MEASUREMENT OF SOCIAL ATTRACTIONS BETWEEN TROPICAL PASSERINE BIRDS

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THROUGHOUT the humid tropics groups of birds of several species are frequently encountered while they feed on fruit and nectar in large trees, or on insects among the canopy and forest floor. The social bonding of such flocks has been well described for insectivores (Moynihan, 1962; Willis, 1966) but the associations of fruit eaters have been much neglected. This paper presents a technique and preliminary results of a quantitative analysis of the social attractions of frugivorous birds in Panama.

METHODS

I selected two fruiting plants in the laboratory clearing of the Smithsonian Tropical Research Institute, Barro Colorado Island, Canal Zone. The plants were *Cecropia* sp. (a second-growth tree) and *Oryctanthus* sp. (a mistletoe shrub), both widespread in the neotropics and heavily exploited by a variety of birds. Each plant was observed for 100 hours at the end of the wet season, a non-breeding period. Census periods sampled the day as follows: 06:30–07:00, 07:30–12:00, and 12:30–17:30 (this temporal spread was designed to avoid bias related to species differences in activity patterns). During the observations I recorded the exact time of arrival of each individual bird that visited the food plant. Each bird was identified as a species or individual (40 birds of the area were color-banded).

RESULTS

At first a simple sequential analysis of the successive arrivals of all birds was used to determine bondings, on the assumption that if one species arrived at the tree after another species more frequently than can be attributed to chance, then the first bird is probably attracted to the second (such an assumption may be applied to both intra- and interspecific relationships). Data from both *Cecropia* (Table 1) and *Oryctanthus* (Table 2) showed that intraspecific attractions were dominant. Most of these were based on pair bonds, as analysed through records of color-banded birds. General intraspecific flocking of six to 10 individuals was important with the Plain-colored Tanager (scientific names in Appendix). Interspecific relationships were not easily revealed with this analysis because of the overriding effect of the intraspecific attractions and because the analysis used only a limited amount of the collected data. More information was incorporated by using the time interval (in minutes) between successive visits as an improved measure of attractive strength. That is, if one bird frequently followed another to a tree within one minute it was likely to have been more strongly attracted than if it usually arrived several minutes later. From this type of analysis for all visits to the plants (Figs. 1 and 2) it is again clear that intraspecific attrac-

TABLE 1

PREDECESSOR-FOLLOWER RECORDS AT *CECROPIA* TREE IN THE CLEARING AT BARRO COLORADO ISLAND, FALL, 1968.

Follower	Predecessor					Totals
	Blue Tanager	Palm Tanager	Plain colored Tanager	Fulvous-vented Euphonia	Others	
Blue Tanager	22*	10	7	5	14	58
Palm Tanager	9	88*	28	6	50	181
Plain-colored Tanager	16	26	191*	3	46	282
Fulvous-vented Euphonia	4	5	1	8*	9	27
Totals	51	129	227	22	119	548

For each predecessor-follower pair the actual number of observations is given. * = Statistically significant intraspecific attractions. Interspecific followings alone are significantly ($p < 0.05$) non-random, except after the Fulvous-vented Euphonia. ("Others" cannot be tested).

tions are stronger (i.e., usually involve shorter time intervals) than interspecific bonds. This technique can be further applied on an individual species basis, with the percentages of predecessor-follower visits that involve one minute or less between the arrival of the two birds (Table 3). The ability of this arbitrary time period to reveal attractions should be greater with shorter periods, and thus the use of the one minute interval criterion

TABLE 2

PREDECESSOR-FOLLOWER RECORDS AT *ORYCTANTHUS* PLANT IN THE CLEARING OF BARRO COLORADO ISLAND, FALL, 1968.

Follower	Predecessor						Totals
	Golden-masked Tanager	Sulphur-rumped Tanager	Paltry Tyrannulet	Ochre-bellied Flycatcher	Social Flycatcher	Others	
Golden-masked Tanager	–	2	8	10	15	27	62
Sulphur-rumped Tanager	5	29*	5	20	6	33	98
Paltry Tyrannulet	6	7	7	17	13	38	88
Ochre-bellied Flycatcher	12	7	13	22	17	83	154
Social Flycatcher	6	10	8	12	40*	51	127
Totals	29	55	41	81	91	232	529

Legend as in Table 1, with significant ($p < 0.05$) intraspecific attractions indicated (*). Interspecific followings alone are non-random ($p < 0.10$) after the Sulphur-rumped Tanager, Paltry Tyrannulet, and Social Flycatcher. ("Others" cannot be tested).

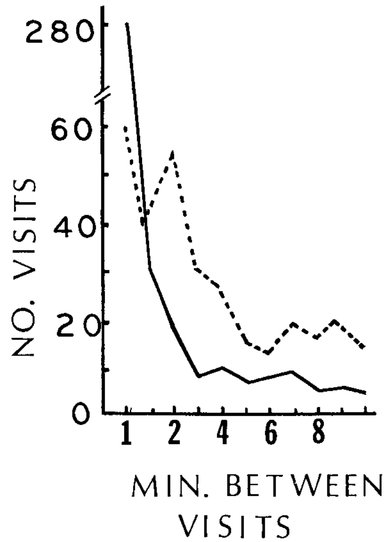

FIG. 1. Number of minutes between individual visits of the same species (solid line; n = 371) and of different species (dotted line; n = 308) to a *Cecropia* tree in the clearing at Barro Colorado Island, Sept.–Nov. 1968.

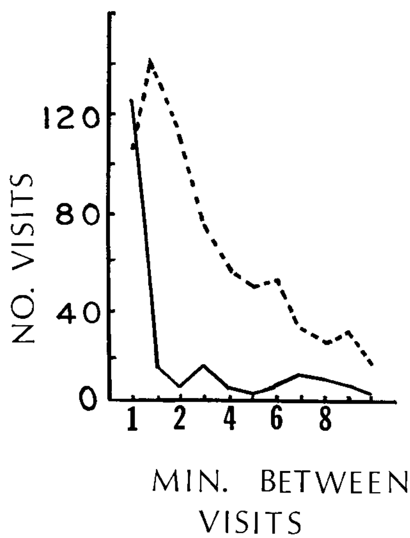

FIG. 2. Number of minutes between individual visits of the same species (solid line; n = 177) and of different species (dotted line; n = 686) to an *Oryctanthus* plant in the clearing at Barro Colorado Island, Sept.–Nov. 1968.

TABLE 3

PERCENTAGES OF FOLLOWING RECORDS OCCURRING WITHIN ONE MINUTE OF THE PREDECESSOR'S ARRIVAL.

Follower	Predecessor				
	Blue Tanager	Palm Tanager	Plain-colored Tanager	Fulvous-vented Euphonia	Others
Blue	91%	30%	57%	20%	14%
Tanager	(20,2)	(3,7)	(4,3)	(1,4)	(2,12)
Palm	56%	61%	46%	17%	18%
Tanager	(5,4)	(54,34)	(13,15)	(1,5)	(9,41)
Plain-colored	19%	35%	76%	33%	22%
Tanager	(3,13)	(9,17)	(145,46)	(1,2)	(10,36)
Fulvous-vented	0%	40%	100%	100%	11%
Euphonia	(0,4)	(2,3)	(1,0)	(8,0)	(1,8)

For each predecessor-follower pair there is in parenthesis the number of records with one minute or less between the two visits and the number with more than one minute between visits, and above these, the percentage of the total that is within the one minute category.

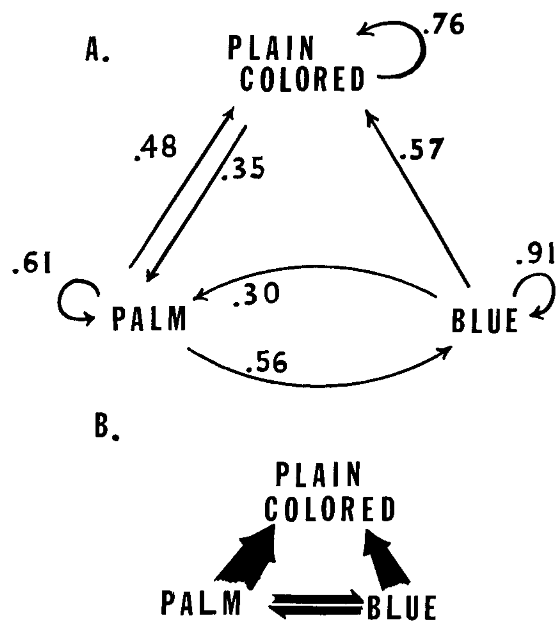

FIG. 3. Strengths of intra- and interspecific attractions of three tanagers at the clearing, Barro Colorado Island. Arrows point from the following (attracted) species to the predecessor. (A) Attractive strengths shown as the percentages of following species arrivals that occurred within one minute of the predecessor. (B) Attractive strengths shown by the relative widths of the arrows (from Moynihan, 1962, p. 65).

(the shortest possible with the data collected). The attractions may be easily diagramed to depict social organizations (Fig. 3A), and the results are seen to be similar to, but less subjective than those of Moynihan (1962) (Fig. 3B). This study also suggests mutual rather than one-way attractions between Palm and Plain-colored Tanagers. The primary contribution of this part of the study is its quantitative nature and its ability to reveal subtle relationships, providing an example of a field study of avian social structure with data adaptable to stochastic analysis.

In other parts of the study area (not reported here) intraspecific flocking of frugivores was common with the larger species (e.g., *Daptrius americanus*, *Crax* sp., *Penelope purpurascens*, *Amazona* sp., and *Ramphastos* sp.). Most of the species showing such gregarious behavior were highly vocal, probably to facilitate group cohesion.

DISCUSSION

As reported by Diamond and Terborgh (1967), the reduced interspecific bonding at fruit trees is in direct contrast to the strong social bonding reported for mixed-species flocks moving through the forest (Sedgwick, 1949; McClure, 1967). There are several possible reasons for these behavioral differences. Species feeding at a stationary food source such as a fruit tree would require less bonding to relocate the food easily than those species feeding at a moving food source, such as ant swarms (Willis, 1967). Second, while interspecific flocking at fruit trees might mainly provide increased awareness of predators, flocks moving through the forest could gain both this protection and an increased availability of food with the mutual flushing of insect prey (Moynihan, 1962). This latter point is probably very important in promoting the social cohesiveness of large mixed foraging flocks, the members of which are mainly insectivorous (Rand, 1954). Finally, competition may reduce social bonds at fruit trees where most species are frugivorous and take the same food, while such competition would probably be less important in mixed-species flocks, the members of which exploit a wide variety of foods through different behaviors (Diamond and Terborgh, 1967).

The methods of gathering data on social interaction at isolated food sources, as described in this report, offer several advantages: (1) an observer is able to take complete notes on the interactions at almost any single tree; (2) by taking notes at similar food sources it is possible to gather comparable data in different habitats, permitting a direct comparative study of social systems in different avian communities; and (3) individual plants which fruit continually provide unique opportunities for studies of seasonal changes in interspecific relationships (Leck, 1970).

SUMMARY

The social behavior of fruit-eating birds was studied in the Panama Canal Zone. Intraspecific attractions, usually pair bonds, dominated the interactions. Interspecific attractions were weak, in contrast to those reported for insectivorous species. The ecological reasons for this behavioral difference are considered.

The method described for gathering social data at single food resources is noted to be of value because of its quantitative nature and wide applicability.

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APPENDIX

Scientific names of species mentioned in the text and tables.

Social Flycatcher (*Myiozetetes similis*)
Paltry Tyrannulet (*Tyranniscus vilissimus*)
Ochre-bellied Flycatcher (*Pipromorpha oleaginea*)
Fulvous-vented Euphonia (*Euphonia fulvicrissa*)
Plain-colored Tanager (*Tangara inornata*)
Golden-masked Tanager (*Tangara larvata*)
Blue-gray Tanager (*Thraupis episcopus*)
Palm Tanager (*Thraupis palmarum*)

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