ECOLOGY AND BEHAVIOR OF THE BUFF-TAILED SICKLEBILL (PARADISAEIDAE: *EPIMACHUS ALBERTISI*)

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ABSTRACT.—I studied the foraging ecology and mating behavior of the Buff-tailed Sicklebill (*Epimachus albertisi*) on Mount Missim, Papua New Guinea, from August 1978 to November 1980. Eighty-nine percent of the feeding records were of insectivory. Birds foraged in the middle levels of the forest primarily by bark gleaning, but also by using their long decurved bill for probing knot holes and dead leaves. On rare occasions the sicklebill took fruit. Of more than 1,000 fruit-foraging records by birds of paradise for this study site, only 7 were by the sicklebill. A single focal male held an exclusive, year-round territory of ca. 14 ha. A single radio-tracked female was observed to travel over a 43-ha range in eight sample days, but spent most time in a 9-ha core area abutting the male's territory. Although the female was silent, the territory-holding male sang daily for more than 6 months each year. The male performed an inverted nuptial display on a sapling near his regular song perch. This species exhibited a court-based mating system typical of many polygynous birds of paradise. This is the first record of non-pair-bonded, court-based polygynous breeding behavior in a forest insectivore. *Received 27 January 1986, accepted 14 July 1986.*

THE birds of paradise (Paradisaeidae) have long been of interest to evolutionary biologists for their extreme sexual dimorphism and polygynous mating behavior (Darwin 1871, Gilliard 1969, Oring 1982, Payne 1984). Until recently, however, little was known of the ecology of this avian family. One novel discovery of recent field studies of a number of species of birds of paradise is that feeding behavior and diet in the different genera are diverse (Beehler 1983b, 1985; Pratt and Stiles 1983, 1985). The postulated causal relationships linking dietary ecology and mating behavior (cf. Emlen and Oring 1977, Bradbury 1981) remain imperfectly understood, especially in regard to the birds of paradise (cf. Pruett-Jones 1985). Knowledge of additional species is useful for socioecological comparisons.

I studied the Buff-tailed Sicklebill (*Epimachus albertisi*), one of the morphologically aberrant birds of paradise, and one that is rare throughout its range. This and the Pale-billed Sicklebill (*Epimachus bruijnii*) comprise the short-tailed sicklebills of the subgenus *Drepanornis*, in which both sexes have a long decurved bill and a comparatively short, rounded tail. The literature provides virtually no information on either of these species (Gilliard 1969, Cooper and Forshaw 1977, Diamond 1981). Recent fieldwork has generated information on the life history of the Pale-billed Sicklebill (Beehler and Beehler 1986). I present here information of a similar nature on the Buff-tailed Sicklebill, for comparison with its closest relative, and for testing the applicability of current mating-system theory to atypical forms such as these.

METHODS

From August 1978 to November 1980, I worked on a 25-ha plot of undisturbed lower montane humid forest at 1,400 m on the southwestern flank of Mount Missim, Morobe Province (for details of the site see Beehler and Pruett-Jones 1983). I was on the study site (known as Missim Camp One) for 249 days. This study was part of a socioecological comparison of four birds of paradise (Beehler 1983a).

Mist nets were used to capture birds for color marking and obtaining fecal samples. Sicklebills were marked with a combination of short, colored Saflag streamers and a numbered aluminum band provided by C.S.I.R.O. Wildlife Division, Australia. The Saflag streamer was sewn in a loop around the tarsus with heavy-gauge thread. During the final three months of the study, birds were trapped for radio-tagging. The single female sicklebill captured was fitted with a 4.5-g battery-powered transmitter, and in tracking we used two portable LA-12 receivers and 3-element Yagi antennas (AVM Company, Dublin, California). The transmitter was attached by thread and epoxy to the ventral side of the base of the four central rec-

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trices. There was no contact between module and living tissue, and the radio was presumably dropped during annual molt.

Before initiation of radio-tagging, it became clear that the movements and home range of the focal adult male (Male A) could be determined by simply following this vocal and slow-moving individual. Thus, it was necessary to use radiotelemetry only with the silent and cryptic female sicklebill. For both sexes, home ranges were determined by plotting all recorded movements of the individuals on a single master map and measuring the area of the polygon defined by the outermost points (see Figs. 1 and 2). Calculations of foraging movement patterns were made using estimates of minimum straight-line distance between perches.

Information on diet and feeding habits of the sicklebill was obtained (1) through chance observation of individuals encountered in the forest, (2) during days when movements of the focal male were mapped, and (3) during periodic observations of avian foraging at fruiting plants (Beehler 1983a). Additional data for analysis were gleaned from the literature (e.g. Gilliard 1969, Schodde 1976).

Throughout the study, regular attempts were made to determine and map the position of all singing male sicklebills within vocal range of the study plot. Methods employed for this survey are presented by Beehler and Pruett-Jones (1983).

Vocalizations of Male A were monitored and recorded with a portable Sony TC-30 cassette recorder. Four times a month, 5-min standard recordings were made near the male's display post. Each recording was initiated 30 min after first light. These recordings measured the frequency of morning singing by Male A. Trial spectrograms were made of the best-quality vocalizations, but most recordings were not suitable for spectrographic depiction.

Information on the mating behavior of the sicklebill was gathered from 93 h of observation of activities at the display perches of the focal male.

RESULTS

DIET AND FORAGING

I assembled 53 dietary records, 45 based on my observations and 8 based on literature and museum records. Because of the territorial nature of this sicklebill, a large proportion of the Missim records are for Male A.

The Buff-tailed Sicklebill is predominantly insectivorous. Forty-five of 53 records (89%) document insect eating. At Missim Camp One, I obtained 1,187 fruit-eating records by nine species of birds of paradise (Beehler 1983b). From these, only 7 (0.059%) refer to fruit feeding by *E. albertisi*.

Insectivory.—The 40 dietary records that included information on foraging method can be classified into five categories: (1) scansorial bark glean ($n = 27$), in which the bird clambers about, creeper-fashion, on sloping limbs and trunks, picking and probing bark and crevices; (2) simple limb glean ($n = 6$), in which the bird perches on a horizontal limb and searches the limb surface, especially by peering at the sides and undersides of the limb; (3) dead-leaf glean ($n = 3$); (4) knot-hole probe ($n = 3$), in which the bird uses its long decurved bill as tweezers or as a probe (during which the jaw is opened wide and the maxilla only is jabbed into the knot hole); and (5) petiole glean ($n = 1$).

The Buff-tailed Sicklebill foraged for insects 8-28 m from the ground (median 17 m, $n = 23$). Forest canopy height on the study area ranged from 25 to 35 m. Sexual dimorphism in foraging height was not evident. The range of heights for females ($n = 6$) was 8-21 m, and for males ($n = 17$) was 9-28 m. Diameter of the branch or trunk used by the foraging sicklebill ranged from 1.5 to 15 cm (mean 6.1 cm, $n = 20$).

Arthropod prey included: Araneida (2), Chilopoda (2, one prey 7.5 cm long), Orthoptera (1 Gryllacrididae, 1 Gryllidae, 1 Stenopelmatidae, 1 Tettigoniidae, 1 unidentified), Dermaptera (1 Chelisochidae), Coleoptera (1 white "grub" larvae, 6 unidentified beetles), Lepidoptera (3 larvae, one a "hairy" caterpillar), and 5 unidentified arthropods.

On a number of days I followed Male A while he foraged through the forest for arthropods, and I never saw him associate either with a conspecific or with other insectivores. In one instance I saw a female-plumaged sicklebill foraging in apparent association with a female Superb Bird of Paradise (*Lophorina superba*). In contrast, Diamond (in litt.) observed this sicklebill join mixed-species foraging flocks in the Foya Mountains of western New Guinea.

Habitat on the study site was relatively uniform. The crest of the main ridge consisted of forest dominated by the oak *Castanopsis acuminatissima*. This oak, also a common subdominant in other parts of the plot, is subject to rapid senescence that produces excellent foraging sites (dead limbs, peeling bark, etc.) for the sicklebill. Nonetheless, this bird showed no special preference for foraging in *Castanopsis*. By stem count of all trees more than 15 cm in diameter on a sample 1-ha plot, the oak rep-

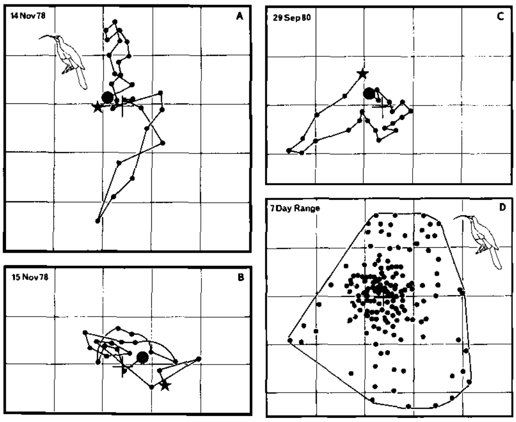

Fig. 1. Movements and home range of Male A sicklebill on Mt. Missim. (A-C) Daily movements, with resting points denoted by small black circles, starting points by large black circles, and ending points by stars. All maps are aligned and the central "crosses" mark the approximate position of the display post of Male A. (D) Seven-day range of Male A, with small black circles indicating perch sites. For all maps the grid is 100 × 100 m (each square = 1 ha).

resented 36% of the forest trees; of 24 instances in which the foraging tree used by the sicklebill was identified, 9 (38%) referred to *Castanopsis.*

Frugivory.—The sicklebill foraged on fruit from three plant species, two with capsular arillate fruits preferred by the paradisaeine birds of paradise (Beehler 1983b) and one canopy vine producing small figs. Five of 7 fruit-foraging records refer to *Chisocheton* cf. *weinlandii*, a food plant known to be visited only by birds of paradise (Beehler 1983b). The small fig vine was defended by the frugivorous Dwarf Koel (*Microdynamis parva*), which dived repeatedly at the foraging sicklebill, attempting to drive it from the vine. I obtained a single record of Male A at *Elmerrillia papuana* (Magnoliaceae).

RANGING HABITS AND USE OF SPACE

Male movements.—I followed and mapped the movements of Male A on 10 days (Fig. 1). The male traveled 1,140 m per day, on average (range 805–1,379, $n = 7$). Each day's travels were composed of a series of foraging flights interspersed with longer periods spent at foraging or resting sites. Unlike the female sicklebill and other birds of paradise, when Male A was silent for long periods it signaled, apparently, that he was resting, and he did not move significant distances from the point where he last called. Presumably, the male always calls when moving about to alert potential mates to his position on the territory.

Data taken between dawn and 1000, when the male was most vocal and easiest to follow closely, accurately characterized the ranging movement of Male A. During the morning, this male traveled, on average, 37 m per foraging flight ($n = 85$, SD = 17 m) and spent, on average, 15 min at each foraging site ($n = 88$, SD = 11).

Female movements.—One adult female was radio-tracked for 10 days (Fig. 2). The radio signal of this individual was difficult to track for unknown reasons. From the data on four complete days when we never lost the female, she traveled 1,053 m, on average (range = 470–1,501 m). Morning foraging flights averaged 97 m ($n = 13$, SD = 27).

Male home range and intermale distance.—Based on all sightings of Male A (data from more than 30 days over 2 yr), a maximum home range was calculated to be 14 ha. The movements of this male over 7 days of intense sampling produced a territory of ca. 11 ha (Fig. 1D). No other male shared this space, nor was any plumed male recorded within 100 m of the boundary of this exclusively held range. I trapped 5 *E. albertisi* on the study site: 1 plumed male (Male A), 3 females, and 1 young male (sexed by mass and bill length). Male A appeared to occupy an exclusive foraging and display territory.

The territory of Male A centered on his display site (Fig. 1D). One can infer information about use of space by the adult males in the population by determining the distance between male display posts, a relatively simple task because of the persistent vocal activities of males from their display sites. Mean nearest-neighbor distance between the display sites of 5 males was 450 m (range 410–520 m) (Beehler and Pruett-Jones 1983). If the size of Male A's home range was typical, it appears that territories of neighboring males are buffered by intervening forest occupied by no vocal male. Calculated from the maximum home range (probably an overestimate of the size of the territory at any single time), the buffer zone is never smaller than 28 m, but using the estimate of home range based on the 7-day range, the buffer would be no less than 75 m. These distances are small, but for a species as sedentary

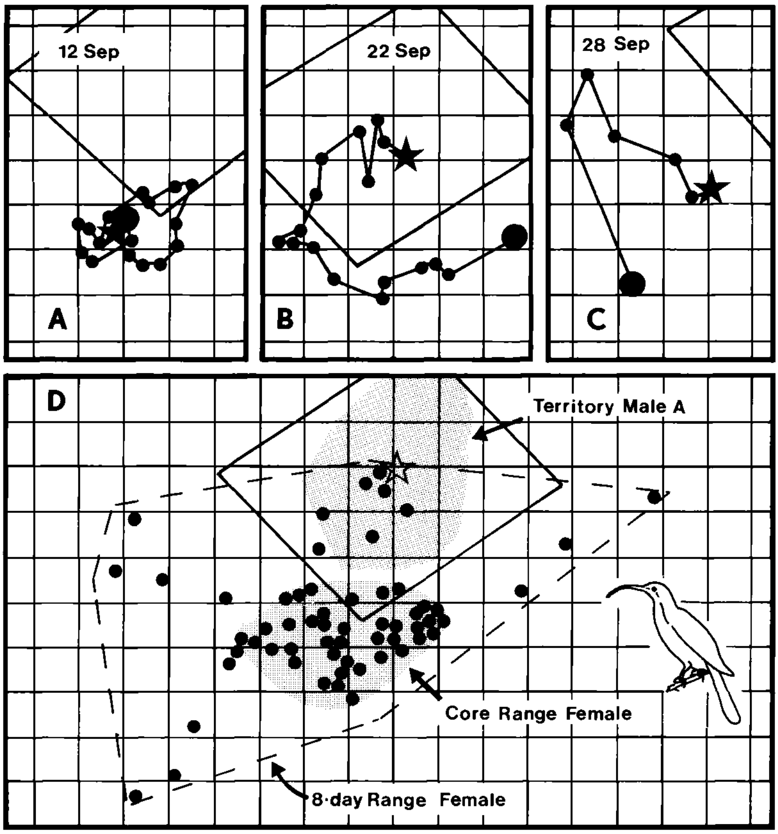

Fig. 2. Movements and home range of radio-tagged female sicklebill. Grid scale as in Fig. 1. The black line forming a tilted parallelogram (or part thereof) delineates the main study plot of Missim Camp One. (A–C) Full-day movements, delineated as for Fig. 1. (D) Eight-day range of radio-tagged female sicklebill. All black dots denote perch sites of this female. Her core range is shaded, as is the territory of Male A. More than two-thirds of all telemetric fixes of the female are located within the shaded "core range." Open star indicates display post of Male A.

as this sicklebill, they are considerable. I never recorded male-male boundary encounters as is typical of territorial species, and which were documented for the Pale-billed and Brown (*Epimachus meyeri*) sicklebills (Beehler and Pruett-Jones 1983, Beehler and Beehler 1986).

Female home range.—Data on use of space by female *E. albertisi* are few, and the results presented here are tentative. The single female that I radio-tagged was captured on the southwestern boundary of the territory of Male A. This female spent more than 75% of her time in a ca. 9-ha patch of forest, but also ranged widely out of this patch and into forest in which other females had been mist-netted and were known to live. During 10 full and partial days of telemetry, the tracked female covered ca. 43 ha, more than three times the area of the territory of Male A (Fig. 2D).

The tagged female occupied a range that only marginally overlapped that of Male A. Also, no adult male was recorded singing within the core range of this female. While on several occasions females were observed at the display site of Male A, on only two occasions were female-plumaged birds observed foraging within the range of Male A. In sum, the tracked female had a larger range than the male, and seemed less predictable in her movements than the male.

VOCALIZATIONS

Male vocalizations.—I identified three vocalizations given by Male A: a simple call note, a

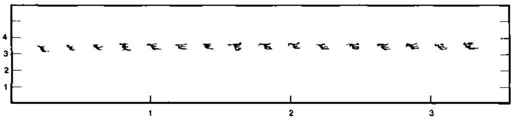

Fig. 3. Spectrogram of advertisement song of Male A, recorded on 30 October 1980. Y-axis = Khz; x-axis = seconds.

whistled series I designate the "advertisement" song, and a display song.

The call note is a quiet, strongly interrogative "wrehn?" The male occasionally gives this note while foraging, but rarely while on the display site. This simple note is similar to call notes of a number of other birds of paradise (e.g. Stephanie's Astrapia, *Astrapia stephaniae;* Raggiana Bird of Paradise, *Paradisaea raggiana*) and is given under similar circumstances. It seems to be a foraging contact note in the more gregarious species, but its function is uncertain in the solitary sicklebill. The male may use it to inform potential mates of his location on the territory when he is not at the display site.

The advertisement song is a loud series of liquid whistled notes that increases and then diminishes in volume: "dyu dyu dyu dyu dyu dyu dyu dyu dyu dyu dyu" (Fig. 3). The number of notes in the series averages 18 (n = 24, range = 13-27, SD = 4). Song length averages 3.2 s (n = 24, range = 2.1-4.2, SD = 0.5). Singing begins before dawn, peaks in frequency at about 0645, then decreases until 0830, continues at a low level throughout the day, and increases again after 1600. This song is delivered from the display site and its vicinity, and while the bird forages throughout the territory. It is delivered from the canopy or middle story of the forest. I could hear the song from 750 m through the forest.

Variants of the typical advertisement song are not uncommon, and are sometimes interspersed with it. One variant is higher pitched, rising in pitch gradually, with the final notes at a high pitch. Another is lower pitched, slower, and slurred, rising slightly in pitch, and is reminiscent of the advertisement song of the Pale-billed Sicklebill (Beehler and Beehler 1986).

The display song is a high-intensity version of the advertisement song, given on the display site. Like the advertisement song, it is a series of whistled notes. The display song differs in being higher pitched, faster, with a greater rise in pitch and intensity toward the end of the series. The terminal notes are hissed more than whistled. This song does not carry as far as the advertisement song, and it is given only when the male is directly involved in courtship or "courtship-practice" (display in the absence of visiting females or other conspecifics).

Male A exhibited a distinct seasonality in vocal activity (Fig. 4). During peak bouts of morning calling, the male gave more than 5 songs per minute. Morning vocalizations (from the first call of the day until 1100) of all types totaled 281 on 23 October 1980, 256 on 14 November 1978, and 169 on 28 September 1980. Male A was vocally active 6.5 months a year (Fig. 4), but from December to early April he called very little. Presumably, vocal activity correlates in some way with courtship and nesting cycles. I have no evidence of any vocalizations from females. The radio-tagged bird was never heard to utter a sound.

COURTSHIP BEHAVIOR

Display site.—All courtship interactions between the sexes were observed at a fixed display site. Unlike in some polygynous birds of paradise (e.g. Lesser Bird of Paradise, *Paradisaea minor;* Beehler 1983c), the display site for Male A was not a single song post or perch, but included at least 3 regular sites, each of which appeared to have a particular function. The advertisement perch was in a group of dead branches in the open crown of a 40-m-tall *Toona sureni* (Meliaceae). The male gave long series of advertisement songs from this perch, and attended the site daily (or nearly daily) for 6 months of the year. Male A carried out most courtship displays ca. 15 m above ground in a small, living sapling near the base of the tall *Toona.* On 12 occasions I observed Male A display on a site near the ground, in a thicket immediately adjacent to the terrestrial display site of a Magnificent Bird of Paradise (*Cicinnurus magnificus*), some 45 m from the central advertisement perch. On one occasion I observed this male sing and display for more than 8 min from another low thicket site, ca. 125 m from the central song post.

Display sequence.—I observed display behavior of Male A on 21 days during April through November. Activity peaked in September-October. Because no single day's observations were

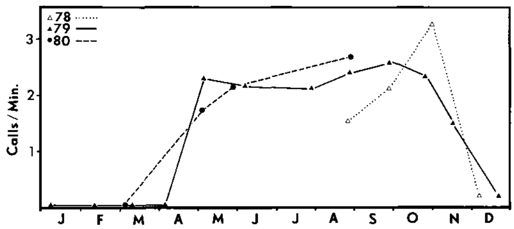

Fig. 4. Seasonality of morning song of Male A over 29 months (1978–1980). Based on a mean of samples (each of 5 min duration) recorded 30 min after first light, from near the male's display post.

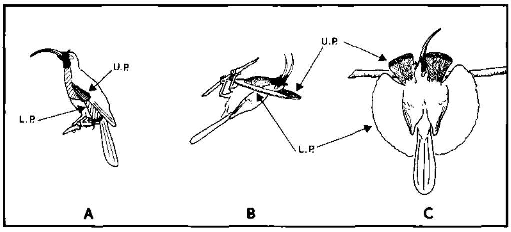

Fig. 5. Inverted display of the male sicklebill. (A) Nondisplay posture, showing position of pectoral plumes. (B) Side and (C) back view of the inverted display. See text for further explanation. U.P. = upper pectoral, L.P. = lower pectoral.

complete, the following description of display sequence is based on a composite of my most detailed encounters, made on 26 September 1979, 19 October 1979, and 23 October 1980. A few of the stated times have been adjusted to fit a realistic single day's sequence.

Male A flew to his open-canopy song perch at 0534 and during the next 30 min gave 69 advertisement songs. At 0603 Male A gave his first display song, and began interspersing this vocalization among repeated advertisement songs. At 0607 Male A dropped to the display sapling in the leafy middle story. Three females moved through the branches close to the male's sapling perch. The females were wary, and hopped about in the branches verging the male's perch. Male A chased the females, and they all flew out of sight; shortly afterward the single male returned to the vicinity of the sapling perch. Male A perched 12 m up on a small horizontal branch and continued to sing rapidly, alternating advertisement and display songs, flaring his flank plumes, and shaking his plumage. Suddenly the male leaned backward to an angle of ca. 50° from upright, flared his flank plumes, and opened his bill, holding the pose without moving for ca. 25 s. Returning to upright, he continued singing for several minutes, then dropped back until he was entirely inverted and flared all of his plumes. He held the position (Fig. 5), while vibrating the body, for 30 s. He gave only one display song while inverted. The male returned upright to the perch and began stripping leaves from branches nearest to his perch.

At 0620 Male A returned to the canopy song perch and continued to sing, occasionally flying to adjacent canopy trees to sing. No females were in sight. At 0645 the bird dropped into the ground display thicket. Hidden from view in the vegetation and perched within 50 cm of the ground, he gave repeated display songs; he remained there for 10 min. After this the male left to forage and sing in the canopy, and then returned to the thicket site to sing from 0720 to 0750.

These observations are incomplete. In spite of my efforts to obtain a complete record of courtship, I did not observe mating, nor did I see all of the male's activities at the ground display site. Throughout the study Male A remained wary; females were difficult to observe when perched in the vegetation, and are apparently even more wary than the male.

Male-female interactions.—I observed male-female contact on 31 August and 26 September 1979. In both instances the females were with the active male at his display site. In the first instance 2 females were observed, and in the second 3 females attended the male.

I observed free-ranging females on only five other occasions, and never in association with conspecifics. On one occasion I captured a female and an immature male together in the same net.

DISCUSSION

The four species of *Epimachus* constitute the paradisaeid sicklebills. The two short-tailed species, *albertisi* and *bruijnii*, are similar in external morphology and in vocalizations that are not shared with the two long-tailed species, the Brown and the Black (*E. fastuosus*) sicklebills. The two short-tailed species show a combination of characteristics that distinguish them from nearly all other birds of paradise: (1) the specialized sickle bill, (2) a diet that includes a significant proportion of arthropods, and (3) males that are exclusively territorial.

The short-tailed sicklebills exhibit non-pair-bonded, polygynous mating behavior typical of the other paradisaeine birds of paradise (Gilliard 1969, Cooper and Forshaw 1977). Although the family shows a wide range of mating behaviors, from monogamous and pair-bonded to true lek systems, typically all members of a genus share a single system (the exception being *Paradisaea*). The polygynous system employed by the sicklebills is best termed "solitary court display," the predominant system in the Paradisaeidae (Beehler and Pruett-Jones 1983).

Presumably because of bill morphology, Sharpe (1877) treated the sicklebills as a discrete subfamily, the Epimachinae. Peculiarities of the sicklebills apparently relate to specialized insectivory. The bill, suited to bark gleaning and knot-hole probing, correlates with the heavily insectivorous diet, which, in turn, is postulated to favor the exclusive territoriality of the males. On the other hand, the sicklebills show a number of traits that are peculiar to the Paradisaeidae. Like the typical paradisaeines (and unlike any of the bowerbirds), the male has a polygynous courtship display based on a fixed set of traditional arboreal perches. Male displays utilize the pectoral plumes peculiar to the family. The sicklebills' known fruit diet consists of capsular angiosperms and figs, which are food plants favored by typical birds of paradise (Beehler 1983b).

SPECIALIZED INSECTIVORY AND MATING-SYSTEM THEORY

The Buff-tailed Sicklebill is exceptional in being a polygynous, court-displaying species that is almost totally insectivorous. The court-displaying manakins, cotingids, bowerbirds, and hummingbirds depend on plant food for much of their diets (Snow 1976, Emlen and Oring 1977, Bradbury 1981, Oring 1982). The court-breeding system of these polygynous species, including the Buff-tailed Sicklebill, involves two behavioral shifts from the prevalent monogamous, pair-bond system: (1) the emancipation of the male from nesting duties and (2) the shift by the male to a promiscuous, site-based mating system. For the frugivorous and nectarivorous court breeders, male emancipation and promiscuity are believed to be promoted by spatially clumped, nutritious, and abundant food resources that cannot be monopolized by males to control the mating habits of the females (Emlen and Oring 1977). Thus, both of the behavioral shifts are difficult to understand for a gleaning insectivore, because it is generally held that provisioning nestlings with "hard-to-harvest" arthropods requires the efforts of two parents. Additionally, such a feeding ecology supposedly promotes territoriality and control of females by the males occupying territories (Orians 1969).

Male emancipation.—Apparently, some aspect of the Buff-tailed Sicklebill's ecology permits (or promotes) uniparental care. By way of explanation, I allude to examples from another group of specialized insectivores, the Dendrocolaptidae, some of which exhibit uniparental nest care (Skutch 1969, 1981; Willis 1972). In some woodcreepers, as in the sicklebill, it appears that males and females preferentially forage on separate ranges. One might speculate that in these species male emancipation may be promoted by the economics of harvesting a rare but predictably renewing crop of arthropods that inhabits knot holes and bark crevices. It may be more economical for a female to feed herself and her nestling in a small, well-known plot than to share this limited but predictable resource with a (hungry) male (Willis et al. 1978). The few data I collected suggest that in this sicklebill the sexes avoid each other except to mate. More fieldwork is needed to clarify the adaptive nature of male emancipation in the insectivorous Buff-tailed Sicklebill.

At present we have no data on nesting by *Epimachus albertisi* except that the clutch is apparently one (Gilliard 1969). Uniparental care in this species is assumed, for four reasons: (1) lack of interaction between sexes except at the display site, (2) evidence of male polygyny in the form of visits to the display site by females in parties, (3) faithful male attendance at the display site for more than 6 months a year, and (4) the two species in the genus *Epimachus* for which data are available are known to exhibit uniparental nest care (Gilliard 1969).

Shift to court display.—Polygynous court breeding by a strict insectivore is unique to this sicklebill. According to prevailing hypotheses, court systems are inherently polygynous and can operate only when there is sufficient "potential for polygyny" (Emlen and Oring 1977). This potential can be high only if a successful male stationed at a fixed display post can expect to attract numbers of mates (Bradbury 1981).

The male Buff-tailed Sicklebill at his song post was observed to be visited by parties of females. In addition, data from the single radio-tagged female indicate she was wide-ranging. More study is needed to elucidate the foraging, nesting, and mate-acquisition strategies of the female sicklebill. Until then, this insectivorous species stands as a striking anomaly in the theory of mating systems in tropical forest birds.

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