FRUGIVORY AND POLYGAMY IN BIRDS
OF PARADISE[1]

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ABSTRACT.—I studied fruit-feeding by nine species of birds of paradise in Papua New Guinea from July 1978 through November 1980 and gathered 1,187 records of foraging at 31 species of trees and vines from 14 botanical families. Fruit consumed was consistently small- to moderate-sized (mean: 1 cm diameter), but fruit of different species of plants showed high morphological diversity. I classify the fruit of 31 plant species into three morphological groups: capsule, fig, and drupe/berry. Each of the primarily frugivorous birds of paradise was recorded taking fruits from 10–21 plant species, including representatives from each class.

The monogamous Trumpet Manucode and Crinkle-collared Manucode were fig specialists. More than 80% of their diet was figs. The polygamous species of paradisaeids were more "generalized" fruit-feeders and took significant amounts of fruit from all three morphological categories. The most important types of fruit among the polygamous birds were capsular species (49% of diet). While fig species were visited by birds from many families, most nonfig trees hosted a narrower range of foragers, and two species of trees, *Chisocheton weinlandii* (Meliaceae) and *Gastonia spectabilis* (Araliaceae), were visited only by birds of paradise.

The frugivorous habits of birds of paradise are similar in several respects to those of the neotropical cotingids and manakins. It is argued that while frugivory is an important component of the evolution of polygamous arena display in these birds, it cannot, by itself, explain why some birds are polygamous and others monogamous. Frugivory in the tropics is a complex syndrome that offers a number of ecological alternatives that, in turn, promote different behavioral adaptations. *Received 22 March 1982, accepted 30 June 1982.*

D. SNOW (1962a, b, 1971a, b) and B. Snow (1970, 1972, 1973, 1977) in their studies of the neotropical cotingas (Cotingidae) and manakins (Pipridae) discovered an apparent relation linking the habit of fruit-eating to non-pair-bonding polygamy. D. Snow (1980: 1197) writes:

Probably as a consequence of the very nutritious fruits that they eat, and of the short time per day that they need spend in foraging, some specialized neotropical frugivores have evolved social systems in which males are emancipated from the nest and spend most of their time in epigamic display. . . . It is probable that the evolution of the birds of paradise in the Australian region was made possible by a similar relationship between the birds and their food supply.

There are fundamental differences between the demands of frugivory and those of insectivory. Insects are elusive, dispersed through the habitat, and difficult to harvest, while fruit is locally abundant, "patchy," and relatively simple to harvest in quantity (Lill 1976). Animals that forage for insects must spend a large portion of each day satisfying their dietary demands, while frugivores can quickly fill their crops with fruit and invest the remaining daylight hours in other activities, such as self-ad-

TABLE 1.   The birds of paradise encountered at fruit trees on the Mount Missim study site.

English name[a]	Latin binomen	Weight[b]	Wing[c]	Abun-dance[d]
Crinkle-collared Manucode	*Manucodia chalybatus*	183 ± 18 (3)	173 ± 8	2–3
Trumpet Manucode	*M. keraudrenii*	171 ± 10 (8)	169 ± 4	7–10
Magnificent Riflebird[e,f]	*Ptiloris magnificus*	194 ± 16 (2)	187 ± 2	1–2
Black-billed Sicklebill	*Epimachus albertisii*	108 (1)	156	1–2
Superb Bird of Paradise[g]	*Lophorina superba*	89 ± 5 (4)	136 ± 2	2–4
Lawes' Six-wired Bird of Paradise	*Parotia lawesii*	166 ± 4 (4)	158 ± 4	4–5
Magnificent Bird of Paradise	*Diphyllodes magnificus*	90 ± 8 (12)	112 ± 2	6–7
Raggiana Bird of Paradise	*Paradisaea raggiana*	246 ± 12 (3)	181 ± 2	5–6
Blue Bird of Paradise[g]	*P. rudolphi*	178 (1)	156	1–2

[a] Nomenclature based on Diamond (1972) with some emendations to be used in a checklist of New Guinea birds presently in preparation (B. Finch, H. Bell, and B. Beehler).
[b] Data include weights of adult males only; listed are mean weight, SD, and sample size.
[c] Males only; wing arc.
[d] Abundance as measured by the number of individuals observed using a fruiting tree during a single day.
[e] Weights from Gilliard and LeCroy (1967).
[f] Wing measurements from skins of three adult males, preserved as study skins, National Museum of Natural History, Washington, D.C.
[g] Data from Diamond (1972).

vertisement, mate competition, and defense of a territory, display perch, or mate(s) (Snow 1976, Foster 1977). The logic of this argument is persuasive, although the generalization as I have presented it is oversimplified. The relationship between fruit-eating and polygamous arena-display is supported by the simple observation that the vast majority of polygamous arena birds in the humid tropics are fruit-eaters (Snow 1976, Bradbury 1981).

Several authors have shown that fruit is a prominent part of the diet of some species of birds of paradise (Rand 1940, Gilliard 1969, Schodde 1976), and, in a few instances, the fruit consumed by these birds has been identified botanically (Cooper and Forshaw 1977, LeCroy et al. 1980). To date, however, no systematic account has been published on frugivory by birds of paradise.

While studying the behavior and ecology of four species of birds of paradise in the mountains of central Papua New Guinea, I gathered data on fruit-eating by all bird species sharing fruit resources with these birds of paradise. The avian fruit-eating community included more than 30 species of birds. In this paper I document the types of fruit eaten by nine species of birds of paradise (Table 1) that share this mid-montane study-site, and I show that, while the fruit-crop of some trees is consumed by a wide range of avian foragers, certain tree species produce fruit eaten mostly, and in some instances wholly, by birds of paradise. In the discussion I point out some family-wide trends,

as well as interspecific differences, and compare these observations with those for frugivorous songbirds from the neotropics. Finally, I examine the characteristics of fruit eaten by polygamous arena-displaying birds and comment on the relation of diet to behavior.

STUDY AREA AND METHODS

I studied birds of paradise on a 17-ha plot of forest on the southwest slopes of Mount Missim, at about 1,430 m. The site is 9 km north-northeast of Wau, Morobe Province, Papua New Guinea (7°16′S, 146°42′E). I worked on this site from July 1978 to November 1980, for 249 field-days. The study-site is mature Pre-montane Moist Forest (Holdrige et al. 1971) on highly dissected and well-drained ridge-and-ravine topography. The area receives an annual rainfall of about 2,000 mm (McAlpine et al. 1975) in a moderately seasonal pattern, with more rain falling from November to April. The 17-ha site supports about 80 species of trees and a community of about 125 species of resident birds. The plot is unusual in having nine resident birds of paradise (Table 1). A tenth species, Loria's Bird of Paradise (*Cnemophilus loriae*), is an occasional visitor. Additional details on the habitat and biota of the study-site are presented elsewhere (Beehler 1983).

I documented the diet of the birds by: (1) recording birds visiting fruiting trees, and (2) collecting and identifying the fruit remains in fecal samples taken from captured birds. I made repeated observations of fruit-feeding at plants producing fruit eaten by birds of paradise. In the early months of the study I monitored visits by birds to many species of fruiting plants that my research assistants encountered in the forest. When I found a tree or vine that was regularly

visited by birds of paradise, I began making standardized observations. I recorded all birds that entered the tree to feed; for selected species of paradisaeids I recorded length of feeding-bouts, number of fruit consumed, and interactions with other foragers. I was assisted in this work by two field technicians employed to find new trees and to help with the foraging censuses. Their help made possible the simultaneous observations of avian foraging at several fruit-trees.

We recorded fruit-foraging by sitting near the fruit-tree and watching birds enter, feed, and depart. We identified birds using 7 × 35 and 8 × 44 binoculars, as well as a 15× telescope, depending upon the conditions. We timed observations with digital watches. We observed at trees in the early morning, usually for periods of 1.5–2.5 h, depending upon the productivity of the observations. Birds usually fed at a tree in the first 1.5 h after sunrise, after which foragers were scarce. Certain species of trees that produced huge synchronously ripening fruit-crops were visited by birds during most hours of the day, but even among these plants attendance by foragers was most frequent in mornings and late afternoons.

Most of the fruiting plants on which birds of paradise foraged were rare in the forest (fewer than 1/ha, occasionally fewer than 1/10 ha; Beehler 1983). With the help of two field assistants I conducted intensive seasonal censuses of all plants producing fruit within the 17-ha study site. Each census required about 70 man-hours. The position of all fruiting plants was placed on a topographic map, scale 1:3,300. While the bulk of the data from these surveys will be published elsewhere, information on abundance of the plants, and periodicity of fruit production will be discussed below. Using this intensive survey method, we were able to find most individuals of a number of important plant species used by the birds of paradise. In addition, during these surveys we collected fruit samples that were measured and preserved for botanical identification.

It was difficult to collect foraging data that were directly comparable from tree species to tree species. Different fruiting plants produce crops of differing size, ease of harvest, and ripening periodicity. As a result, birds used these different food sources in different ways that are nearly impossible to account for in the censusing process. I collected data to maximize the number of foraging observations per tree species. These data make it possible to document which birds dominate foraging at particular trees. At trees with large crops of fruit, where birds were abundant, the data came quickly; for smaller resources, or those with gradually ripening fruit crops, more hours of observations were needed to obtain a sufficiently comparable set of data. This biases the data in a way that makes it more difficult to compare the relative popularity of differing fruit trees. Nonetheless, foraging preferences differed so strongly among the

species of birds of paradise that these were not lost in the sampling bias.

The unit of measure in this project was the "feeding-bout": a record of a bird entering a tree and taking at least one fruit. I discovered early in the study that birds of paradise foraged for fruit in a behaviorally stereotyped fashion (see Results section). Consequently, I treat paradisaeid foraging bouts as equivalent. Avian use of fruit resources are quantified and compared in terms of these foraging bouts.

I collected additional data on fruit eaten by birds of paradise by examining fecal samples. I mist-netted birds and placed them in a darkened holding cage with a wire-mesh floor of ½-inch hardware screen. Beneath this was a tray with an aluminum foil liner that trapped all excreta. Some of the material trapped was probably the result of regurgitation, as well. Birds of paradise are known to regurgitate seeds (LeCroy 1981). I released a caged bird after 1 or 2 h of captivity. The feces/regurgitated matter were preserved in 70% ethanol and placed in small vials labeled with data on the bird and date of capture. In the laboratory I washed the samples and separated fruit from arthropod contents. I matched seeds by comparison to a botanical reference collection made on the study site and identified with the assistance of several botanists and the resources of the National Herbarium, Lae, Papua New Guinea. We were able to identify nearly all fruit material to genus, and some material was referred to particular species by direct comparison to dried or alcohol-preserved specimens at the National Herbarium. Fruit samples are presently held by the author; voucher specimens are deposited at the herbarium of the Wau Ecology Institute, Wau, Papua New Guinea.

For analysis, the data from the two sampling methods are united. The observations at fruit trees (1,000+) far outnumber the data from fecal samples (100+). A fruit-in-feces record is given equivalence to a single "feeding-bout" at a fruit tree. A fecal sample is considered a measure of presence in the diet of particular fruit species. Each sample is counted as a single record regardless of the number of seeds contained.

RESULTS

Method of harvest.—When I began observing paradisaeid fruit feeding, I conjectured that the different bird species would use the fruit resources in measurably different ways. After an initial period of observation, I got the clear impression that the birds were behaving in a similar fashion: the typical individual would enter the tree warily, forage nervously but discriminatingly (testing and rejecting fruit), and would leave after 2–5 min. On many occasions a single individual would visit the same tree

TABLE 2. Record of feeding bouts by nine bird of paradise species at 31 food plants.

Plant name	Fruit type[b]	Birds of paradise[a]									Tree species totals
		CCM	TMA	MRI	BBS	SBP	LSW	MBP	RBP	BBP	
Aglaia	C	—	—	—	—	—	1	—	3	—	4
Aporusa	C	—	—	—	—	1	—	—	—	—	1
Canthium	D	—	—	—	—	—	—	1	—	—	1
Chisocheton[c]	C	1	7	16	5	23	10	13	13	3	91
Cissus hypoglauca[c]	D	—	13	1	1	1	2	4	5	3	28
C. aristata	D	1	—	—	—	—	—	1	—	—	2
Dysoxylum[c]	C	—	1	—	—	—	1	12	17	—	31
Elmerrillia[c]	C	1	8	—	1	2	2	12	2	—	28
Endospermum[c]	D	—	2	—	—	9	2	15	2	—	30
Ficus drupacea[c]	F	—	2	—	—	—	—	—	—	—	2
Ficus gul[c]	F	25	155	—	—	1	12	8	45	1	247
F. odoardi[c]	F	19	55	2	—	1	6	8	20	—	111
Ficus #202	F	1	2	—	—	—	—	1	—	—	4
Ficus #181	F	—	7	—	—	—	2	—	—	1	10
Ficus #217	F	—	9	—	—	—	—	—	—	—	9
Ficus #246[c]	F	1	4	—	—	—	—	2	—	—	7
Ficus #275[c]	F	8	40	—	—	2	1	5	13	4	73
Ficus #371	F	1	6	—	1	4	4	—	3	7	26
Gastonia[c]	D	—	17	7	—	—	22	58	24	3	131
Glochidion	C	—	—	—	—	—	—	1	—	—	1
Homalanthus[c]	C	—	4	8	—	17	10	104	75	23	241
Myristica	C	—	3	—	—	—	3	1	1	—	8
Pandanus[c]	D	—	—	—	—	2	—	5	2	1	10
Piper	D	—	1	—	—	—	—	—	—	—	1
Schefflera	D	—	—	1	—	—	47	2	—	10	60
Sloanea aberrans	C	—	—	—	—	—	—	2	—	—	2
S. sogerensis	C	—	2	—	—	2	2	4	1	—	11
Sterculia	C	—	—	—	—	—	1	—	—	—	1
Syzygium	D	—	8	—	—	—	1	—	1	—	10
Uvaria	D	—	2	—	—	—	—	—	—	—	2
Zingiberaceae	C	1	—	—	—	—	—	2	—	1	4
Bird feeding totals:		59	348	34	7	65	129	261	227	57	1,187

[a] The three-letter abbreviations are formed from the first letter of the generic name plus the first letters of the specific name. Decoded, they are: CCM = Crinkle-collared Manucode; TMA = Trumpet Manucode; MRI = Magnificent Riflebird; BBS = Black-billed Sicklebill; SBP = Superb Bird of Paradise; LSW = Lawes' Six-wired Bird of Paradise; MBP = Magnificent Bird of Paradise; RBP = Raggiana Bird of Paradise; BBP = Blue Bird of Paradise.

[b] The abbreviations for fruit-types are: C = capsule, F = fig, and D = drupe/berry.

[c] Plants marked with this footnote are illustrated in Fig. 1.

several times in a morning, but each visit would be relatively brief.

Initially, I measured length of foraging bouts for three species: Trumpet Manucode, mean length of foraging bout = 220 s ± 89 SD, n = 18; Raggiana, mean = 178 ± 122 SD, n = 26; Magnificent, mean = 171 ± 101 SD, n = 26. These data show no significant difference (one-way ANOVA, F = 1.2, P = 0.3). In addition, I compared data for the number of fruit taken per bout: Trumpet Manucode, mean number of fruit eaten per bout = 7.6 ± 5, n = 11; Raggiana, mean = 5.4 ± 7, n = 20; Magnificent, mean = 5.3 ± 6, n = 17.

The different species of birds of paradise tended to forage for fruit in a stereotyped fashion. They rarely or never rested or preened in the tree where they were feeding; to perform such activities they invariably moved to adjacent vegetation. They preferred to feed in a tree that was already occupied by other foragers, although this generalization does not hold for small fruiting plants that could accomodate one or two birds at a time. Once a foraging group assembled in a fruit tree, foraging was kinetic. The bustle of activity was punctuated by rapid evacuations of the tree, in what I presume were predator-escape maneuvers. Many times I watched groups of birds flush from fruit trees, dropping nearly vertically toward the ground, then veering into the nearest vegetation. I never observed predators in these instances, but predators were present on the study site, and I did find carcasses of birds that had been con-
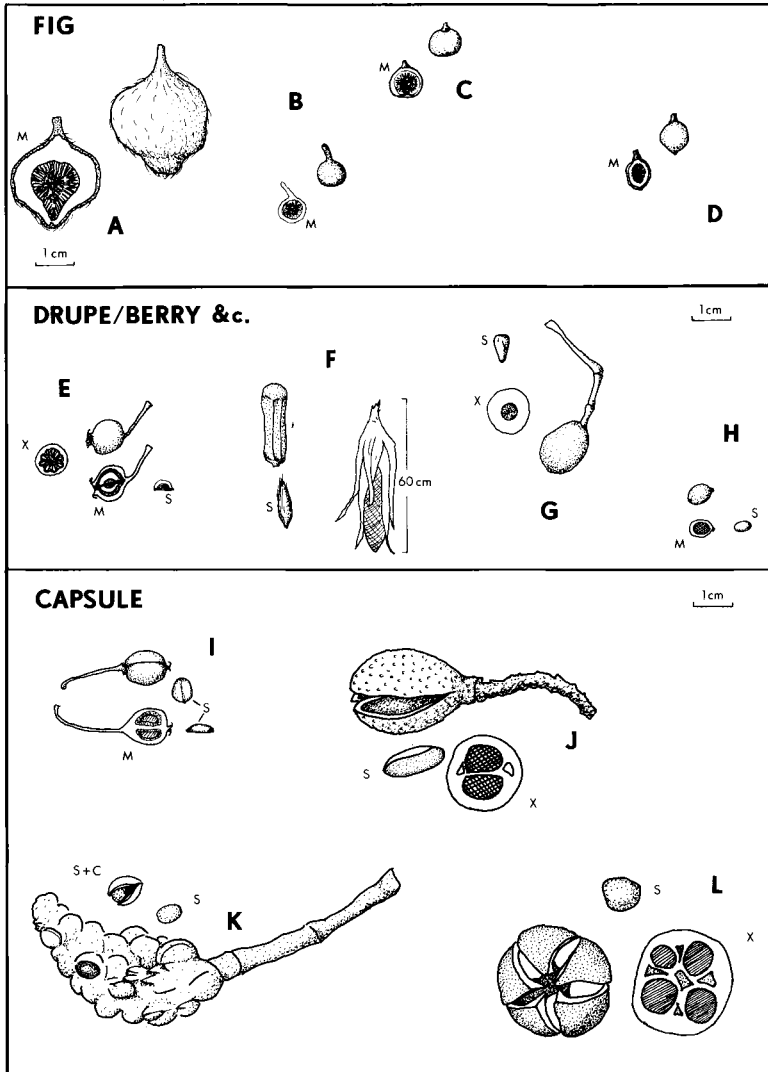
Fig. 1. Selected fruits from the three morphological classes. Abbreviations are: S = seed; M = longitudinal/medial section; X = transverse/medial cross-section. A. *Ficus odoardi*. B. *Ficus gul*. C. *Ficus* #275. D. *Ficus* #246. E. *Gastonia spectabilis*. F. *Pandanus conoideus*. G. *Cissus hypoglauca*. H. *Endospermum medullosum*. I. *Homalanthus novoguineensis*. J. *Dysoxylum* cf. *macrothyrsum*. K. *Elmerrillia papuana*. L. *Chisocheton weinlandii*.

sumed by forest hawks. I believe that the fear of predation may be one of the forces modifying fruit-foraging behavior in the species of birds of paradise. It is a conservative force, inadvertently suppressing the acquisition of interspecifically different foraging methods among the species (Howe 1979).

Birds of paradise harvest fruit while perched and never take items in flight, as is characteristic of the prominent neotropical fruit-eaters, the cotingids and manakins (Snow 1976).

The fruit.—For the nine species of birds of paradise at the Mount Missim study site, I obtained 1,187 records (Table 2) of foraging at 31 species of trees and vines of 14 botanical families (see Appendix for data on plants, their taxonomy, and morphology). The fruit of the 31 species varied from 3 mm in diameter (edible portion) for *Glochidion* to 28 mm for *Ficus odoardi*. This difference in size did not appear to limit edibility to birds of paradise. The smallest bird in the group, the Magnificent Bird

of Paradise, consumed both the smallest and largest fruits. The largest bird, the Raggiana Bird of Paradise, was recorded taking the largest and second smallest fruits.

Morphology of the fruits varied interspecifically (Fig. 1 a–l). I classify the fruits into three morphological groups. (1) *Fig* (Fig. 1 a–d), fruits from plants of the genus *Ficus*, "an aggregate fruit formed by enlarged fleshy cups containing numerous small achenes" (Johns 1976: 107). The bird either swallows the entire fig or, when the fruit is large, pecks off fleshy pieces of it. (2) *Capsule* (Fig. i–l), fruit that has a seed with edible aril encased within an inedible, dehiscent capsule (included in this general class are: legume, follicle, pod, and etario; Foster and Gifford 1974, van der Pijl 1972). To feed, the bird plucks the seed with attached aril from the opened capsule and swallows it, later either regurgitating or defecating the seed. (3) *Drupe/berry* (Fig. e–h), simple, compound, and aggregate fruits with seeds surrounded by fleshy edible pericarp. In all species listed in Table 2, the fruit (or fruitlet) in the drupe/berry class is eaten whole (see Jensen and Salisbury 1972).

Of the 31 plant species whose fruit was taken by the nine birds of paradise, 12 were capsular (412 observations), 10 were from the drupe/berry class (275 observations), and 9 species were figs (500 observations).

Figs ranged in diameter from 6 to 28 mm (mean 12 mm). Color of ripe figs varied from orange (4 species), green (2), red (1), and pink (1) to whitish (1). The most common growth-form was hemiepiphytic strangler, which is epiphytic in its early stages, then develops into a free-standing tree after it grows large and kills the host tree that originally supported it. Five species were stranglers, two were vines, and two were canopy trees. Fig fruit-crops ranged from huge (100,000) to small (5,000); in the larger species, with large crops, the fruit ripened synchronously over a season as short as 1½ months. Many species of foragers were attracted to these large crops, and the figs were, in most cases, simple to harvest, being arrayed on the twigs and smaller limbs.

The 10 species in the drupe/berry category varied from 6 to 20 mm (mean 13 mm). The most common color of the ripe fruit was red (4), with two each of yellow and white, and a single purple fruit. These fruits were displayed on vines (5 species), canopy trees (3), and understory trees (2). Their crops ranged from small (2,000 for *Schefflera pachystyla*) to moderate (15,000 for *Cissus hypoglauca*), with fruiting seasons from 2 to 12 months long and low synchrony of fruit ripening within the crop.

The fruits of the capsule category ranged in size from 3 to 16 mm (mean 10 mm). Coloration is two-part in this class. The outer shell of the dehiscent capsule is one color, and the edible aril is invariably another color, often contrasting with that of the capsule. In the species of this class, the arils were: red (5); orange (3); pink, brown, and white (1 each). The color of the outer capsule ranged from brown (6) to green (4) and orange-tan (1). Plants producing capsular fruit were predominately canopy trees (6) or understory trees (4). The fruit-crops were very small (less than 300) to moderate (12,000), with low synchrony of ripening and a season lasting from 1½ to 5 months.

Summarizing, the fruits eaten by the birds of paradise ranged in size from 3 to 28 mm diameter (mean 10 mm). These measurements of external diameter are not indicative of the volume of edible material because of the variation in seed size; they are an important indication, however, of the average size of the nutritional "package" acceptable to foraging birds of paradise. The two most common fruit colors were red and orange. Van der Pijl (1972) notes that red and blue/purple are the most popular colors for bird-dispersed fruits. Growth forms varied: canopy tree (11), understory tree (7), vine (7), strangler (5), herbaceous shrub (1).

The birds and their feeding preferences.—For five species of birds of paradise, I have fewer than 100 feeding observations per species (Tables 2 and 3). For these, I can make only guarded comments on feeding preferences. Of 59 feeding observations of the Crinkle-collared Manucode, 55 (93%) were at figs. This bird was a fig specialist. Data on foraging by Black-billed Sicklebill and Magnificent Riflebird (Beehler 1983; unpubl. data) show that these birds were largely insectivorous. Both spent a preponderant amount of time gleaning for insects on bark and dead wood. This agrees with data from Schodde (1976). The Superb and Blue birds of paradise were recorded at 12 and 11 species of fruiting plants, respectively, from all three fruit categories.

The four species for which I have more than 100 observations each merit individual accounts. Like the Crinkle-collared Manucode, the Trumpet Manucode was a fig specialist. I recorded the Trumpet Manucode at 21 species of

TABLE 3. Paradisaeid preference for fruits from the three morphological classes.[a]

Bird species[c]	Fruit classes[b]		
	Fig	Capsule	Drupe/berry
Crinkle-collared Manucode	55 (93%)	3 (5%)	1 (2%)
Trumpet Manucode	280 (80%)	25 (7%)	43 (13%)
Magnificent Riflebird	2 (6%)	24 (71%)	8 (23%)
Black-billed Sicklebill	1	6	—
Superb Bird of Paradise	8 (12%)	45 (69%)	12 (19%)
Lawes' Six-wired Bird of Paradise	22 (17%)	33 (26%)	74 (57%)
Magnificent Bird of Paradise	24 (9%)	151 (58%)	86 (33%)
Raggiana Bird of Paradise	81 (36%)	112 (49%)	34 (15%)
Blue Bird of Paradise	27 (47%)	13 (23%)	17 (30%)
	500	412	275

[a] See text for identification of fruit classes.
[b] First number is total of field observations of bird taking this type of fruit; second number, in parentheses, is percentage of bird's diet of fruit.
[c] See Table 1 for full data on bird nomenclature.

fruiting plants; this list includes all nine species of figs. This fig component made up 80% of the bird's foraging records. The two species of *Manucodia* showed a foraging preference unlike any other birds of paradise in the study.

Lawes' Six-wired Bird of Paradise was recorded feeding at 18 species of fruiting plants from all three categories. The vine, *Schefflera pachystyla*, accounted for 36% of my observations for this bird, and this bird made 78% of the recorded avian visits to the *Schefflera*.

I recorded 261 foraging bouts of the Magnificent Bird of Paradise. This species was the numerically dominant forager at two species of fruit trees: *Homalanthus novoguineensis* and *Gastonia spectabilis*. While the Magnificent Bird of Paradise dominated at these two fruit sources, the bird also visited 19 other species of fruiting plants. The bird's preference for figs (9% of its diet) was low; capsular fruits formed the bulk of the diet (58%).

The Raggiana Bird of Paradise was recorded taking fruit of 16 species of plants. It dominated none of the larger fruit-tree species but did account for 55% of avian visits to *Dysoxylum*. Raggiana specialized on no single food item but took small amounts from a broad array of fruits from the three morphological categories.

These nine birds of paradise can be grouped into three categories: the primarily insectivorous Black-billed Sicklebill and Magnificent Riflebird; the fig-specialist manucodes (two species); and the five species of fruit-eating generalists: Superb, Lawes' Six-wired, Magnificent, Raggiana, and Blue birds of paradise.

Bird foraging: the plant's perspective.—I now examine fruit consumption from the plant's point of view. I include for analysis data for all species of avian foragers that visited the food plants. Fruit sources differed in the extent to which they were dominated by birds of paradise. For analysis, I compare five food plants that exhibit the range of variation.

Ficus #275 (Fig. 1c) is a large strangler with a massive branching canopy of limbs. Mature individuals produced a prodigious number of tiny figs, arrayed on the twigs and outer limbs. The figs ripened synchronously and were simple to harvest. Flocks of birds would visit and forage during the peak period of fruiting. I recorded 22 species of foragers from 10 bird families. Birds of paradise accounted for 35% of the recorded visits.

Ficus gul (Fig. 1b) is a free-standing tree, similar in most aspects of its fruiting to the previous species except for *gul*'s smaller canopy and smaller crop. This fig attracted 15 species of foragers, and birds of paradise accounted for 85% of the feeding records.

Homalanthus novoguineensis (Fig. 1i), a small subcanopy tree, produced a modest crop of fruit that ripened over a 3-month period. The fruits of this species required more effort to harvest than the two figs. For this fruit the bird of paradise plucked the entire capsule from its attachment, held it with one foot, and pecked it open, taking out the two arillate seeds. I recorded 11 species of birds foraging at *Homalanthus*; birds of paradise made up 93% of these records.

Gastonia spectabilis (Fig. 1e) produced a large crop of fruit (40,000 ±) that was available over a short season (1½ months). I recorded 131 feeding visits to the tree and found that only

six species of birds took the fruit, all birds of paradise.

Chisocheton weinlandii (Fig. 1l) was even more extreme in its attractiveness to birds of paradise. I recorded 91 foraging bouts by nine bird species, all birds of paradise. *Chisocheton* produced a crop of about 4,500 fruits that ripened over a 3-month season. The arillate seeds required some effort to harvest from their capsules. The tree attracted no large crowds of birds but instead was visited by a small steady stream of birds of paradise that rarely took more than two or three arillate fruit per visit.

DISCUSSION

I believe aspects of frugivory are of great importance to the evolution of polygamy in birds of paradise. I review this issue against a background of hypotheses that have been presented in the literature to explain the evolution of polygamous lek behavior in neotropical songbirds, and I consider the birds of paradise as examples that can either support or refute these hypotheses.

Of the nine species of birds of paradise that I studied on the Mount Missim site, seven are polygamous and two are monogamous (Gilliard 1969, Beehler 1983). The two monogamous species are congeneric and apparently are similar in many of their habits (unpubl. data). In contrast, the polygamous species show both morphological and behavioral diversity (Gilliard 1969, Cooper and Forshaw 1977). The Raggiana Bird of Paradise displays in a true lek. The Magnificent and Lawes' Six-wired birds of paradise display at solitary terrestrial courts. The remaining four species display solitarily in the middle levels of the forest vegetation.

Much has been written to explain the ecological conditions that predispose tropical songbirds to promiscuous arena behavior (D. Snow 1971a, 1976, 1980; Snow and Snow 1979, Willis et al. 1978, Willis 1979, Ricklefs 1980). The common theme in all of these relates to two factors: (1) the advantages of fruit-eating, and (2) the exigencies of nesting in the tropical forest.

Apropos of frugivory, Snow (1976: ix) writes:

It is, apparently, the relief from the need to spend most of the day in search of food that has given the fruit-eaters the opportunity to develop other activities to a degree not seen in the insect-eaters. In a few of the bird families that have entered into close part-

nership with forest trees as legitimate fruit-eaters there has been an extraordinary proliferation of species with fantastic and beautiful plumages and courtship displays.

With respect to nesting ecology, several factors are involved: (1) feeding nestlings efficiently, (2) nest predation, (3) size of the clutch, and (4) the need to have a small and cryptic nest (Snow and Snow 1979, Willis 1979). It is argued that, because nest predation in the tropics is high, individual investment per nesting attempt should be low (hence a small clutch is best); the nest should be small and cryptic to avoid attracting predators (again, promoting small clutch size). Under these conditions, presumably one parent will be sufficient to provision the nestlings, especially if the parent can efficiently feed the nestlings on regurgitated fruit pulp (Snow and Snow 1979). These factors promote male emancipation and increase the opportunity for polygamy.

If there are real links between nesting ecology and the evolution of polygamy, one might expect consistent differences between monogamous and polygamous species. One might expect that monogamous species build better-protected or invulnerable nests, or have larger clutches, or both. Among the nine species addressed in this paper, there is no such dichotomy. Clutch size for the two monogamous species is two eggs. For the 7 polygamous species it is two in 4 cases and one in 3 cases. In fact, most forest songbirds in New Guinea produce a clutch of two, with occasional deviations to single- or triple-egg clutches (from data in Rand and Gilliard 1967).

All nine species of birds of paradise build simple open nests attached to tree limbs, at various heights above the ground. Again, there is no consistent difference between monogamous and polygamous species. Because the nine species live together in the same forest on Mount Missim and elsewhere, one can presume that nest predation is equivalent among the nine species, and any argument about the relation between nesting ecology and polygamy breaks down. Snow and Snow (1979) state that the evolution of promiscuous arena display has not developed in hole-nesting birds (another aspect of the nest-predation hypothesis). This, too, is contradicted by birds of paradise. The King Bird of Paradise (*Cicinnurus regius*) nests in a hole and displays in an arena

system (Gilliard 1969; Cooper and Forshaw 1977).

Addressing the relation of frugivory and polygamy, Ricklefs (1980: 476) writes:

> I would predict that the fruits eaten mainly by promiscuous species and those eaten by monogamous frugivores (mainly tanagers among passerines in the New World tropics) have distinctly different patterns of dispersion, availability, and, perhaps, nutritional value.

Within limits, this suggestion appears to have real merit, especially as it relates to birds of paradise. The two monogamous birds of paradise in the group that I studied were both fig specialists. The seven polygamous species took a wide range of fruits, but many from the capsule and drupe/berry categories. What can be made of these different dietary preferences and behaviors? Data on avian visitors to fruiting plants show that figs are exploited by a wide range of bird families, while many of the fruits from the other two categories are visited by a narrower segment of the bird community, and some are used only by birds of paradise. I suggest that aspects of this coevolutionary relationship between birds of paradise and some fruiting plants may contain an answer to why the birds were able to evolve their remarkable polygamous mating systems. One aspect may be nutritional. The capsular arillate fruits are richer in proteins and lipids and poorer in water and carbohydrates than the simpler and smaller fruits, typified here by many species of figs discussed (Crome 1975, Foster 1978, Frost 1980). Thus, much of a bird's nutritional needs can be supplied by these specialized fruits. In addition, the specialized food plants have, on the whole, longer fruiting seasons that offer regular visitors a small daily complement of ripe fruits (strategy I of Howe and Estabrook 1977; see also McKey 1975, Frost 1980, Beehler 1983). The fruits are predictable, fixed in space, and can offer nutritional rewards usually available only from arthropods, a resource that is considerably more costly to harvest (Snow 1976, Snow and Snow 1979). The specialized fruits, then, provide the nutrients needed for adult and nestling nutrition, yet are simpler to harvest than the elusive insect resource. The gain in time and nutrition can allow more time for the female alone to care for the offspring and for the emancipated male to pursue a polygamous mating strategy.

How do paradisaeid diets compare with those of other species in other tropical bird families? The polygamous Bearded Bellbird (*Procnias averano*) was recorded to take the fruit of 32 species of food plants, including five families used by birds of paradise: Araliaceae, Myrtaceae, Rubiaceae, Euphorbiaceae, and Myristicaceae (B. Snow 1970). The lek-displaying White-bearded Manakin (*Manacus manacus*) took fruit of 105 species, including members of five plant families also used by birds of paradise: Zingiberaceae, Moraceae, Euphorbiaceae, Araliaceae, and Rubiaceae (Snow 1962a).

There are morphological similarites between the specialized fruits from New Guinea and the neotropics. Some of these similarities are based on taxonomic affinities. The capsular species of Meliaceae and Myristicaceae in both regions are strikingly alike, with golden-brown capsular exocarps and orange-red arils (cf. *Viola* and *Myristica* in Central America and New Guinea, respectively). In this same vein, these specialized fruits are arranged on the plant in patterns that make them available only to a select group of foragers, who often expend considerable energy to harvest these fruits [exemplified by *Nectandra* (Lauraceae) and its cotingid foragers (B. Snow 1977) and *Chisocheton* and its paradisaeid foragers (Beehler 1983)].

There are some nonconformities in the fruit-polygamy relationship. Two of the birds of paradise that I studied, the Black-billed Sicklebill and Magnificent Riflebird, take many arthropods in their diets. In the case of the Sicklebill, most of its diet is arthropod matter. On an intercontinental scale, the New Guinea species that are polygamous tend to take many arthropods in their diets, while some, or many, of the polygamous species in the neotropics are close to being entirely frugivorous (Snow 1976, Beehler 1983). In New Guinea, species of cuckoo-shrikes (Campephagidae), honeyeaters (Meliphagidae), and berrypeckers (Dicaeidae) form a large assemblage of the passerine frugivore community (Beehler 1981). No members of any of these groups, however, show any evidence of the polygamous arena behavior exhibited by the birds of paradise. In fact, the majority of fruit-eating birds of the world are monogamous, while most of the species of Paradisaeidae and Pipridae are polygamous.

I believe the reason for this apparent anomaly to be correctly stated by Bradbury (1981), whose studies of bats in tropical Africa offer

other examples of rainforest vertebrates that are both frugivorous and polygamous. Bradbury argues that the peculiarities of frugivory are important but do not constitute the sole sufficient factor promoting the evolution of arena polygamy. It is the fruit diet that promotes large home ranges, with high overlap, which, in turn, raises the potential for high interindividual contact rates. Frugivores share ranges and fruiting plants. Birds are highly vagile. Thus an individual male who attempts to attract and court numbers of females will have greater success if the population is frugivorous, rather than insectivorous, site-faithful, and territorial. As discussed in the earlier arguments, frugivory also increases the likelihood of male emancipation from nesting duties. These two phenomena, occurring together, create an environment with high potential for polygamy.

Given the diversity of fruit in the tropics (Fig. 1), and the range of nutritional constituents of various fruit types (Crome 1975, Frost 1980), in conjunction with great potential differences in production strategies and spatial dispersions (Beehler 1983), it is evident that the term "fruit-eating" subsumes a multitude of ecological situations that can, in turn, produce varied responses in an animal's behavior (Emlen and Oring 1977). I agree with D. Snow (1980) that frugivory is an obligatory field for study in the quest to understand the evolution of polygamous arena display in birds of paradise and other tropical forest songbirds. I stress, however, that the key to understanding the frugivory-polygamy relationship will require analysis of such factors as: (1) percentage of fruit in a bird's diet, (2) spatial dispersion of the different food plants, (3) size of fruit crops, (4) intraspecific synchrony of plants, (5) predictability of fruiting cycles of individual plants as well as species populations, (6) the ripening synchrony of crops and length of fruiting season, and (7) nutritional constituents of the fruit taken. These and additional factors define the spatio-temporal availability and quality of a bird's food resources, which influence ranging and foraging patterns and ultimately affect social and sexual habits.

LITERATURE CITED

BEEHLER, B. 1981. Ecological structuring of forest bird communities in New Guinea. Pp. 837–861 *in* Biogeography and ecology in New Guinea (J. L. Gressitt, Ed.). The Hague, Junk.

———. 1983. The behavioral ecology of four birds of paradise. Unpublished Ph.D. dissertation. Princeton, New Jersey, Princeton Univ.

BRADBURY, J. W. 1981. Evolution of leks. Pp. 138–169 *in* Natural selection of social behavior (R. D. Alexander and D. Tinkle, Eds.). New York, Chiron.

COOPER, W., & J. FORSHAW. 1977. The birds of paradise and bowerbirds. Sydney, Collins.

CROME, F. 1975. The ecology of fruit pigeons in tropical Northern Queensland. Australian Wildl. Res. 2: 155–185.

DIAMOND, J. M. 1972. Avifauna of the eastern highlands of New Guinea. Cambridge, Massachusetts, Publ. Nuttall Ornithol. Club. No. 12.

EMLEN, S. T., & L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197: 215–223.

FOSTER, A., & E. GIFFORD. 1974. Comparative morphology of vascular plants. San Francisco, W. H. Freeman.

FOSTER, M. S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit resource. Ecology 58: 73–85.

———. 1978. Total frugivory in tropical passerines: a reappraisal. Tropical Ecol. 19: 131–154.

FROST, P. 1980. Fruit-frugivore interactions in a South African coastal dune forest. Pp. 1179–1184 *in* Acta 17th Congr. Intern. Ornithol. (R. Nohring, Ed.). Berlin, Deutsche Gesellsch.

GILLIARD, E. T. 1969. The birds of paradise and bower birds. Garden City, New York, Natural History Press.

———, & M. K. LECROY. 1967. Annotated list of birds of the Adelbert Mountains, New Guinea. Bull. Amer. Mus. Nat. Hist. 138: 53–81.

HOLDRIDGE, L., W. GRENKE, W. HATHEWAY, T. LIANG & J. TOSI. 1971. Forest environment in tropical life zones: a pilot study. Elmsford, New York, Pergamon Press.

HOWE, H. 1979. Fear and frugivory. Amer. Natur. 114: 925–931.

———, & G. ESTABROOK. 1977. On intraspecific

competition for avian dispersers in tropical trees. Amer. Natur. 111: 817–832.

JENSEN, W., & F. SALISBURY. 1972. Botany: an ecological approach. Belmont, California, Wadsworth.

JOHNS, R. J. 1976. Common forest trees of Papua New Guinea. Vol. 8, part 3. Angiospermae. Bulolo, Papua New Guinea, P. N. G. Forestry College.

LECROY, M. K., A. KULUPI, & W. S. PECKOVER. 1980. Goldie's Bird of Paradise: display, natural history, and traditional relationships of the people to the bird. Wilson Bull. 92: 289–301.

———. 1981. The genus *Paradisaea:* display and evolution. Amer. Mus. Nat. Hist. Novitates 2714: 1–52.

LILL, A. 1976. Lek behavior in the Golden-headed Manakin *Pipra erythrocephala* in Trinidad (West Indies). Fortsch. Verhalt. 18: 1–83.

MCALPINE, D., G. KEIG, & K. SHORT. 1975. Climatic tables for Papua New Guinea. Division of Land Use Tech. Pap. No. 37. Melbourne, C.S.I.R.O.

MCKEY, D. 1975. The ecology of co-evolved seed dispersal systems. Pp. 159–191 *in* Coevolution of animals and plants (L. Gilbert and P. Raven, Eds.) Austin, Texas, Univ. Texas.

PIJL, VAN DER, L. 1972. Principles of dispersal in higher plants, 2nd ed. New York, Springer-Verlag.

RAND, A. L. 1940. Breeding habits of the birds of paradise *Macgregoria* and *Diphyllodes.* Amer. Mus. Novitates. 1073: 1–14.

———, & E. T. GILLIARD. 1967. Handbook of New Guinea birds. Garden City, New York, Natural History Press.

RICKLEFS, R. 1980. Commentary. Auk 82: 476–477.

SCHODDE, R. 1976. Evolution in the birds-of-paradise and bowerbirds, a resynthesis. Pp. 137–149 *in* Proc. Intern. Ornithol. Congr. No. 16 (H. Frith and J. Calaby, Eds.). Canberra, Australian Acad. Sci.

SNOW, B. 1970. A field study of the Bearded Bellbird in Trinidad. Ibis 112: 299–329.

———. 1972. A field study of the Calfbird *Perissocephalus tricolor.* Ibis 114: 139–162.

———. 1973. Notes on the behavior of the White Bellbird. Auk 90: 743–751.

———. 1977. Territorial behavior and courtship of the male Three-wattled Bellbird. Auk 94: 623–645.

SNOW, D. 1962a. A field study of the Black and White Manakin, *Manacus manacus,* in Trinidad. Zoologica 47: 65–104.

———. 1962b. A field study of the Golden-headed Manakin, *Pipra erythrocephala,* in Trinidad, W. I. Zoologica 47: 183–198.

———. 1971a. Evolutionary aspects of fruit-eating in birds. Ibis 113: 194–202.

———. 1971b. Observations on the Purple-throated Fruitcrow. Living Bird 10: 5–17.

———. 1976. The web of adaptation. New York, Quadrangle.

———. 1980. Regional differences between tropical floras and the evolution of frugivory. Pp. 1192–1198 *in* Acta 17th Congr. Intern. Ornithol. (R. Nohring, ed.). Berlin, Deutsche Gesellsch.

———, & B. SNOW. 1979. The Ochre-bellied Flycatcher and the evolution of lek behavior. Condor 81: 286–292.

WILLIS, E. O. 1979. Commentary. Condor 81: 324.

———, D. WESCHLER, & Y. ONIKI. 1978. On behavior and nesting of McConnell's Flycatcher (*Pipromorpha macconelli*): does female rejection lead to male promiscuity? Auk 95: 1–8.

APPENDIX. Taxonomic and morphologic information on the food-plants of nine birds of paradise.

Botanical family[a]	Latin binomen	Author/field number[b]	Plant type	Fruit morphology	Dimensions of edible part[c]
Annonaceae	Uvaria sp.	252	Vine	Berry	8 × 18 mm
Araliaceae	Gastonia spectabilis	(Harms) Philipson	Canopy tree	Berry	9
	Schefflera pachystyla	Harms	Vine	Aggregate berry	9 × 15
Elaeocarpaceae	Sloanea cf. aberrans	A. C. Smith	Canopy tree	Capsule	5 × 12
	Sloanea cf. sogerensis	E. G. Baker	Canopy tree	Capsule	5 × 16
Euphorbiaceae	Aporusa cf. nigro-punctata	Pax & K. Hoffman	Subcanopy tree	Capsule	9
	Endospermum medullosum	L. S. Smith	Canopy tree	Drupe	6
	Glochidion sp.	—	Subcanopy tree	Aggregate capsule	3
	Homalanthus novoguineensis	K. Schum.	Subcanopy tree	Capsule	7
Magnoliaceae	Elmerrillia papuana	Dandy	Canopy tree	Aggregate capsule	7
Meliaceae	Aglaia cf. versteeghi	M. & P.	Subcanopy tree	Capsule	7 × 16
	Chisocheton weinlandii	Harms	Canopy tree	Capsule	10
	Dysoxylum cf. macrothyrsum	Miq.	Canopy tree	Capsule	6 × 12
Moraceae	Ficus drupacea	Thunb.	Canopy strangler	Fig	18
	F. gul	Laut. & K. Schl.	Canopy tree	Fig	6
	F. insculpta	Summerhayes	Vine	Fig	9
	F. obliqua	Forst. f.	Canopy strangler	Fig	6
	F. odoardi	King	Vine	Fig	28
	F. strangler #3	202	Strangler	Fig	14
	F. sp.	217	Canopy tree	Fig	10
	F. sp.	275	Canopy strangler	Fig	11
	F. sp.	371	Canopy strangler	Fig	6
Myristicaceae	Myristica subalulata	Miq.	Subcanopy tree	Capsule	11
Myrtaceae	Syzygium sp.	343	Canopy tree	Drupe	10
Pandanaceae	Pandanus conoideus	Lam.	Subcanopy "palm"	Aggregate drupe	4 × 20
Piperaceae	Piper sp.	284	Vine	Aggregate drupe[d]	5 × 10[d]
Rubiaceae	Canthium cf. brevipes or valetonianum	M. & P. S. Moore	Subcanopy tree	Berry	12
Vitaceae	Cissus hypoglauca	A. Gray	Vine	Drupe	10 × 18
	C. aristata	Blume	Vine?	Drupe	8 × 10
Zingiberaceae	(unidentified)[e]	—	Shrub?	Capsule	?

[a] Listed alphabetically, not systematically.
[b] Field number is listed in absence of specific identification; see text for location of voucher material.
[c] The size of the swallowed part; species that are significantly aspherical are given in two dimensions.
[d] Each fruitlet is tiny (ca. 2 mm), and the bird swallows pieces of the aggregate fruit, each piece containing many fruitlets.
[e] Found in fecal samples; not assignable to a botanical specimen from the study site.