

khoturov Island (Kharkevich and Vyatkin 1977) and Karaginsky Island (Gerasimov 1970).

The first new colony encountered was at Skalisty Cape, where some 20,000 pairs of light-phase fulmars nested on about 200,000 m² of a 40-m high cliff. A few dark-phase individuals were seen among the predominantly light-phase fulmars in this colony. Fulmar nest sites appeared to be evenly distributed from 20 m above sea level to the top of the cliff at 300–400 m. Two kilometers south of Skalisty Cape, 20 pairs of fulmars nested on an 80-m high cliff and 90 pairs nested on a 150-m high cliff.

Olutorsky Cape is formed by the 600-m high sea-cliffs of Ukiyn Mountain. Three separate fulmar colonies were observed there. About 5,500 pairs were counted in the first colony (from north to south), 12,000 pairs in the second, and 500 pairs in the third colony. Only light-phase individuals were seen at this location, which lies about 40 km south of Skalisty Cape on the Olutorsky Peninsula.

Finally, four fulmar colonies were discovered at Iren Cape (20 km west of Olutorsky Cape), where cliffs are about 400 m high. A colony on the northern side of the Cape contained about 4,000 pairs, and three colonies on the southern side had 5,000, 7,000, and 1,000 pairs, respectively. Only light-phase fulmars were observed. These breeding sites were part of a large com-

plex of seabird colonies that occupied about 5 km of coastline at Iren Cape.

In all, 55,000 pairs of Northern Fulmars were counted in 10 colonies during the survey, which more than doubles the previously known populations of this species on the western Bering Sea coast. Fulmars number about 490,000 pairs in the eastern Bering Sea and Aleutian Islands (Sowls et al. 1978).

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BEHAVIOR, VOCALIZATIONS AND POSSIBLE RELATIONSHIPS OF *XENORNIS SETIFRONS* (FORMICARIIDAE), A LITTLE-KNOWN CHOCÓ ENDEMIC¹

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Many taxa of birds are restricted to the very wet forests of the Chocó region, a small area extending from eastern Panama through Pacific Colombia to northwestern Ecuador (Chapman 1917:106, Haffer 1975). One of the most distinctive and distributionally limited of these endemics is *Xenornis setifrons* (Spiny-faced or Speckled Antshrike) which represents a monotypic genus in the subfamily of "typical antbirds," *Thamnophilinae*,

within the *Formicariidae*. Although its separation as a monotypic genus has never been challenged, the relationships of *Xenornis* within the family remain obscure. In the type description of the genus, Chapman wrote, "A formicariian bird, possibly a member of the thamnophiline group but without close resemblance to any known species." Wetmore (1972) remarked, "The bird is peculiar, possibly a relict of an older group from which some of the more widespread antshrikes may have had their origin." Only a handful of specimens exists, and *Xenornis* remains virtually unknown. In this paper we present the first observations on vocalizations, foraging, and some other behaviors of *Xenornis*, and compare these aspects of the biology of this enigmatic antbird with those of some other thamnophilines.

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STUDY SITE

Our observations were conducted at the Kuna Indian Reserve near its headquarters at the tourist/research lodge "Nusagandi" (approximately 9°13'N, 78°58'W), about 75 km ENE of Panama City along the road to the coastal town of Carti in western San Blas province, Panama. Nusagandi, at an elevation of about 390 m, is situated within the general ridge system making up the Continental Divide. It faces the Caribbean versant of the cordillera and has a very wet climate owing to showers spawned by moisture-laden trade winds. In contrast, the Pacific slope, only a few kilometers away, is in a rain shadow and is arid for much of the year. The general area is characterized by ridges and steep-sided valleys and ravines with clear, fast-flowing, rocky streams. Forest within the reserve is largely undisturbed, with an irregular canopy ranging in height from 15 to 25 m. The canopy is rather open (crowns of taller trees often not interlocking), allowing sunlight to penetrate to the forest floor, although it is denser locally. The larger trees carry a heavy epiphytic load, and the trunks of these trees generally are lightly coated with mosses. Large lianas are common, and vines form a network through the mid- and understory, although rarely forming dense tangles. The forest understory is dense up to a height of about 2.5 m, above which it opens significantly. One of the most conspicuous elements of the vegetation is the abundance and variety of palms in the understory, with some species reaching the canopy.

We observed 7–9 different individuals (both sexes included) of *Xenornis setifrons* over parts of three days in February 1987 (both authors) and January 1992 (Whitney alone), totaling about three continuous hours. The shortest length of time that a pair was watched was about 10 min. Our interpretation of foraging moves is based upon a minimum of 40 foraging attempts observed mostly by Whitney. All reported distances, times, and heights above ground are estimates. Whitney made tape recordings with Nagra 4.2 and Sony TCM-5000 tape recorders and a Sennheiser ME-80 microphone. Recordings have been or will be archived at the Library of Natural Sounds, Cornell University, Ithaca, New York.

BEHAVIOR AND VOCALIZATIONS

We found *Xenornis* between about 180 and 390 m elevation, mostly on the sides of steep slopes below ridges, but also noted that it ranged into the damp bottoms of ravines below ridges. At Nusagandi it is a fairly common bird although difficult to detect. Pairs foraged exclusively as members of mixed-species flocks in the undergrowth of undisturbed forest. Wetmore's (1972) statement that "The birds range in pairs in undergrowth in forest like some of the common antshrikes, but more secretively" does not indicate whether he found *Xenornis* in solitary pairs or with mixed-species flocks. Ridgely and Gwynn (1989) report that "Birds seen at Nusagandi have foraged mostly as pairs, generally not with mixed-species flocks, favoring dense viny tangled growth." It is possible that *Xenornis* undergoes some seasonal or temporal shift in flocking behavior (perhaps during breeding activities, for instance) that would account for the observations of

Ridgely and Gwynn (1989). Nonetheless, we believe that *Xenornis* is most accurately regarded as a regular member of mixed-species foraging flocks.

Within these mixed-species understory flocks *Xenornis* foraged between about 0.5 and 2.5 m above the ground, but ranged from practically on the ground to as high as about 5 m (where noted only once). No foraging moves were initiated from a perch higher than 2.5 m above ground. We never saw more than one pair of *Xenornis* in a flock, but on one occasion Whitney saw an adult male and two female-plumaged birds with a single flock. Members of a pair typically foraged from about 2–7 m apart, but density of vegetation in the understory sometimes made this distance difficult to judge. The birds perched on thin vertical stems and vines as well as more horizontal perches, often in situations where surrounding vegetation was fairly open. This may have allowed them to scan foliage at a variety of distances and heights. While scanning for prey, *Xenornis* sat nearly motionless for long periods of time (ranging from about 2 sec to about 1 min, usually about 20 sec). Typical posture on a horizontal perch resembled the upright attitude of *Thamnomanes* antshrikes (see color plate in Hilty and Brown 1986) and the Pearly Antshrike (*Megascictus margaritatus*) (pers. observ.) although *Xenornis* did not hold the tail quite so perpendicular to the ground as in *Thamnomanes*. The wings and tail were not moved but the head was in constant scanning motion and flying insects were tracked visually (although none were seen to be pursued in flight) in the manner of jacamars (Galbulidae). Individuals frequently reversed on perches, rapidly turning the body 180°, sometimes moving short distances up (but never down) vertical vines with this motion. They often changed perches with a sudden, leaping motion during which the wings seemed to remain closed. Such "closed-winged leaps" were usually short-range in any direction, but occasionally spanned approximately 1 m of open space in a lateral plane. The birds also occasionally shuffled along perches with a rapid side-stepping of the legs and feet. In one instance, a *Xenornis* that had been perched for several seconds on a sloping vine about 2 m above ground suddenly inverted itself so that its back was toward the ground and its neck and head were craned over its shoulder, and hung from the vine for about 5 sec peering intently at one particular spot before darting downward out of sight.

All foraging moves of *Xenornis* were, in order of most-commonly to least-commonly observed, rapid sally-strikes, sally-stalls, and sally-pounces to live foliage (terminology follows Remsen and Robinson 1990). These attacks were executed in any direction, but were most often laterally or upward-directed in a variably arcing swoop. Such moves were usually less than 1 m in range, but some sallies in excess of 2 m were also noted. *Xenornis* took prey from all surfaces of leaves, perhaps most often from the tips and upper surfaces. Palm leaves apparently were more often the target substrate than one might expect from the number of palm leaves relative to other leaves present (although palm leaves had much larger surface-areas than other types of understory plants in the area). Sally-strikes frequently involved rather violent contact of the bird's head with leafy foliage. The peculiar spine-like feathers concentrated in the loreal region of *Xenornis* may serve to

protect the eye during such strikes, perhaps allowing it to remain open fractionally longer. Prey items were apparently quite small and were swallowed quickly as we were not able to see anything more than tiny legs on any of the items captured. No surface-maneuver attacks (gleans, reaches, hangs, or lunges) were observed.

In one instance, Whitney observed both members of a pair of *Xenornis* move the tail in a distinctive manner. This was in response to close-range playback of a recording of the call. The birds were perched about 1 m above ground on horizontal palm petioles, and raised the tail rather sharply through about 45° then lowered it slowly, repeating this three of four times. No vocalization was given. We interpret this as an annoyance-triggered "cocking" of the tail; this is not performed during route foraging.

Three "core" species [*Myrmotherula fulviventris* (Checker-throated Antwren), *M. axillaris* (White-flanked Antwren) and *Microbates cinereiventris* (Tawny-faced Gnatwren)] were present in all flocks containing *Xenornis*. Other species that were present in most flocks with *Xenornis* were: *Automolus ochrolaemus* (Buff-throated Foliage-gleaner), *Xenops minutus* (Plain Xenops), *Glyphorhynchus spirurus* (Wedge-billed Woodcreeper), *Thamnophilus punctatus* (Slaty Antshrike), *Dysithamnus puncticeps* (Spot-crowned Antwren), and *Rhynchocyclus olivaceus* (Olivaceous Flatbill). Sometimes canopy/subcanopy mixed-species flocks appeared to be loosely associated with these understory flocks. The role of *Xenornis* within flocks may be impossible to determine, but playback of a recording of *Xenornis* (call or song) seemed to stimulate not only *Xenornis* but also the other "core" species in a flock to approach the tape recorder in a scolding attitude.

While engaged in routine foraging and in the absence of abnormal stimulation (i.e., tape playback, conspicuous presence of an observer), *Xenornis* was often quiet and inconspicuous. Although Wetmore apparently encountered *Xenornis* in the field on at least two occasions, he stated "I heard no calls that I could attribute to them" (Wetmore 1972). We previously (*in* Ridgely and Gwynn 1989:267) described the primary song and most common call of *Xenornis*: "The song is a series of three to nine (most often five) high-pitched and evenly spaced notes which rise steadily in pitch, the call a fairly loud fast *chak-chak-chak* (sometimes only one or up to five or more syllables); both song and call are given by both sexes." The birds give the explosive *chak-chak-chak* call (Fig. 1a) while foraging, especially if the flock is moving quickly or if the birds are alarmed. Under such circumstances members of a pair call frequently. This call seems to function to keep members of a pair in contact, and perhaps also as a general "heightened awareness" call; it does not function as a scold. Only very quiet, short songs were heard in an unsolicited context (i.e., no tape playback or whistled imitation), but *Xenornis* invariably responded to playback of a recording or Whitney's whistled imitation of its song by singing loudly and repeatedly, sometimes including up to 12 notes in the song. Female songs are very similar to male songs, but rise less rapidly (especially initially) and are slightly lower-pitched and shorter. A typical male song followed by a female song is shown in Figure 2.

Whitney observed two different individual female *Xenornis* give a slightly drawn-out descending, single-note call. In both instances the calling bird and several other species in the same mixed-flock appeared to be mobbing or scolding following the initiation of tape playback of *Xenornis*. This distinctive vocalization was not heard in any other context.

Xenornis also gives a variety of other vocalizations in the context of such behaviors as flying between perches and intra-specific interactions that are difficult to define (displacement, pair contact, mate solicitation, etc.). Some of these calls seem to be given rarely.

INTRA-FAMILIAL COMPARISONS

The foraging and flocking behavior and frequency of occurrence in mixed-species flocks of *Xenornis* are similar to the behavior of *Thamnomanes*. Both are regular members of understory mixed-species flocks and are nearly pure sally-attackers, employing an erect "sit-and-wait," long-range prey-search and capture method. Schulenberg (1983) suggested that this foraging strategy was unique to *Thamnomanes* within the Formicariidae, but it appears that it is shared by *Xenornis*. Whitney's observations of the foraging behavior of *Megastictus* (also a poorly known, monotypic genus) in eastern Ecuador and northeastern Peru reveal that it is also a sally-attacker, performing strikes, stalls, and pounces. *Megastictus* forages in the understory and mid-story of undisturbed forest and old second-growth, ranging from very near the ground to as high as about 10 m, most often between about 2 and 8 m. It scans for prey from both horizontal and vertical perches. In this regard, *Megastictus* is more similar to *Xenornis* than is *Thamnomanes*, the members of which rarely perch on vertical stems and vines (pers. observ.). *Megastictus* often changes perches every few seconds, hopping from perch to perch almost continuously before settling on a new prey-scanning perch. During these hopping motions prey items are sought and gleaned in short sally-pounces. These behaviors are less commonly employed by *Xenornis* and are virtually never performed by *Thamnomanes*. Sally-strikes are usually initiated from scanning perches that have been maintained for about 10–30 sec, and are usually 1–2 m in range. Prey items include caterpillars, moths, and orthopterans up to about 3 cm in length. *Megastictus* appears to forage primarily in solitary pairs or family groups of up to four individuals, only occasionally and peripherally joining understory mixed-species flocks. Finally, *Megastictus* regularly pumps the tail rather sharply up and down, although it tends to stop if a perch is maintained for approximately 15 sec or so. With regard to its solitary foraging behavior and characteristic tail movements, *Megastictus* is further distinguished from both *Xenornis* and *Thamnomanes*.

The *chak-chak-chak* call of *Xenornis* is given in the same context as a similar call shared by *Thamnomanes caesius* (Cinereous Antshrike) (Fig. 1) and *T. schistogynus* (Bluish-slate antshrike) (pers. observ.). This distinctive call-type (function described above) apparently is not given by other thamnophilines. The analogous call of *Megastictus* is a single note that members of a pair exchange rapidly for a few seconds (pers. observ.). The series of high-pitched, evenly spaced notes rising in frequency that characterizes the song of *Xenor-*

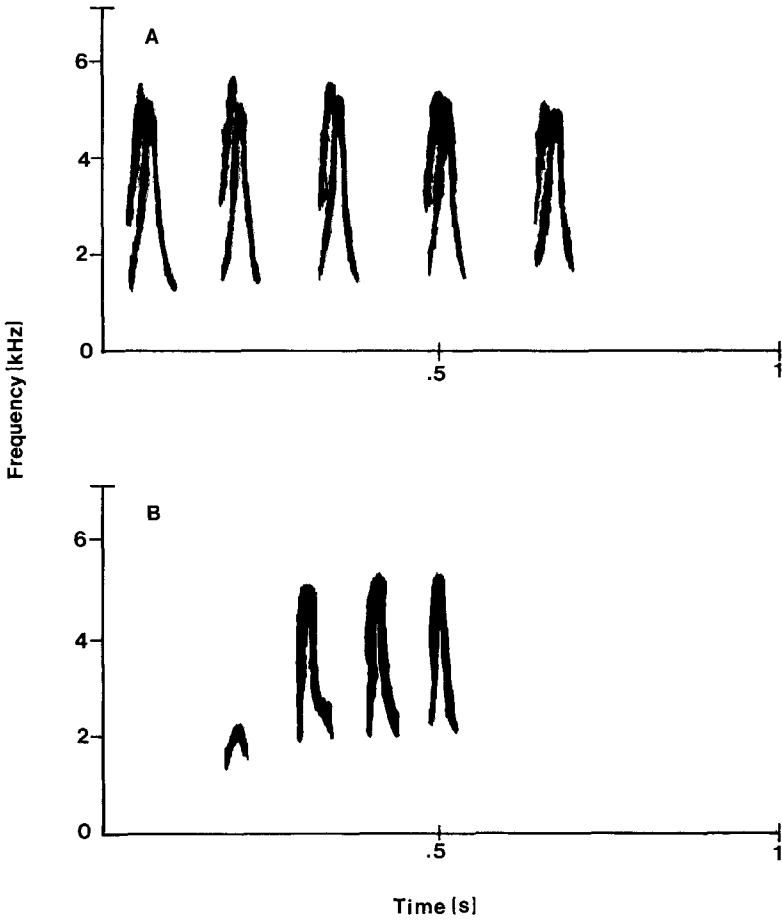


FIGURE 1. (A) The *chak-chak-chak* call of *Xenornis setifrons*. (B) Analogous call (*rattle-call*) of *Thamnomanes caesius*. Number of syllables is variable for both species.

nis is, in contrast, a common theme in the Thamnophilinae (pers. observ.).

Whether parallels in foraging behavior and calls between *Xenornis* and *Thamnomanes* and similarities in

the song of *Xenornis* and several other thamnophilines represent varying stages of advancement on convergent strategies or an undifferentiated ancestral state in *Xenornis* is impossible to determine in the absence of a

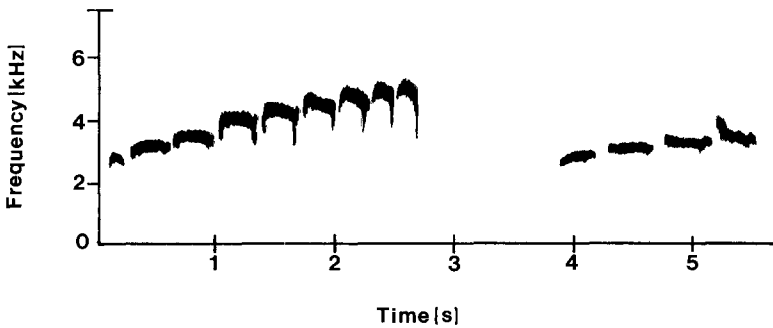


FIGURE 2. Male (left) and female songs of *Xenornis setifrons*.

well-corroborated phylogeny for the Thamnophilinae. Nevertheless, *Xenomnis setifrons* and the allopatric, sibling species pair of *Thamnomanes caesius* and *T. schistogynus* appear to be ecological counterparts, sharing a niche rare within the Thamnophilinae.

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PREY TRANSPORT BY LOGGERHEAD SHRIKES¹

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Key words: *Foraging; Loggerhead Shrike; Lanius ludovicianus; prey transport; Florida.*

Recent studies demonstrate that avian single-prey loaders preferably transport larger prey to their nests (e.g., Gronlund et al. 1970, Carlson 1985, Krebs and Avery 1985, Sonerud 1989). For central-foraging predators that carry prey for further handling and caching or for feeding of mates or young, the value of the prey is influenced by the energetic cost of transport (Orians and Pearson 1985).

Shrikes (Laniinae) are birds of open-savannah habitats that exhibit central-place foraging and caching behavior. Northern Shrikes (*Lanius excubitor*) transport whole arthropods and reptiles to the nest, but decapitate mammalian prey (Gronlund et al. 1970). This species usually transports a higher-than-optimal load size, compared to other avian predators such as the Eurasian Kestrel (*Falco tinnunculus*) (Sonerud 1989). Sonerud (1989) reasoned that the optimal load-size carried by a Northern Shrike made up a higher percent of the body mass than it did for a Kestrel, because the relative cost of flying increases with increasing body mass. Sonerud also found that central-place foraging birds which differed in size and exploited the same prey type, differed in their selection of prey for trans-

port over the same distance. Carlson (1985) found that Red-backed Shrikes (*Lanius collurio*) delivered to females prey collected close to the nest; he reasoned that the range of prey sizes economically worth returning decreased with distance and, inversely, the range of prey sizes available for self-feeding increased with distance.

Studies of hunting by Loggerhead Shrikes (*Lanius ludovicianus*) are limited to foraging behavior (e.g., Bohall-Wood 1987), prey selection (e.g., Kaufman 1973), and reproductive requirements and capabilities (e.g., Kridelbaugh 1982, Novak 1989), and opportunistic observations wherein large prey are reported (e.g., Balda 1965). Shrikes are reported carrying prey of approximately their own body mass in their feet (e.g., Conley 1982, Ingold and Ingold 1978), and carrying smaller prey in their beaks (e.g., Chapman and Casto 1972). However, mode of prey transport and distance flown with prey as functions of prey body mass are unstudied.

The Loggerhead Shrike (mean body mass on study site 47.9 ± 3.3 SD, $n = 103$) is an exclusive carnivore. Because prey carried in the bill should destabilize a flying bird and consequently increase energetic costs, I postulated that to maintain a more stable center of gravity, prey items weighing more than some threshold value would be carried in the feet rather than in the bill.

I studied post-breeding Loggerhead Shrikes during October-December 1991 at the 4,300 ha MacArthur

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