264-269.
- LECK, C. F. 1971. Overlap in the diet of some neotropical birds. *Living Bird* 10:89-106.
- LECK, C. F. 1972. Seasonal changes in feeding pressures of fruit- and nectar-eating birds in Panama. *Condor* 74:54-60.
- LECK, C. F., AND S. HILTY. 1968. A feeding congregation of local and migratory birds in the mountains of Panama. *Bird-Banding* 39:318.
- MORTON, E. S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. *Am. Nat.* 107:8-22.
- PAYNTER, R. A., JR. 1955. *The ornithogeography of the Yucatan Peninsula*. Peabody Museum of Natural History, Yale University, New Haven, CT.
- PIANKA, E. R. 1969. Sympatry of desert lizards (*Ctenotus*) in western Australia. *Ecology* 50:1012-1030.
- SCHOENER, T. W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2:369-404.
- SCHOENER, T. W. 1974a. Resource partitioning in ecological communities. *Science* 185:27-38.
- SCHOENER, T. W. 1974b. The compression hypothesis and temporal resource partitioning. *Proc. Natl. Acad. Sci.* 61:4169-4172.
- SHEPHERD, J. D. 1975. *The phytosociology of a tropical seasonal forest in southeastern Mexico*. M.S. thesis, Univ. of Wisconsin, Madison.
- SNOW, B. K., AND D. W. SNOW. 1971. The feeding ecology of tanagers and honeycreepers in Trinidad. *Auk* 88:291-322.
- TERBORGH, J. W., AND J. M. DIAMOND. 1970. Niche overlap in feeding assemblages of New Guinea birds. *Wilson Bull.* 82:29-52.
- WILLIS, E. O. 1966. Competitive exclusion and birds at fruiting trees in western Colombia. *Auk* 83:479-480.

Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706. Accepted for publication 4 August 1980.

Condor 83:187-189
© The Cooper Ornithological Society 1981

INHERITANCE OF COLOR PHASES OF FERRUGINOUS HAWKS

SHEILA M. SCHMUTZ

AND

JOSEF K. SCHMUTZ

Color polymorphism occurs quite commonly among birds (Huxley 1955, Paulson 1973). In the Snow Goose (*Anser caerulescens*) color is thought to be determined by one gene, the dark, or blue allele being dominant (Cooke and Cooch 1968). As part of an ecological study of buteos in southeastern Alberta (Schmutz et al. 1980), we recorded the color phase of adult and nestling Ferruginous Hawks (*Buteo regalis*). Two phases were observed on our study area: a light phase with predominantly white undersides and rufous thighs, and a dark phase, appearing black in flight except for the white undersides of the remiges and the rectrices (Godfrey 1966). The nestlings are very similar to the adults and were easily categorized as light or dark phase. We recorded the color phase of each adult in 1976 and 1977 in all cases where both members of a pair were seen (85 of 97 pairs), and the color phase of each nestling for 48 pairs.

Since light- and dark-phased birds are so distinctive, we considered it unlikely that color phase is polygenically determined. The simplest hypothesis is that one gene determines color phase. Table 1 summarizes the color phases of offspring born to parents of known

phase. Our hypothesis is that the dark phase is produced by a dominant allele for melanism. The occurrence of one dark nestling born to a pair of light colored parents contradicts this hypothesis. However, this could be an anomalous case resulting from fertilization by a dark male who did not stay mated to this light female, a new mutation, or an error in recording data. For example, we once saw a female carrying nest material and displaying to a male with whom she did not copulate at that time. Then she flew approximately 1 km to a location where she copulated with another male before rejoining her original "mate." Possibly we

TABLE 1. The number of light and dark nestlings produced in 1976 and 1977 where phase of all offspring was recorded.

Year	No. nests	No. nestlings	
		Light	Dark
Light × light matings			
1976	15	37	0
1977	21	54	1
Light × dark matings			
1976	4	4	5
1977	6	8	5
Dark × dark matings			
1976	1	2	2
1977	1	1	0