

## EXAMPLES OF TROPICAL FRUGIVORES DEFENDING FRUIT-BEARING PLANTS

THANE K. PRATT

**ABSTRACT.**—In the tropics, birds have not been shown to defend fruit-bearing trees or vines, even though tropical birds defend other sources of food at high density, particularly flowers. I studied foraging of frugivorous birds in New Guinea and describe here four examples of feeding territories at fruiting woody plants: 1) a female Blue Bird of Paradise (*Paradisaea rudolphi*) at *Schefflera pachystyla*, 2) a male Indian Koel (*Eudynamis scolopacea*) at *Chisocheton* sp., 3) a male Cinnamon-breasted Wattlebird (*Melidectes torquatus*) at *Dendrocnide ternatensis*, and 4) a Reinwardt's Long-tailed Pigeon (*Reinwardtoena reinwardtsi*) at *Schefflera chaetorrhachis*. The birds of paradise, wattlebird and pigeon were individually recognizable. All four holders of feeding territories ("defenders") attempted to chase away all other visiting birds ("visitors") and succeeded, except in the case of the wattlebird, where some visitors were larger than it was. Chases were not always followed by feeding. Defenders either spent long periods at their feeding territories or visited them repeatedly. They held their feeding territories over several days.

Despite the burgeoning study of frugivory and seed dispersal (Howe and Smallwood 1982), birds in the tropics have not been shown to defend fruit-bearing plants. Outside of the tropics, only the Northern Mockingbird (*Mimus polyglottos*) has been demonstrated to defend a fruiting tree (Moore 1977, 1978). That more cases have not been reported is surprising, because birds do defend other sources of food occurring in temporary patches of abundance, e.g., flowers (Stiles and Wolf 1970; Gill and Wolf 1975a, b; Carpenter and MacMillen 1976; Pyke 1979) and prey fleeing from army ant swarms (Willis and Oniki 1978). A few observers have noted aggressive behavior by tropical birds at fruit-bearing plants (Leck 1972, Bourne 1974, Howe 1977); however, most investigators have either given the problem little attention or have commented on the low level of aggression at the trees they observed (Willis 1966, Terborgh and Diamond 1970, Cruz 1974, Crome 1975, Foster 1977, McDiarmid et al. 1977, Howe and Vande Kerckhove 1979, Howe and De Steven 1979).

As part of a larger study of seed dispersal at a mid-elevational forest in New Guinea, I recorded visits by frugivores to 29 individual fruit-bearing plants (Pratt 1983). In the present paper, I show that four of these plants were defended as feeding territories by individual frugivores. I use the term "defender" for a bird defending a fruit-bearing plant and "visitor" for any other visiting frugivore. Brown and Orians (1970) defined the essential characteristics of a territory as: "(1) a fixed area, which may change slightly over a period of time, (2) acts of territorial defense by the possessor which

evoke escape and avoidance in rivals, so that (3) the area becomes an exclusive area with respect to rivals." As an alternative hypothesis, aggressive behavior by a frugivore may enable such a bird to gain access to fruit at many plants, at the expense of subordinate frugivores. Therefore, in order to establish that a bird is defending a fruiting plant as a feeding territory, one must show that (1) the same, recognizable, aggressive individual (the defender) makes repeated feeding visits to the fruiting plant within and among observation periods, (2) the defender successfully drives other birds from the fruiting plant and thereby reduces their feeding rate at the plant, and (3) the defender returns to the fruiting plant to rout visitors even when it does not intend to feed immediately. In considering the four cases I ask the following questions: Do these cases represent defense of feeding territories? When should a frugivorous bird defend a fruiting plant? And why has such behavior previously gone unnoticed?

### STUDY AREA AND METHODS

The study was conducted from September, 1977 through March, 1980, on Mt. Missim, 12 km northeast of Wau, Morobe Province, Papua New Guinea, at an elevation of 1,600 m. This site was remote from human disturbance. The tree flora is very rich (ca. 180 species in six ha); epiphytes and vines are diverse and abundant. The community of avian frugivores includes 36 arboreal species, the predominant families being pigeons (Columbidae), birds of paradise (Paradisaeidae), honeyeaters (Meliphagidae), and berrypeckers (Dicaeidae). Av-

TABLE 1. Blue Bird of Paradise defending *S. pachystyla*; numbers of visits to the feeding territory by the defender and visitors for each observation period. Values in parentheses show numbers of visits to branches A, B, and C.

Day April 1979	Time	Defender visits			Visits by visitors	
		Feeding	Chases	Total	Feeding	Non-feeding
19	15:00-18:00	3 (2A, 1?)	4	7	i (C)	5
20	15:00-18:00	3 (2A, 1B)	2	3	6 (4B, 2C)	4
21	06:40-07:45	2 (2A)	3	5	4 (1A, 1B, 2C)	0
21	07:46-09:40	0	0	0	7 (7A)	1
22	14:40-16:10	0	0	0	5 (4A, 1B)	0
22	16:11-18:00	2 (2A)	1	4	2 (1A, 1B)	0
27	06:50-08:50	0	0	0	0	0
Totals:						
First 4 periods (740 min)		10 (8A, 1B, 1?)	10	19	25 (13A, 7B, 5C)	10

erage mass is taken from birds captured during banding and from specimens at the American Museum of Natural History; measurements from other authors are cited accordingly.

Observation periods varied in length and number for each of the four cases. However, during each period the activities of the birds were recorded at two-minute intervals. Birds were viewed with binoculars and a telescope. Marked birds were color-banded at least one month before observation; in most cases they had been banded for much longer.

## RESULTS

### PARADISAEA RUDOLPHI DEFENDING SCHEFFLERA PACHYSTYLA

*Schefflera pachystyla* Harms (Araliaceae) is an epiphytic shrub with ropy branches 5–7 m long. Each branch periodically produces a terminal inflorescence composed of three to six radiating branches, each about one m long and bearing 20–50 “cones.” Ten to 20 hard conical berries are tightly anchored in the cone. Each berry (ca. 15 × 20 mm) contains 15–20 flat seeds. Ripening fruits turn color from red to purple and are available year-round within the population (Pratt 1983).

I monitored a fruiting *S. pachystyla* shrub in 1978 when it was not defended and in 1979 when a defender was present. Observation periods for 1978 totaled 975 min: 27 July (15:00–18:00), 3 August (14:35–17:50), 4 August (7:00–11:00), 9 August (14:45–17:45), and 10 August (14:45–17:45). Observation time in 1979 totaled 920 min (Table 1). The quantity of fruit at the shrub differed between the two years; much more fruit was available the second year. In 1978 the shrub bore only one fruiting branch with 26 fruiting cones, while the next year it bore fruit on three branches (A, B, and C), which were visited differently by the defender and visitors. At the beginning of the study, branch A (38 cones) was just ripening, B bore 35–40 ripe cones, and C had

remaining 13–15 partly eaten ripe cones. By the end of the study 18 cones were on A, 13 on B, and none on C. The distance A to B was an estimated 8–10 m, A–C 5 m, and B–C 8 m. In 1979 a large vine, *Palmeria arfakiana* Becc. (Monimiaceae), 30–35 m away, attracted some of the birds also feeding at the *S. pachystyla*.

At my study site virtually the only birds to feed on *S. pachystyla* fruit were four species of partially frugivorous birds of paradise: the Blue Bird of Paradise (*Paradisaea rudolphi*, ♀ 145 g), Lawes's Six-wired Parotia (*Parotia lawesii*, ♂ 165 g, ♀ 145 g), Superb Bird of Paradise (*Lophorina superba*, ♂ 90 g, ♀ 65 g), and Magnificent Bird of Paradise (*Diphyllodes magnificus*, ♂ 80 g; Pratt 1983).

In 1978, only Lawes's Parotia and Superb Bird of Paradise made feeding visits, and I witnessed only one possible case of aggression.

In 1979, a banded female Blue Bird of Paradise repeatedly visited and defended the *S. pachystyla* on the first four days of observation: eight visits for feeding only, two visits for feeding followed by defense of branch A, two visits for defense of branch A followed by feeding, and seven visits for defense alone. The Blue Bird of Paradise visited the shrub only briefly; it either attacked trespassers from outside the shrub when they arrived, or flew to the shrub shortly before the visitor. I do not know how the bird of paradise kept the shrub under surveillance because it was difficult to tell where she went upon leaving it. Once I saw her perch in foliage close by, at other times she moved through the crowns of nearby trees, and I also observed her leaving in the direction of the *Palmeria* vine. My impression was that the bird restricted her other activities to the vicinity of the *S. pachystyla*.

Active defense behavior included vocalizing, supplanting visitors, chasing, or redirected aggression, when the Blue Bird of Paradise bit leaves on branch A and ripped them to pieces. In addition to the 19 visits by the defender, I

witnessed 17 visits by Lawes's Parotia, 16 visits by Superb Birds of Paradise, and 2 visits by Magnificent Birds of Paradise. The sole interaction between visitors occurred when a parotia supplanted a Superb Bird of Paradise on branch A.

The Blue Bird of Paradise focused her defense on branch A, rather than on all three fruiting branches. She did not forage randomly in the shrub but instead took fruit almost exclusively at A ( $P < 0.05$ , two-tailed binomial test for a one-sample case, Siegel 1956): A, eight feeding visits; B, one; C, none; and branch unrecorded, one visit. Though visitors made 13 feeding visits to A and 12 feeding visits to B and C, the temporal distribution of these visits followed a pattern, with visits to A clustered into two periods when the Blue Bird of Paradise was apparently absent: on 21 April at 7:46–9:40 and on 22 April at 14:40–16:10, for a total of 11 feeding visits. When the Blue Bird of Paradise was defending the shrub, the only two feeding visits by visitors at A were disrupted by the defender. Feeding visits by visitors took place at B and C once when the Blue Bird of Paradise was away and 11 times when it was present; in three of these instances the defender was actually in the shrub, perched on A. The choice of fruiting branches by visitors, as influenced by the presence or absence of the defender, was statistically significant ( $P < 0.005$ , Fisher exact probability test, one-tailed, Siegel 1956).

In order to measure the effect that the defender might have on feeding visits by visitors, I counted the numbers of fruit swallowed by the birds on each visit for 1978 and 1979 (Table 2). Individual feeding rates could not be determined because in both years most visitors were not banded; however, it was evident from plumage differences that more than one individual of each species was involved. Instead, I recorded the numbers of fruits consumed per visit. In both years some birds entered the shrub, but did not feed; these data were not included in the analysis since the birds may have to inspect the fruit crop before deciding whether to feed or not. However, all visits are entered in Table 2. A factorial analysis of variance (using the GLM procedure of SAS statistical package) with years and species as classes, showed a significant difference between species ( $P < 0.0001$ ) and significant interaction between years and species ( $P < 0.01$ ). A Duncan Test of the means showed significant differences (at the  $\alpha = 0.05$  level) between the Superb Bird of Paradise and the two larger species, but not between the parotia and the Blue Bird of Paradise. For the two visiting species, the years also differed significantly, chiefly because

TABLE 2. Blue Bird of Paradise defending *S. pachystyla*; quantities of fruit taken per visit for three bird species are given.

Bird of paradise species	Year	Number of fruit eaten per visit						
		1	2	3	4	5	6	0
Blue	one	absent						
Blue	two	0	1	4	2	0	1	0
Parotia	one	0	1	2	4	2	0	5
Parotia	two	3	0	3	1	0	0	5
Superb	one	5	0	0	0	0	0	0
Superb	two	8	4	1	0	0	0	1

the parotias took less fruit in 1979 when the defender was present; means for the Superb Bird of Paradise increased. The latter species posed several problems for data analysis since the amount of food it took per visit was often equivalent to the unit of measurement (i.e., one fruit) and because fruit fragments swallowed by these birds were difficult to quantify; I gave these a cumulative score of one fruit per visit.

#### *EUDYNAMIS SCOLOPACEA* DEFENDING *CF. CHISOCHETON* SP.

This fruiting tree, cf. *Chisocheton* sp. (Meliaceae), was monitored on 20, 22, and 27 December 1978. Its small spherical crown reached a height of about 20 m. The fruits were woody capsules (2.0–2.5 cm diam.), dehiscent to expose two to four black seeds enclosed at the base by a bright orange aril; the seed-aril unit measured  $12 \times 16$  mm. Initially the tree bore ca. 1,200 fruits in loose clusters within the foliage. On the last day of observation 250 fruits remained. The reproductive phenology of this rare species is unknown.

The defender at this tree was an adult male Indian Koel (*Eudynamis scolopacea*, ca. 170 g), a large black cuckoo. The bird was not marked, but its extraordinarily long visits to and rigorous defense of the tree suggested that the same individual made all visits. During the 482 min of observation (Table 3), the koel spent 130 min (27% of the time) perched near the feeding tree and 253 min (52%) in the tree, of which 63 min (13%) were spent feeding. Thus, the defender was definitely present on the territory for 383 min (79%). The only bird permitted to feed in the tree was a female koel. I saw eight attacks on other visitors: six times against Black-eared Catbirds (*Ailuroedus melanotis*, 200 g) in bands of three to five birds, once against a fruitdove (*Ptilinopus* sp., 125 to 150 g) and once against an unidentified bird of paradise. Catbirds never entered the fruiting tree and were attacked nearby. The two other species alighted in the tree but were driven out before they could feed. Four of the attacks were

TABLE 3. Indian Koel defending *Chisocheton* sp.; rates of visitation, feeding, and attacks on potential visitors are shown.

Observation periods		Koel behavior		
Day				
Dec. 1978	Time	Visits to tree	Feeding bouts	Attacks on visitors
20	14:50-17:54	15:00-17:54	5	5
22	14:30-17:30	15:05-17:30	2	1
27	14:42-16:40	15:36-16:40	3	2

not immediately followed by feeding. Agonistic behavior included singing, rushing flights at visitors, and supplanting.

*MELIDECTES TORQUATUS* DEFENDING  
*DENDROCNIDE* CF. *TERNATENSIS*

*Dendrocnide* cf. *ternatensis* (Miq.) Chew (Urticaceae) is a fast-growing tree that colonizes forest gaps. Annually, during the early wet season (August to October), female trees bear numerous loose panicles of several hundred fruit each; fruiting may also occur at other times of year (Pratt 1983). The fruit consists of a disk-shaped nut (1-2 mm diam.) enclosed at the base by a fleshy lavender stem (2-6 mm diam.).

In 1978, I observed a *D. ternatensis* tree for 11 h. Cinnamon-breasted Wattlebirds (*Melidectes torquatus*, 47 g) were absent from the tree that year. Of the 30 visits by other birds, four were by larger birds, the Rainbow Lory (*Trichoglossus haematodus*, ♂ 135 g, ♀ 120 g, Diamond 1972) and Superb Bird of Paradise. Twenty-six were by small birds, the Common Melipotes (*Melipotes fumigatus*, 47 g) and three species of berrypeckers (*Melanocharis* spp., 12 to 20 g). Aggressive interactions did not take place.

A color-banded male Cinnamon-breasted Wattlebird defended the tree in 1979 (Table 4). This aggressive honeyeater forages for insects, nectar, and occasionally small fruits (pers. observ.). The male was sometimes joined at the tree by a smaller conspecific, probably a female, which was marked with only an aluminum band. Of 36 visits by wattlebirds, the banded male was identified on 19 visits, including six of the nine attacks on other birds; the female was identified on five visits. I did not see any wattlebirds without bands or with different bands at the tree. The six species of visitors included the Rainbow Lory, Lawes's Parotia, Superb Bird of Paradise, Magnificent Bird of Paradise, Common Melipotes, and Mid-mountain Berrypecker (*Melanocharis longicauda*, 15 g). Some of the birds of paradise were color-banded; individuals of other species were not. The wattlebirds and all visitors made brief feeding trips and did not linger in the tree

TABLE 4. Wattlebird defending *D. ternatensis*; number of visits for the color banded male wattlebird, for visitors the same size or smaller than the wattlebird, and for visitors larger than the wattlebird are shown.

Day		Number of visits		
Sept. 1979	Time	Wattle-bird	Small	Large
21	15:00-18:00	3	0	0
22	06:30-09:40	10	5	10
27	06:30-09:30	2	1	2
27	15:00-18:00	4	5	2

between foraging bouts. When a bird left this tree it usually disappeared immediately into the surrounding forest. My impression was that few of these birds hid in nearby foliage between foraging bouts.

Feeding visits by the wattlebirds were more frequent than visits by other species, with at least 30 visits by the two wattlebirds in contrast to 25 visits by all other species combined (Table 4). Most of the visitors (14 visits) were larger than the wattlebirds. Certain of the color-banded larger birds (a male and a female Superb Bird of Paradise and a female Magnificent Bird of Paradise) were seen to visit the tree repeatedly (data including casual inspection outside of the observation periods). In 14 visits by large birds, the wattlebird attacked five, of which 3 left; in 11 visits by birds smaller or the same size as the wattlebirds, 4 were driven away. Only once did the male wattlebird return to the tree to attack a visitor but not to feed. Agonistic behavior included loud vocalizations, supplanting, and chasing.

*REINWARDTOENA REINWARDTSI* DEFENDING  
*SCHIFFLERA CHAETORRHACHIS*

Similar in many respects to *S. pachystyla*, the shrub defended by the Blue Bird of Paradise, *S. chaetorrhachis* Harms. differs in being larger in all proportions except for its tiny fruits. The inflorescence is composed of numerous sinuous branchlets, each 0.5-0.7 m long and bearing ca. 100 fruiting heads. These branchlets radiate from a central axis and give the inflorescence a medusa-like appearance. The fruiting heads (1.5 cm diam.) are composed of clustered fruitlets, each 6 × 4 mm and containing three to five seeds. I counted 20-30 fruitlets per head and estimated the crop to be 10<sup>5</sup> fruitlets. Fruitlets ripen from white to pale violet; however, because of a rusty tomentum, the color change is apparent only at close range. *S. chaetorrhachis* appears to bear fruit annually at the end of the dry season (June to August).

A Reinwardt's Long-tailed Pigeon (*Reinwardtoena reinwardtsi*, 200 g) defended the shrub I watched (Table 5). I have observed this

TABLE 5. Long-tailed Pigeon defending *S. chaetorrhachis*; visitation and feeding times for the pigeon and the numbers of visitors that visited the shrub and the numbers attacked are shown.

Day Aug. 1979	Time	Pigeon		Visitors	
		Visits	Feeding	Visits	Attacked
22	16:12–18:02	16:30–16:47	—	0	
		17:26–17:46	17:16–17:46	0	
23	15:00–18:00	15:00–15:04	—	0	
		15:59–17:48	17:17–17:48	6	5
24	15:15–18:00	16:29–17:51	16:29–17:39 (34 min.)	5	4
		absent		1	
25	06:50–09:50	06:50–07:35	07:19–07:26	0	
		08:54–09:50	—	11	11
		absent		17	
29	15:10–18:10	absent		8	
30	06:55–09:55	two short visits, 3 min.	—	0	
		absent		41	
31	06:55–09:50	absent		13	
7 Sept.	06:50–09:52	absent		20	

species feeding only on the unripe and ripening fruits of four species of trees and shrubs in the Araliaceae; this pigeon may digest seeds as well as fruit pulp. I recognized the defender on all visits by the condition of its molting plumage and by a white chip in its bill. When not feeding, the pigeon spent long periods at the shrub or conspicuously perched nearby. Visitors included ten species of passerines: the Trumpet Bird (*Phonygammus keraudrenii*, ♂ 180 g, ♀ 160 g), Lawes's Parotia, Superb Bird of Paradise, Magnificent Bird of Paradise, Black-eared Catbird, Common Melipotes, Grey Honeyeater (*Pycnopygius cinereus*, 46 g; Diamond 1972), Tit Berrypecker (*Oreocharis arfaki*, 20 g), Mid-mountain Berrypecker, and Streaked Berrypecker (*Melanocharis striativentris*, ♂ g 18, ♀ 20 g; Diamond 1972). Visits by these birds lasted less than 10 min and seldom included more than one feeding bout. Few visitors were color-banded. The pigeon attacked all other species. Of the 22 visitors that did enter the shrub when the pigeon was present, 20 were driven away. The pigeon called rarely. It behaved agonistically by clapping its wings loudly while attempting to alight on the visitor. The pigeon did not immediately feed after 17 of these attacks.

## DISCUSSION

The three criteria essential to defining a territory, as set forth by Brown and Orians (1970), are met by three of the four cases, and are partially met by the fourth case, the wattlebird at *D. ternatensis*:

(1) In all cases, the fruiting plant defined the "fixed area" visited and defended. The Blue Bird of Paradise defended only the part of the plant in which it fed. I did not determine if defended areas included other fruiting plants.

(2) In all cases, the defender acted by supplanting behavior (all cases), chasing (all but the wattlebird), and redirected aggression (Blue Bird of Paradise). Defenders vocalized infrequently, and only the koel and wattlebird occasionally called immediately before or during a supplanting or chase. Perhaps vocalizations more effectively deter conspecifics, by advertising the feeding territory from a distance. I did not observe conspecifics at feeding territories except at two territories defended by males (koel and wattlebird) where in each case a single female fed. The Blue Bird of Paradise and koel ambushed visitors from perches near the feeding territory. In this way, they may have discouraged visitors even when they were absent, since experienced visitors could not tell whether or not they would be attacked. Alternatively, because fruiting plants may attract predators (Howe 1979), defenders may have been avoiding predation by leaving the plant.

(3) In three cases (all but the wattlebird), the defended area was exclusive to rivals when the defender was present. Visitors fed at the territories of the Blue Bird of Paradise and pigeon when these defenders were absent. Only the wattlebird failed to evict visitors; it successfully routed birds smaller than or the same size as itself, while larger birds often remained. However, the wattlebird's defense could have accounted for the lower numbers of smaller species recorded in the year when the wattlebird was present, compared with the year when it was absent. All species visiting the territories elicited aggressive responses from territory holders, a pattern in common with many cases of interspecific territoriality (Murray 1981).

Arguably, the aggressive behavior observed in the four cases was not defense of feeding territories, but instead behavior enabling these

individuals to gain access to fruit at any plant. If so, more than one aggressive conspecific could have been observed at each plant, and aggressive birds should have been aggressive only during feeding visits. However, I show that these cases were feeding territories because:

(1) In three cases (all but the koel), the same recognizable, aggressive individual was the only bird defending the plant. No other aggressive birds visited the fruiting plants; indeed, few conspecifics were recorded. Also, the recognizable individuals repeatedly fed at the fruiting plant within and among observation periods.

(2) In all cases feeding by other birds was reduced or prevented, as explained above. Although parotias fed at the shrub defended by the Blue Bird of Paradise, they ate fewer fruits per visit than the defender and fewer than parotias in another year when the defender was absent. Presence of the Blue Bird of Paradise, and particularly, defense of the most desired part of the shrub, were associated with lessened feeding by parotias.

(3) In three cases (all but the wattlebird), the defender frequently chased away other visitors even when it was not feeding. The defender either returned to the territory specifically to rout visitors (especially in the case of the Blue Bird of Paradise) or waited in or near the fruiting plant between feeding bouts (koel and pigeon). Defense not associated with feeding suggests that defenders were actually protecting fruit for later consumption.

When should a frugivorous bird defend a fruiting plant? The defender must choose a fruit crop large enough to sustain itself. If a fruit crop is too small, the defender must forage elsewhere and could lose too much food to other birds visiting the territory in its absence. A large fruit crop would be impractical to defend because: (1) if other birds seldom visited, the defender could give up defense and still get enough to eat; (2) if other birds visited often, defense would require too great an effort; and (3) defense would be logistically impracticable if many visitors were to arrive simultaneously. For example, foraging in flocks enables mockingbirds to invade feeding territories (Merritt 1980). Howe and Vande Kerckhove (1979) showed that frugivore visitation rates depend directly on the size of the food crop for a single species of tree in one season. This suggests that, to avoid high encounter rates with visitors, a defender should choose a territory of intermediate crop size.

Feeding territories are defended only under certain conditions, so frugivorous birds forage uncommonly in this way. I observed bird vis-

itation at 29 fruiting plants, and only these four cases represent feeding territories. Other factors help to explain why defense of fruiting plants has not been previously reported for the tropics. Field biologists most often notice and choose to study fruiting trees with large crops and high visitation rates by birds. My data show that defended fruiting plants are seldom visited by other birds. It is difficult to observe defense by frugivores; chases are few, and feeding territories are even more inconspicuous when defenders station themselves outside the plant. Lastly, since some nonterritorial birds behave aggressively at fruiting plants, individuals must be recognizable in order to identify a feeding territory.

## ACKNOWLEDGMENTS

I wish to thank: assistants Diro and Meparon, the staff of Wau Ecology Institute, and the Government of Papua New Guinea for making this study possible. M. LeCroy made available the collections of the American Museum of Natural History. J. Burger, C. F. Leck, M. LeCroy, E. W. Stiles, and D. W. White provided critical comments and discussion. Fieldwork was supported by fellowships granted by the Smithsonian Institution.

## LITERATURE CITED

- BOURNE, G. R. 1974. The Red-billed Toucan in Guyana. *Living Bird* 13:99-126.
- BROWN, J. L., AND G. H. ORIANS. 1970. Spacing patterns in mobile animals. *Annu. Rev. Ecol. Syst.* 1:239-262.
- CARPENTER, F. L., AND R. E. MACMILLEN. 1976. Threshold model of territoriality and test with a Hawaiian honeycreeper. *Science* 194:639-642.
- CROME, F. H. J. 1975. The ecology of fruit pigeons in tropical northern Queensland. *Austr. Wildl. Res.* 2: 155-185.
- CRUZ, A. 1974. Feeding assemblages of Jamaican birds. *Condor* 76:103-107.
- DIAMOND, J. M. 1972. Avifauna of the Eastern Highlands of New Guinea. *Publ. Nuttall Ornithol. Club* No. 12.
- FOSTER, M. S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* 58:73-85.
- GILL, F. B., AND L. L. WOLF. 1975a. Economics of feeding territoriality in the Golden-winged Sunbird. *Ecology* 56:333-345.
- GILL, F. B., AND L. L. WOLF. 1975b. Foraging strategies and energetics of East African sunbirds at mistletoe flowers. *Am. Nat.* 109:491-510.
- HOWE, H. F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. *Ecology* 58:539-550.
- HOWE, H. F. 1979. Fear and frugivory. *Am. Nat.* 114: 925-931.
- HOWE, H. F., AND D. DE STEVEN. 1979. Fruit production, migrant bird visitation, and seed dispersal of *Guarea glabra* in Panama. *Oecologia* 39:185-196.
- HOWE, H. F., AND J. SMALLWOOD. 1982. Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13:201-228.
- HOWE, H. F., AND G. A. VANDE KERCKHOVE. 1979. Fecundity and seed dispersal of a tropical tree. *Ecology* 60:180-189.
- LECK, C. F. 1972. Seasonal changes in feeding pressures of fruit- and nectar-eating birds in Panama. *Condor* 74:54-60.
- MCDIARMID, R. W., R. E. RICKLEFS, AND M. S. FOSTER.

1977. Dispersal of *Stemmadenia donnell-smithii* (Apocynaceae) by birds. *Biotropica* 9:9–25.
- MERRITT, P. G. 1980. Group foraging by mockingbirds in a Florida strangler fig. *Auk* 97:869–872.
- MOORE, F. R. 1977. Flocking behavior and territorial competitors. *Anim. Behav.* 25:1063–1065.
- MOORE, F. R. 1978. Interspecific aggression: toward whom should a Mockingbird be aggressive? *Behav. Ecol. Sociobiol.* 3:173–176.
- MURRAY, B. G. 1981. The origins of adaptive interspecific territorialism. *Biol. Rev.* 56:1–22.
- PRATT, T. K. 1983. Seed dispersal in a montane forest in Papua New Guinea. Unpubl. Ph.D. diss., Rutgers University, New Brunswick, NJ.
- PYKE, G. H. 1979. The economics of territory size and time-budget in the Golden-winged Sunbird. *Am. Nat.* 114:131–145.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.
- STILES, F. G., AND L. L. WOLF. 1970. Hummingbird territoriality at a tropical flowering tree. *Auk* 87:467–491.
- 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.
- WILLIS, E. O., AND Y. ONIKI. 1978. Birds and army ants. *Annu. Rev. Ecol. Syst.* 9:243–263.

*P.O. Box 354 CHR, Saipan, CM 96950.* Received 22 May 1981. Final acceptance 26 August 1983.

*The Condor* 86:129

© The Cooper Ornithological Society 1984

## RECENT PUBLICATIONS

**The New Guide to the Birds of New Zealand.**—R. A. Falala, R. B. Sibson, and E. G. Turbott. Illustrated by Elaine Power. 1981. Collins, Auckland and London. 247 p. \$39.95. First published in 1966, this field guide was revised, extended, re-illustrated, and re-set in larger format for a 1978 edition. That, in turn, was subsequently reprinted with Addenda, resulting in the present version. The book presents the native and introduced birds, living or recently extinct, of New Zealand and its outlying islands, for a total of approximately 320 species. Thus the Kakapo (*Strigops habroptilus*), the Huia (*Heteralocha acutirostris*), and the New Zealand Thrush (*Turnagra capensis*) are included, moas are not. With fewer species and a smaller area to cover than most other field guides, the species accounts can be longer than usual while keeping the book in standard size. The accounts are conventionally organized, yet they go into considerable detail where appropriate, particularly on habitat, range, and breeding. Line drawings and 48 color plates portray most of the birds, and include many variations of sex, age, and molt. The Addenda (as of October 1980) comprise four additional species, changes in scientific names, and recent information concerning some of the rarer birds already mentioned. Glossary, references, index, end-paper maps. Clearly indispensable for field identification, this well-prepared guide can also serve stay-at-homes as a handy source of information about the habits of New Zealand's breeding birds.

**The Native Forest Birds of Guam.**—J. Mark Jenkins. 1983. Ornithological Monographs No. 31, American Ornithologists' Union, Washington, DC. 61 p. Paper cover. \$9.00 (\$7.00 to AOU members). Source: Assistant to the Treasurer of the AOU, Dr. Frank R. Moore, Dept. of Biology, University of Southern Mississippi, Southern Station Box 5018, Hattiesburg, MS 39406; all orders must be prepaid and include a \$0.50 handling charge. Situated approximately 1,800 km north of Papua New Guinea, the island of Guam currently has a resident avifauna of 25 species. A megapode (*Megapodius laperouse*) has long since been extirpated, populations of most of the remaining land species have declined drastically, and ten species are officially being considered as endangered. Information needed for a conservation program was sought through a two-

year study, of which this report is a major result. Eleven of the 12 native land birds are considered as to habitats, behavior, food, nesting, distribution, and status. (Jenkins has already published on the endemic rail, *Rallus oustoni*.) The causes of the population declines are briefly discussed and steps toward the conservation of habitats and birdlife are recommended. One appendix gives a complete list of the birds of Guam, another gives data on the abundance of the 11 species of forest birds. Maps, graphs, color photographs, list of references.

**Tropical Seabird Biology.**—Edited by Ralph W. Schreiber. 1984. Studies in Avian Biology No. 8, Cooper Ornithological Society. 114 p. Paper cover. \$12.00. Source: Allen Press, Inc., P.O. Box 368, Lawrence, KS 66044; all orders cash in advance; make checks payable to Cooper Ornithological Society. This book is a collection of six papers that were presented at a symposium of the Pacific Seabird Group in December 1982. The theme of the symposium arranged by Dr. Schreiber, was "the seabirds of the low latitudes and the relationship between those species and the various components of the marine ecosystem found along the temperature-salinity gradient to the north and south." The papers are: "An ecological comparison of oceanic seabird communities of the South Pacific Ocean" by D. G. Ainley and R. J. Boekelheide, "Feeding overlap in some tropical and temperate seabird communities" by A. W. Diamond, "Physiological ecology of incubation in tropical seabirds" by G. C. Whittow, "Growth strategies in marine terns" by N. P. Langham, "Some considerations of the reproductive energetics of pelagic seabirds" by R. E. Ricklefs, and "Contrasts in breeding strategies between some tropical and temperate marine pelecyaniformes" by J. B. Nelson. While these reports will clearly appeal to specialists on these birds, they deserve to be seen by other ornithologists as well, for comparative insights into the different ways that birds feed and reproduce. The discussions that surely followed the original presentations, and that are among the chief values of a symposium, are regrettably lacking. On the other hand, all those who had a hand in producing the volume deserve applause for managing to publish it so soon after the event, yet still have it nicely printed. Illustrations and lists of references.