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Cooperative Breeding by Rufous Hornbills on Mindanao Island, Philippines

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Hornbills (Bucerotidae) are unique in their nesting habits; females seal themselves within the nest cavity, where they lay the clutch and remain with the growing young for most or all of the nesting period. In some species the male helps with the sealing process from outside the nest cavity. The nestlings and female are fed by the male through a narrow vertical slit in the sealed nest opening (Kemp 1979 and references therein). Thus far, four species of hornbills have been found to have cooperative breeding systems with helpers at the nest; nonbreeding birds assist the male in feeding the nest mates (Stacey and Koenig 1990). These are the Bushy-crested Hornbill (*Anorrhinus galeritus*; Madge 1969), Southern Ground Hornbill (*Bucorvus cafer* [=*leadbeateri*; see Browning 1992]; Kemp and Kemp 1980), White-crowned Hornbill (*Aceros comatus*; Leighton 1982), and Brown Hornbill (*Ptilolaemus tickelli*; Poonswad et al. 1983). I report helpers at the nest in another hornbill species, the Rufous Hornbill (*Buceros hydrocorax mindanensis*) on Mindanao Island in the Philippines.

Each of the three subspecies of Rufous Hornbill (*B. h. hydrocorax*, Luzon and Marinduque; *B. h. semigaleatus*, Bohol, Leyte, Panaon, and Samar; and *B. h. mindanensis*, Mindanao and Basilan [McGregor 1909]) has a distinct casque morphology and bill coloration (illustrated in Hachisuka 1934). In all subspecies the sexes are similar and all show the same pattern of plumage maturation (McGregor 1909). The juvenal plumage is distinct with white feathers on the head, neck, chest, and belly. Subsequently, the pale juvenal plumage is replaced by the dark black and chestnut body plumage of adults. The casque and bill develop more slowly; many birds have adult plumage coloration but incomplete development of the casque and bill coloration. Maturation is probably complete in about four years (Kemp 1979). Mindanao Rufous Hornbills develop from a black bill with a low, humped casque in juvenals to an ivory bill with a prominent, red, anvil-shaped casque in mature adults (see Hachisuka 1934). I use "immature" to designate birds that have adult plumage coloration, but which have not yet developed the definitive adult morphology and coloration of the bill and casque ("adult" refers exclusively to these birds).

I observed breeding activity at two Rufous Hornbill nests on the island of Mindanao, Philippines: one at Mt. Apo National Park near Davao City, Davao del Sur Province (7°1'N, 125°22'E) from 31 July to 25 August 1984; and the other at Lake Sebu, South Cotabato

Province (6°12'N, 124°41'E) from 4 to 14 August 1985. Both sites are approximately 1,000 m in elevation. The primary forest vegetation is tropical lowland evergreen rain forest (Whitmore 1984) dominated by trees in the family Dipterocarpaceae (Lewis 1988). I also recorded Rufous Hornbill group sizes at the Paper Industries Corporation of the Philippines (PICOP) logging concession (7°50'N, 126°14'E) during two weeks in November and December 1986. The PICOP site is 600 m in elevation with vegetation of approximately 20-year-old selectively logged forest.

The Lake Sebu nest was found on 4 August 1985. I opportunistically observed hornbill activities at and around the nest daily through 14 August; total observation time was 12 h. The nest cavity was 30-m high in the trunk of a huge emergent dipterocarp (40-m high, 220-cm dbh). This hornbill group was in the initial phases of breeding activity and included four adults and one immature (black bill and casque; the undeveloped casque of this hornbill suggests that it was an immediate postjuvenal bird). I was not able to individually identify the adults.

An adult hornbill, probably the female, spent 49% of the total observation time (5.88 h) in the nest chamber. This bird excavated the chamber by chiselling at the cavity walls and dumping out beak-fulls of wood chips. Other group members, including the immature, often perched outside of the cavity entrance, facing the nest hole, and hammered at the outer rim of the cavity opening.

The presumed female was fed by at least two adults seven times during the two days (10 and 11 August) that she spent the most time (104 and 127 min) within the cavity. Foods transferred included fruits (9 of 10 visible items) and arthropods (1 item).

On 4 and 8 August I observed copulation. The first copulation took place in the nest tree and the second in an adjacent tree. With the pair perched on the same branch facing the same direction, the male sidled up next to the female and lowered his head forward low under the female's chin, gently shaking his head. After 1 to 2 s, he hopped laterally over her to land on the same branch, where he repeated the behavior from the opposite side. With each successive hop the male appeared closer to mounting the female. After five or six of these hops, the male mounted the female for 1 to 2 s. In the first observation the male then performed three or four more of the precopulatory hopping displays and mounted the female again (with his tail to the right side of hers) for about 5 s. Just prior to the 8 August copulation, the female had allopreened with another of the adult hornbills.

On 4 August three adults moved about the tree in a close group, while the immature bird lagged behind. On 13 August one of the adults chased and billfenced with the immature bird as the immature tried to approach the other three adults, which were perched close together.

The Mt. Apo nest was discovered on 21 July 1984. I began observations on 31 July and watched the nest from a ground blind located 20 m from the nest tree for a total of 62 h on 9 days (5–8 h per day) from 4–25 August. On 5 September a single nestling fledged. The nest was a cavity about 14-m high in a 20-m-high rotten tree trunk (102-cm dbh). I could see no seal at this nest; the female had apparently broken out of the nest by the time I began observations, and the cavity was either left unsealed or I was unable to discern remaining sealing material. Thus, I observed these hornbills during the final 45 days (nest discovery to fledging) of a presumed four-month nesting cycle (see Kemp 1979), during which time the female was out of the cavity and feeding the nestling.

Three Rufous Hornbills tended this nest. Both adults, presumably the mated pair, had blue-gray eyes. These birds could be individually identified by differences in tail molt and bill coloration; one had a short central rectrix and a dirty-white bill tip (adult A), while the other had a complete tail with three new feathers that were lighter than the rest of the tail and an ivory-white bill tip (adult B). The other hornbill seen at the nest was an immature bird, recognizable by a dark-gray bill tip and maroon casque. This bird's casque was a raised anvil-shaped protuberance, but it was not as prominent as in the adults; its eyes were yellow-brown.

During the nine days of observation I was able to recognize the individual feeding the nestling for 66 of 72 feeding visits: 22 (33%) by adult A; 29 (44%) by adult B; and 15 (23%) by the immature. The feeders tended to arrive and depart together when delivering food to the nest; group feeding visits were followed by long periods of inactivity at the nest. The feeders visited the nest singly, in rapid succession, perching on the bottom lip of the cavity entrance to regurgitate food to the nestling. Individual feeders usually stayed at the nest cavity for less than one minute. The mean number of hornbills tending the nest during a group visit was 1.8 ± SD of 0.76 ($n = 35$). Rates of visitation to the nest by these three birds were notably constant. Intervals between feedings by the group (defined as a visit by any or all of the feeders) averaged 1.35 ± 0.75 h and ranged from 0.25 to 3.00 h ($n = 32$). Known visit intervals were not significantly different between individual birds (ANOVA, $F_{2,35} = 0.04$, $P = 0.96$). Of 83 individual items that I observed being transferred to the nestling, 78 were fruits and 5 were animal prey (2 cicadas identified).

Repeated sightings of territorial Rufous Hornbill groups at the two nest sites and at the PICOP site enabled me to determine the number of individuals in these groups. Family group sizes ranged from three to seven birds ($\bar{x} = 4.3$, $n = 7$). Stott (1947) also observed groups of Rufous Hornbills in western Mindanao of from three to seven birds. Because hornbills in the genus *Buceros* usually produce a single young per nesting attempt and nest no more than once per year (Kemp 1979, Poonswad et al. 1986, this study),

these territorial groups are probably composed of the breeding pair and their young (Stacey and Koenig 1990) from previous years' nestings.

The behavior of the Lake Sebu hornbills is comparable to descriptions of early nesting activity for captive (Poulsen 1970) and wild (Poonswad et al. 1986) Great Hornbills (*Buceros bicornis*), as well as captive (Reilly 1988) and wild (Johns 1982) Rhinoceros Hornbills (*B. rhinoceros*). The nest site is visited for several months prior to nesting and the female alone excavates the nest from within the nest cavity. The male begins feeding the female when she starts to seal the nest, although she still exits to forage on her own. Poonswad et al. (1986) also noted copulation during this period when the female emerged from excavating and plastering the nest. Nest-sealing behavior and materials have yet to be reported for Rufous Hornbills. The use of living trees for nesting, in addition to the frequent hammering within the nest cavity and on the cavity rim by the Lake Sebu hornbills, suggests that Rufous Hornbills may use tree resin for nest sealing, as observed for Rhinoceros Hornbills (Hose *in* Shelford 1899, Johns 1982). Feeding of the nestling by both the male and female breeders at the Mt. Apo nest during the later stages of nesting is similar to reports for Rhinoceros Hornbills (Johns 1982, Reilly 1988) and Great Hornbills (Poonswad et al. 1983). Synchronized group feeding visits have also been observed in Brown Hornbills (Poonswad et al. 1983). This pattern of nest attendance by feeding groups may minimize the duration of disturbance at the nest, reducing the chance of revealing the nest to predators.

My observations document helpers at the nest in Mindanao Rufous Hornbills. One breeding group consisted of four adults and one immature; the other group consisted of two adults and one immature. Presumably, nonbreeding birds were affiliated with a monogamous pair. Helpers assisted breeding adults in nest preparation as well as feeding the nestling. The immature helper at the Mt. Apo nest contributed a substantial amount of provisioning to the nestling.

Cooperative breeding is likely to be common for Mindanao Rufous Hornbills because territories are usually occupied by three or more birds. The breeding systems of the other subspecies of the Rufous Hornbill have yet to be described. Kemp (1979) noted the association between unique coloration of juvenal and immature birds compared to adults and cooperative breeding systems in hornbills, suggesting that all subspecies of Rufous Hornbill have helpers at the nest. The other three species in this genus have been reported to breed monogamously without helpers (Rhinoceros Hornbill, Johns 1982, Leighton 1982; Helmeted Hornbill [*B. vigil*], Leighton 1982; Great Hornbill, Poonswad et al. 1986), although helping behavior has been observed in Rhinoceros Hornbills (Hose *in* Shelford 1899, Reilly 1988). Because of the diversity of breeding systems within this genus, comparative ecological work on these hornbills might be useful in investigating the causes of cooperative breeding.

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An Early Miocene Passeriform from Argentina

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The fossil record of Passeriformes from South America had previously been restricted to the Pleistocene of Argentina, Brazil and Venezuela (Brodkorb 1978, Tambussi and Tonni 1986, Cuello 1988, Noriega 1991). In this contribution we report the first passeriform fossil from the Miocene of South America (Noriega and Chiappe 1991).

Recent joint paleontological expeditions of the State University of New York (Stony Brook) and the Museo Argentino de Ciencias Naturales have recovered abundant avian remains from the Miocene deposits of southern Patagonia (Chiappe 1991). The material on which we report comes from beds of the middle part of the Pinturas Formation, which outcrops at the locality of "Portezuelo Sumich Sur" (Bown and Larriestra 1990), northwestern Santa Cruz Province, Argentina. The age of these deposits has been considered to be Early-Middle Miocene by several authors (Marshall et al. 1983, Bown and Larriestra 1990, MacFadden 1990).

Description.—The fossil is a nearly complete distal end of a right humerus (MACN-SC-1411; Museo Argentino de Ciencias Naturales, Sección Paleontología de Vertebrados, Buenos Aires; Fig. 1B). In cranial view, the brachial fossa (Fossa M. brachialis) is shallow, not well delimited, and of subelliptical shape. The ventral supracondylar tubercle (Tuberculum supracondylare ventrale) is large and subtriangular. This area is situated just distal and lateral to the brachial fossa.

The distal condyles are globose and well defined. The dorsal condyle (Condylus dorsalis) is very convex and its proximal area curves medially. The distal margin of the ventral condyle (Condylus ventralis) is remarkably convex, and it projects distally with respect to the dorsal condyle. On its medial half, the ventral condyle exhibits a smooth depression, which is proximally bounded by the superior margin of the condyle.

Proximal to the dorsal condyle there is a subelliptical papilla of insertion of the ventral head of the M. extensor metacarpi radialis. The dorsal supracondylar process is well-developed, hook-shaped, and proximally projected. The ventral epicondyle (Epicondylus ventralis) is missing. However, the large area of break indicates that it must have been extensive and directed distocaudally. In caudal view, the olecranal fossa is superficial and the scapulo-tricipital groove (Sulcus M. scapulotricipitis) is pronounced.

Discussion.—Comparisons of the specimen were made with members of the Passeriformes and with those taxa considered closely related to Passeriformes, the so-called "perching birds" of Feduccia (1977; i.e. Trogoniformes, Coraciiformes and Piciformes). Despite its fragmentary nature, the fossil can be unquestionably assigned to the Passeriformes because the ventral epicondyle is prominent and distally directed. The ventral epicondyle is not projected mediocranially as in the nonpasseriforms (Fig. 1A), but