

displays and, more generally, into why the Mimidae apparently have a propensity for this use of the wings.

These observations were made while conducting research supported by the Frank M. Chapman Memorial Fund of the American Museum of Natural History and the Society of Sigma Xi.—TERRELL D. G. RICH, *Dept. Biology, Idaho State Univ., Pocatello, Idaho 83209.* (Present address: *P.O. Box 204, 518 S. Alta, Shoshone, Idaho 83352.*) Accepted 3 Aug. 1979.

Wilson Bull., 92(4), 1980, pp. 513–519

A comparison of avian foraging at flowering trees in Panama and New Guinea.—

Mixed-species foraging aggregations at fruiting and flowering trees are striking features of the humid tropics, where in some instances, 10–15 species of birds, from 5 or more families, may share the same, temporarily super-abundant resource (Moynihan, *Smithson. Misc. Coll.* 143:1–140, 1962; Land, *Wilson Bull.* 75:199–200, 1963; Diamond and Terborgh, *Wilson Bull.* 79:273–282, 1967; Terborgh and Diamond, *Wilson Bull.* 82:29–52, 1970). Birds visiting flowering trees consume nectar, pollen and insects. Though it is often difficult for the field observer to discern which item is being taken by which species (Snow and Snow, *Auk* 88:291–322, 1971), the tree represents a locus of high abundance for all 3 resources, and the result is aggregations of invertebrate and vertebrate foragers.

In this note I discuss observations made at a single flowering tree in Panama in January 1978, and compare these with data of a similar nature that I gathered in Papua New Guinea in 1975–1976. My short-term observations in Panama cannot be generalized for the Neotropics or even for Panama in all seasons; but the data, limited as they are, indicate potentially significant differences among foraging by Neotropical honeycreepers and New Guinea honeyeaters and lories. In treating these data, I ask 2 questions: (1) to what extent is there some sort of flocking organization, as opposed to unstructured aggregation, at flowering trees; and (2) does the pattern of resource-use in Panama differ from that in New Guinea?

Methods.—I watched a single flowering tree in relatively undisturbed mature second-growth forest along the Pipeline Road, Canal Zone, Panama. The tree was a 27-m high *Luehea seemanii* (Tiliaceae), surrounded by an uneven canopy varying in height from 22–33 m. During the period of observation, 12–15 January 1978, the *Luehea* was festooned with small, whitish, pedicellate blossoms. There were no other flowering trees in the immediate vicinity. Observations were made from a 28-m aluminum tower that stood about 30 m from the tree and afforded an unimpeded view of the entire crown of the *Luehea*. I censused all birds visiting the tree every 15 min, for a period of 5 min. Each 5-min census is considered an “instantaneous snapshot” of avian use of the tree. I also noted all instances of intra- and interspecific aggression. At no point were more than 16 birds in the tree at once; I had no difficulty watching and taking notes simultaneously. All identifications were made using 8.5 × 44 Swift binoculars, with the aid of Ridgely’s *Guide to Panamanian Birds* (Princeton Univ. Press, Princeton, New Jersey, 1976).

My observations in New Guinea were made sporadically from April 1975 through June 1976. I observed at several localities on New Guinea proper (Wau, 1100 m, June–July 1975; Goroka, 1500 m, September 1975; Mt. Missim, 1050, 1400 and 1750 m, December, January and March 1975–1976; and Bulldog Road, 2600 m, on 10 occasions during 1975–76). I also watched on New Ireland in February 1976 and on Goodenough Island in April 1976. Nearly 100 different flowering trees were watched during the period, from sea level to 3000 m. Because the observations were incidental and not the focus of my main research, I did not

TABLE 1
OBSERVATIONS OF BIRDS FORAGING AT FLOWERING *LUEHEA*, 12-15 JANUARY 1978

Species	12 Jan.				13 Jan.				14 Jan.				15 Jan.			
	10:45	11:00	17:30	07:15	09:15	09:30	09:45	10:00	10:15	11:00	11:15	07:45	08:00	08:15	08:30	08:45
Shining Honeycreeper (<i>Cyanerpes lucidus</i>)					3	3	1	3	3	3	6	4	5	1	5	2
Red-legged Honeycreeper (<i>C. cyaneus</i>)					3	5	4	1		4	2	3	3	4	3	1
Blue Dacnis (<i>Dacnis cayana</i>)					3	2	2	1		3	2	3	4	2	2	2
Green Honeycreeper (<i>Chlorophanes spiza</i>)					2	1	2	2	1				1	2	1	2
White-necked Jacobin (<i>Florisuga mellivora</i>)	1					1	1					1			1	
Summer Tanager (<i>Piranga rubra</i>)	1	1						1	1	1				1		
Tennessee Warbler (<i>Vermivora peregrina</i>)								1			1	1	1			
Unidentified hummingbird (Trochilidae)																
Other visitors ^a				1	1											
Total individuals/census	2	1	0	1	11	12	10	5	8	0	1	4	3	0	9	12

^a Four species each visited only once: a wood warbler (13 Jan., 07:15), *Euphonia* (13 Jan., 09:30), a *Lophornis* hummingbird (14 Jan., 10:00) and a Great Crested Flycatcher (*Myiarchus cinerascens*) (15 Jan., 15:15).

TABLE 2
DETERMINATION OF THE STATISTICS OF CONSOCIATIVE FLOCKING BY HONEYCREEPERS AT
A FLOWERING TREE

Species	No. observation periods = 27			
	No. times observed		Probability of occurrence	
Shining Honeycreeper	19		0.70	
Red-legged Honeycreeper	15		0.56	
Blue Dacnis	14		0.52	

	No. species present	1 species	2 species	3 species
Prob. of chance	$(1 - P_1)(1 - P_2)$	$P_1(1 - P_2)(1 - P_3) +$	$P_1P_2(1 - P_3) +$	$P_1P_2P_3$
co-occurrence:	$(1 - P_3)$	$P_2(1 - P_1)(1 - P_3) +$	$P_1P_3(1 - P_2) +$	
		$P_3(1 - P_2)(1 - P_1)$	$P_2P_3(1 - P_1)$	
Expected:	1.71	8.02	11.76	5.5
Observed:	7	4	4	12
	$\chi^2 = 31.18, P < 0.001$			

Chlorophanes flock association

Number of periods of observation when at least 1 honeycreeper was present in the tree = 22. *Chlorophanes* was present on 18 occasions; $P_4 = 18/22 = 0.82$. All 4 honeycreepers will co-occur by chance at a frequency of $P_{123} \times P_4$, where $P_{123} = 0.55$; on 55% of my 22 observations I saw all 3 "flockers." By chance, then, all 4 honeycreepers should co-occur at a frequency of $0.55 \times 0.82 = 0.45$.

	All together	All not together
Expected:	$0.45 \times 22 = 9.92$	$0.56 \times 22 = 12.32$
Observed:	10	12
	$\chi^2 = .0226, P > 0.70$	

collect normalized and systematic data as I did in Panama. Instead, I monitored relative inter-individual aggression and species-abundance at the different locales.

Panama flowering tree.—During the 31 censuses made at the Panamanian flowering tree (*Luehea*), 12 species of birds were noted, but only 8 were regular visitors (Table 1). Of the 206 observations of individual foragers, 178 (86%) were of honeycreepers (either Blue Dacnis [*Dacnis cayana*], Red-legged [*Cyanerpes cyaneus*], Shining [*C. lucidus*], or Green [*Chlorophanes spiza*]). These 4 species were the key foragers at the flowering tree, coming in pairs and small parties. Other species invariably visited the tree as solitary foragers, represented by a single regular individual that visited each day for a period of time (Table 1).

Snow and Snow (1971) discussed the ecology and morphology of the 4 honeycreepers that were the dominant foragers during my observations (for biometric data and a comparative photograph of the birds, refer to that paper). Of these 4 species, the *Dacnis* and 2 *Cyanerpes* seemed to come and go from the tree as a heterospecific flock. *Chlorophanes* was often in the tree with the other 3, but neither associated, nor came and went with the "flock."

To determine if the 3 honeycreepers acted as a coordinated flock (see Table 1), I tested whether their presence together in the tree or mutual absence from the tree deviated from a random association produced by their respective temporal distributions at the tree (Table 2). Censuses in which I saw no birds at the tree were excluded from the test, so that the

birds would not appear more gregarious than they really were. The average probability for presence of each species in the tree at any random census was computed by dividing total number of censuses with the species present by absolute total number of censuses with any birds in any tree. From these probabilities, the expected frequency of co-occurrence, if the birds were acting independently, was computed and compared with observed frequencies. Table 2 shows that *D. cayana*, *C. cyaneus* and *C. lucidus* were forming a non-random consociation at the feeding tree. The fourth species, *Chlorophanes spiza*, segregated from this flock (Table 2).

My observations on inter-individual aggression further confirmed the census results. The 3 flocking species showed very little inter-individual aggression—I recorded no interspecific aggression and only 1 case of intraspecific aggression. When a small flock of 5–10 birds entered the tree, the birds foraged in clumps rather than spreading out for maximum spacing of individuals. In some cases, 3–4 birds would forage within the same m³ of vegetation.

In contrast, *Chlorophanes* showed entirely different dispersion and interspecific behavior. This species chased the other honeycreepers on a number of occasions, and never foraged near the others. Rather, a pair of these birds (male and female) defended an apparent feeding territory in a discrete portion of the tree. I saw no other conspecifics enter the tree, and the other honeycreepers seemed to forage away from the “territory” established by the pair of *Chlorophanes*. The pair of *Chlorophanes* was rather sedentary, and while the flocking birds arrived and departed frequently, the *Chlorophanes* remained in their territory for long periods. During all 4 days of observation the pair remained in the same restricted area of the flowering *Luehea*.

New Guinea flowering trees.—Birds that fed in flowering trees in New Guinea were dominated by honeyeaters (Meliphagidae) and lorries (Psittacidae). In addition, flycatchers (Muscicapidae), warblers (Acanthizidae), drongos (Dicuridae), birds of paradise (Paradisaeidae), sunbirds (Nectariniidae) and white-eyes (Zosteropidae) often fed in flowering trees. Table 3 shows assemblages from 3 diverse localities in Papua New Guinea. These 3 samples vary in composition, although their behavior was similar.

The 3 visitors to the cocoanut palm (*Cocos nucifera*) comprise the simplest feeding group. The interactions that took place among these birds typify all New Guinea observations. The brush-tongued lorries (in this case *Charmosyna placensis*) visited the tree in monospecific flocks of 3–4 birds. The sunbird and honeyeater visited solitarily. All intra- or interspecific actions between individuals were aggressive—supplanting, threatening and even chasing. There was no evidence of heterospecific flocking nor any form of inter-individual cooperation.

Among all New Guinea feedings assemblages that I have observed, only lorries, white-eyes and the warbler, *Acanthiza murina*, form flocks that feed in flowering trees. All are monospecific. Even in these cases there is inter-individual aggression among flock members.

Honeyeaters usually dominated in a flowering tree, whatever the elevation or locale. Although honeyeaters feed in multispecies aggregations, they are invariably solitary and aggressive. In no instance have I observed organized heterospecific flocks visit New Guinea trees to feed on flowers.

My brief observations at the tree in Panama indicated a quiet, even orderly, aspect of group feeding. My New Guinea experiences involved avian assemblages that were veritable riots of inter-individual aggression. In general, the organizing factor among the New Guinea birds seemed to be dominance hierarchy, based on size and aggressiveness. The larger species were usually more successful; thus, they occupied the favored feeding spots with minimum harassment. But, even under the best of circumstances, the dominant species in a tree spent most of the time supplanting and chasing conspecifics and smaller heterospecifics. This is documented by Terborgh and Diamond (1970) and Ripley (Am. Nat. 93:127–132, 1959).

TABLE 3
REGULAR AVIAN VISITORS TO 3 FLOWERING TREES IN PAPUA NEW GUINEA

Cocoanut Palm (<i>Cocos nucifera</i>) (Coastal scrub, New Ireland Province, 7-8 February 1976)				
Species	Abundance ^a	N ^b	\bar{x} weight ^b	SD ^b
Yellow-fronted Blue-eared Lory (<i>Charmosyna placensis</i>)	3-4	9	35.5	±4.3
Black Sunbird (<i>Nectarinia sericea</i>)	1-2	1	9.7	—
Red Myzomela (<i>Myzomela cruentata</i>)	1-2	3	9	±0
<i>Rhus taitensis</i> (Anacardiaceae) (Mid-montane second-growth forest, Morbe Province, July 1975)				
Species	Abundance	N	\bar{x} weight	SD
Rainbow Lory (<i>Trichoglossus haematodus</i>)	5-10	4 ^c	113.1	±10.6
Spangled Drongo (<i>Dicrurus hottentotus</i>)	1	3	78.8	±2.3
Long-billed Honeyeater (<i>Melilestes megarrhynchus</i>)	1	10	46.6	±1.7
Mt. Red-headed Myzomela (<i>Myzomela adolphinae</i>)	3-4	2 ^c	7.1	±1.3
White-marked Honeyeater (<i>Meliphaga albonotata</i>)	1-2	14	30.7	±2.3
Tawny-breasted Honeyeater (<i>Meliphaga flaviventer</i>)	2-3	12	47.3	±4.2
Marbled Honeyeater (<i>Pycnopygius cinereus</i>)	2-3	7	48.8	±3.9
Cinnamon-breasted Wattlebird (<i>Melidectes torquatus</i>)	4-7	7	52.4	±3.6
Black-fronted White-eye (<i>Zosterops atrifrons</i>)	10-25	11	11.5	±0.7
<i>Xanthomyrtus papuanus</i> (Myrtaceae) (Upper montane primary forest, Morobe Province, October 1975)				
Species	Abundance	N	\bar{x} weight	SD
Fairy Lory (<i>Charmosyna papou</i>)	2	1 ^c	119	—
Plum-faced Mountain Lory (<i>Oreopsittacus arfaki</i>)	5-10	2	22.4	±0.1

TABLE 3
CONTINUED

<i>Xanthomyrtus papuanus</i> (Myrtaceae) (Upper montane primary forest, Morobe Province, October 1975) (continued)				
Species	Abundance	N	\bar{x} weight	SD
Orange-billed Mt. Lory (<i>Neopsittacus pullicauda</i>)	4-6	3	35.7	±2.4
DeVis Tree Warbler (<i>Acanthiza murina</i>)	3-5	1 ^c	9	—
Black and Red Honeyeater (<i>Myzomela rosenbergii</i>)	3-6	15	11	±2.5
Black-throated Honeyeater (<i>Meliphaga subfrenata</i>)	1-2	4	33.75	±2.4
Brown-backed Streaked Honeyeater (<i>Ptiloprora guisei</i>)	2-3	10	24.2	±1.7
Belford's Melidectes (<i>Melidectes belfordi</i>)	1-2	4 ^c	82	±6.4
Sooty Honeyeater (<i>Melidectes fuscus</i>)	1	1 ^c	44	—

^a Abundance indicates average number of individuals observed in the tree simultaneously during active periods of foraging.

^b Data are from Diamond (Nuttall Ornithol. Club, Cambridge, Massachusetts, 1972).

^c Beehler field data, taken 1975.

Discussion.—During my studies, Panamanian honeycreepers foraged in a fashion different from the honeyeaters and other New Guinea visitors to flowering trees. My Panamanian data, limited to observations at 1 tree and in 1 season, cannot show that this difference is apparent year-round, or even from tree to tree. Moynihan (1962) mentions aggression among the species of honeycreeper that I discuss, but his observations are vague, not necessarily related to activities at flowering trees and often discussed out of context of foraging activities. (He was more concerned with the ontogeny of flock development and behavioral hierarchies without relation to the energetics and ecology of the situation.) In periods of high forager abundance, levels of aggression in feeding trees seem to be increased (Leck, Condor 74:54-60, 1970). Carpenter and MacMillen (Science 194:639-641, 1976) show that in Hawaii, the Iiwi (*Vestiaria coccinea*) is territorial in a flowering tree when the nectar resource is rich enough for defense to be justified, but not so rich that it would be a waste of time to try to monopolize it.

In Panama, the 3 flocking honeycreepers came and went as a group, while *Chlorophanes* did not. Diets may give an indication of why this foraging difference may exist. The 3 flocking species spent much of their time taking primarily nectar (Snow and Snow 1971), which can be quickly depleted during the day. The nectivorous birds must compete with bees and other insects; thus, it pays them to work efficiently to maximize caloric intake. By feeding as an organized group, the flock of honeycreepers can systematically "crop" the nectar resource in the manner of Cody's finch flocks in the Mojave Desert (Cody, Theoret. Pop. Biol. 2:142-158, 1971). This might explain why the honeycreeper flocks congregated in 1 section of the tree when they foraged. *Chlorophanes*, on the other hand, spends less time nectar-feeding (Snow and Snow 1971) and more time taking arthropods that visit flowers. It may pay *Chlo-*

rophanes to stake out a space in the tree and systematically to feed on foraging insects. The arthropods are probably a rapidly renewing resource that is difficult to harvest, but which pays a relatively high nutritional reward. Renewal may be so rapid as to be "instantaneous"—making the resource temporally stable, quite unlike the rapidly depleted and slowly renewing nectar resource. The sedentary and aggressive characteristics of *Chlorophanes* may reflect the most economical foraging strategy.

I can only speculate as to why my limited Panamanian observations are so radically different from those I made in New Guinea. The birds that regularly visit flowering trees in New Guinea are more diverse and include many birds that are much larger than the honeycreepers. The Panamanian species all resemble the *Myzomela* honeyeaters—a small specialized subset of the diverse New Guinea assemblage. The majority of flower-visitors in New Guinea are only opportunistically nectivorous; most spent their time gleaning insects from the flowers and foliage (pers. obs., unpubl. data, Terborgh and Diamond 1970). Probably the level of insectivory makes cohabitation in the tree more difficult (as with *Chlorophanes*). The result in New Guinea is higher levels of aggression. The 2 specialized New Guinean groups, the lories and *Myzomela* honeyeaters, have probably been unable to form cooperative alliances (as in Panama) because of the effect of continual interference from aggressive and solitary species that share the feeding trees.

Acknowledgments.—Support for fieldwork in New Guinea was provided by the Thomas J. Watson Foundation, Smithsonian Institution and Sigma Xi. The government of Papua New Guinea kindly gave permission to study in the country. Princeton University provided support for the trip to Panama. I thank John Terborgh for guidance in the field, and Jared Diamond and James Karr for criticism of an earlier draft of this note.—BRUCE BEEHLER, *Dept. Biology, Princeton Univ., Princeton, New Jersey 08544. Accepted 2 Jan. 1979.*

Wilson Bull., 92(4), 1980, pp. 519–523

Foraging by Yellow-bellied Sapsuckers in central Illinois during spring migration.—Yellow-bellied Sapsuckers (*Sphyrapicus varius*) breed throughout the coniferous and deciduous forests of the northeastern United States and Canada, and overwinter primarily in the southeastern U.S. (Howell, Auk 70:118–126, 1953). They regularly pass through the deciduous forests of central Illinois during spring and fall. In this note, I report on observations made on the foraging of these birds during the springs of 1974 and 1975.

My first 2 study areas were located in Hart Memorial Woods along the Sangamon River near Mahomet, Champaign Co., Illinois. The woods contained 2 distinct areas—a relatively dry upland (9.6 ha) and a wetter flood plain (3.4 ha). My third study site, called Briarwood (6.2 ha), was an open, pastured woodlot. A detailed analysis of vegetation composition and vertical structure for all 3 areas is presented in Williams (Ph.D. thesis, Univ. Illinois, Champaign, Illinois, 1977). Root et al. (Trans. Ill. State Acad. Sci. 64:27–37, 1971) provide a description of seedlings and saplings.

Hart upland, containing 565.3 trees/ha, was dominated by white (*Quercus alba*), black (*Q. velutina*) and red (*Q. rubra*) oaks. The floodplain area (239.9 trees/ha) was dominated by silver maple (*Acer saccharinum*). Briarwood, with the fewest trees (24.2/ha), contained mostly bur oak (*Q. macrocarpa*), shagbark hickory (*Carya ovata*) and white oak.

I examined the foraging of Yellow-bellied Sapsuckers by quantifying: (1) activity of the bird; (2) tree species occupied; (3) height of bird in tree; (4) condition of substrate (dead or alive); and (5) limb diameter, at signals given every 10 sec by an electronic metronome (Weins et al., Ecology 51:350–352, 1970). Observations were begun in March and ended in