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LEK BEHAVIOR AND NATURAL HISTORY OF THE VELVET ASITY (*PHILEPITTA CASTANEA*: EURYLAIMIDAE)

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ABSTRACT.—Observations of territoriality, vocalizations, display behavior, and nesting of the Velvet Asity (*Philepitta castanea*: Eurylaimidae: Philepittinae) indicate that this species is polygynous. Males defend nonresource-based, display territories that are distributed in dispersed leks. Male display repertoires include six elaborate secondary sexual display elements which are performed in both intrasexual and intersexual contexts. Pairs of female-plumage birds construct the nest outside of male territories, and females perform post-fledging parental care. Occasional observations of adult males in association with female-plumaged birds at the nest indicate potential plasticity in breeding behavior within the species. The evolution of the breeding system, display behavior, plumage, delayed male plumage maturation, and molt of the asities is discussed in a phylogenetic context. Two displays of *P. castanea* originally evolved in the common ancestor of the asities. The distinctive appearance of *P. castanea* in the breeding season is a worn basic plumage which has evolved by acquisition of a sexually dichromatic basic plumage and the loss of the prealternate molt. Delayed plumage maturation originally evolved in the common ancestor of the genus *Philepitta.* An additional, distinctive, predefinitive plumage stage-class has evolved in Schlegel's Asity (*P. schlegeli*). *Received 27 Feb. 1996, accepted 7 April 1997.*

The asities are a monophyletic group including two distinct genera—*Philepitta* and *Neodrepanis*—that are endemic to Madagascar. *Philepitta* includes two species of medium-sized (~40 g), forest birds with diets that consist of fruit and nectar. *Neodrepanis* includes two species of sunbird asities—very small (6–8 g; Goodman and Putnam, 1996), forest nectarivores with long decurved bills that are remarkably

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Frontispiece. The Velvet Asity (*Philepitta castanea*). Alternate, definitive plumage male (upper left) performing the Hanging Gape Display; basic definitive plumage male (middle right); and female (lower left). Inflorescence in upper right is *Bakerella clavata* (Loranthaceae).

convergent with many sunbirds (Nectariniidae), hummingbirds (Trochilidae), and Hawaiian honeycreepers (Drepanidae). Traditionally treated as a separate, isolated family of suboscines (Amadon 1951, 1979; Raikow 1987), asities have long been recognized as a striking example of adaptive radiation (Salomonsen 1965). Recent phylogenetic analysis of the group has documented that the asities are a Malagasy lineage of the Old World tropical broadbills (Eurylaimidae; Prum 1993). In the phylogenetic context of the broadbills, the adaptive radiation of the asities is even more extreme given that *Neodrepanis* species could be appropriately called "sunbird-broadbills."

The Velvet Asity (*Philepitta castanea*) is an understory forest frugivore that is distributed throughout the rain forests of eastern and northern Madagascar (Langrand 1990). Recent field studies have documented that the diet of Velvet Asity is composed of a wide variety of fruit species and nectar from various plants (Goodman and Putnam, 1996; V. R. Razafindratsita and S. Zack, unpubl. data). Most other aspects of the natural history of *P. castanea* remain poorly known.

P. castanea shares a number of striking ecological and morphological similarities with several groups of well known, polygynous tropical passerines. Like many manakins (Pipridae), cotingas (Cotingidae), birds of paradise (Paradisaeidae), and bowerbirds (Ptilonorhynchidae), *P. castanea* is primarily frugivorous, is highly sexually dimorphic in plumage, has elaborate secondary sexual characters (e.g., brightly colored, fleshy caruncles), and delayed male plumage maturation. The presence of this unusual and distinctive combination of characters first lead us to investigate the nature of the breeding system of this species. Our observations indicate that *Philepitta castanea,* like many other species of frugivorous tropical passerines, is polygynous and breeds in a dispersed lek system. These preliminary observations document that the behavioral diversity of the Old World suboscines is even broader than currently realized.

STUDY AREA AND METHODS

The observations were made in an area of secondary humid tropical forest in Ranomafana National Park, Ranomafana, Ifanadiana, Madagascar (21°16'S 47°28'E). The study site included a roughly 10 km^2 area near the park entrance. Specific localities of territories and nests found in the study area are referred to here by the trail name and the meter number nearest the site (e.g., A-1100—meter 1100 of trail A).

Initial observations of territorial males were made during the 1993–94 breeding season by V. R. Razafindratsita between 24 Nov.–15 Dec. 1993 and 23 Jan.–1 Feb. 1994, and by R. O. Prum on 22–25 January 1994. The second field season was from 2–29 November 1994. Twenty-four Velvet Asities were banded with distinct color combinations in the study area between 1991–1993 by S. Zack and colleagues. An additional seven individuals were banded by the authors in November 1994. Three of these latter birds were subsequently observed as territorial males.

All observations were made with binoculars and without blinds between 5 and 20 m from the birds. Tape recordings of vocalizations were made using a Sony TCM-5000 with a Sennheiser ME-80 microphone. Spectrograms were prepared using Canary 1.2 (Charif et al. 1995). Video tape recordings of Velvet Asities were made using a Canon L2 high-8 mm camera. Data for ethograms of focal territorial males was taken using 5-min observation periods. During each 5-min observation period, we recorded whether the male was present in, exited, or entered the territory; the position and height of its perch; changes in perch; vocalizations or displays; intraspecific and interspecific interactions; foraging events; regurgitation; and preening. A total of 40 h of observations of eight territorial males was completed.

Information on plumage and morphology was gathered from observation of museum skins in the collections of the American Museum of Natural History (AMNH), New York, the Field Museum of Natural History (FMNH), Chicago, and the Muséum National d'Histoire Naturelle (PM), Paris.

RESULTS

Plumage and morphology.—The plumage of female *P. castanea* is dull green above with wide green and gray longitudinal stripes below (see Frontispiece). The legs are grey, the bill black, and the iris dark brown. The definitive plumage of adult male *P. castanea* changes seasonally. Adult males go through a complete prebasic body molt sometime between February and May (earliest in northern Madagascar). The fresh, definitive basic plumage male (or adult nonbreeding aspect) is black on the face, throat, and flight feathers, and black with olive green feather edgings over the rest of the body (See Frontispiece). The green feather edgings wear off and ultimately produce a distinctive, black appearance during the breeding season (which is refered to here as the breeding aspect of the definitive basic plumage). The definitive male breeding aspect is velvety black with a bright yellow spot on the upper marginal alular wing coverts (See Frontispiece). These yellow "wrist" feathers are usually concealed when an adult male is perched. There is no prealternate molt. Thus, the definitive male breeding aspect is a worn basic plumage, not a distinct plumage produced by a distinct molt. During the transitional period from nonbreeding to breeding aspect, males are individually identifiable by the distinctive patterns of wear of the green feather edgings. Little is known about the molt of females, predefinitive males, or flight feather molt in either sex. There is no sexual dimorphism in size (Goodman and Andrianarimisa 1995).

Definitive breeding aspect males also have a pair of brilliant fleshy supraorbital caruncles (Prum et al. 1994). The caruncle is mostly bright, vivid green with a central horizontal sky blue stripe above the eye. At rest, the caruncle is a flaccid and wrinkled flap of unfeathered skin above the eye (Fig. 5). The rostral portion of the caruncle is a flat, rounded lobe that lies over the culmen. The caudal portion of the caruncle is a narrow, wrinkled strip that lies above the eye and curves ventrally below and behind the eye. The horizontal blue stripe is concealed within a prominent horizontal wrinkle or fold in the center of the caruncle above the eye. The caruncle is covered with tiny cone-shaped, keratinized papillae that include macrofibrils of collagen that produce the structural color (Prum et al. 1994). At rest, the caruncles vary in size and shape within and among males. Some males are individually distinguishable by particular features of their caruncles, particularly the wrinkled dorsal margin and the extent of curvature below and behind the eye. Males can immediately erect the caruncles into two straight planes above the eyes (Fig. 2). When the caruncle is erect, the rostral and caudal portions of the caruncle straighten, and extend upward, exposing the bright blue central stripe. The erection of the caruncles is a prominent feature of the erect posture and wing-flap display performed by territorial males (see below). The shape and position of the caruncles are under immediate muscular control. Video tape recordings of males document that they can move the caruncle instantaneously. Histological sections of the caruncle also show prominent striated muscle tissue in the caruncle that presumably controls its shape (Prum et al. 1994: fig. 2, lower left).

The caruncles of males are absent in nonbreeding, basic plumage males. They apparently develop annually before the breeding season (between June and November, depending on latitude). Nothing is known about the mechanism of development of the caruncles.

Predefinitive males have enlarged gonads, essentially female-like plumage and lack developed caruncles (Rand 1936; Benson 1976:367–369; S. M. Goodman, pers. comm.). At least some, and perhaps all, predefinitive males can be distinguished from females in the hand by a whitish, featherless patch of skin above the eyes, which is the precursor of the definitive caruncle of adult males (Prum et al. 1994; R. O. Prum, pers. obs.; FMNH 345697). Predefinitive males also vocalize and perform rudimentary displays (see below). Nothing is known about the amount of time male *P. castanea* spend in predefinitive plumage before they acquire definitive male plumage and caruncles.

Male territoriality.—Observations were made of eight territorial, adult male *castanea* in two subsequent breeding seasons (Table 1). Male territories are approximately 10–20 m in diameter. Most territories identified were adjacent to another male territory, with territory centers less than 50 m apart (ER-0 and ER-35; A-1100 and A-1110; π-25, π-75, and π-125). In all of these cases, males in adjacent territories were within

TABLE 1

TERRITORIAL ATTENDENCE BY MALE VELVET ASITY (*PHILEPITTA CASTANEA*) IN RANONOMAFANA NATIONAL PARK, MADAGASCAR

Individual	Locality	1993–1994			1994–1995
		Dec	Jan	Feb	Nov
UB#1-GRWW[a]	A-1100	*	*	*	*
UB#2	A-1110	*	*	*	
UB#3	ER-0	*			*
WYRR[a]	ER-35				*
UB#4-GWOO[a]	E-10	*	*	*	*
UB#5	π-25			*	
UB#6	π-75			*	
UB#-7	π-125			*	

* Territorial, adult male was cited at this locality during that month.

[a] Banded during November 1994.

auditory range of one another. Only a single male (GWOO, E-10) was out of immediate hearing range of other known territorial males; he was 125 m from the closest other male. Three males banded in early November 1994 were subsequently observed defending territories later that month. Two of these three males occupied the same territories and used the same vocalization perches as unbanded males in January 1994, during the previous breeding season. An unbanded male (UB#3) was also observed in the same territory in two consecutive breeding seasons. This male was individually identifiable by plumage and caruncle shape during ten observation days in late November 1994. Males were not observed defending territories until they had completed a majority of the transition from the nonbreeding basic asect to the worn, breeding aspect of the basic plumage (i.e. were mostly black). Additional observations are required to confirm this conclusion. Predefinitive males were not observed defending territories.

Males advertise and defend territories by perching on a horizontal branch or liana between 1–5 m above the ground (x = 2.5 m, N = 218) and calling (see below). Males were observed using more than 20 different vocalization perches within a territory, but a few specific perches were usually preferred. Male territorial attendance varied with season. From December 1993 through early February 1994, males were present on territory for 63–92% of 5-minute observation periods between 05:30 and 16:00. In early November 1994, males were not territorial. Between 20–29 November 1994, apparently at the beginning of this breeding season, males were present on territory between 40–70% of 5-minute periods

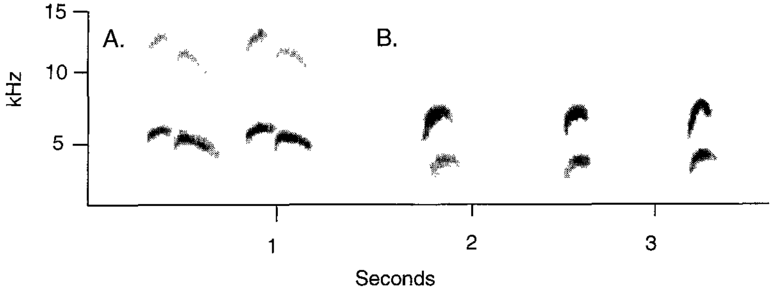

FIG. 1. Spectrograms of vocalizations of the Velvet Asity *Philepitta castanea* at Ranomafana National Park, Madagascar. (A) The advertisement call (*weee-dooo*); and (B) the long call (*weet . . . weet . . .*).

between 05:30 and 8:30. Later in the day, territorial attendance dropped off completely.

Males frequently left their territories for short periods to forage or interact with other birds (N = 99; 28% of observation periods with male in attendance). Limited food resources were located within male territories and males occasionally did forage within their territories, but males most frequently left the territory to forage elsewhere.

At Ranomafana, female *castanea* build nests exclusively in a single species of tree (*Tambourissa obevata,* Monimiaceae; see Nesting below). Five male territories that were carefully surveyed did not include a single individual of this common tree species (A-1100, A-1110, ER-0, E-10, π-25).

Vocalizations and mechanical sounds.—Males give a high, thin, squeaky advertisement vocalization that is a pair or short series of *weee-dooo* notes, with a conspicuous emphasis on the first syllable. Each *weee-dooo* phrase is characterized by an initial note that rises from ~5.5 to 6.3 kHz over 100 ms, a 50 ms pause, and a final note that descends from ~5.4 to 4.8 kHz over 150 to 190 ms (Fig. 1A). This vocalization is inconspicuous, low in amplitude, and can be difficult to detect at more than 20 m away.

During male-male interactions (see below), males give a long call, which is an energetic, nearly continuous series of call notes similar to the initial syllable of the advertisement call—*weet . . . weet . . . weet . . . weet.* Each *weet* note rises ~1–3 kHz over 80 ms from between 5.5–6.3 kHz to 7.4–8.2 kHz, and are separated from one another by 0.75 to 1.5 s (Fig. 1B). Series of long calls can be given continuously for minutes.

A third rare vocalization, a high thin *seeeeee* call, was heard on several

TABLE 2

FREQUENCY OF VOCALIZATION AND DISPLAY ELEMENTS BY MALE VELVET ASITY (*PHILEPITTA CASTANEA*) IN RANONOMAFANA NATIONAL PARK, MADAGASCAR

	N	Frequency over all observation periods[a]	Frequency with male in attendance[a]
Territorial Attendance	335	65%[c]	—
Advertisement Call	495	10.9	16.7
Long Call Bouts	36	0.80	1.23
Wing Flap Pump	75	1.70	2.50
Open-Gape Display	15	0.33	0.50
Hanging Gape Display	5	0.11	0.17
Perch-Somersault Display	2	0.04	0.62

[a] Mean observations per hour over all 542 5-min. observation periods.

[b] Mean observations per hour over the 355 5-min. observation periods with the male in attendance.

[c] % of the 542 5-min. observation periods with male in attendance.

instances during interactions between territorial males. This vocalization was not recorded.

Presumed predefinitive males with female-like plumage were observed and recorded giving both the advertisement and long calls during visits to established territories and while following foraging females.

Adult males produce a notable whirring sound during flight that is presumably produced by the wings. This sound was heard during both display and foraging, and did not appear to be modulated or controlled by the male. Female-plumage birds were not observed making this wing noise, but this may be a result of limited observations at close distances. It is not known whether this wing sound serves as a sexually dimorphic acoustic advertisement, or whether their is sexual dimorphism in the shape of the remiges.

Territorial male *castanea* vocalize relatively infrequently (Table 2). The *weee-dooo* advertisement call was given an average of 10.9 times per observation hour (16.7 times per hour during the five-minute observation periods when the male was on territory). Long call bouts were observed 36 times at an average frequency of 0.8 bouts per observation hour. Vocal activity is greatest in the morning between 06:00 and 10:00, but precise measures of daily temporal variation are skewed by the greater number of morning observation periods.

Display elements.—Six complex male display elements were observed: (1) the erect posture, (2) the wing-flap pump display, (3) the horizontal posture, (4) the open gape display, (5) the hanging gape display, and (6) the perch-somersault display.

In the erect posture, the male assumes an erect, "rooster-like" pos-

FIG. 2. The erect posture of the Velvet Asity *Philepitta castanea.*

ture with its neck and body elongated and leaning forward over the perch, and erecting the brilliant green and blue caruncles (Fig. 2). When erect, the caruncles are raised into two planes running from the base of the beak to above and behind the eye, resembling two sides of a tricornered hat, and exposing the light blue horizontal stripe above the eye. The erect posture is strikingly different from the typical inert, pear-shaped appearance of perched *P. castanea* when perched. (An accurate account of the frequency of the erect posture was not recorded because this display was not identified as a distinct element until late in the observations).

Performances by two different males of the wing-flap pump display were observed well. One male maintained the erect posture for 1–2 s, and suddenly leaned forward and horizontal over the perch. The male then briefly pumped up and forward, pointing its beak, fully extending its neck, raising up on its long tarsi, and returning back to erect posture on the perch. Then after a short pause, the male performed a second vertical pump and opened and closed both its wings simultaneously

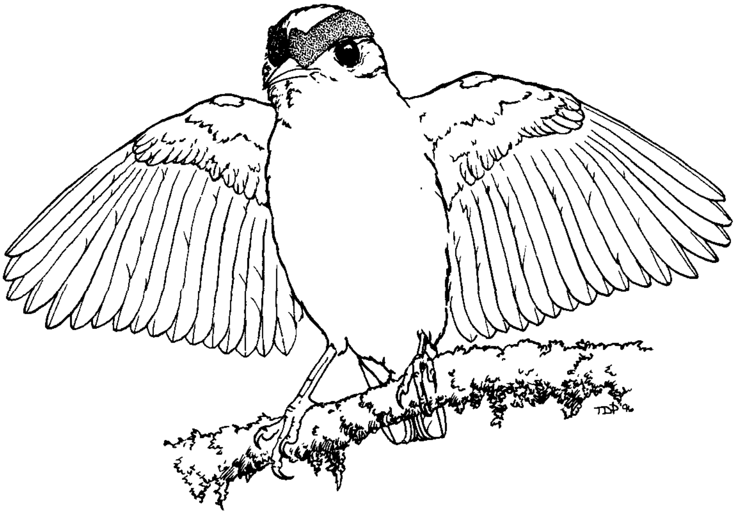

FIG. 3. The wing-flap pump display of the Velvet Asity *Philepitta castanea.*

(Fig. 3). At this moment, the body is at its most erect position, and the broad black wings were held open vertically at the sides and parallel to the body (Fig. 3). The yellow alular covert wing spots were also prominently flashed against this dark, bat-like profile. In a single video tape recording of this male displaying, the first and second pumps were 0.23 and 0.26 s long, respectively, with a single 0.1 s pause in between them. In the wing-flap pump display of a second male, the two pumping movements were immediately followed by a series of two to five asynchronous, single wing flaps that were performed without pumping movements. The order in which each wing was flapped appeared random. Each male always performed the display in the same fashion. The display is performed silently. A total of seventy-five performances of the wing-flap pump by five different males were observed, for a frequency of 1.70 displays per observation hour (Table 2). Males were observed assuming the erect posture without proceeding to the wing-flap or pumping movements.

In the horizontal posture, the male assumes a sleek horizontal position on the perch with the neck elongated (Fig. 4). Typically, the horizontal posture is assumed after a male has heard the call of another neighboring male. The male then peers intently for a brief period and then flicks his wings once or twice before leaving the perch. (An accurate account of

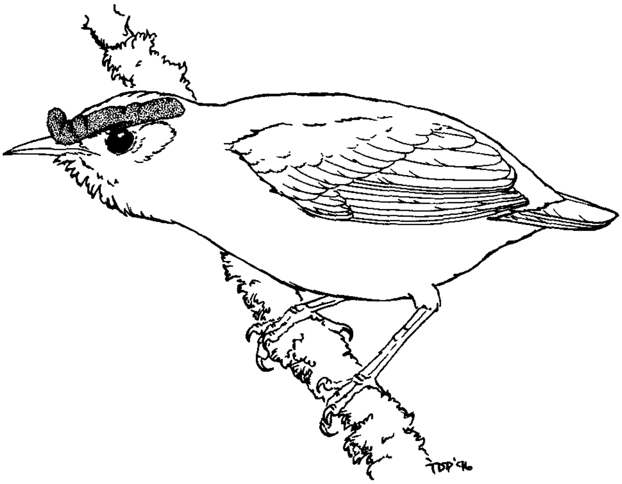

FIG. 4. The horizontal posture of the Velvet Asity *Philepitta castanea.*

the frequency for the horizontal posture was not recorded because this display element was not identified until late in the observations).

In the open gape display (N = 15), a male perches with its head pulled in, and its mouth open wide held up at a slight angle, prominently exposing the bright yellow gape (Fig. 5). While perched in this posture, the male may open its mouth silently or give an extended and energetic series of long calls. Frequently, the male flies from perch to perch, giving con-

FIG. 5. The open gape display of the Velvet Asity *Philepitta castanea.*

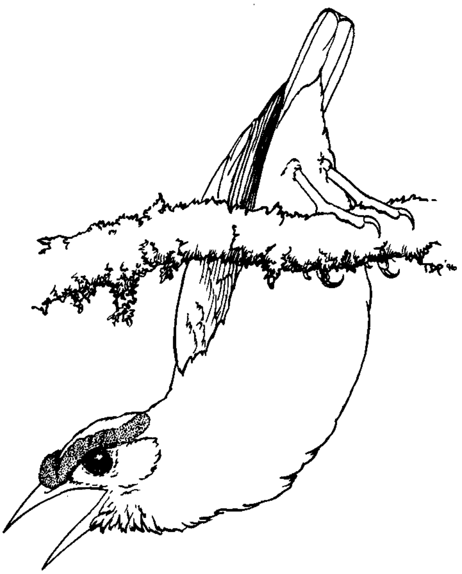

FIG. 6. The hanging gape display of the Velvet Asity *Philepitta castanea.*

tinuous long calls, and assuming the open gape posture on each perch. The caruncles are not raised during the open gape display. The open gape display was infrequently observed (Table 2).

On several occasions (N = 5), males performed a fifth elaborate display movement. In the hanging gape display, a male in the gape posture suddenly throws itself forward and downward with an awkward flap of the wings and hangs from the perch (Fig. 6). The hanging male faces forward with its head held horizontal, its wings closed, its tail nearly vertical and above the perch, and its gape open. After 0.5 to several seconds, the male flies from the perch. Sometimes, the male continues giving long calls throughout the display. The sudden initiation of the hanging gape display looks as if the male were about to fly from the perch but accidentally tripped over its long toes while leaving.

A distinct perch-somersault display was observed twice (N = 2) being performed by two different males. During this display, the male appeared to initiate a hanging gape display, but instead of hanging, it completely rotated around the perch to resume a normal open gape display posture.

Presumed predefinitive males in female-like plumage were observed performing the erect posture, the wing-flap pump display, and the open gape display.

Intraspecific interactions.—Territorial males frequently interact with other individuals including adult males, and presumed predefinitive males and females. Interactions among adult males usually began as bouts of countersinging between territorial neighbors (N = 29). After a few calls each, countersinging males frequently left their perches, and approached each other along their mutual territorial boundaries. Neighboring adult males were never observed intruding directly on a male's territory. Interactions with predefinitive males (N = 7) were similar but predefinitives occasionally enter a male's territory directly. Predefinitive males were identified by their female-like plumage, advertisement vocalizations, postures or displays, and frequent aggressive perch changes.

The open gape and hanging bow displays were most frequently performed during competitive male-male interactions. Two males commonly perch <5 m apart at the boundary of their territories, vocalized energetically, chased one another, and performed repeated open gape displays and occasional hanging gape displays.

On most occasions, the erect posture and the wing-flap pump display were performed in response to a second, unobserved bird. On five occasions, visits to male territories by presumed females were observed. These female-plumage individuals did not call, posture, or act aggressively toward the resident males, as did presumed predefinitive males. After excited advertisement calling, territorial males became silent and performed the erect posture and wing-flap pump displays repeatedly until the female exited the territory. Interactions between territorial males and presumed females were frequently disrupted by the distracting activity of neighboring males. On several occasions, two adult males pursued a presumed female off their territories with repeated calls and displays. No copulations were observed.

In general, the horizontal, open gape, and hanging gape displays appear to serve an intrasexual, competitive function, whereas the erect posture and the wing-flap pump display serve an intersexual function. On some occasions males performed the erect posture or the wing-flap pump display during interactions with other males, but in several of these cases it appeared that another unseen individual, perhaps female, was present.

Interspecific interactions.—Territorial male Velvet Asity occasionally responded to intrusions of other species on the territory. Several times, wing-flap pump displays were performed by males in response to a bird of another species—e.g., Blue Coua (*Coua caerulea*), Madagascar Pygmy Kingfisher (*Ispidina madagascariensis*), and Wedge-tailed Jery (*Hartertula flavoviridis*). On two occasions, a territorial male performed the wing-flap pump in response to our arrival at its territory early in the morning.

Preening.—Territorial males preen their plumage with their bills and feet persistently throughout the day. Preening was observed in 128 5-min observation periods (23% of observation periods, or 36% of observation periods in which the male was present on his territory). Preening behavior was often extensive. For example, on one occasion a male was observed preening continuously on a single perch for over 25 min. In another instance, a male seized a 1 cm-long ant and rubbed it in on body plumage for about 10 sec. No other unusual movements were associated with this "anting" behavior.

Nesting and fledgling care.—All of the more than 25 nests of *P. castanea* that have been observed at Ranomafana over the last decade were placed near the end of long overhanging branches of a single common species of forest tree: *Tambourissa obevata* (Loret Rasabo, pers. comm.; Prum and Razafindratsita, in prep). *Tambourissa obevata* has simple, entire leaves about 15 cm long with pointed "drip tips." Nest trees are frequently reused over a number of years. In November 1994, a single large tree at Ranomafana included remnants of six *castanea* nests that had been constructed on different branches in previous seasons.

The nest of *P. castanea* is a hanging sphere of moss and fine plant fibers about 25 cm long and 12 cm wide. Nest construction and fledgling attendance were observed on several occasions by Razafindratsita in the 1993–1994 breeding season. Three partial or complete nests were observed in late November and December 1993 (C-125, C-275, and F-0). Construction was observed at the C-125 and C-275 nests. Each nest was built by two female-plumaged birds that were closely associated with one another and frequently perched within one m of each other near the nest. One of the pair of individuals at the C-125 nest in 1993 was certainly female since it was banded in female plumage in 1991. Nests were built over more than ten days. One nest that was nearing completion on 27 November 1993 had no eggs inside on 8 December 1993. No nests were found in November 1994.

Nests were not placed in known male territories, but adult males were observed in the vicinity of two nests. One male was observed exiting from the C-125 nest on 26 November 1993, and associating briefly with the two female-plumaged birds. An adult male was also observed in association with two female-plumaged birds near the C-275 nest on one occasion. This male called and chased the two female plumage birds. These males, however, were not consistently associated with these nests, and were not observed constructing the nests.

A single female-plumaged bird was observed attending a group of three dependent fledglings for one hour by Razafindratsita on 26 January 1994 at C-300, just 25 m from one nest observed in the previous month. The fledglings had female-like plumage but were distinguished by having few-er stripes below, shorter tails, and conspicuous yellow gape marks. The three fledglings begged and chased the presumed female. The female-plumaged bird foraged for fruits and placed them whole in the mouths of the begging young.

Diet.—The diet and ecology of *P. castanea* is being studied intensively at Ranomafana by V. R. Razafindratsita and S. Zack (in prep.). Their observations confirm that *castanea* is extensively frugivorous. However, our observations during November 1994, when the weather was unusually dry and fruit was extremely scarce, indicate that nectar feeding is a seasonally important food source for *castanea.* Of particular importance is *Bakerella*—a common parasitic mistletoe (Loranthaceae) with abundant, bright pink flowers (See Frontispiece). Male UB#3 was observed foraging on the *Bakerella* nectar on 12 occasions during ten observation days in late November 1994.

Salomonsen (1965) states that the tongue of *castanea* is unspecialized for nectar feeding. However, observations of the tongues of spirit specimens show that the tongue of *P. castanea* is bifid distally, and that each side is divided into numerous, fine brushy tips, as found in other nectarivorous birds (FMNH 345696-7, 345708-10).

Annual cycle.—Langrand (1990) states that nesting has been observed from August through January, but this includes records from the entire range of *castanea.* At Ranomafana, *P. castanea* breeds between November and February. Nest construction was observed in November and December 1993, and fledgling attendance was observed on 26 January 1994. The beginning of the 1994–1995 breeding season was apparently delayed. Territorial males were not encountered until 20 November 1994 and no nest were observed by the end of the month. This delay may have been due to the unusually extended dry season at this locality in November 1994.

Further north in Madagascar, breeding occurs earlier in the year (Lambert and Woodcock, in press). For example, Rand (1936) reports collecting a nest with eggs and specimens of males and females in breeding condition in late August and early September west of Andapa. The initiation of breeding across Madagascar appears to follow the arrival of the spring rainy season.

The acquisition of breeding aspect and the development of caruncles also varies with latitude. In northern Madagascar, most adult males acquire worn basic plumage and complete caruncles by August-September, and some as early as late June (Rand 1936, specimens in AMNH). In five breeding seasons at Ranomafana, >90% of male Velvet Asity have acquired entirely black appearance and caruncles by October (S. Zack, pers. comm.). However, in 1994, all males observed in early November had extensive yellow-green feather edgings of the nonbreeding aspect of the male definitive basic plumage. Most adult males were in transition from green to black appearance (showing partial remnants of yellow-green edgings) throughout the month of November.

DISCUSSION

Breeding system of Philepitta castanea.—Our field observations of *Philepitta castanea* indicate that this species breeds in a display polygyny system. Males apparently occupy non-resource based territories that are distributed in dispersed leks. Males defend these territories from other males, and perform elaborate, secondary sexual displays. The display repertoire includes both intersexual courtship elements (the erect posture and wing-flap pump display) which are performed during male–female interactions, and intrasexual competitive elements (the horizontal posture, open gape, and hanging gape displays) which are performed during male–male competitive interactions. At least some male territories are occupied in successive breeding seasons, probably by the same males (Table 1). Male display territories lack resources necessary for reproduction. They are too small to include significant food resources, and even territorial males leave the territory frequently to forage. Furthermore, three nests observed during these observation periods were not placed within any male territories. Indeed, two nests observed in December 1993 (at C-125 and C-275) were 100 and 50 m, respectively, from the territory of male UB#4/GWOO (at E-10). This male remained on its display territory consistently throughout the day during the construction and attendance by female-plumaged birds at these two nearby nests. Lastly, five male territories lacked any individuals of the tree species in which *P. castanea* exclusively nests at this locality.

Although most males appear not to develop pair bonds with females during the breeding season, single adult males were observed near nests in association with female-plumage birds on several occasions. These males were not consistently present at these nests and took no part in nest construction or parental care. However, some males in the population may establish a pair bond or social association with females outside of the display territory system. Further, Langrand (1990) states that both parents feed the young, but this conclusion has not been documented. Thus, *P. castanea* may be characterized by significant behavioral plasticity among males.

Even with this small sample of observations, some of the display elements of *castanea* appear to be quite variable. For example, two males performed the wing-flap pump display in strikingly different fashion. Such ethological variation is unknown in most polygynous birds (e.g., manakins, Prum 1990) with some conspicuous exceptions (e.g., Ruff, *Philomachus pugnax*; Rhijn 1973).

An additional peculiarity is the independent observations at multiple nests of two female-plumage birds during nest construction. Cooperative breeding currently is known in few species of frugivorous passerine (Brown 1987). It seems likely that both female-plumage individuals observed at the nests were actually females. It is possible, however, that the additional female-plumage birds were predefinitive males that are pursuing an alternative breeding strategy. More detailed observations of multiple territorial males and nests throughout entire breeding seasons are required to further understand the nature of the breeding system and behavioral variation of *P. castanea.*

Evolution of breeding systems, display behavior, plumage, and diet of the asities.—Little is known about the breeding systems of the three other species of asity (Lambert and Woodcock, in press). Schlegel's Asity (*Philepitta schlegeli*) is restricted to deciduous dry forests of northwestern Madagascar (Langrand 1990). A recent observation of nest construction in *schlegeli* indicates that a male and female have a pair bond and construct the nest together (Hawkins 1994). However, other observers have encountered 6 male *schlegeli* calling simultaneously from separate perches spaced along 150 m of trail during the breeding season, in a spatial pattern reminiscent of dispersed leks (P. Morris and B. Wright, pers. comm.). Additional observations are required to determine whether *schlegeli* populations exhibit polygyny or variation in breeding system. In the Common Sunbird Asity (*Neodrepanis coruscans*), there is a pair bond between the sexes, but the nest is constructed entirely by the female (Prum and Razafindratsita, in prep.). Similarly, in the Yellow-bellied Sunbird Asity (*Neodrepanis hypoxantha*), there is a pair bond with female-only nest construction (S. M. Goodman, F. Hawkins, and M. Putnam, pers. comm.).

Several elaborate display elements have been observed in other species of asities. A male *P. schlegeli* was observed displaying next to a female by "drooping his wings, fluffing up breast feathers and lifting his tail so that it almost touched his rump feathers" (Hawkins 1994). This display appears to be unique among asities; none of the details of this tail-cocked posture appear to be homologous with the display elements of the congeneric *P. castanea* (Fig. 7). However, male *N. hypoxantha* have been observed performing a display in which the male leans forward with its body held below the perch with its tail held above the perch, the throat feathers fluffed, and the bill and head held horizontal; in this posture the male flicks his wings and vocalizes energetically (S. M. Goodman, F. Hawkins, and M. Putnam, pers. comm.; F. Hawkins, photograph). This

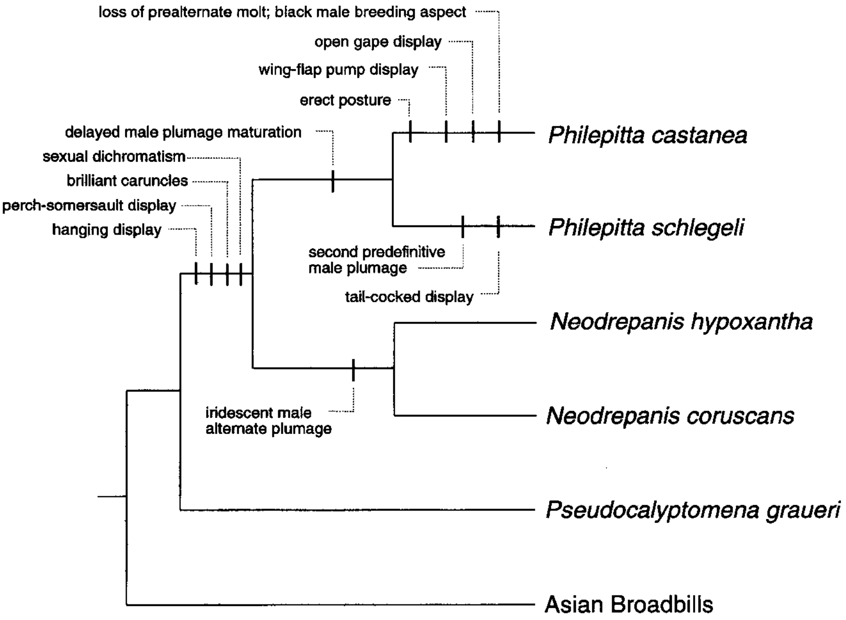

FIG. 7. Phylogenetic patterns in the evolution of display elements and plumages of the asities. Tick marks indicate the lineages during which various traits are hypothesized to have originally evolved (see Discussion; relative position of trait changes on a single lineage is arbitrary). The phylogenetic hypothesis is based on morphology (Prum 1993). The sister group to the asities is the African Green Broadbill *Pseudocalyptomena graueri*; the sister group to this group is a clade including Asian broadbills except *Calyptomena* (Prum 1993).

display is extremely similar to the hanging gape display performed by male *castanea* (Fig. 6). In addition, a male *hypoxantha* has also been observed doing a repeated perch-somersault display while fluttering its wings in response to playback (P. Morris, pers. comm.). This display element is also extremely similar to the perch-somersault display of *castanea.*

The detailed similarities between the hanging display and perch somersault displays of *castanea* and *hypoxantha* support the hypothesis that these two display elements are behavioral homologs that originally evolved in the common ancestor of the asities, prior to the differentiation of *Neodrepanis* and *Philepitta* (Fig. 7). The detailed similarities between these displays make the alternative hypothesis of convergence unlikely. This evidence supports the prediction that a similar, homologous display element is performed by *P. schlegeli* and *N. coruscans,* or that it has been lost in these species. Since the origin of these display elements in the common ancestor of asities, the displays have continued to evolve. Thus, a male *hypoxantha* shivers its wings and fluffs out its throat throughout the hanging gape display, whereas male *castanea* holds the gape open broadly and calls; a male *hypoxantha* flutters its wings and somersaults repeatedly, while the homologous display of *castanea* is simpler. These novel differences have probably evolved subsequent to the origin of these display elements. Interestingly, the open gape display appears to be an evolutionarily novelty that has been added to the hanging display in *castanea.* Although the hanging gape display looks like an elaboration of the open gape display, the opposite conclusion appears to be correct.

During the breeding season, all species of asities are sexually dichromatic and have brilliant, secondary sexual caruncles. Sexual dichromatism apparently evolved in the original common ancestor of the asities (Fig. 7; Prum 1993). All asities except *castanea* have two annual molts- the prebasic and the prealternate- and sexually monomorphic, basic (nonbreeding) plumages. Primitively within the asities, sexual dichromatism is achieved by the sexually dimorphic, alternate male plumage which is produced by the prealternate molt. The primitive male alternate plumage in asities was probably yellow below and green above. *Neodrepanis* subsequently evolved the iridescent blue upper parts in the male alternate plumage.

In contrast to other asities, *P. castanea* has lost the prealternate molt and has evolved a unique, sexually dimorphic basic plumage. The fresh, nonbreeding male basic plumage is scaley green. The novel, black, male appearance during the breeding season is a worn basic plumage. Thus, the beautiful, breeding aspect that gives the Velvet Asity its English name has evolved through the derived loss of the prealternate molt that was primitively present in the asities (Fig. 7). The seasonal variation in sexual dichromatism found in male asities is rare in tropical passerines, but the type of annual molt and plumage wear found in *castanea* may be unique among all tropical passerines.

The brilliant colors of the caruncles of *castanea* and other asities are produced by constructive reflection, or interference, of incident light by highly ordered collagen lattices in the dermis; this structural color mechanisms is apparently unique among animals (Prum et al. 1994; Prum, in prep.). These multicolored caruncles have also differentiated extensively among the species of asities since their origin in the common ancestor of the group (Prum 1993; Prum et al. 1994). The size, shape, colors, and surfaces textures of the caruncles vary among species. Further, the ultrastructural organization of collagen fibers has continued to evolved. In *castanea,* the arrangement of collagen fibres is much more orderly than in either species of *Neodrepanis,* resulting in more vivid, brilliant color production (Prum et al. 1994; Prum, unpubl. date). No histological specimens exist of the caruncles of *P. schlegeli.*

Both species of *Philepitta* also have delayed male plumage maturation. In *castanea,* the predefinitive male plumage resembles female plumage. Males acquire definitive plumage and caruncles in the same season. Interestingly, since *castanea* has only a single annual, prebasic molt, the first definitive plumage acquired by any male is the basic plumage in the non-breeding season. The first male caruncles are apparently developed prior to the subsequent breeding season. However, in *schlegeli,* there are two stages, or probable age-classes, of predefinitive males. The first stage has female-like plumage and lacks caruncles as in *castanea*; the second stage-class has female-like, predefinitive plumage but has completely developed caruncles, as in the definitive male. The third stage-class has the definitive male plumage and caruncle morphology. The second stage-class, predefinitive male *schlegeli* have been observed singing like definitive males (P. Morris and B. Wright, pers. comm.). The age at which predefinitive males assume definitive adult plumage is unknown in either species of *Philepitta.*

Delayed plumage maturation originally evolved in the common ancestor of *Philepitta* with the retention of a female-like, predefinitive male plumage (Fig. 7). Delayed plumage maturation continued to evolve after its origin with the evolution of a second, distinct stage-class of predefinitive males in *schlegeli* (Fig. 7). Natural or sexual selection on the function of predefinitive plumages as social signals apparently led to the diversification of new status or age-indicating morphologies. Our limited observations indicate that predefinitive male *castanea* enter adult male territories more frequently than definitive adult males. Predefinitive male plumages may have evolved by selection to reduce the costs to young males of male-male aggression, and allow access and experience at male display sites. McDonald (1993) and Collis and Borgia (1993) have found evidence for this hypothesis in the polygynous manakins and bowerbirds, respectively.

Prum (1993) hypothesized that the primitive diet within the asities was frugivory and that nectarivory was derived in the genus *Neodrepanis.* However, observations of significant nectarivory by *castanea* at Ranomafana and our observations of the tongue morphology of *castanea* indicates that *castanea* is significantly more nectarivorous than hypothesized by Salomonsen (1965). Facultative nectarivory probably evolved in the mainly frugivorous common ancestor of the asities (Fig. 7). Extensive nectarivory in *Neodrepanis* evolved subsequently through specialization on nectar and the loss of frugivory within a diverse, diet (Fig. 7), rather than the adoption of an entirely new food source (Prum 1993).

Conclusions.—The evolution of the numerous secondary sexual characters in the asities has likely been influenced by intersexual selection. The extreme sexual dichromatism in *castanea* is likely to be a derived, evolutionary consequence of the intense intersexual selection that occurs in lek display polygyny breeding systems. The numerous striking similarities between *P. castanea* and the polygynous/lekking manakins (Pipridae), cotingas (Cotingidae), birds of paradise (Paradisaeidae), and bowerbirds (Ptilonorhynchidae) first lead us to initiate this study of its breeding system. As hypothesized by Snow (1971, 1976), frugivory, in combination with nest predation, can result in the evolutionary "emancipation [*sic*]" of males from parental care. This change establishes the opportunity for female mate choice, and can initiate the evolution of elaborate sexual dimorphism, intersexual display behavior, and lek behavior.

Although more observations are required, *P. castanea* is apparently the first known lekking bird in Madagascar. *P. castanea* belongs with the manakins, cotingas, birds of paradise, bowerbirds, hummingbirds, and others as another, phylogenetically independent example in support of the relationship between diet, parental care, and the evolution of lek behavior proposed by Snow (1971, 1976). Further, natural and sexual selection have lead to coherent phylogenetic patterns in the evolution of display elements in asities that are similar to those of the Neotropical manakins (Pipridae; Prum 1990). *P. castanea* constitutes an extreme example of the behavioral diversity within the Old World suboscine clade, and further substantiates this group as a premier example of avian evolutionary radiation that deserves further study.

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COLOR PLATE

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