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BREEDING AND OTHER HABITS OF CASQUED
HORN BILLS (*BYCANISTES SUBCYLINDRICUS*)

(WITH 6 PLATES)

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PREFACE

I went to Uganda at the invitation of the East African High Commission to carry on virus research as a visiting scientist at the Virus Research Institute, Entebbe, where I worked from August 1954 until mid-May 1955. My ornithological observations were made as an amateur in the early mornings and evenings, and on weekends. It had been my hope to study some particular field problem in addition to making a general acquaintance with African bird life. The nature of the problem was determined soon after my arrival. In my bird notes, black-and-white casqued hornbills [*Bycanistes subcylindricus* (Sclater)] soon took up more pages than any other species. They came to our garden frequently. In addition, a pair of them roosted and carried on courtship activities in a tree above our house. When I discovered a concentration of hornbill nests in the Mpanga Research Forest, it was apparent that I had an unusual opportunity to study the natural history of casqued hornbills. Present studies did not begin until many females were already walled in. A few pairs of late-nesting hornbills, however, enabled me to witness the beginning stages of nesting activity. Observations on 16 nesting pairs gave, in the aggregate, a rounded picture of breeding and other habits of these birds. As far as I am aware, this is the first detailed description published on the natural history of *Bycanistes subcylindricus*. Moreau (1936), however, has written of a related species, *Bycanistes brevis*. His account is based on the histories of two nests that he observed in Usambara, Tanganyika.

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L. K.

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INTRODUCTION

Description of area.—Casqued hornbills were studied in an area extending from Entebbe, Uganda, to the Mpanga Research Forest located 13 miles to the west. This area is situated on the north flank of Lake Victoria. It is a few miles north of the Equator, at an altitude of approximately 3,750 feet. The rainfall is about 50 inches a year, with a peak in November and a peak of heavier rains in April. Temperatures vary little from a range of 60° to 85° F. Entebbe is the administrative center of British Government and is beautifully situated on a peninsula in Lake Victoria. Its extensive gardens and natural features make it attractive to an incredibly rich bird fauna. There are few trees, however, large enough for nesting hornbills. The Botanical Gardens have a small patch of forest where a single pair nested.

Eastern Uganda consists principally of rolling hills covered with small native farms or shambas. Excellent climate and abundant rainfall enable natives to raise crops continuously and in wide variety, including bananas, coffee, sugarcane, cotton, and cassava. Small fingers of forest persist along bays of the lake and swampy valleys. Zika Forest, 7 miles from Entebbe, is somewhat more extensive and consists of medium-sized trees. Most of these forest patches are under attacks from natives. Africans are continually collecting firewood or trying to enlarge their shambas. The Mpanga Research Forest was the only place I visited with any concentration of large trees furnishing suitable nesting sites. In a sense it is an island, preserved from encroachment of the ever increasing native shambas. The forest is largely second growth. Some of its trees, however, are 150 feet in height. A network of well-kept trails enabled me to move

rapidly and quietly from one nest tree to another. Most of the nest trees I discovered were within a quarter mile of the headquarters clearing. There were undoubtedly more at a greater distance. The forest covers 1.75 square miles and is $2\frac{1}{2}$ miles long. An African ranger and his assistants who lived at the headquarters clearing (pl. 1, fig. 1) were most helpful in putting up ladders and erecting scaffolds.

Life in Mpanga Forest.—A remarkable feature of the tropical forest was that during many hours I saw and heard few living things, whether I was sitting or moving quietly about. Throughout the day, especially in the first part of the nesting season, casqued hornbills were noisy and conspicuous. Other wildlife activity reached a crescendo early in the morning and again late in the afternoon, set off by the screaming of gray parrots (*Psittacus erithacus*). Great blue turacos (*Corythaëola cristata*) often came to feed on fruit of the same trees as the casqued hornbills. Their rolling calls were tremendous in volume. On the other hand black-billed turacos (*Tauraco schütti*), running squirrel-like along high branches, were quiet and difficult to find. Two other, smaller hornbills (*Tockus alboterminatus* and *Tockus fasciatus*) occasionally came through the forest in small groups. I never saw or heard an owl at Mpanga. Hawks and eagles were not frequent, but they raised a commotion among hornbills whenever they appeared. Most magnificent was the crowned hawk eagle (*Stephanoaëtus coronatus*). The harrier hawk (*Polyboroides typus*), somewhat vulturine in appearance, would search crevices and holes of dead trees for birds' nests and other prey. Lastly, I encountered the great sparrow hawk (*Accipiter melanoleucus*) for some weeks in the hornbill area. It made a continual shrill call, "ker-kee-kee." I had a strong suspicion, but could not prove, that this powerful bird sometimes preyed on casqued hornbills. Smaller birds were rather retiring. It usually took some searching to see such birds as the West African nicator (*Nicator chloris*), the yellowbill (*Ceuthmochares aereus*), and Narina's trogon (*Apaloderma narina*). Among mammals, troops of redbill monkeys (*Cercopithecus ascanius schmidti*) were much in evidence at the extremes of the day.

METHODS

Finding nests.—Knowledge of hornbill habits facilitated the finding of nests. The various ways in which 16 nests were located, with the number of nests discovered by each method, may be summarized as follows: Search for the largest tree in an area where hornbills were suspected of nesting (5 nests); chance observation of a male at the

nest hole (3 nests); hearing the feeding chuckle of the male and following it through the forest (2 nests); rattle of female bill in nest opening (1 nest); shrill screaming of female hornbill from behind wall when her nest was approached by foreign hornbills (1 nest); commotion of a group of hornbills surrounding an eagle (1 nest). Two other methods involved observations of a male bird: When on a direct, purposeful flight into the forest (1 nest); and following a bird after it picked up dirt from the ground (1 nest). Finally, one nest located in the Botanical Gardens was first noted by other observers. A helpful clue in finding an actual nest tree, once the general territory had been localized, was the presence of the elliptical stones of *Canarium schweinfurthii* on the ground. This fruit is a main item of hornbill diet. Feces were of little help as signs. They are mostly brown in color, disintegrate rapidly on vegetation, and are expelled away from the nest.

Identification of individuals.—Adult hornbills, as well as young emerging from the nest, have the same pattern of black and white plumage. Males, however, are readily distinguishable from females. As adults they are a third larger and have the huge, forward-projecting casque on the upper bill. Young males, even at time of nest leaving (pl. 1, fig. 2), have a larger bill than adult females. There is an ivory-white patch at the base of the upper mandible. As illustrated by my young hornbill (pl. 2, fig. 1), this patch is very large and is well supplied with blood vessels. It is probably an area of growth. In adult males it is smaller, but can be seen at a distance and, owing to variations in size and configuration, it proved to be of considerable value in recognition of individual birds. It is unknown at what age a young male develops a forward projection of his casque.

Watching hornbills.—Observations on nesting hornbills were made from the ground close to nest trees, using 8 x 50 Zeiss binoculars. A few males were shy and rarely seen at the nest. Ordinarily, however, males came to feed their mates if I sat still and waited. A blind was not essential. I usually watched from the spot which gave the best possible view. Along some trails in Mpanga Forest and in the Botanical Gardens the hornbills were accustomed to seeing people passing below. Hornbills were less shy when constructing nests, possibly because of preoccupation with the work. Many nests were inconveniently located. I therefore concentrated my watching on nests most favorably situated. Only one nest was located low enough for construction of a scaffold, reached by ladders tied in place. One could look inside by pointing a flashlight through the aperture. Ob-

servations were all made by myself except in two instances, both of which I was able to check to some extent on a subsequent occasion.

Captive hornbills.—Field studies have been supplemented with observations on four young captive hornbills, three of which were removed from nests when approximately 6 to 7 weeks of age. A male (pl. 2, fig. 1) and a female (pl. 2, fig. 2), named "Mpanga" and "Zika" respectively, were both taken from nests and have lived in my house for a year. This paper does not present full observations on these captive birds. It is hoped to make a more complete study over a number of years.

GENERAL HABITS OF HORNBILLS

Flight.—Casqued hornbills, with large bills and black and white plumage, were conspicuous birds in the vicinity of Entebbe, especially when they flew over open spaces. They were usually in pairs, the male flying about 20 feet in front of the female. Occasionally she took the lead. Their flight was remarkable. There would be a series of wingbeats, then a glide with head and bill held well up. These glides could be without apparent loss of altitude. If a bird was going downhill, as from our hilltop garden toward the lake, a glide might extend 200 or 300 yards. Either phase of flight was noisy. The wingbeats made a "wush, wush" noise and the glide a prolonged "woo-oosh." These noises were helpful, especially in Mpanga Forest, as they enabled me to know, even at some distance, when a male hornbill was returning to his nest.

Roosting.—There were several opportunities within the Institute Compound for observing roosting habits. From August, when we arrived, until October, a pair of hornbills spent every night in a tree in our garden. They would come in with fair regularity at about 6:50 p.m. and sit together for 10 or 15 minutes in the dusk. Then they would separate to roost on individual perches. These perches were at the periphery of the tree where branches were about one inch in diameter. They were about 20 feet apart and 25 feet above the ground. The male always used his own perch and the female hers. In the period of perching together, either one of the two perches might be used. During my first nights at Entebbe, I was mystified by strange noises coming from the tree, not knowing that they came from hornbills. There would be an occasional "woof" or a whacking of bills on bark. By dawn at 6 a.m. noises increased, especially the bill whackings. The hornbills again perched side by side but were in no hurry to leave. They would finally move to other branches of

the tree, then fly off about 6:45 a.m. They thus spent nearly 12 hours roosting. When I returned from a short safari on October 19, I found that the pair had left. I presumed they had started to nest. Unfortunately, I had not discovered at this time that male hornbills can be identified by the white patch on the bill. I had spent many evenings watching the pair and wondered if they would return. Later I had some evidence that the male continued to roost alone in the Institute Compound. This evidence was most suggestive. On the evening of January 19 I heard a familiar bill whacking outside of my window. A male hornbill was roosting on the same male perch observed early in October. He spent only one night. I now recognized, by the white patch on his bill, that he was the same bird I had observed some weeks before roosting in an unusual place just beyond our garden. At night he was perched on a bare limb 20 feet over a driveway. On the nights of January 28 and 29, he was on the same perch, silhouetted against the sky. On the evening of January 31, this hornbill again came to our big tree, alighting first on the female perch, then settling on the male perch. Apparently the lone male alternated roosting places. Although territory among casqued hornbills was not obvious much beyond the vicinity of the nest tree, it would appear possible that the area used for roosting might be more permanent. This situation would be worth further investigation. My captive hornbills, Mpanga and Zika, became extremely nervous at the approach of the evening. This was true even when in a room with artificial illumination. They appeared to have a strong desire to be on a roost they were used to and where they felt secure. Each bird perched on exactly the same place on the roosting pole night after night.

Courtship behavior and the pair bond.—Casqued hornbills remain closely paired the year around, as far as I could determine. Some of their activities prior to nesting appeared to be courtship behavior. The pair of hornbills that roosted in our garden from August to October could be readily observed. They would come flying in about dusk. Soon after they were perched side by side, the male would jerk his head and pop a cherry-sized fruit to his bill tip. Then he would bend over and try to feed the "cherry" to his mate. Usually she would not accept. This never discouraged his efforts. For example, on September 18 he hung his head and with a few slight heaves ejected a "cherry" from his gullet. He held it delicately in the tip of his huge bill as he offered it to his mate. She refused. The male then opened his bill with an upward toss which sent the "cherry" flying back into his throat. In a few minutes he again produced the

fruit and again she refused to take it. She finally touched the "cherry" with her bill. The male then swallowed the fruit for the fourth and last time. Although this "cherry" presentation was observed on six evenings between September 25 and October 5, she accepted only once. On other evenings the ceremony climaxed in a touching of bills. There was never more than a single fruit involved.

Presentation of a piece of bark, a stick, or a leaf was commonly observed during the nesting period. It was almost always the male who did the offering. On one day, November 20, I observed the reverse process. A male perched in Mpanga Forest was joined by his mate who held a large winged insect in her bill. She gave it to him. He then gave it back and she swallowed it. Possibly she simply liked to have things handed over, even if she had to provide the objects herself.

Mutual preening was another late evening activity of the two hornbills in our garden. On September 15, the female sidled up to the male on his perch. Preening now went on for 20 minutes. The male nibbled at the feathers of his mate's head and neck. She appeared to enjoy this attention. Her head moved slowly backward until the occiput rested on her back and her bill pointed upward. The male meanwhile kept nibbling at her exposed throat. Later it was his turn and she went over the feathers of his head and neck. He did not put his head way back as she had. I seldom saw males do this, once being on March 7 in the Botanical Gardens. A pair of hornbills were together for the first time in 4 months. The recently emerged female, in soiled plumage, was perched close to her mate as she nibbled at the feathers of his exposed throat. Mpanga and Zika, my captive hornbills, were preening each other at 3 months of age. Zika has always enjoyed having her throat tickled gently. Even when sitting in my lap, her head has gone way back in the manner of the wild bird which roosted in our garden. Mpanga has often invited preening. He does this by turning the back of his head to Zika, then ruffling up the feathers. In going over each other's feathers, hornbills take special delight in finding small bits of horny material. They may stop to toss these about, small as they are.

Playing with sticks and bill whacking.—Bill whacking was predominantly a male activity. It was usually done after a male had fed his mate on the nest, but might take place on waking up at dawn or most any time of day. The huge bill would resound like a castanet as it was whacked from side to side on a limb. Females scrape their bills on a perch after feeding.

A favorite occupation of resting male hornbills was to toss a stick

in their bills, continually clamping on it to get a fresh grip. On November 20 I saw one knock off a piece of bark and juggle it about until it dropped. He then fell straight from his perch toward the ground and retrieved the bark with surprising agility. On November 29 a male, after much knocking on dead wood, finally broke off a piece 10 inches long. This fell toward the ground and the bird swooped down 50 feet but failed to catch it. My captive hornbills, male and female, would seize a stick or piece of crumpled paper with great gusto. Their clamping and tossing, however, would soon cause them to loose it. They were amazingly quick at catching any piece of food thrown at them, and when placed by a sunny window, they would try to seize bits of floating dust.

Notes and calls.—In addition to noises made by wings in flight and whacking of bills, casqued hornbills made a din with their notes and calls. At times they sounded somewhat like domestic hens. A pair, perched in separate trees, would keep in touch with a series of hoarse "cuk, cuk's." At times they made single notes such as "ugh" or "woof." Most lugubrious noises might come from a male in search of or temporarily separated from a mate. Thus on September 24 I saw a lone male and a nearby pair of hornbills. The single bird made "ka-ka-ka" and "ka-wack, ka-wack, ka-wack" noises of considerable volume. He broke off a small stick, and when he bounced along a limb with it in his bill, the pair flew away at his approach. The male of nest 1 made Mpanga Forest resound with his cries when his mate lost interest in nest building after weeks of futile effort. He was apparently trying to entice her back to the nest hole. Calls associated with nesting were of help in studying hornbills, for I could hear much farther than I could see in the forest. A feeding visit might be announced by a croak when a male came to perch near the nest. Then, when clinging to the entrance and transferring food, males usually made a low, rapid feeding chuckle as bills touched. Females sometimes responded with low guttural notes. These birds, walled within the nests, had a repertoire of their own. Two different noises were made with the bill. The first was a rapid, woodpecker-like tapping made with the tip of the bill, used broadside. Females tapped not only in constructing the original nest wall, but also when walled inside the tree. Sometimes they were repairing the nest wall, but at other times I conjectured that they were tapping on the sides of the hollow tree by way of idle amusement, for the persistence of tapping in some nests was greater than could be expected from repair work alone. My captive hornbills tapped in similar fashion on the walls of their cage when 7 and 8 months old. Two further noises of nesting females

expressed alarm. One was a rattling of the slightly opened bill in the aperture of the mud wall. The bill was visible from the ground. A second alarm noise was a loud, wailing screech. I never heard this call except from a nesting female in distress. Nest 15 was first located by following such screaming through 700 yards of forest. A foreign pair of hornbills was by the nest when I arrived. Such intrusions were a frequent cause of screaming. Similar screams were heard from another female whose mate, early in the nesting season, fed her comparatively infrequently, and from another female whose mate had been recently killed. I seldom heard chirping of the young inside a nest. A newly hatched chick observed in nest 10 made a "chirpee, chirpee" note. Older young ones, as I learned from my captives, can make an assortment of chittery, whistling, and screaming noises. The whistling somewhat resembled that of a smaller species of hornbill, *Tockus fasciatus*.

NEST CONSTRUCTION

Hole hunting.—I first noted nesting activities of hornbills late on the afternoon of October 13. A male flew to the top of a high tree by the lake shore and peered into a hole. He was soon joined by his mate, who took her turn, looking into the hole for 10 minutes. Then she went inside and excavated pieces of rotten wood up to 8 inches long which she tossed out. The male hung his head down to watch what was going on. When his mate finally came out, he started to inspect a second hole nearby. He changed his mind, however, and flew away with a dismal wailing to alight by a hole in another tree. Here he called to his mate with a succession of "caks" and "ughs." He put his head into the hole and pecked at the sides. Within a few minutes his mate joined him. It was apparent from this episode that the male pioneered exploration of possible nesting holes and enticed the female to follow. This observation was borne out by subsequent experience. On November 11, again late in the afternoon, I noticed a male hornbill perched next to a likely looking hole. He flew away and shortly returned with his mate. For the next 5 minutes she kept hanging her head down into the hole and pecking at the entrance. Then she lit on the lower rim, putting head and body inside. When she flew up by the male, he hopped down for another inspection. In Mpanga Forest, I had other examples of the lead taken by the male. Nest 1 had too large an opening for successful nesting. A pair of hornbills spent weeks trying to wall up the aperture, the male's interest persisting longer than that of his mate. On November 7 I found the pair inspect-

ing a hole in a stump 25 feet above ground. I suspected that they were trying to find an alternative to their other nest cavity. They both lit on the rim together, but he kept bending in to remove bits of rotten wood up to 2 inches long. She took a few of these from his bill, but let him continue the excavating. In January I observed further pioneering by a male under unusual circumstances. The male of nest 5 had been killed and his mate had broken out by January 2. I arrived shortly after 9 a.m. To my surprise, I saw a male picking up dirt in the forest clearing. I had seen no signs of nest construction for many weeks. The male's flight led me to the abandoned nest. Here he perched by his mate, then clung to the lower rim of the hole and spent some minutes poking his bill about inside. His mate scrutinized the hole carefully before flying to it. She clung to the rim momentarily, but dropped away as if frightened. This desultory type of inspection went on for 3 weeks. After losing interest in the hole, presumably due to lateness of the season, the pair continued to use the tree as a perch.

Location of nests.—Locations of nests are summarized in table 1. It was apparent that casqued hornbills preferred the largest trees and a hole as far from the ground as possible. Very large trees were scarce, even in Mpanga Forest. Nest 3 was in one of the finest trees (*Antiaris toxicaria*) in the forest, a huge specimen 6 feet in diameter at breast height and possibly 150 feet tall. The large branches supported a growth of epiphytic plants and were draped with lianas. Text figure 1 is a sketch of the nest opening in a limb 85 feet above the ground and shows the male as he always perched preparatory to bending over to feed his mate. Such large trees, free of limbs for 60 or 70 feet, were impossible to climb. Nests were often located where a large limb had broken off, exposing an area of decay. Such a site is illustrated by text figure 2. Plate 3, figure 1, is a photograph of a large tree in the open, showing location of a nest entrance in the stub of a broken branch. Nest 5 was located in a huge arching limb of a *Piptadenia*, as shown in plate 3, figure 2. Some few nests were in less favorable sites. Nest 16, for example, was only 30 feet from the ground in a comparatively small tree. It was relatively easy for an African to climb up and open it. Three nest trees were isolated and in the open and the remainder were in forests. Nest 2 was in a unique position. The cavity was located in a crotch in the top of an exceedingly tall, dead stump. Since the entrance faced vertically upward, one wondered what might happen in a heavy rain storm.

Gathering dirt for building at nest 1.—I learned the most about wall building from a pair of hornbills in Mpanga Forest. Their hole was

TABLE 1.—Location of nests of *Bycanistes subcylindricus*

Nest No.	Date discovered	Location	Tree	Location in tree	Height in feet (approx.)	Date found open	Remarks
1.....	10-24-54	Mpanga	<i>Cellis saoyourii</i> Engl.	Trunk	70	—	Unsuccessful nest
2.....	10-24-54	Kisubi	Dead stump	Top	75	—	—
3.....	10-30-54	Mpanga	<i>Antiaris toxicaria</i> (Pers.) Lesch.	Branch	84	1-15-55	Eggshell 11-28-54
4.....	11- 4-54	Mpanga	<i>Cellis zenkerii</i> Engl.	Trunk	50	1- 2-55	Male killed 1-1-55. Female broke out.
5.....	11- 6-54	Botanical Gardens	<i>Piptadenia africana</i> Hook. f.	Branch	70	4- 7-55	Female walled in 119 ± 2 days
6.....	11-14-54	Mpanga	<i>Cellis zenkerii</i> Engl.	Trunk	75	1-23-55	Eggshell 12-9-54
7.....	11-14-54	Mpanga	<i>Albizia grandibracteata</i> Taub.	Trunk	50	2- 6-55	—
8.....	11-24-54	Near Zika	Unidentified	Branch	54	1-25-55	—
9.....	11-20-54	Mpanga	<i>Antiaris toxicaria</i> (Pers.) Lesch.	Trunk	60	—	Eggshell 11-28-54
10.....	11-21-54	Mpanga	Dead stump	Trunk	30	—	Chick removed 1-22-55
11.....	12- 4-54	Mpanga	<i>Loxoa brownii</i> Sprague	Trunk	85	2- 5-55	—
12.....	12- 4-54	Mpanga	Unidentified	Branch	60	1- 1-55	—
13.....	12- 7-54	Near Entebbe	Unidentified	Trunk	50	1-24-55	Tree in open
14.....	12-17-54	Zika	Unidentified	Branch	45	—	Chick removed 1-21-55
15.....	1-22-55	Mpanga	<i>Antiaris toxicaria</i> (Pers.) Lesch.	Branch	60	—	—
16.....	1-30-55	Mpanga	Unidentified	Trunk	30	—	Chick removed 1-30-55



1. Headquarters clearing, Mpanga Research Forest.



2. Young male hornbill 2 days after emerging from nest 5.



1. "Mpanga," hand-reared male hornbill 10 months of age.



2 "Zika," hand-reared female hornbill 10 months of age.



1. Location (shown by arrow) of nest 13 in stub of broken limb.



2. Nest 5 (location shown by arrows) in *Piptadenia* tree in Botanical Gardens, Entebbe.



1. Termite mound at headquarters clearing, Mpanga Research Forest, where female hornbill collected earth.



2. Entrance of nest 10, showing cement wall.

ideally located. It was 70 feet up in the trunk of a huge tree (*Celtis saoyouxii*), as illustrated by a sketch (text figure 2). Unfortunately the hole was about a foot in diameter and apparently too large. The sketch shows the small wall built across the lower portion. Its rate of construction was exceedingly slow, even though the female worked for

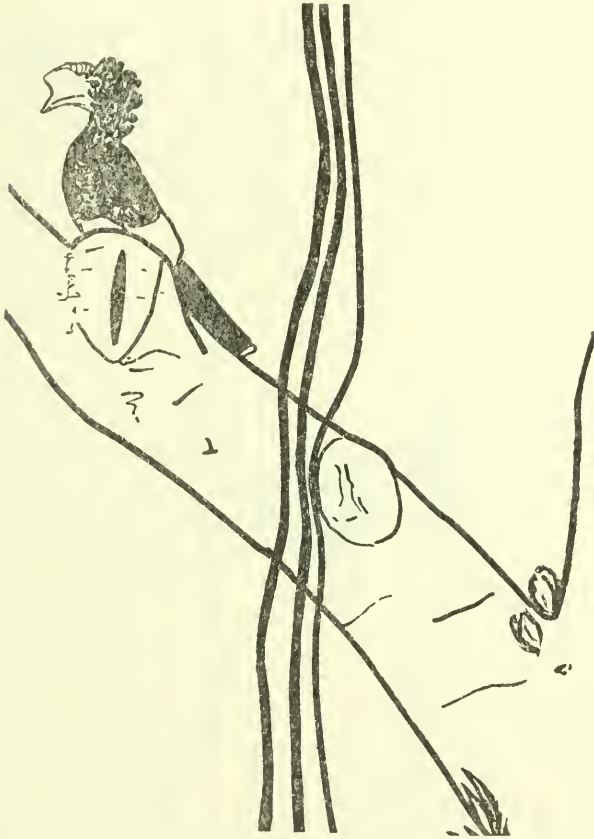


FIG. 1.—Nest 3, Mpanga Forest.

many hours, usually in the morning. On October 24 the pair flew to the hole at 8:45 a.m. The female went inside and the male perched close by. He offered her a mud pellet 5 or 6 times, but she was occupied and paid no attention. At 9 a.m. the male flew to the forest clearing, then down to a path among the shambas. Here he picked two gobs of damp earth, swallowing the first and holding the second, an inch in diameter, in his bill. Then he flew back in stages to the nest tree. I watched him cough up and pass three small mud pellets

to his mate. She took them at her bill tip in rapid succession. The male then remained quietly by for some time while she continued working inside. Twenty minutes later the male again flew to the forest clearing, alighting in a patch of maize. I crept up to within 30 feet and found him perched on a stump several feet above the ground.

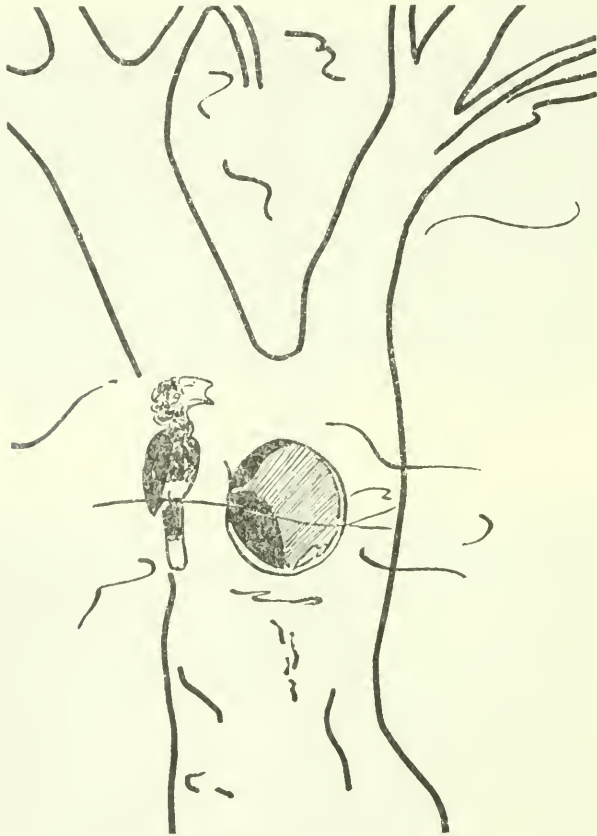


FIG. 2.—Nest 1, Mpanga Forest, never completed.

He was bending over repeatedly, and I could see that he was picking up lumps of earth and swallowing them. To my surprise the female flew over. Both birds now perched together at the forest edge while he coughed up and transferred 5 or 6 pellets to the bill of his mate. Then he hopped away a few feet, broke off a 2-inch piece of bark, and bounced back to offer it to her. She refused it. When the pair had flown into the forest with loud squawking, I examined the stump. A termite nest clung to the side of it. Freshly opened tunnels, now

lined by soldiers, showed where the hornbill had collected earth. On October 27 the male again visited the stump. At 12:30 noon he flew from his nest tree to the maize patch where I was able to observe him from a distance of 25 feet by using a screen of corn stalks. This time he picked up considerable earth from the stump and a little from the ground. Then he flew back to his nest hole, where he spent some time perched on the rim, moving his head about inside where his mate was working. Both birds were silent. So far it appeared that his job was to gather dirt and hers to build with it. However, at 8:20 a.m. on October 31 both birds flew to the forest clearing. She flew to the ground and hopped behind a mud-wattle hut. I moved around to see her bounce up against the wall and knock off a piece of dry mud the size of a plum, which she swallowed. She next hopped around a corner and knocked off another piece. From here she flew up to rejoin her mate. Shortly afterward she followed him to a distant pawpaw tree, where he fed her some fruit. Within 15 minutes they were back at the nest. By 9:10 a.m. the female was working on the nest wall, making a rapid tapping noise like a woodpecker. The male flew away for a short time, apparently to collect dirt. On his return, he perched beside his mate outside the hole, then gave her 11 pellets which she accepted at the tip of her bill and swallowed. She did not use them immediately, for the pair flew away from the nest hole and were gone for a half hour or more.

These observations showed that female hornbills as well as males collect dirt, although they probably do so less often. The female from nest 1 did not always use pellets immediately after swallowing them. Dirt might be retained in her gullet for half an hour or more. The same was true of the male. Since earth was generally hard and dry when collected, the period of retention would give it a chance to become moistened by glandular secretions and by juices from such fruit as paw-paws retained in the gullet at the same time. A larger part of the moistening may be done by the male. I noticed with my captive hornbills that the male could swallow more than twice as much as the female. He is, of course, a third larger in size. It was of interest that hornbills came to termite nests to gather building material, as these nests are exceedingly durable; each grain of earth is selected and coated with a cement substance by the termites. I saw the birds from nest 1 visit a termite nest on another occasion. The pair flew to the edge of the forest clearing at 9:08 a.m. on November 7. The female flew to a low tree, then over the shambas to the tall termite mound shown on plate 4, figure 1. Clinging to its steep sides, she took up 15 chunks of dirt and swallowed them. Finally her mate flew over to

join her. Developments which took place in the next few minutes were unexpected.

Coition.—The pair had been nest building for at least 2 weeks when they perched together on the termite mound. There was a touching of bills, and the male acted as though he were trying to give her a few extra pellets, but he apparently had none to give. At 9:15 a.m. the female flew from the termite nest, closely followed by the male who made a loud, wailing noise. The two headed toward the nest tree, but lighted on a branch at the forest edge. I had to run across the clearing for a better view. Within this short time the male had mounted the female. He came off a few moments later. Then he mounted on her back again, without hurry, and got securely placed. There was no noise. She had her tail held way over to one side. When he mounted he pressed his tail downward and somewhat under her body. His wings were kept closed. After some moments he got off and flew alone to the rim of the nest. She continued to hold her tail to one side. I could see against a background of white feathers that her vent was extroverted but was retracted shortly afterward. From at least 9:45 a.m. until 12:20 p.m. the female apparently worked from inside the nest on the wall, as she had on previous mornings.

Gathering of dirt at other nests.—At 5 p.m. on November 7 I was watching nest construction by a pair of hornbills in the Botanical Gardens. The male flew toward me and lighted on the ground 35 feet away. Here he picked up 15 or more chunks of earth. After he had flown away, I examined the spot which proved to be a low termite mound. Freshly opened tunnels showed where the bird had been working. Although hornbills appeared to be especially attracted to termite nests they are not invariably so. Sometimes they pick up ordinary dirt. On October 31 the male from nest 4 lighted on a stick close to the ground of a native shamba. He repeatedly bent over, took up chunks of black cultivated soil, and swallowed them. His next move was to an adjacent banana tree. Here he tore off pieces of leaf and bark, 1 to 2 inches long, three of which he swallowed. His subsequent flight to the forest led to the discovery of his nest hole. The wall of this nest was unusually black.

Construction of the nest wall.—At various times I watched four pairs of hornbills constructing their nest walls. There was variation in the time of day when work took place. Three pairs worked in the morning and one pair, from the Botanical Gardens, late in the afternoon. Experience at nest 2 was typical. On October 24, the male returned to his tall, isolated nest stump at noon. He leaned over the nest opening as he heaved up pea-sized pellets of dirt. These he

passed with his bill tip to that of his mate directly below. At least 10 pellets were passed in rapid succession. The male then bounced along to another part of the stump and tried to whack off bits of dead wood. In a few moments he bounced back to the hole. He shook his head from side to side, with bill half open, as though a pellet had gotten stuck. Then for a while he held his head low over the hole to watch what was going on. A week later I found him carrying on much the same. He spent considerable time looking down and even putting his head and neck through the hole. Sometimes his mate accepted two pellets and refused a third. At such periods of active construction, the only sound was the rapid tapping of the female's bill, which could be heard some distance away.

Male hornbills did no work on the walls, although they might peck and explore about a nest entrance. A male usually sat by like a bricklayer's helper. He would fetch building material and supply it to his mate as needed. The pair at nest 1 would spend the larger part of a morning in this fashion, settling down to work at about 8:30 a.m. Work at the Botanical Garden nest was done from midafternoon on. At this time the sun shone directly into the nest entrance. Possibly this pair was taking advantage of the illumination. I could see the female's bill tapping inside. Details of how the tapping was done could not be perceived readily in high nests. I had a better opportunity at nest 7 which was comparatively low. The female was already walled in but on January 29 she was repairing the entrance with material from the nest floor. She applied this material with rapid tapping of the side of her bill tip. Tapping was again seen to good advantage in my captive pair of hornbills. In September 1955, when 9 months of age, both birds would get in a corner of their cage and plaster the wall with any litter, feces, or food matter which might serve as mud. Both sexes did the tapping. This activity was carried on daily, as judged by the appearance of the wall and the amount of tapping we heard.

Abortive nesting.—On November 7, following coition, the pair of hornbills from nest 1 had worked all morning on the nest wall. By the following weekend their interest had obviously declined. The hole was too large to wall in. On the afternoon of November 13 the male kept returning to the nest rim. Then he would fly back to the forest to join his mate. Sometimes the pair would fly together to the nest tree, making a tremendous noise. It was a dismal wailing. The male, however, would look into the nest alone. On the following day I observed the same behavior from 7:15 a.m. until 12:30 p.m. These two were the noisiest hornbills in the forest. It appeared that he was

anxious to continue with the nest, but that she had lost interest, as during the whole morning she never came near it. He would put half of his body inside and make low grunts as he poked about with his bill. The same performance continued on a following weekend. She entered the nest several times, started tapping, then flew out again after a short time. The male persisted for two more weeks in his efforts to have her return. December 4 was the last time I ever saw her in the nest. This was 6 weeks after I had first found her at work. My final view of the pair was on December 12. They were perching near the nest cavity but showed no interest in it.

Structure of wall and the inside of the nest.—Nest entrances were usually elongate slits, $1\frac{1}{2}$ to 2 inches wide and 4 to 10 inches high, depending on the size of the natural cavity. These measurements are approximate. Plate 4, figure 2, a photograph of nest 10, shows a representative nest entrance. Walls were remarkably strong. Neither Africans nor myself, by putting a hand into the slit and pulling hard, could budge or loosen them in three nests opened for removal of young. Much hacking and prying with a curved bush knife were needed to effect an entrance. Another indication of the stoutness of walls was provided at the time of natural nest openings. One-half of the entrance cement of 2 nests (3 and 12) was knocked out entire, apparently by the emerging female. These pieces fell 60 to 85 feet to the ground, where I picked them up unbroken. They were roughly 4 inches long, 3 inches in width and thickness, and were built in concentric layers. Possibly each layer represented a day's work. Odd bits of insects, bark, and plant material were incorporated in the cement in haphazard fashion. In two of the three pieces, one side was dark brown. It did not run with the concentric layers and it had faced the inside of the nest. Females had probably made this addition after being walled in. For lack of earth they had used fruit stones, seeds, and what appeared to be darker fecal material. It did not appear that feces was an integral part of the main cement structure in any of the five nest walls I examined closely.

There was nothing organized about the inside of a nest. Nests 10 and 14, examined at time of opening for removal of young, had fragments of rotten wood at the bottom. Nest 10 also contained many large contour feathers. When I pulled away the cement from this nest, hundreds of small ants swarmed out from behind the edges. My hand and arm were covered with them as I explored the cavity which was roughly a foot in diameter. An African who broke open nest 14 for me had a similar experience. These ants are presumably attracted by feces and other debris, for an amazing amount of fruit

appears to go right through a hornbill's intestinal tract undigested. This is especially true of young birds, as I discovered with my captive specimens. Feces from younger individuals does not always clear the entrance. This was observed from the scaffold by nest 10. There was, therefore, ample organic matter to attract ants, and their presence in great numbers may explain why I failed to find insects, in the nature of parasites, scavengers, or others, in examinations of nest debris.

ACTIVITIES OF NESTING PAIRS

Walling in of female.—As far as I can determine, I was watching nest 5 on the evening when the female began her 4 months of voluntary confinement. On November 7, the male was active late in the afternoon bringing termite earth to his mate, and giving her pellets as she worked. On the following day I arrived at 5:15 p.m. to find him bending over the entrance. The sun shone into the hole. I could see that the nest wall was complete and that no more building was in progress. For the next hour the male stayed close by. At 6:30 p.m. he flew to a large tree (*Canarium schweinfurthii*) and picked some fruit, then returned to his nest with loud wailing. He gave his mate five or six fruits and she made low guttural notes. Dusk was now coming on. The male flew to a limb 15 feet away, then took a long flight which carried him out of sight over the brow of the hill. His mate remained alone. It was not until March 7 that I was to see her again.

Feeding and other attentions of male to mate in nest.—Once walled in the nest, the female was entirely dependent on the male for food until she emerged with her young one some months later. Nest 5 was well situated for observations. I would station myself below the huge *Piptadenia* tree in the Botanical Gardens (pl. 3, fig. 2) every few days during the week, before breakfast and again late in the afternoon. The male was accustomed to people passing beneath the arching limb containing the nest hole. Some days I would wait nearby an hour without seeing him approach the nest. I discovered, however, that there was some regularity to his visits, one usually taking place close to 7:30 a.m. Forty feeding visits were observed in the course of 4 months. A visit on November 13 was typical. At 5:40 p.m. the male came flying over the open lawns, head held high, and wings making a "woo-ooshing" noise. He held a chip of wood 5 inches long in his beak. It looked as though he were flying with a cigar. He landed on the big limb, then bounced sideways until he was on the bole above the nest entrance. Then he leaned over and pushed the

stick of wood through the entrance. When his mate had taken it, he coughed up eight blackish fruits in succession, swinging his head down each time to place them in the tip of her bill. By the time the feeding was done, the stick had come out of the hole. He picked it up and pushed it in again. Then he flew to a perch 15 feet away. At such times he would usually whack his bill loudly back and forth on a limb as one would whet a knife. This male, like most of the others I observed, did not linger in the nest tree after a feeding visit.

Stick or bark presentation was a common prelude to feeding. It occurred in 13 of the 40 visits observed. Objects presented ranged from curled pieces of bark, 1 by 6 inches, to smaller bits an inch in diameter. Discarded and dropped pieces accumulated on the ground below the nest. The male was persistent about these offerings. On December 8 he lighted above the nest and swung his bill down into the entrance 23 times to offer a piece of bark. His mate gave no response. When she accepted on the twenty-fourth try, he fed her four fruits.

The male usually made a feeding chuckle when a fruit was transferred. Numbers of fruits offered varied from 2 to 17 per visit, but counting was often difficult. Thus on February 7 the male fed his mate 17 small fruits. Some of these were offered 4 or 5 times before she accepted. On February 28 he fed her 2 "cherries." A third one, however, had to be held down 11 times before she took it. Possibly the female is at times occupied with the young chick, so that she is not in a position to accept. Fruits brought to the nest ranged from the size of a pea to that of a small plum.

In addition to bringing sticks and fruit, the male of nest 5 cleared away accumulations from the entrance. The approach to the nest, formed by a broken-off limb, sloped slightly upward from the wall. It thus collected fecal and other matter expelled from the nest. The male lingered to clear away this debris after 14 of 40 feeding visits. Sometimes he swallowed a few items. More often he would pick up small bits with his bill and toss them outward in a rapid and systematic fashion. On February 9 he did this 30 times after one visit and on February 28, 25 times. Usually he made only a few tosses before flying away. Nest 7 was the only other nest where I observed a male clearing the entrance.

Observations at other nests, while generally similar to those made in the Botanical Gardens, differed with the individual character of hornbill pairs. Sometimes physical peculiarities of the nest cavity led to differences of behavior. Nest 6 was in the straight trunk of a huge tree and the female often rested with her tail protruding from the



1. Female hornbill at time she was removed from nest 10, approximately two-thirds of the way through nesting period.



2. "Mpanga" and "Zika" when approximately 2 months of age.



1. "Mpanga" at 6 months of age.



2. Young crowned hornbill (*Tockus alboterminatus*).
(Photograph by Dr. Herbert Friedmann.)

entrance. When the male bent over to offer food, she would not always bother to turn around. One day he gave her a fresh green leaf before coughing up four yellow fruits. At nest 12, also at Mpanga, the female would put her whole bill out of the entrance to take food. Possibly females in these last two nests were crowded for space. Some of the holes, such as those of nests 4 and 7, were on straight trunks without boles. Consequently, the visiting males had to cling to the lower rim of the nest with tail fanned out against the trunk. An occasional visiting male would bring bark to his mate but no food.

Expulsion of feces, and other activities of female in nest.—Watching and listening from the ground gave some insight into activities of nesting females. At infrequent intervals one might see a stream of fecal matter shoot 2 to 3 feet out of an entrance hole, glisten in the sun, then land with a splash on the leaves below. The white feathers of the female's rear end were, in some nests, clearly visible as she maneuvered her vent to the opening. Hornbill vents are protrusible and mobile. This could be well seen in our young birds 6 to 8 weeks of age when, standing way up on their legs, they would back up over the edge of the box they were in and expel feces on the floor. Expulsion was not as forceful as seen in some hawks. Tree trunks and foliage below nests were not appreciably stained by expelled feces. This was partly due to the dark color of the droppings resulting from a fruit diet. Some streaking of white appeared in feces with development of the young. On January 8, as I was sitting on the scaffold beside nest 10 in Mpanga Forest, the 4-weeks-old chick backed to the entrance and deposited a cylinder of feces 4 inches long on the lower cement. This feces had a white film over one end. The ladder leading to nest 10 became increasingly spattered with feces as weeks went on. Observations on my captive birds indicate that the white substance in the feces increased with ingestion of animal protein. I saw one nesting female toss debris out of the entrance with her bill. Doubtless this method also contributes to nest sanitation.

Females within the nest did not lose their constructive instincts. Bill tapping continued, but was carried on far more by some females than others. I frequently heard tapping from nests 7 and 10, which were only 120 feet apart, at the same time. Much of the time I could not see a bill in the aperture. It is conceivable that these birds plaster debris against their nest cavities either because habit is strong or just by way of idle amusement. My young captive hornbills plastered the walls of their cage, possibly for the same reasons. Entrance walls, however, sometimes needed repair. On November 28, the female of nest 6 was repairing her nest entrance at noontime. I could see her

bill tapping rapidly on either side of the lower aperture. The shape of this aperture changed somewhat from one week to another and the repaired areas were darker in color. Presumably feces and other debris present by the opening were used, for I later obtained half of the cement from this nest and found that the dark areas had seeds and fruit stones embedded in it.

Nesting females may enlarge their nest cavities by pecking at rotten wood surrounding them. The female of nest 10 had an escape attic above her nest. I could hear her scuttling into it when I climbed up the ladder, and on looking through the opening all I could see was the tip of her tail. When nest 14 was opened on January 21, there was no female in sight. The African who had removed the chick swept the whole length of his arm inside without encountering the mother bird. His position was too precarious for him to look inside. It seemed probable that the mother had crawled into some remote recess.

EGGS, YOUNG, AND NEST OPENINGS

Eggs.—Nest 10 was in a dead tree 30 feet above the ground in Mpanga Forest. On December 4 I climbed the scaffold to this nest for the first time and peered through the aperture, using a flashlight. The mother bird was almost out of sight in her escape attic. There were two white eggs, similar to those of a domestic fowl in size and shape. My next visit was on December 11. The forest ranger said that he had climbed to the nest at 6 a.m. and had seen two eggs. I approached the nest tree at 1:30 p.m. and saw two-thirds of an egg-shell on the ground directly below the nest hole. The shell was so fresh that ants were still swarming over its moist inner surface. I climbed the scaffold to find the mother hornbill facing me at the entrance. This was the only time she ever did so. As far as I could determine before she climbed to her escape attic, she had a complete plumage. When she left I saw one egg and one blind, completely naked, rather blue young one. This was a first view of my subsequent pet, Mpanga. When I looked in on the following morning, I could not see him, but he soon emerged from under some debris, giving a feeble "chirpee, chirpee." His lower bill was larger than the upper one. Early in the morning of December 14 the ranger found the second egg chipped, and by afternoon he saw the shell on the ground and a second chick in the nest. I was able to visit the nest two days later and see the two chicks together. The larger one was chirping lustily. He had brown mash over his bill and throat, and there was more mash in the nest. I wondered whether the mother hornbill had regurgitated food onto the nest floor and then fed it to her offspring.

It was January 1, 1955, before I was able to visit the nest again. There was now a single young one, the size of a plucked pigeon, which begged and peeped a few times when I looked in. The forest ranger reported that the second chick had disappeared a week after hatching. The remaining chick had its eyes open. They were dull but mobile. Pinfeathers were just beginning to emerge on its head and wings. The entrance hole was becoming stained with feces, whereas it had been clean previously. On January 8, the young bird had black pinfeathers one-fourth of an inch long on head, neck, and wings. There were smaller, colorless pinfeathers on back, tail, and in two tracks bordering the breast bone. Feet and an inch-long fleshy tail appeared large for the size of the bird. The chick seized my finger when I pushed it in. He also chewed pieces of wood. This bird was removed from its nest when 6 weeks old and has lived well in captivity for over a year.

Periodic inspections of the ground below nest trees gave clues as to the number of eggs and approximate time of hatching in four other nests. For example, on November 27 I found pieces amounting to two-thirds of an eggshell, with its membranes, below nest 4. I carefully removed all pieces, and on November 28 there were no further eggshells. Six days later, however, I found a second eggshell, three-fifths intact, with an additional one-fifth in pieces. It appeared that two eggs had been laid and that they had probably hatched on different days. This had happened at nest 10. There, it may be recalled, the eggshell was tossed from the nest soon after the hatching of the chick. On the ground below nest 9, I removed most of an eggshell on November 28, and three-fourths of a shell on December 4. These and other data are tabulated in table 1. Data from two other nests were less complete. I found over half of an eggshell below nest 3 on November 28, but it was not until January 1 that a second shell turned up. Possibly it had been covered with debris, either in the nest or on the forest floor. On December 9 there were pieces of one shell below nest 12. I did not, as in the other cases, know how long they had been there.

Breaking open nests to obtain young. Molting of female.—Inaccessibility made it difficult to study the molt in nesting females, but I was able to gather some information. Nest 10 could be reached by ladders. The female was usually in her escape attic and I did not want to interfere with her by making an opening. The nest was well lined by remiges when I looked in on December 4. In retrospect I should have removed them with a pair of long forceps for arrangement and counting. All I could see of the mother bird was her tail. The tail feathers remained soiled with no evidence of renewal. On December 11 I had

my only full view of the mother when she briefly defended her chick. Her plumage appeared complete, but I did not see her outstretched wings. My next view of her was when I broke open the nest on January 22. After putting the 6-weeks-old chick in a bag, I reached into the hollow trunk and pulled the mother bird down. She was kept in captivity for a few days of observation. Plate 5, figure 1, shows that her plumage was complete. The only sign of molting was one tail feather, a few inches long, which was still enclosed in a sheath. She was not shy in captivity, but she remained motionless, as if stunned, and refused to eat. I liberated her on January 24. In spite of a long period of confinement in the nest and having had no food for 2 days, she flew to a tree, squawked a few times, then took a flight of 300 to 400 yards. She was headed back in the direction of Mpanga Forest, 13 miles away.

It was apparent that this female, viewed when roughly one-third, and again at two-thirds through the nesting period, had not experienced any sudden or complete molt. On January 30, we opened nest 16 to remove a chick 6 or 7 weeks of age. The mother bird struggled vigorously, striking the African who held her a sharp blow on the chin, so that he fell over backward. When I took hold of her it was obvious that she was in no weakened condition. Her plumage appeared to be complete except that her tail feathers, although well grown, had sheaths at the base. She flew readily to a tree when liberated.

Premature escape of female due to loss of mate.—When I entered Mpanga Forest on the afternoon of January 1, I heard the wailing screech of a female hornbill in distress. The calls were given twice a minute. I followed them to nest 4 where I found a pair of foreign hornbills. These flew away at my approach. The female in the nest kept screeching for the next 2 hours in a most pitiful manner, but her mate failed to return. I examined the ground below the nest tree and found that he had been killed. There were two large patches of feathers directly below his usual perch. These patches were $2\frac{1}{2}$ to 4 feet across. One consisted principally of small body feathers and the other of large feathers from wings and tail. I suspected that the hornbill had been struck from his perch by some bird of prey, and, after falling directly to the ground, had been plucked on the spot. The female was still screeching when I left the forest late in the afternoon. On the following morning I reached the nest shortly after 9 a.m. The mud wall was partially broken out. A new pair was inspecting the nest and it was evident that the original female was no longer there.

Natural nest openings.—I observed how nests were opened naturally

in five nests with entrances visible from the ground. In each the cement had been knocked away from one side of the aperture. This left ample room for the mother and young to emerge. I was interested to find that the missing cement was lying in an intact piece on the ground below three of the five nests. These five nests (Nos. 3, 6, 11, 12, and 13, table 1) all opened between January 1 and February 5. Some of these may have been open for a week before I noticed them. Nest 6, however, was closed on the afternoon of January 22 but open by 9:15 a.m. on the following day. There were no hornbills in the vicinity.

Emergence of mother and young.—On February 5 I noticed that the female of nest 7, which I had had under observation for 84 days, was still walled in. By the following morning she had left. I began to search the adjacent forest and was able to locate the pair 100 or more feet from the nest tree. The female was recognizable by her soiled plumage, the white patches of which were muddy. The male, recognizable by his bill markings, sat close by her. For the next 2 hours I hunted back and forth through uncut jungle. It was raining hard and I thought that if I could find the young, I could probably catch it if its plumage was water soaked. The parents expressed great alarm, coming down within 20 feet of my head. Unfortunately I could not find the young. I wondered if it had crawled into some hollow limb.

I had better success in the Botanical Gardens. The female was walled in on November 8, 1954, and had emerged with her young one on March 7, 1955. She was confined for 119 days, with a possible error of 2 days. There were no signs of activity by the nest on the morning of March 7. Late in the afternoon, however, I found the male perched by his mate 50 yards from the nest tree. He made continuous noises. Several times he hung his head way back, allowing her to nibble the feathers of his throat. Her plumage was in poor condition. The white parts of her feathers were soiled, her tail ruffled, and the small feathers on the back of her head and neck were worn. There was no sign of the young one. At 7:15 a.m. on March 8 I located the pair by cries coming from a patch of forest. They were together in a tall tree, and a young hornbill was close by. His plumage was in fine condition, pure black and white, his tail nearly full length, and his upper bill had the large, light-colored growing patch of a male (pl. 1, fig. 2). He made squawks similar to those of my captive birds. Everything appeared well when I left.

The tragedy that overtook the family during the morning may be reconstructed from the chance observations of another bird watcher,

Mrs. Iris Darnton. At 10:30 a.m. Mrs. Darnton was attempting to photograph the parent hornbills where I had seen them earlier. The young one was perching on a low branch by a roadway. He flew with some difficulty to a higher perch. At this moment an intruding female hornbill attacked the young one and the two fell grappling to the ground. The parents made a great commotion. Their young one lay flat on the road, but soon flew onto the lawn, then into a low tree. After 5 p.m. I came to the gardens and found the family where last seen by Mrs. Darnton. The young bird was perched precariously near the top of a spindly tree and one foot hung limp and useless. He was using half-spread wings to maintain his perch. The male parent made a great noise when he saw me, but soon quieted down, hopped closer, and fed the young one four fruits. Ten minutes later he tried to feed him again, but without success. The mother bird did not attempt to feed the young one. She remained inactive. A foreign female hornbill stayed about 50 feet away. On the following morning I found the parents in the same area, but the young bird was not in the trees, so I searched the underbrush and found him on the ground. When placed on the lawn, he was unable to fly. The male parent swooped repeatedly at my head. I was reluctant to take away the young bird, but it was obvious that any passing dog or individual could kill it. I therefore took it home. Plate 1, figure 2, shows his appearance 2 days after leaving the nest. I estimated that he was 10 to 11 weeks of age, using as a guide my captive male of known age. One of his feet was broken. When placed in a splint, it healed completely in 3 weeks. This bird was the only one of my four captives that did not become tame.

Parental devotion.—No large hornbills had come to our garden regularly since departure of the roosting pair in October. However, from April 1 until May 15, when we left, a pair of hornbills came every day, often remaining for some time. I soon recognized the male. It was the one I had watched for 4 months in the Botanical Gardens, which were 2 miles away. The parent hornbills had located their young in his outdoor cage, and our garden resounded off and on all day with their wailing and commotion. They perched on adjacent trees, and frequently swooped down low over the wire. "Mutesa," as we called the young one, never responded in any perceptible way.

TERRITORY, AND RELATIONS OF HORNBILLS WITH ONE ANOTHER

Specific interference.—Nesting hornbills were interfered with by members of their own species to a surprising degree. Experiences at nest 5 illustrate the persistence of such interference. On November 6

the pair of hornbills were working on their nest late in the afternoon. An adult male kept coming into the tree and the male in possession repeatedly drove him away. By November 8 the female was walled in, and a more serious attempt at interference was now made by a foreign female. I first noticed her on November 19. She was following the male and lighted in the nest tree when he lighted above his nest hole. On November 23 the same course of events took place, except that the male was less tolerant. He fed his own mate, then drove the intruder away. A week later I again saw her fly in close behind the male and light 25 feet from the nest hole. The male gave his mate a piece of bark followed by some fruit, and then bounced from one branch to another toward the foreign female. The intruder called and the female within the nest screamed a number of times. I wondered whether the interloper could seduce the male, but from subsequent observations it seemed unlikely that she would. The male returned again to the nest hole, and a few minutes later was in the upper part of the tree knocking about on dead branches until he dislodged a piece of bark. He clamped his bill on the bark until it was largely fragmented. Then he moved toward the foreign female. If he presented the bark, one would suppose that she had some attraction for him. After a moment, however, he changed his direction, flew down to the big limb below, bent over the nest hole, and gave the token to his mate, accompanied by a feeding chuckle. Subsequently he returned to perch quietly within 8 feet of the intruding female. At 7:30 a.m. the two of them flew away together. As the nesting season progressed, he became less tolerant of her intrusions. On my next visit, a week later, he made several swoops in an effort to drive her away, but she was not discouraged. On February 3 I again watched her fly in behind the male and alight in the nest tree, making considerable noise. The male stopped feeding his mate, swooped at the interloper and drove her down toward the ground. However, when he flew away, she followed a short distance behind. It generally appeared that her interest was in him rather than in the nest. On March 2 I observed a more serious situation. Late in the afternoon I found a foreign female clinging to the nest entrance. This time she was alone. She worked industriously, removing debris from the entrance and knocking from the cement wall chunks which she broke in her bill before dropping them. There was no noise. After 5 minutes the male arrived and she flew a short distance away. He tossed some debris from the entrance, then drove the foreign female to another tree, flying at her so hard that he knocked leaves from intervening branches. He returned to his nest with a small stick held like a cigar.

His mate, who had remained silent, now began her wailing screeches. I also heard her bill tapping. The intruding female, persistent as usual, had followed the male back to the nest tree. In a few minutes he flew at her again, flying faster than hornbills usually do as he chased her from one tree to another. Five days later, mother and young emerged from the nest. As already related, a foreign female attacked the young bird and apparently broke its foot. After I had picked up the helpless young one on March 9, I returned to the Botanical Gardens late in the afternoon. The pair of hornbills were perched side by side in their nest tree. Not long after I heard a great flutter of wings. I looked back to see both members of the pair pursuing a foreign female. This was the last I saw of her. When the parents later came to our garden, she did not follow. I have presumed that the same foreign female was involved in all these incidents relating to nest 5. This presumption was based on her consistent behavior, general appearance, and bill shape. I never saw another female with which to compare her near the tree.

At 5 p.m. on January 26 I witnessed an intrusion by a pair of hornbills. A foreign female was on the lower rim of the nest entrance, poking her bill about the aperture. She made no noise. After some minutes a foreign male lighted on a limb above. He had a fruit in his bill tip. The female moved toward him, took the fruit, and kept offering it down inside the hole. It was not accepted. The foreign female would toss the fruit about in her bill, then try again. Finally the rightful male returned, drove the intruding pair away, and fed his mate a number of fruits. The whole incident appeared odd. I wondered whether the foreign pair were unsuccessful nesters, who, having a strong, though thwarted instinct to feed something, dropped in on the female in nest 5.

Interference by foreign hornbills was not limited to the nest in the Botanical Gardens. It happened not infrequently at other nests. A pair of hornbills were involved in each of the following intrusions. On November 19 a foreign pair were perched by nest 4 in Mpanga Forest. The female flew to the entrance, clinging to the lower rim with tail outspread for support. She then gave some hard pecks against the mud wall and grappled at bill point with the female inside the nest. Neither bird made any noise. However, when the intruder withdrew, the nest owner rattled her bill in the entrance. The foreign male sat quietly by without participating. In a period of 10 minutes the intruding female attacked the nest entrance 12 times, but did no significant damage. In the next 5 minutes she attacked only twice. Then the rightful male returned and drove the trespassers away.

Since this episode took place early in the nesting period, I conjectured that the foreign pair had, perhaps, not found a suitable nesting site and the female was trying to take possession of one already occupied. A second episode was difficult to interpret. It took place late in the nesting period, on January 23. I saw a foreign pair fly into the tree containing nest 15. The male repeatedly bent over the nest rim and there was a rattling of bills. He produced a "cherry" at his bill tip. Then he either gave it to the nesting female or dropped it into her nest. The female rattled her bill at the strange male. Ten minutes later the foreign female swung dramatically on a long tangle of epiphytic roots, then landed on the nest rim. This was the only time I ever saw a pair of foreign hornbills perched together on a nest. The intruding female wagged her bill vigorously in the opening. A few minutes later the owning male swooped in and drove the intruders away. He fed his mate some yellow fruit. She now screamed repeatedly.

On one occasion I saw a lone male attacking a nest. This was on November 21 at nest 6 in Mpanga Forest. The foreign male came quietly to a limb above the nest, then dropped to the nest rim. He appeared wary, bending his head to one side, then to the other, as he hung his head down to look through the entrance. The female had her bill ready but made no noise. He finally struck at the cement, then sparred with the female within the nest through the opening. I could hear their bills clashing. After 12 minutes the returning male owner drove the trespasser away. He had a leaf in his bill tip which he gave to his mate along with some fruit. It should be mentioned that a male may attack his own nest. At midmorning on November 28 the male from nest 7 flew down and rattled his bill in the opening. He was apparently in a bellicose mood for he next flew to a limb directly over my head, which was unusual. I could see his bill markings clearly. Meanwhile, his mate rattled her bill in the entrance.

Lone females were the most frequent intruders at hornbill nests. I often saw one at nest 11. She had a favorite perch 10 feet from the entrance where she would sit for some periods. The nesting female would rattle her bill and scream repeatedly, but her mate, on feeding visits, paid little attention to the intruder. On December 12 a foreign female perched calmly on the bole above nest 6. She repeatedly leaned down into the opening, giving the feeding chuckle eight times as she did so. The female in the nest rattled her bill. After 15 minutes the male returned and drove the foreign female away. A final and most unusual case of interference occurred at nest 16, which was 30 feet above the ground. On January 30 we had placed some

ladders and an African was preparing to climb up and open the nest. As we stood below, a foreign female flew in and lighted on the edge of the nest. I thought that the mother had already emerged, but it was later discovered that the mother and young were inside.

Territory.—Neighboring pairs of hornbills tolerated each other well. For example, nests 7 and 10 in Mpanga Forest were within 120 feet of each other and a third pair made persistent attempts to nest within an equal distance. Within this triangle I could watch activities of all three pairs at one time. They paid no attention to each other, their sense of territory apparently being limited to the nest tree and its immediate vicinity. Some trespassing was accidental and without interest in the nest itself. Thus nest 4 was centrally located in Mpanga Forest so hornbills engaged in their various activities frequently came near it. The male from this nest did more chasing than any other I had under observation. He had a peculiar habit of perching during the day within 10 feet of his nest hole. No other male perched close to its nest. Some might occasionally perch within 100 feet, but usually I saw males near their nest trees only on feeding visits. Females were frequently alone for 45 minutes to an hour at a time, and during these periods the nest tree was open to intruders. Hornbills may have a sense of territory in relation to roosting areas; I did not make sufficient observations to determine whether this was so.

Aggregations of hornbills.—Sometimes a number of hornbills would come together, usually owing to a common attraction such as a flight of insects, a fruiting tree, or a passing hawk. This did not appear to be true flocking. Nine was the largest number of hornbills I ever saw together. They were in our garden on August 26. Other observers told me that they had seen larger gatherings. On November 28 I watched two males and four females closely besetting a harrier hawk. A week later I came across what appeared to be the same group in the same area of Mpanga Forest. This time a band of redbill monkeys were working along the forest edge. Six female and two male hornbills followed along with them sitting in the same trees but making no noise. I believe that the association was an idle one, for the hornbills were playing with sticks and showed no alarm. The excess of females was of interest. Pairs of hornbills were also frequent during the nesting season. I wondered if there had not been enough nesting sites to go around. On February 15 I saw a curious association of two adult male hornbills. They came to our garden and hunted together closely, going over cracks and crevices in a big tree. Two

weeks later I found the same pair a mile away and still closely associated.

RELATIONS WITH OTHER BIRDS

Hornbills became much disturbed when a hawk or eagle appeared in Mpanga Forest. A crowned hawk eagle perched on a tall tree at the edge of the headquarters clearing. Then he sailed into the forest and was lost from view. An hour later I heard a great noise and found the hawk eagle surrounded by casqued and the smaller pied hornbills (*Tockus fasciatus*). None came closer than 20 feet. On November 28 I was watching nest 8 when I heard a number of hornbills making short flights from one perch to another. This drew my attention to a harrier hawk in a dead tree. Two female hornbills were perched within a few feet of him, one on either side. Two males were in the same tree. When the hawk flew, all four hornbills followed him closely but made no noise. The bird that upset hornbills the most was a great sparrow hawk. On December 11 he flew up close to me in Mpanga Forest, calling "ker, kee, kee" in plaintive fashion. Three male hornbills accompanied him. None of them made any noise. Whenever the hawk circled and returned, the hornbills pursued closely and even swooped at him. On January 2 I again heard the cry of the great sparrow hawk. When he lighted above me, a male hornbill lighted within 6 feet of him, and when he flew, two hornbills followed within 20 feet. Hornbills are occasional predators themselves. Their presence, however, seldom caused any disturbance among smaller birds. I saw one hornbill momentarily beset by sunbirds and colies when he was robbing a nest of the latter. Broad-billed rollers (*Eurystomus afer*) would pursue hornbills passing by the lake shore. These aggressive birds attack everything from aningas to starlings.

FOOD

Fruit.—Food brought by male hornbills to their nests consisted largely of fruits, ranging in size from a pea to an olive. Some fruits, such as figs and pawpaw, were brought in as amorphous pieces. The elliptical fruits of *Canarium schweinfurthii* were conspicuous and prevalence of their stones on the ground were a helpful clue to the location of nest trees. I was able to collect various seeds and fruit stones by cleaning the ground below nests. Following is a list of all fruits identified. Such indigestible matter passes through the digestive tract of the hornbills and is expelled with the feces. This was observed in both wild and captive birds. I have never seen hornbills go near

water and my captives do not seem to know what it is. Apparently they get enough water from fruit.

FRUITS IDENTIFIED FROM SEEDS, STONES, AND PIPS RECOVERED FROM
FECES BELOW HORNBILL NESTS

<i>Canarium schweinfurthii</i> Engl.	<i>Antiaris toxicaria</i> (Pers.) Lesch.
<i>Pycnanthus angolensis</i> (Welw.) Exell.	<i>Chlorophora excelsa</i> (Welw.) Benth.
<i>Pseudospondias microcarpa</i> (A. Rich.) Engl.	<i>Eugenia jambolana</i> Lam.
<i>Maesopsis eminii</i> Engl.	<i>Dracaena steudneri</i> Engl.
	<i>Ficus natalensis</i> Hochst.

Animal food.—Bannerman (1953), writing of *Bycanistes subcylindricus*, states that "this bird lives entirely upon fruit, as indeed do most of the large hornbills." During initial observations I had no reason to doubt this statement. By closer watching, however, I found that hornbills take a wide variety of animal prey. On December 6 a male went from one low perch to another among our garden trees, sometimes only 7 feet from the ground. Five minutes later I saw him fly up from the foot of a jacaranda with a 5-inch lizard squirming in his bill. He flew to a perch over a native shamba. Here he tossed the lizard about in his bill for some time, holding it by the tip of the tail, then chewed along until he reached the head. Finally the hornbill lost hold and the lizard fell. In a feat of acrobatics, the hornbill fell down after his prey, disappearing from sight in the vegetation. Fifteen minutes later the bird was back in our garden. A completely limp lizard hung from his bill as he flew over the hill in what I suspected was the direction of his nest. On January 31 another male hornbill was hunting in our garden. He hopped onto a perch, looked around slowly in all directions, then hopped to another perch and did the same. After some minutes he flew to a thick bushy tree, where he scrutinized the foliage carefully, then hopped directly to the end of a branch where a mouse bird had its nest. The hornbill picked up a small egg with his bill tip, sent it flying back into his gullet with a toss of his head, then did the same with a second egg. To finish off, he seized some nest material and dropped it. What followed was an example of the delicate control casqued hornbills have with their bills. The male coughed up one egg from his gullet and held it again in his bill tip. By this time his mate had arrived in a tree across the lawn. He flew over to her, still holding the egg, and settling beside her, presented her with the egg; then heaved and presented her with the other, both intact. She swallowed both. On February 15 I watched two male hornbills hunting in our garden. A double-toothed barbet (*Lybius bidentatus*) was excavating in a tree when the hornbills flew

directly to the hole. One male repeatedly drove his bill into the excavation. I was not sure whether the barbet was inside or not. For the next 15 minutes the hornbills quietly examined the hole, knocked off dead bark, and searched leaves and seed pods. Their hunting was not successful while in the garden. However, hornbills probably catch other birds on occasion. On January 29 a male in Mpanga Forest glided to his nest with a sparrow-sized bird, chewed beyond recognition, hanging from his bill. He saw me and quickly flew away. My captive hornbills have been maintained to a large extent on left-over laboratory mice which they swallow whole. They appear to thrive on animal protein.

Hornbills catch insects both large and small. I found the remains of some insects which they had fed upon by examining fecal matter below nest 5 in the Botanical Gardens. Dr. V. G. L. van Someren was able to identify the following:

REMAINS OF INSECTS RECOVERED FROM FECES BELOW HORNBILL NEST 5

- Dicranorrhina micans* (Drury)
- Longicornis* beetles of cerambycid group
- Rhyparobia grandis* (Sauss.)—large cockroach
- Long-horn cricket
- Tenebrionid beetle, *Metallonotus*
- Slender-winged mantis

Some were not adequate for species identification. Large bark beetles were a frequent finding. Activities of a male hornbill observed on February 1 indicated how these might be captured. For a half hour in midmorning he worked on the dead portion of a large tree. He would strike slanting blows to loosen a piece of bark, then pry under it and appear to pick out something from underneath. The next step was to knock the loose bark to the ground. This hornbill showed acrobatic skill, often leaning way over on its long legs, with head and neck outstretched, in an effort to reach more bark. He removed at least 3 square feet before flying away. Praying-mantis nests were not infrequent in accumulations below nest 5. They had come through the digestive tract more or less intact, as indicated by adherent feces.

I would not have supposed that casqued hornbills could catch small insects on the wing. They are, however, quite resourceful in this respect. On April 18 three hornbills were perched on a casuarina tree late in the afternoon. They were gulping at a close swarm of insects that were whirling about in a small cloud near the treetop. These insects were black-winged termites. Some were still moving upward

from the ground. The hornbills made a clapping noise as they snapped at the passing termites and were at the game for over 10 minutes. On May 1 I witnessed a similar spectacle, again late in the afternoon. Compact swarms of small insects (not lake flies) were hovering at the tops of tall trees adjacent to the Institute Compound. Smaller birds were catching them, mostly by perching on a topmost spray. These birds included splendid starlings (*Lamprocolius splendidus*), bulbuls (*Pycnonotus tricolor*), Abyssinian gonoleks (*Lanarius erythrogaster*), and didric cuckoo (*Chrysococcyx caprius*). Two casqued hornbills were catching insects along with the smaller birds. For over 20 minutes they kept turning their heads to snap at the swarm around them.

Dr. W. H. R. Lumsden has contributed an observation which further indicates the agility of these large hornbills. On September 6, 1953, he was in the woods of the Botanical Gardens. Three or four hornbills were perched about 60 feet from the ground. They would swoop down across an open space, pick up something in midair, then rise to a perch in an opposite tree. They were after winged ants which were swarming on ground and vegetation below the clearing.

SOME ANATOMICAL FEATURES IN RELATION TO FUNCTION

Some peculiarities of hornbill anatomy came to have more significance with continued watching. The large eyes are unusually mobile for a bird. Casqued hornbills can look up and down to a moderate extent without cocking their heads as many birds do. This gives them, by human interpretation, a more intelligent expression. The upper and lower eyelids are continuous and in sleeping this fused eyelid is pulled over the eye from back to front. The combined eyelids are white in adult females. Considering that the eye is dark and surrounded by blackish feathers, I have wondered whether these white eyelids enable the male to see his mate better when looking into a dark nest cavity. The head is covered by fluffy feathers, $1\frac{1}{2}$ to 2 inches long. These are used in emotional expressions and when fully erect the head is like a small, round feather duster. From front view the topmost feathers, which may be the only ones erected, may resemble two horns. My young captive hornbills demonstrate how these feathers may be used. If I toss grapes to them, Mpanga may grab them all. Zika, the female, then feels left out. This is obvious by her expression. Her head feathers stand straight out in all directions as though to say "Where do I come in?" When alarmed or excited, her head feathers lie tightly back. If she next investigates some object,

like a crumpled piece of paper, they stand out partially again. In young birds the feathers just above the eyes and forming the horns are brown. By the age of 10 months these are almost entirely replaced by black feathers.

The bill tip can be used as delicately as a pair of forceps. In females, only the tips may be in apposition, leaving a slightly open space for several inches behind. This space is more exaggerated in older females and may suggest, to a mild degree, the bill of an open-bill stork (*Anastomus lamelligerus*). At first I thought the space was due to wear. However, my captive Zika had this space at an early age when wear was not apparent. The bill tip itself is very sensitive. It is, for example, continually used to investigate strange objects. If I give my captive hornbills a fruit they have not seen before, they will toss and squeeze it in their bill tips for some time before swallowing. The bill of the male is huge, and that of a young one is larger than a female's before he leaves the nest. This is shown in the photograph (pl. 5, fig. 2) of two young hornbills, male and female, at 7 to 8 weeks of age. Plate 6, figure 1, shows Mpanga's bill at 6 months of age and plate 2, figure 1, at 10 months. The white patch is apparently an area of growth. With some transillumination one can see that it is full of blood vessels. The patch becomes smaller in older males. No one knows, as far as I am aware, how long it takes the bill of the male to reach full development, with a forward projecting knob. At present I can only speculate on the function of this huge structure. It would appear to have no strictly practical use, for the smaller bill of the female serves more immediate functions. Her bill not only is used to plaster the wall of the nest, but is also a formidable weapon for defending the nest opening. Its inner capacity is no less than that of the male's. In addition, males and females are equally adept at catching small objects with their bills. I wonder, therefore, if the casqued bill is not chiefly sexual in function. Possibly it is comparable to the mustache stripe of the male flicker or the red breast of the cock robin. In this sense it would serve to release behavior patterns in the female which promote successful breeding and pair formation.

The feet of hornbills, with three front toes somewhat webbed, do not grasp tightly. I have never felt any real grip from the birds perching on my arm. Hornbills can, however, hang down from a perch, almost parrotlike, without losing their hold. The long tail is remarkable in that it can be neatly folded over the back. This adaptation is convenient for females walled within nest cavities, as is the fact that they are a third smaller than males.

DISCUSSION OF FACTORS CONTROLLING HORNBILL POPULATIONS

Birds such as hornbills which rear a single young one are, one may suppose, relatively safe from enemies. This was probably true before the original rain forests had been cut. A female walled in a nest 70 feet above the forest floor, in the trunk of a huge tree without lower branches, is in an almost impregnable position. Such trees, however, are now entirely absent over large areas. Natives' shambas, elephant grass, and patches of second growth cover the countryside, leaving only thin fringes of large trees along lake shore and swamp. Eastern Uganda is good agricultural country and the native population is rapidly expanding. Interference by man's activities is, I believe, the greatest factor limiting hornbill populations. Mpanga Research Forest remains as a needed refuge. Even here, observations suggested that suitable nesting sites were way below the demand. Some pairs of hornbills were nesting in unfavorable situations. For example, nests 10 and 16 (table 1) were only about 30 feet from the ground and were easy to reach. Also, I continually saw pairs of hornbills that were not nesting during the nesting period. Two pairs tried without success to build nests in unsuitable locations. When nest 4 suddenly became vacant owing to the death of the male, another pair of hornbills took it over immediately. Some of the incidents of specific interference already narrated indicate the degree of competition. The disastrous effects of forest destruction on casqued hornbills is well described by Capt. C. R. S. Pitman (1955, personal communication). He writes that "ever since I first went to Entebbe in 1925 forest destruction in the vicinity of Entebbe and Kisubi, and in fact all along the NTB-Kampala Road, has been on such an appalling scale, that annually large numbers of trees, with the best nesting sites, are being destroyed. *Bycanistes* therefore is constantly having to move farther and farther afield to find suitable nesting sites. When I first went to Entebbe there must have been at least two dozen *Bycanistes* nests within a 2-mile radius . . . but now good nest sites are fewer and far between and *Bycanistes* resorts to hollows, some readily accessible, which it would have ignored in the past."

Fortunately Africans in eastern Uganda do not molest birds to any extent. Ease of growing food and comparative prosperity probably puts less pressure on them to do so. But in Bwamba, where hornbills were considered fair prey, I continually came across Pygmies and other natives wandering about with slingshots and small bows and arrows. Under these conditions I found the birds more wary and difficult to observe than near Entebbe.

COMPARATIVE STUDIES OF OTHER HORNBILLS

Genus Tockus.—There were two other species of hornbills in the vicinity of Entebbe, the crowned hornbill (*Tockus alboterminatus*) and the pied hornbill (*Tockus fasciatus*). These two smaller hornbills are somewhat similar in size and appearance. I could never discover any basic difference in their habits. Their high piping cries, erratic type of flight with many rises and dips, and greater concentration on insect food readily distinguished them from casqued hornbills. All three species occurred in the same stretches of open country and forest.

On March 20, 1955, I noticed a crowned hornbill flying through Zika Forest. He lighted on a treetop, then suddenly dropped downward. Searching the area, I found a leaning tree with a bole, 40 feet above the ground, with a 2-inch hole in the center. There was almost no suggestion of a mud wall. I watched for 20 minutes. At one time white feathers closed the entrance as the female pushed her vent to the opening, and a stream of excreta shot out. The maneuver was the same as I had witnessed with *Bycanistes*. Later the male returned to perch on the bole and feed his mate a large insect (mantis?). He did not linger, the briefness of his visits apparently being due to the fact that he carried only one item in his bill tip; there was no heaving up of fruits from the gullet such as characterized visits of male casqued hornbills to their nests. On March 25 an African, well trained at the Institute, climbed up and inspected the nest for me. There were three white eggs. The mother bird, when poked, backed to the rear of the cavity. Unfortunately, preparations for leaving Africa prevented an adequate study of these birds. I am indebted to Dr. Friedmann (1925) for the following account, hitherto unpublished, of the opening of a nest of this species in Kenya Colony.

On April 7, at Taveta, some natives cut down a large tree in which there was a nest of this hornbill containing the adult female and two young birds. The nest was about 50 feet up in the tree and was in a large hole, the entrance of which measured roughly 10 inches in long diameter and 3 inches wide. This entrance was plastered up with dry mud, bird feces, and bits of bark all mixed together, leaving an opening about 2 inches long and 1 inch wide. As I picked away at the mud the adult female pecked at me with its bill, about an inch and a half of which could protrude through the opening. When finally I opened the nest and took out the birds I found that the two young birds were of different ages, the older of the two [pl. 6, fig. 2] being feathered on the back, wings, sides, legs, and crown, while the tail feathers were free of their sheaths for their distal thirds and the sheaths of the neck and breast feathers were beginning to burst. The other bird was less well feathered, the wings and flanks being the only parts really well covered. The tail feathers were about the same as in the older bird and the under

tail coverts in both were well developed. In both nestlings the bill showed no trace of a casque and was a yellowish-horn color; the feet were dark lead color; the skin light pinkish; the iris bluish gray. The tail folded up against the back so well as to look like a definite adaptation to living in crowded quarters. In fact it seemed to be muscularly easier for the birds to hold their tails up than to straighten them out [pl. 6, fig. 2]. One of the nestlings when put on the ground fell over forward on its head and breast and the tail remained sticking straight up in the air as though the bird were unable to drop it into what would be considered the normal position. The adult female when about to enter a nest before egg-laying usually begins to molt and is for some time thereafter in quite a helpless condition. New feathers grow in while the eggs are incubating and the young growing to the flying stage. The female taken from the nest had all the new tail feathers well developed but all of them were still basally enclosed in their sheaths. The bird was still missing the outermost secondaries and innermost primaries but the other remiges were there, most of them more or less still in their sheaths basally. The bird could fly only very poorly and seemed dazzled by the light. Several times I let it go and each time it flew or rather half fluttered, half flopped through the air very laboriously for a short distance and stopped by smashing against a tree or the side of my tent.

I had some evidence that pied hornbills also breed in March. From November on I had been observing a pair of casqued hornbills in the Botanical Gardens and had kept watch on a squirrel hole 50 feet up in a nearby tree. It was not until March 1 that I noticed a pair of pied hornbills showing any interest. At 7:30 a.m. a pair were preening nearby. Between them they made 10 visits to the hole, poking their bills inside. When a crowned hornbill appeared, they chased it away. The following day the pair were at the hole morning and evening. On March 8 I saw them putting their bills into the hole and tossing out debris. I had no subsequent evidence that the pair nested. The hole may have been occupied by a squirrel which I had seen using it previously. Apparently smaller hornbills may compete with hole-nesting mammals. On February 18 I was driving near Kaboona, in the arid country of Karamoja, when I noticed a pair of Jackson's hornbills (*Tockus jacksoni*) catching insects and flying to a 2-inch hole in a dead tree. When I returned 4 days later the pair were still inspecting the nest hole. Thinking young hornbills might be in the tree, I cut it down. To my surprise, the cavity contained a mother bush baby (*Galago senegalensis*) with a mouse-sized young one. These limited observations may have interest because I could find no breeding dates for these three species of *Tockus* in eastern Uganda.

The investigations of Gordon Ranger (1949-52) offer an opportunity to compare the habits of *Bycanistes* with those of *Tockus* in some detail. These investigations on African hornbills are the most complete known to me. They have extended over many years and concern

another crowned hornbill (*Tockus alboterminatus*) which occurs in South Africa. Comparisons will be made first in regard to differences of behavior, then to points of similarity with *Bycanistes*. All observations and quotations on the crowned hornbill are from Ranger's publications.

Differences in behavior between Bycanistes and Tockus.—(a) Crowned hornbills have a definite territory which is fairly extensive, is defended against trespassing hornbills, and is maintained year after year by the same pair which temporarily share it with the offspring of each season. I found little evidence that *Bycanistes subcylindricus* maintains a definite territory other than the immediate vicinity of the nest tree.

(b) Crowned hornbills live more extensively on insects. This greater consumption of animal protein is reflected in their white excreta. In feeding his mate at the nest, the male carries the food, usually a single insect, at his bill tip. He does not load his gullet, then cough up fruits one at a time as do male casqued hornbills. Furthermore, crowned hornbills make casts of indigestible seeds, pips, and hard parts of insects. Casqued hornbills, on the other hand, pass everything out in the feces—even large fruit stones, whole baby mice, and mantis nests.

(c) There are a number of differences in the manner of plastering nest walls. Crowned hornbills make plaster of feces, finer soil from the floor of the nest, and insect remains. According to Ranger "the female does not swallow anything for the purpose of disgorging it in the form of plaster," and "the male plays no part whatever in plastering the nest hole." *Bycanistes* collect soil and lumps of earth from the ground. Both sexes do this, but the male brings the most and is a kind of "bricklayer's helper," supplying his mate who does the actual plastering.

(d) A distinction between *Bycanistes* and *Tockus* lies in the time of emergence of the female from the nest. Ranger (1955, personal communication) has extensive data on this subject. He has found that the female may emerge 62 to 74 days after being walled in. At this time the precocious young reseal the entrance. Both parents then feed the young which emerge 19 to 34 days later. Moreau (1936) has collected similar information in regard to *Tockus deckeni* and *T. alboterminatus*.

Similarities in behavior between Bycanistes and Tockus.—A close relationship between the two genera of hornbills is indicated by similarities in their behavior patterns. Many of Ranger's descriptions (1949-52) of the habits of *Tockus alboterminatus australis* apply

equally well to *Bycanistes subcylindricus*. I have quoted a number of these verbatim.

(a) Food. The crowned hornbill's handling of larger prey is the same as for *Bycanistes*. Speaking of a grasshopper, Ranger writes "the hornbill . . . subjects the creature to prolonged chewing and pulping between the mandibles before swallowing, turning it about and tossing it to secure new holds. . . ." Chameleons and nestling birds are treated in the same manner. Among insects taken by crowned hornbills, those as diverse as winged termites, long-horned beetles (cerambycids) and, curiously enough, mantid egg cases were all fed on by *Bycanistes*. After feeding, cleaning "is performed by scraping and wiping the outside of the bill against a branch."

(b) Roosts. The crowned hornbill has roosting sites which are used in rotation. Each member of the family, however, has its own private perch. The two casqued hornbills in our garden always used the same individual perch each night. Like *Bycanistes*, the crowned hornbill is not an early riser. The birds stretch and make gruff utterances to each other for some time in the morning before leaving their roosts.

(c) Play and agility. The following odd traits are also true of casqued hornbills. Ranger wrote that the crowned hornbill reveals "its dexterity when by diving it recovers an object that falls from its bill before it reaches the ground." Speaking of a captive bird he writes that "Conkie was adept at catching objects cast at her over intervals of many yards." The bill whacking of male casqued hornbills was a characteristic sound in the forest. Ranger wrote as follows of the crowned hornbill: "The meaning of the exaggerated scraping of the bill against a branch, indulged in more particularly by the male, has not become apparent."

(d) Basking. "The foliage bath is followed by basking, advantage being taken of the sun's appearance in a clouded sky, but basking is independent in purpose. The body with wings extended is relaxed and spread limply upon branch or foliage, the head and neck upturned. Conkie assumed the most limp, lifeless, unbirdlike attitudes, neck curled with throat uppermost, eyes obscured by the relaxed third eyelid." Such postures are the ones assumed by my pet hornbill, Zika. It is not a matter of drying her plumage but love of sunshine for its own sake. As soon as the sun comes from behind a cloud, whether she is indoors by a window or outside, Zika assumes the grotesque attitudes so well described by Ranger.

(e) Courtship. In describing breeding habits of *Bycanistes*, I have included various activities under a heading of courtship and main-

tenance of the pair bond. This is a matter of interpretation. Ranger uses other phraseology, but the activities he describes are similar. For example, he wrote of the following behavior as having taken place 26 days before final entry. "Investigation of a knocking and rattling near Site I disclosed the hornbill pair, one striking its bill with vibratory rapidity against a branch. The side of the terminal part of the bill was used, and the point, vibrating, traveled around the surface of the branch till in turn the opposite side came into play . . . then the other bird . . . became enlivened and extending its bill performed the same rattling action." Ranger believed this rattling was the same motion employed in plastering and made special note that both sexes were involved. I am not sure whether this performance is entirely related to the onset of nesting in *Bycanistes*. My captives, Mpanga and Zika, do a good deal of tapping. They began when 9 to 10 months of age and sometimes do it against my clothes. Ranger has stated further that his crowned hornbills made increasing visits to the nest tree as the season progressed. Such flights were initiated by the male. A new behavior was noted 19 days before final entry into the nest when the male began to present food to the female. This was done anywhere, not necessarily near the nest tree. Finally, bark presentation was frequent among crowned hornbills. Ranger found that the female would take bark with ready interest from her mate, then bite it to pieces.

(f) Intruders. I have described intrusions on nesting casqued hornbills by members of their own species. Apparently a similar phenomenon takes place among crowned hornbills. Speaking of a feeding visit Ranger wrote "the male and a young intruder arrived, and this drew a single sharp cry from the female. . . . The male then delivered an item and resumed his chasing of the intruder." This male subsequently delivered "13 items of food and bark, but all the time was worried by the young trespasser who followed him again and again to the nest. . . ." I was unable to tell whether the female intruders I saw by *Bycanistes* nests were young birds or not. The male intruders were all adults. Ranger has also written of the nesting female rattling her bill in the entrance. He describes this "habit rattling" as useless activity. This was not true of casqued hornbills. Every time I saw a female rattling her bill there was some cause, such as presence of intruders, to evoke this alarm signal.

(g) Plastering. Photographs of nest entrances presented by Ranger show that the cement walls look much the same as those constructed by *Bycanistes*. The female crowned hornbill has the same technique of plastering. "Always the bill works rapidly in vibratory

fashion, the side of the end portion . . . beating against the surface, to which the moist dung is applied." Ranger has also noted that the cement walls are built up in layers.

Ranger has been fortunate in having many years in which to study crowned hornbills. If I had had at least a second year to study *Bycanistes* I should have been specially interested in finding out (1) whether these hornbills remain paired from one season to another; and (2) whether the same pair returns to the same nest tree in succeeding years. Both of these situations, true for the *Tockus alboterminatus*, presumably hold for casqued hornbills.

Ground hornbills.—I had only casual views of the huge ground hornbills in Karamoja and in Murchison Falls National Park. These form the third main group of hornbills that occur in British East Africa. The following unpublished account of *Bucorvus cafer* (Schlegel) is contributed by Dr. Friedmann. It is of interest from the point of view of comparative biology.

This giant hornbill was seen in rather small numbers in the open bushveldt at Taveta, Kenya Colony, during March and April. The birds were usually seen walking around on the ground in loose groups of three to six individuals. They really walk, not hop. In East Africa they are protected as scavengers and are not molested by big-game hunters and settlers. Although they feed on the ground they sleep high up in tall trees and can fly remarkably well for their bulk. The original "take-off" seems to give them some little difficulty, but when once under way they fly more directly than do most hornbills, their heavy wings causing a very audible *woof woof* with every stroke. The call note is a deep *boom boom*, a rather hollow, and reverberating note. During the mating season the birds become more vociferous and call to each other with great frequency.

The natives in Kenya Colony have a story to the effect that the female ground hornbill says, "*boom boom, I'm going home; boom, I'm going home*" and the male counters with, "*you always say that; boom, you always say that; I'm tired of hearing it; go on home; boom boom.*" It was, therefore, with considerable interest that I learned from Mr. Rudyerd Boulton that the natives in Angola have another interpretation of the calling of these birds. They say that the female says, "*boom boom, I'm going home, I'm going home,*" while the male replies with, "*you must not do that, you must hold up the corn.*"

Like all hornbills these birds feed by picking up bits of food with the bill, then tossing it in the air and catching it far down in the bill or even in the open mouth as it descends.

DISCUSSION OF HORNBILL BIOLOGY

An early impression at Entebbe was that many of the nonmigratory tropical birds, from hadadas (*Hagedashia hagedash*) to red-bellied shrikes (*Laniarius erythrogaster*), remained paired throughout the year. Casqued hornbills were usually encountered in pairs. They are presumably mated for life and one would like to know when pair

formation takes place. It may have no immediate relation to the breeding season. I had three young captives, hand-reared and approximately of the same age, in a cage at Entebbe. Mpanga and Zika were definitely paired before they were 3 months of age. Zika would work through Mpanga's throat feathers as he let his head fall back, then he would do the same for her. The other hornbill, and later a fourth, both males, led independent lives except for roosting. Unnatural conditions undoubtedly favored this early pairing. Young birds, however, do not necessarily pair up when confined together. This was shown by three magpies (*Pica pica hudsonia*), taken before they left the nest, which I kept in a large cage in the same manner as the hornbills. They showed no inclination to pair.

Maintenance of close pair formation demands mutual attentions. When casqued hornbills are perching in different trees, the members of a pair are almost always in communication with each other, sometimes only with single notes such as "cak" or "ugh." When together, mutual preening, in which the female may take the lead, is a common activity. This preening about the head and nibbling of feathers under the throat went on regardless of the time of year. I saw it going on at dusk in the pair which roosted in our garden in October and again with the pair in the Botanical Gardens, on the day the female emerged with her young one in March. It took place early in the life of Mpanga and Zika.

I have interpreted as courtship, activities which bring a pair of hornbills into the rhythm needed for the close cooperation involved in nesting. The lead is taken by the male. He feeds his mate and presents her with sticks and pieces of bark. In addition he becomes noisier in his calls and wailing. Similar activities are not uncommon to the courtship of many groups of birds. The male hornbill also takes the lead in exploring possible nest holes. By his cries and wailings, and his flights back and forth, he tries to induce his mate to look at them.

Stonor (1937) has given an interesting account of a pair of trumpeter hornbills (*Bycanistes buccinator*) which attempted to breed in the London Zoological Gardens. Courtship consisted principally of the male feeding the female. She would fly down to the feeding dish, then wait expectantly for him to feed her. Sometimes he would do so. At other times he would swallow the food himself. Then, as if stricken with remorse, when she would fly to a higher perch, he would at once follow to feed her a morsel. Stonor wrote of a "curious ceremony, wherein the female flew up from the ground with food in her beak which she passed to the male, who then returned it to her,

when she swallowed it." I have previously described an almost identical situation which took place in Mpanga Forest.

Important differences in appearance of hornbills are located about the head, the region which can be seen best through a nest opening. Head feathers in birds of all ages express emotions. In young birds the feathers at the base of the upper mandible are brown instead of black. The huge, forward-projecting casque of the male is his chief sexual characteristic and white skin around the eye is a peculiarity of the female. Many African hornbills have brightly colored patches of skin and wattles about the head and neck. These, however, are entirely lacking in *Bycanistes subcylindricus*. One would like to know what part these bright colors may play in courtship performances.

Coytation in one pair of casqued hornbills took place without any special courtship other than some touching of bills. The pair were returning to their nest, after gathering termite earth. Moreau (1936) found that copulation took place in *Bycanistes brevis* just after the female had emerged from her morning's work and about 10 days before the nest wall was complete.

Good nesting sites are probably used annually. Pitman (personal communication, 1955) believed that the nest hole that I watched in the Botanical Gardens had been used in 1947 and in 1949. At nest 1 the pair tried for weeks to close the opening. Interest, however, began to fall off a week after coytation, a situation that paralleled one described by Moreau (1936) in Usambara. Pairs of *Bycanistes brevis* tried for 2 years to nest at one site without success. "In both years," Moreau wrote, "building continued after copulation had taken place, and when work had ceased, both birds still showed a keen interest in the nest hole." Failure at the nest in Mpanga Forest may have been due to the large size of the opening. Other factors could have been operative also. The pair, or perhaps only the female, for example, may have been young and inexperienced. It is difficult to follow Moreau's hypothesis that in Usambara, failure to complete nests was due to the male's running out of saliva.

Casqued hornbills probably lay two eggs to insure that a single healthy chick is produced. The young bird becomes so large that the nest might be overcrowded if two chicks survived. Crowned hornbills have two to three young. The mother, however, leaves the nest some weeks ahead of time. This not only makes more room for the young but enables her to help in the feeding.

The length of time a female is walled in a nest (119 days for nest 5) does not appear unusual for a bird of hornbill size to lay eggs, incubate, and rear a young one. One can use Wahlberg's eagle

(*Aquila wahlbergi*) for comparison. It is approximately the size of a casqued hornbill and has been studied by Leslie H. Brown (1952) in Kenya Colony. He observed an incubation period of 46 days and a fledgling period of 72 days at a nest where a single eaglet was raised. This gave a total of 118 days. The total time is about the same as for the casqued hornbill, which, I have estimated, leaves the nest when 10 to 11 weeks of age. I would have supposed that young hornbills would grow more slowly on a fruit diet—they had animal food only occasionally. However, as indicated by white matter in the feces, they may have had more animal protein, particularly in the form of smaller insects, than I realized. It was almost impossible to feed my young captive hornbills on fruit alone. The volume required was exhausting. We reduced the number of feedings, first by coating pieces of pawpaw with powdered milk, then by giving each bird six to eight half-grown mice a day.

Intrusions of foreign hornbills on nesting pairs of their own species presented an interesting study. In a few instances the intruders came in pairs. There were many free pairs of hornbills throughout the nesting season and I wondered if these were not an index of an increasing shortage of suitable nest trees. Intrusions by single female hornbills were more difficult to explain. At one nest the same female apparently stayed around for months, and possibly attacked and crippled the young one soon after it left the nest. Several explanations suggest themselves. First, intruding females may have been offspring of the season before, unwilling to leave their parents or, second, they may have been unmated adults attracted by a seemingly lone male; possibly they fell into both categories. Some of them seemed to be more attracted to the nest itself and others to the male, coming and going with him as he made his feeding visits. I had an impression that there was an excess of females in the hornbill population.

In conclusion, the pleasure of watching hornbills comes from their love of play, unexpected agility, clownishness, and seeming intelligence. This last quality is difficult to assess. The intelligence of the crow family is well recognized. I have kept tame blue jays, crows, and magpies and rate my captive hornbills on the same level. Both groups are playful and curious, examining new objects with interest. They have a wide range of vocal expression. The large eyes of hornbills, together with expressive movements of head feathers, give an impression of intelligence which is hard to disregard. Whatever their mental capacity, however, it is difficult to see how these birds can adapt themselves to civilization, as they are destined to inhabit large

forest trees. My unusual opportunity to study their breeding and other habits in the vicinity of Entebbe has been most fortunate.

SUMMARY

Sixteen nesting pairs of casqued hornbills (*Bycanistes subcylindricus*) have been studied in the vicinity of Entebbe, Uganda. An unusual concentration of nests was found in the Mpanga Research Forest.

In courtship the male presented his mate with food and bits of bark or sticks. Mutual preening and calls back and forth were important in maintenance of the pair bond.

The male did the pioneering in exploration of possible nest sites and tried to entice the female to them with wailing cries. Plastering was done by the female from the inside of the nest cavity, using a rapid tapping with the side of her bill tip. Both sexes flew to the ground to collect dirt for building. Most of this, however, was done by the male. He attended the female, furnishing her with pellets for construction of the nest wall. Termite earth was preferred for building.

Two eggs are laid. Although both may hatch, only one chick is raised.

Male hornbills feed their mates about every 30 to 60 minutes, heaving up fruits held in their gullets. Often a stick or piece of bark is presented first.

Nest sanitation is accomplished by female and chick expelling feces through the entrance. The female may also toss debris out with her bill. If such debris collects outside of the entrance, it is regularly cleared away by the male.

Ants which swarm in some hornbill nests may act as scavengers and keep down insect fauna.

Females walled within nests can be extremely noisy if alarmed.

Observations made at one-third and two-thirds through the nesting period indicate that females have a gradual molt. Two females removed when two-thirds through their nesting could fly readily.

The total period a female was walled in one nest was 119 ± 2 days. A young hornbill, captured two days after emerging, was in full plumage.

The majority of casqued hornbills in eastern Uganda probably begin nesting in September and break out in January.

A hornbill territory is confined largely to the vicinity of the nest tree.

Occasionally a foreign pair of *Bycanistes* would visit a nesting female and attempt to feed her.

Lone female hornbills interfered persistently with a number of nesting pairs. At one nest this interference had serious consequences.

Male hornbills fed their mates largely on fruit but also caught insect and vertebrate prey. Lists are given of such fruits and insect remains as could be identified.

Roosting habits are described for one pair before and for a lone male during the nesting season.

Casqued hornbills were much alarmed by hawks and eagles.

They prefer the largest of forest trees to nest in. Rapid destruction of forests in Uganda threatens the future of these birds.

Three hornbills, removed from nests when 6 to 7 weeks of age, have been reared in captivity, largely on a diet of animal protein. The exact age of one captive was known. Two of them have remained closely paired from the age of 3 months. Bill tapping and plastering against the walls of their cage were done by the male and the female, beginning at 9 to 10 months of age.

A comparison has been made of *Bycanistes* and *Tockus*. There are many points of similarity in the habits of the two genera.

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