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BREEDING BEHAVIOR OF THE HARPY EAGLE (*HARPIA HARPYJA*)

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ABSTRACT.—The breeding behavior of a pair of Harpy Eagles (*Harpia harpyja*) in southwestern Guyana, South America was observed over 947 h between 13 May and 6 December 1974 and 15 March to 5 April 1975. The nest was located 38.4 m above ground in a huge silk-cotton tree (*Ceiba pentandra*). The pair constructed most of the nest between 14 May and 1 June. From 1 to 17 June copulation in the nest tree occurred nine times but on no occasion were preliminary courtship displays noticed. Also during this period, both sexes frequently collected green sprigs to line the bowl of the nest. With but two exceptions, only the female collected green sprigs during the incubation and early rearing period. The male resumed vigorous sprig collecting when the young was half grown. The first of two eggs was laid on or just before 17 June and the second around 19 June. Incubation began after the second egg appeared and continued for 56 days, when one of the eggs hatched. The remaining egg did not hatch and was eventually buried with nesting material. The female performed 97% of the incubation, fed the eaglet (usually in the morning and late afternoon), and protected the chick from insects, potential predators, and inclement weather. The male arrived with prey about once every 7 days during incubation and once every 3.5 days during the first half of the nestling period. He incubated while the female fed. His attendance at the nest became irregular in the second half of the nestling period, when the female resumed hunting. With both adults hunting, prey were brought to the nest about once every 2.5 days.

At 115 days of age, the nestling, which we believe was a male, weighed 4,032 g and was 5/6 as large as the adult male. Fledging occurred at 141–148 days. After fledging, the juvenile was generally inactive and made only occasional short flights within the vicinity of the nest tree. From 15 March to 5 April, the adults arrived six times with prey. During this time, the juvenile was totally dependent on the adults.

Fifteen species of mammals were identified from prey remains, 13 of which were arboreal.
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THE Harpy Eagle (*Harpia harpyja*, see Frontispiece), largest of eagles, inhabits tropical rain forest from southern Mexico to northern Argentina. Strictly a forest species, this huge raptor is largely inaccessible to field observation and until the present study little was known concerning its breeding behavior. Most previous accounts of the species' habits are general in nature (Schomburgk 1848, Brown 1876, Quelch 1890, Lloyd 1897, Chubb 1916, Bond 1927, and Friedmann 1950). Fowler and Cope (1964) discovered two nest sites in 1960 in Guyana, South America (formerly British Guiana), providing data on nest sites, nest construction, habits of adults and fledged juveniles, prey, food requirements, and plumage variations. The present study was made at one of the nest sites discovered by Fowler and Cope.



Frontispiece. Adult female Harpy Eagle and 54-day-old eaglet. Crest, cheek, mantle, back, scapulars, remiges and upperwing coverts are evident on young. Adult female's breast and belly feathers show trace of nest stain.

STUDY AREA AND METHODS

Between 13 May and 6 December 1974, and from 15 March to 5 April 1975, we studied the nesting cycle of a pair of Harpy Eagles in the Kanuku Mountains of southwestern Guyana. The Kanuku Mountains cover about 56 km from north to south and 120 km from east to west and range up to 1,036 m in height. The slopes support montane tropical rain forest, while the creek valleys contain mixed lowland rain forest. Forests extend 5 to 8 km beyond the mountains and end abruptly, giving way to the Rupununi Savannah.

Temperatures in the mountain valleys from January to April 1960 varied from a nighttime low of 22°C to a daytime high of 33.6°C (Fowler and Cope 1964). Rainfall measures about 200 cm annually. In 1974 the main rainy season lasted from early June until early September. Normally the rains are concentrated between April and September and between December and February. Since the area is 3.3° north of the equator the length of daylight varied little.

Over 947 h of surveillance were made during 8 months, utilizing 6 vantage points: a ground blind 18 m from the base of the nest tree; a tree blind 53 m from the nest, and 38 m off the ground in a mora tree (*Mora excelsa*); a blind in the nest tree 8.5 m from the eyrie and 40 m from the ground; and 3 observation platforms located in the tops of trees in the vicinity of the nest. Behavior was recorded on 35-mm still film and 16-mm motion picture film. Weights were measured with a spring scale.

DESCRIPTION OF THE NEST SITE

At 1500 on 13 May 1974 we first visited the silk-cotton tree (*Ceiba pentandra*) that contained the old eagle nest. The massive tree was 56 m tall and measured 2 m in diameter above the buttresses, which spread to a maximum width of 7 m. The first limb was 27 m from the ground. The nest was seated 2.4 m above the main fork (the main fork was the position of the nest discovered by Fowler and Cope 1964) where two large limbs crossed and fused together (Fig. 2). This point was 38.4 m above the forest floor. The silk-cotton was the tallest tree in the area and dominated the creek valley. Unlike many other large rain forest trees, including other silk-cottons, it was notably devoid of epiphytes and its open canopy allowed sunlight to illuminate nearly every major branch. The height of the surrounding forest canopy averaged 30 m though some mora trees attained heights of about 45 m.

The silk-cotton tree was located at the base of a valley (elevation about 135 m) surrounded on the north, south, and east by mountain slopes. It was 30 m from the north branch of Moco-Moco Creek and 5.6 km east of a point where Moco-Moco flows into the open Rupununi Savannah.

During the course of our observations, the nest changed appearance notably although the basic size and shape remained about the same: diameter = 137 cm; height = 78.7 cm. During incubation green sprigs were basically confined to the bowl, which was 40.6 cm in diameter and 15.2 cm deep, and to the perimeter of the bowl. When the eaglet was 21 days old, the nest was generously decorated with green sprigs (Fig. 3b). The entire upper half of the nest was composed mainly of dried and fresh sprigs collected primarily by the female (Fig. 2). The actual height of the structure increased only about 5.2 cm as the new material was compressed due to constant trampling.

The nest seemed to be ideally located in conjunction with the abundance of wild-life in the creek valley. This was especially true during the dry seasons when we noted increased populations of terrestrial mammals attracted to the creek for water.

THE NESTING CYCLE

Pre-egg-laying period.—At 1400 on 14 May, we sighted an eagle on the nest and found fresh nesting material there. To avoid human interference, we limited our



Fig. 1. Eagles copulating on the nest (1-17 June).

observations to a mountain clearing 0.4 km north of the nest until 18 May. During 8 h we did not observe any activity from this point. On 18 May we visited the nest site again. At 1250 an eagle alighted on the nest and began to utter various croaking and chirp-like calls and to arrange nest material. As it adjusted the material, it would commonly correct its balance by wing flashing. This eagle was later confirmed by its smaller size and vocalizations to be the male. Within an hour he visited the eyrie five times bringing sticks. On one additional occasion, he flew from the nest to a limb nearby with what appeared to be the leg of a monkey. Both the male and the female landed on the nest at 1350. Soon after their arrival they rubbed their mandibles together for about 4 s, and while chirping softly began to adjust nest material.

Between 18 May and 1 June the activity of the eagles consisted of periodic visits to the nest, most commonly between 0530 and 1130, when sticks were collected. During the time nest material was collected, we judged from their vocalizations (since we were in the ground blind) that they radiated no more than 180 m from the nest tree.

Movements of the pair were recorded on 19 May. With the first trace of daylight at 0530, we saw the female on the nest, thus indicating that she probably roosted on the structure. The male arrived on the nest sometime between 0635 and 0640. The eagles departed from the eyrie to collect sticks five times between 0605 and 0750 with each round trip averaging 7.4 min. From the ground blind, we could not always distinguish the sex of the departing bird. At 0805 the male departed and was



Fig. 2. Female Harpy arriving at nest with green sprig. Young is 38 days old. Upper half of the nest is composed of fresh and dried sprigs.

not seen again that day. The female left the nest at 0808 and perched on a limb of the silk-cotton tree until 1350 when she returned to the nest for 10 min and then departed for the remainder of the day.

Detailed observations were far too limited from the ground, and we therefore decided to construct a tree blind in a 44-m mora tree growing 53 m west of the nest tree. The canopy of the mora afforded a well concealed position to build the blind without creating a shocking change in the surroundings of the eagles. From this point the entire silk-cotton crown was exposed and activity at the nest was clearly visible.

At 1230 on 1 June, we observed copulation for the first time. We saw the pair copulating on eight more occasions: once on 3 and 17 June and twice on 7, 9, and 11 June. The sporadic copulation was not preceded by displays and occurred on the nest or a limb of the nest tree (Fig. 1). During copulation the male would mount the female without any visible ritualistic behavior and would usually drop onto his tarsometatarsal joints, balancing with half-extended wings. The tail of the female usually shifted to her left and the male's to his right. Four mating intervals were timed at 13, 13, 11.3, and 9.5 s (average 11.7 s). During mating, the crest feathers lay flat against the nape. This was also observed when the birds were excited or alarmed. During the period of copulation, the male was present in the area nearly every day.

Though we observed the first signs of nest construction on 14 May when only a



Fig. 3. A. Adult female Harpy with 10-day-old eaglet and unhatched egg. Remaining egg was ignored by adults after the first hatched. B. Female eagle and 35-day-old eaglet. Female calling after departure of the male. C. Female feeding 110-day-old young. Damage to wing coverts visible on the nestling. D. Nestling (115 days old) with kinkajou skull and spine in foreground. Weight of nestling = 4,032 g.

trace of the old structure was present, an Amerindian saw an eagle at the nest site in the middle of April. The bulk of the nest was completed between 14 May and 1 June and was composed of sticks as large as 5.1 cm in diameter and 1.2 m in length. After 1 June, green sprigs (22–75 cm in length) comprised about 90% of the nest material added. Both adults collected green sprigs until incubation began. The female continued to gather them through the early rearing period. Though the male collected sprigs twice during early incubation, he did not collect them routinely again until the chick was half grown.

The male and female differed notably in the methods used to collect green sprigs. The female would usually bob her head and would direct her attention to a chosen treetop, sometimes taking as long as 5 min to finally make the decision to move. Flying directly to a crown and using feet, mandibles, or both, she would dislodge the sprig from the tree. Often there was violent wing beating and unwieldy grappling with her feet, actions that could easily be confused with the capture of prey. She often took 4–5 min to sever the sprig from the tree and after doing so would then fly to the eyrie and place it on the perimeter of the bowl. We noted that smaller sprigs and sticks were carried in her bill while larger pieces were transported in her talons (Fig. 2). The female seemed to favor sprigs of mora trees and normally collected from the same tree or group of moras within 75 m of the nest, but on occasion she collected from the silk-cotton and other trees close to the nest location.

Unlike the female, the male quickly initiated green sprig collections. He would fly directly to the outer branches of trees and would grapple with the green sprigs, habitually hanging upside down. He often hung for 15–20 s while either plucking the sprig with his beak or dislodging it with his feet. The hanging

position seemed to be the only stable way he could remain on the delicate branches long enough to secure a sprig. The male showed no preferences when gathering sprigs and sticks. They were collected from the nest tree or apparently at random from trees surrounding the silk-cotton. When collecting a sprig from the silk-cotton, he often launched up at a 60° angle and gracefully secured the green sprig. Since sprig collecting by the male abruptly terminated soon after incubation began, it may have been a display directed at the female. However, because it occurred again late in the cycle, we believe that it was a normal technique used by the species to collect nest material.

Fowler and Cope (1964) observed a female grappling in the top of a mora tree. "For three minutes she was either fighting the branches, upside down with her legs drawn tightly to her body, or was holding on to the top of the mora with her wings outspread." Based on the similarity to the techniques for sprig collecting we saw, we believe that their observation refers to this activity.

From 1 June to 17 June both the male and female prepared the bowl of the nest. They lined it with fresh greens and often assumed an incubation-like posture to shape it. The male spent more time in this attitude than the female. Once he remained in this posture continuously for 1.5 h.

In the last 17 days of nest construction prior to incubation (1–17 June), the male brought kills to the nest on 1, 5, 7, and 17 June. Prey was brought to the eyrie between 1100 and 1300 on these days. Once we observed copulation following the arrival of the male with a carcass. We noted that the female preferred to carry a kill away from the nest before feeding on it.

Egg-laying period.—On 11 June the female began to reveal signs of lethargy. Nest decorating decreased and she showed no interest in feeding. That day a troop of six spider monkeys (*Ateles paniscus*) passed directly under the silk-cotton about 15 m from her. She paid little attention to them as they moved on from tree to tree below the eyrie. Between 11 and 17 June the female spent most of the day perched near the nest. She limited her activity to two sprig collections and to occasional visits to the nest where she often assumed a position similar to incubation.

On 17 June a climber found one egg in the nest; it was partially covered by green leaves. We suspect that the leaves covering the egg helped maintain a cooler temperature, possibly to delay embryonic development until the completion of the clutch. We do not know exactly when this egg was laid. A second egg was deposited on or near 19 June, when she began to incubate. Intervals between the first and the second egg of 6 days (von Eberhard 1973) and 9 and 14 days (Hanif 1970) have been reported for captive Harpy Eagles.

Bond (1927) found the nest of a pair in Brazil in which two eggs were laid. He collected one fresh egg (the only one present in the nest) on 27 April and on 9 May secured a second slightly incubated egg. Fowler and Cope (1964) thought that the second egg may have been a replacement. Since the pair we studied laid two eggs (Fig. 3a), we suspect that the first was collected soon after it was laid and that the second egg was deposited shortly afterward, thus completing the normal clutch size.

Incubation period.—At 0650 on 20 June the female left the nest, and an hour later the male arrived and incubated the eggs. As the male incubated, he began making whispy screaming or wailing calls with a forced exhaled *Wheeeeeeeeeee-whheeeeeee-whheeeeeeeee*. Call sequences of 5–7 vocalizations were heard for durations of 30–40 s; pauses between sequences lasted over 10 s. The female began

calling in a similar manner, though her calls were pitched somewhat differently and in sequences of 8–10. The pair seemed to be duetting because they alternated calling with a degree of overlap. Similar calls were commonly heard through the balance of the nesting cycle but were uttered mostly by the female.

During the 56-day incubation period, details on behavior were noted. Usually at dawn (0545 to 0600) the female would take the first of many short daily breaks from incubation. These occurred at intervals of about 1.5 h and usually lasted 9.5 min (range 2–45 min). Her pattern of behavior was consistent. On rising off the eggs, she would turn and hop to a position on her favorite limb near the nest. Next she normally stretched, preened, and called, and then rested or collected a green sprig. Sprigs were collected about three times a day (during our usual 8 h of daily observation) until the female resumed hunting around 1 November. The period of incubation, 19 June–14 August, was in the midst of the 1974 main rainy season; this likely influenced her strict nest attendance. With the occurrence of rain, breaks were terminated immediately and the female returned directly to the eggs.

During the first 3 weeks of incubation, the female rolled the eggs 1–3 times daily. After that time and until one egg hatched on 14 August, the eggs were turned each time the female resumed incubation after a break. This was observed about five times daily.

When the female entered the nest bowl, she gently raised her feet with hind claws turned forward under the ball of the foot. The foot, in this position, was also utilized to rake or remove leaves covering the eggs before she settled down. The wings acted as stabilizers as she slowly entered the bowl and would flash out if balance correction were required. When in the bowl, she habitually rocked from side to side for about 3–4 s to adjust herself properly on the eggs. She would then rest her lower mandible on the nest in low profile for a moment before lifting her head to observe the activities in the rain forest.

The female performed about 97% of the incubation and the male supplied her with food an average of once every 7 days through this period. She normally vocalized (*Wheeeeeeee* repeated 9–12 times) after fasting for 4–5 days. If the female detected the male in the area, she normally increased the intensity and frequency of calling until he arrived. Often she was aware of his presence for 45 min before his arrival on the nest. We assume that the male utilized certain perches within sight of the female where he usually removed the hair of the prey and consumed its head and upper torso.

When the male delivered the remainder of a carcass to the nest, the female would grasp it and would either fly to a favored mora tree nearby to feed or would consume it on the nest. The male would incubate the eggs until his mate returned 1–4 h later and would relinquish his duties without hesitation. When the male incubated, his beak was frequently open as if affected by the heat or exhausted from his previous hunting excursion.

Late incubation and hatching.—On 7 August we began building a blind in the silk-cotton tree, 40 m from the ground and 8.5 m from the eagle eyrie. Construction was limited to favorable weather and to one hour daily for 6 days. The blind was completed at 1400 on 13 August. During the last hour of construction we could faintly hear vocalizations coming from the eggs.

Rettig remained in the silk-cotton blind from the time it was completed until 1700 on 15 August to record the behavior of the adults during pipping and emergence of the chick. From 0015 to 0400 on 14 August, he heard curious sounds from the nest

similar to the female ruffling her feathers (rousing) and fanning her wings. During this time the chick apparently hatched. At 0600 the female left the nest briefly revealing the eaglet, which was pure white and completely dry. At that time, the chick was totally uncoordinated, but by late afternoon it could hold its head upright for 1–3 s before tiring. The female closely brooded the newly hatched eaglet that day, and took only three brief (1–3 min) breaks to her favorite limb near the nest.

At 0630 on 15 August, the female took a 30-min break and collected a green sprig before returning to brood the eaglet. As the day progressed the female shaded the chick from direct sunlight. At 2 days old, we heard the eaglet vocalizing: *Peeeeeeee-
peeeeeeeee*, etc. The male arrived with an unidentified kill at 1700 and shortly afterward the female fed the eaglet.

Feeding was performed slowly and with great care due to the eaglet's uncoordinated attempts to take offered meat during the first week. The chick was given pieces of meat (5–15 mm) moistened by salivary and nasal secretions. Feeding usually occurred twice daily (range 1–4 times): once in the morning between 0730 and 0930 and once in the afternoon between 1500 and 1730. The average feeding session lasted 35 min. We estimated that a feeding would consist of about 56–84 g in the first 1–2 weeks. After feeding, his crop seemed only comfortably full (not bulging or filled to its capacity). Carcasses on the nest lasted 1–4 days, but usually were consumed within 72 h. Decomposing meat was often utilized.

As soon as the egg hatched, the behavior of the female toward the male changed radically. When he arrived at the nest she would quickly secure any prey from him, and then begin to mantle and call loudly. The female would continue to mantle and call while the male was present and for up to one hour after his departure (Fig. 3b). When she stopped calling, she usually fed the eaglet.

Just after the first egg hatched, the female quickly lost interest in the remaining egg. We observed the egg for 4 weeks lying idle in the bowl of the nest (Fig. 3a). Eventually, it was buried under accumulated green sprigs.

We suspect that in this eagle, incubation terminates after the first egg hatches, or, if it does not hatch, continues until the second egg does. In this way only one chick would ever be reared. In certain species of eagles in the genus *Aquila* that lay two eggs both often hatch, but one chick will sometimes kill the other.

Nest attendance of the male.—During incubation, the male brought food to the nest once every 7 days, but after the egg hatched he frequented the nest about once every 3.5 days until the eaglet was half grown (Table 1). He normally arrived on the nest between 0850 and 1100. A similar schedule has been reported (Brown and Amadon 1968) in the Crowned Eagle (*Stephanoaetus coronatus*) where the male brings food every 3.5 days during incubation and about twice as often after the chick hatches.

The behavior of the male changed somewhat in October during the second half of the rearing period. These changes consisted of longer periods at the nest site (up to 1 h 40 min), a sudden increase in green sprig collecting, more interest in the juvenile, and a slightly irregular schedule in delivering prey.

The male collected green sprigs only twice from the time the first egg was laid to when the chick was half grown. However, on 4 October after he delivered an opossum (*Didelphis marsupialis*) to the nest, he resumed gathering green sprigs. He continued doing so often through October while he was near the nest site. He commonly collected sprigs in an energetic manner in rapid succession. On 12 October, he arrived at the nest tree without prey and proceeded to collect two greens

TABLE 1
THE ATTENDANCE OF THE ADULT HARPY EAGLES AT THE MOCO-MOCO NEST SITE

Date	Time of arrival	Prey	Time on nest (approx.)
Nest attendance of the male			
August			
15	1700	unknown	unknown
19	1000	three-toed sloth	5 min
22	unknown	<i>Cebus</i> monkey	unknown
23	1130	unknown	5 min
24	1100	<i>Cebus</i> monkey	5 min
26	1045	unknown	unknown
30	1030	<i>Cebus</i> monkey	5 min
September			
2	1200	unknown	3 min
4	0930	<i>Cebus</i> monkey	8 min
10	unknown	unknown	unknown
15	0930	<i>Cebus</i> monkey	2 min
18	0900	three-toed sloth	unknown
20	0945	unknown	unknown
23	0805	unknown	3 min
25	1505	unknown	unknown
28	unknown	kinkajou	unknown
October			
4	1010	opossum	14 min
6	0900	opossum	unknown
20	a.m.	monkey	unknown
21	0930	— ^a	unknown
24	1300	unknown	2 min
29	1000	opossum	2 min
November			
4	1700	monkey	2 min
7	unknown	unknown	unknown
10	1715	two-toed sloth	unknown
15	1630	unknown	unknown
20	1420	kinkajou	3 min
23	a.m.	<i>Cebus</i> monkey	unknown
30	unknown	unknown	unknown
Nest attendance of the female ^b			
November			
3	1445	two-toed sloth	—
11	0945	two-toed sloth	—
16	1600	two-toed sloth	—
21	unknown	unknown	—
27	1030	three-toed sloth	—
29	unknown	unknown	—

^a The male arrived without a prey.

^b The female remained in the vicinity of the nest except when she departed to hunt.

from canopies about 90 m from the nest. When he brought the first sprig to the nest, the female flew in immediately and mantled over the bowl even though there was no carcass present. At this time, both female and juvenile appeared hungry. The last prey we observed brought by the male was an opossum 6 days earlier (6 October). This prey lasted 3 days. We did not see any prey delivered from 6–19 October. The 13-day period was the longest span we recorded between successive deliveries of prey. On 20 October, the female had what appeared to be half of an adult red howler monkey (*Alouatta seniculus*). From remains seen, we judged this monkey to have weighed 6.3 kg. The condition of the carcass (not dehaired) and its size indicated that the female probably captured it.

The male arrived on 21 October, again without food. He collected five green



Fig. 4. Juvenile male Harpy Eagle (7 months old) calling near the old nest site. Note absence of wing coverts, and white wing bar composed of down.

sprigs in succession and then remained at the nest site for 1 h 40 min. After vigorous collecting, he often adjusted greens on the eyrie and investigated the nestling, who would chirp rapidly and beg for food. The male, however, never attempted to feed the chick. In October after he attended the nest, he often perched in the silk-cotton tree for as long as 1 h before departing. During this month, he averaged one arrival every 5 days.

During incubation and especially after the eaglet hatched, the male vocalized nearly every time he arrived at the nest site. Vocalizations consisted of rapid chirps, goose-like calls, and occasional sharp screams. From 20 November, the frequency

with which he vocalized decreased to the point where he would either chirp only a few times as he landed on the nest or remain totally silent. We did not hear the adults vocalize in March and April.

Development and care of the young.—During the development of the chick, the adults maintained relatively consistent behavioral modes. When the eaglet was 14 days old, the female began spending more time off the eyrie though she normally remained nearby. If the eaglet called in distress (*Chi-chi-chi . . . chi-chi-chi-chi*) when it rained, or when the nest was exposed to the sun, she usually returned to the nest immediately to brood or sun-shade the eaglet.

At 22 days the eaglet began to pick at kills, but it could not tear off any sizeable portions. At 26 days it attempted to stand and began to watch and snap at insects around the nest. By 36 days the eaglet was capable of standing and actually walking, though clumsily. During this period we often observed the eaglet moving towards the edge of the nest (Fig. 3b) especially when the female perched on an adjacent limb. At times it looked in danger of slipping off, but the female seemed to detect the danger and would move into the center of the nest and the chick would follow her there.

The young called three times (*wheeee-wheeee-wheeee*) at 38 days in a manner similar to the females but softer, especially towards the end.

The remiges began to emerge at 45 days, and at 54 days the following feathers became evident: crest, cheek, mantle, back, scapulars and upperwing coverts (Frontispiece). At 59 days, wing exercising began. Rectrices were evident at 77 days.

In November and December, the juvenile could feed itself, though with some difficulty, but it preferred to be fed by the female (Fig. 3c). It fed more easily on partially decomposed remains since the flesh was softened.

We observed wing exercising often through November and early December. Flapping sessions often occurred when gusts of wind or strong breezes swept through the silk-cotton tree. Sometimes it actually lifted off the nest for an instant while exercising. When left unattended for any long period of time, it would call repeatedly much like the female. When the female was present at the nest, the juvenile became submissive and would not mantle food items as it would when other raptors (such as a vulture or hawk) passed nearby. When the juvenile mantled, it would sometimes scream in a weaker variation of the adults' *wheeeeeeeee*.

Deterioration of the wing coverts began soon after they emerged when the juvenile was 70 days old. Figure 3c clearly shows the damage when the juvenile was 110 days old. The damage appeared to have been caused by ectoparasites as the webs of the feathers were eroded leaving on many only the rachis. When the juvenile was two-thirds feathered, the ventral apterium was exposed and there was poor development of the underwing coverts (Fig. 3d).

At 115 days the juvenile weighed 4,032 g and appeared to be 5/6 the size of the male. From its weight and size, we judged it to be a male.

Fledging and post-fledging.—We discontinued observations on 6 December when the juvenile was 116 days old and about two-thirds feathered. At that time, we estimated that he would become a "brancher" in 15–21 days and would fly in 25–32 days.

On 7 February 1975, Jim Fowler (pers. comm.) visited the nest site and found the juvenile to have full flight capabilities. When we returned to the nest site on 15 March, the nest had fallen and the juvenile was flying but was still dependent on the adults. The most striking change in the 7-month-old juvenile was the total

absence of the greater and lesser secondary wing coverts which had apparently been destroyed by ectoparasites. The "naked" area was marked with a bright white wing bar that consisted of down feathers that protruded from the area above the radius (Fig. 4).

The light plumage and the bright downy wing bars (Fig. 4) of the juvenile contrasted sharply to the greens of the forest and made him conspicuous; however, when he perched in the silk-cotton tree and faced away from us, he was very camouflaged. The mottled ash greys of his back blended cryptically with the grey limbs of the tree. The young bird was also easily located because he frequently called (Fig. 4), especially when unattended by the adults for more than 2 or 3 days. Often during 7–8 h of surveillance, we would not see him fly. He perched in the upper middle branches of the nest tree (39–48 m from the ground) about 80% of the time. Other perches utilized were mora crowns, densely foliated trees, and dead snags, all of which were near the nest tree. His flights were limited to no more than 270 m around the nest tree.

During our 3 weeks in March and April, the adults brought food to the juvenile in the silk-cotton tree six times (both birds on 16 March and one bird on 25, 30, 31 March, and 1 April). Each adult arrived about once every 6 days. The juvenile usually detected the presence of an adult several minutes before one actually arrived. He responded to their presence by screaming (a series of *wheeeee*) and flashing the wings vigorously. On all but one occasion when the adults arrived with prey, he would instantly rush them to possess the carcass. Once acquired, he would mantle the prey and continue to scream for a while. On 16 March, the adult male delivered a carcass to the nest tree at 1030. The juvenile waited 2 h before flying to the prey, although before the adult arrived, the young bird screamed and flashed his wings for 20 min, apparently very hungry. At 1230, when the juvenile began feeding, the female came in with food and was immediately rushed by the juvenile which caused the female to drop her prey to the ground. The juvenile slowly returned to the carcass brought earlier by the male and resumed feeding.

COLORATION OF THE ADULTS AND JUVENILE

The adult plumage of the Harpy Eagle is described by Friedmann (1950) and the juvenile plumage by Fowler and Cope (1964). These descriptions apply to the adults and juvenile in our study except for the condition of the wing coverts of the young bird described above. The adults differed only in size (the male was one-third smaller than the female) and in eye color. The color of the iris in the male was dark brown and in the female light brown.

During the incubation period the breast and belly feathers of the female became heavily stained by tannins leached from the green sprigs lining the bowl of the nest (Fig. 3a, 3b, and Frontispiece). The eggs were also heavily stained. The stain on the female gradually disappeared and was nearly gone 5 months later in November, when she began to hunt again. The adults gradually moulted their feathers throughout the study.

AGGRESSIVE ACTIONS TOWARD INTRUDERS NEAR THE NEST

Before we constructed our blinds, we noted the reactions of the eagles to climbers and objects alien to them (camera cases, ropes, climbing gear, etc.). In May, the eagles expressed only slight concern with humans on the ground and with loud

TABLE 2
PREY REMAINS AT THE MOCO-MOCO NEST SITE OVER 328 DAYS OF NESTING

Prey Species	Typical remains	Minimum-number of individuals represented	Average weight of species (kg) ^a
Opossum (<i>Didelphis marsupialis</i>)	skull, pelvis	2	3.5
Monkey (<i>Cebus</i> sp.)	spines, pelvis, femora	13	2.25
Red howler monkey (<i>Alouatta seniculus</i>)	sight record	1	8.0
White-faced saki (<i>Pithecia pithecia</i>)	tibia	2	1.25
Red-backed saki (<i>Chiropotes satanas</i>)	vertebrae	2	1.0
Kinkajou (<i>Potos flavus</i>)	skulls, spines	4	2.0
Coati-mundi (<i>Nasua nasua</i>)	sight record	?	?
Olingo (<i>Bassaricyon beddarti</i>)	sight record	1	?
Gray-headed tayra (<i>Eira barbara</i>)	sight record	1	1.8
Agouti (<i>Dasyprocta aguti</i>)	femur	5	3.0
Prehensile-tailed porcupine (<i>Coendou prehensilis</i>)	skull, pelvis	3	2.5
Three-toed sloth (<i>Bradypus tridactylus</i>)	skulls, forelimbs	6	3.5
Two-toed sloth (<i>Choloepus didactylus</i>)	skulls	15	5.0
Tamandua (<i>Tamandua tetradactyla</i>)	sight record	1	?
Red brocket deer (<i>Mazama americana</i>)	femur	1	5.0

^a References: Walker (1975), Robert Izor (pers. comm.).

^b The red brocket deer was a fawn.

sounds from falling trees or distant gunshots. During the 4 days (1–4 June) we built the mora blind, most of our movements were confined to the trees. The eagles were not alarmed by our activities, and in fact, actually appeared slightly curious.

During the construction of the blind in the nest tree (7–13 August) and afterward when we approached the blind or departed from it, the female attacked dozens of times. She would normally fly directly at the intruder and would veer off a few meters away. Sometimes, however, she would strike the trespasser, usually in the middle of the back with closed talons. We prevented her from striking us on many occasions by shouting and raising our arms when she was about 2 m away. While we were in the blind, she ignored us.

The aggressive reactions of the eagles to climbers entering the nest tree assured us that they would boldly defend their nest and would not abandon the area. The male paid less attention to climbers. He attacked only once, the first time a man climbed into the silk-cotton tree.

When insects, especially bees and wasps, and in one instance a 20-cm centipede appeared on or near the nest, the female would snap at or remove them and would sometimes swallow them in the process.

On one occasion, the female responded to a Turkey Vulture (*Cathartes aura*) attracted to carcasses on the nest. When the vulture neared the canopy of the silk-cotton tree, the eagle launched off the nest and pursued it. Though she easily overtook it, she flared off and did not strike the fleeing bird.

FOOD

During 235 days of observation at the nest, the adults arrived with prey 52 times; 43 by the male, 9 by the female. Table 1 lists the arrival schedules for the adults from 15 August to 30 November. The male provided all the kills during nest construction, incubation, and the first 2.5 months after the eaglet hatched. Table 2 lists the genera or species identified from prey remains brought to the nest and from remains found under the nest, all of which were collected over 328 days of nesting.

Of the 15 genera and species identified, all but two, the agouti (*Dasyprocta aguti*) and the red brocket deer (*Mazama americana*), were arboreal. The age distribution for members of the genera *Choloepus*, *Cebus*, and *Bradypus* was random and indicated that the Harpy Eagle does not select individuals of any particular age group.

Animal remains brought to the nest by the adults weighed between 0.5 and 3.2 kg. The male brought kills or portions of prey ranging from about 0.5 to 2.3 kg (average 1.1 kg); the female brought portions of prey weighing up to 3.2 kg. We estimated that the live weight of the animals she captured ranged from 2.7 to 9.0 kg. The largest animal was an adult two-toed sloth (*Choloepus didactylus*).

Several of the mammals taken by the adults are normally nocturnal. They apparently catch them at twilight or find them curled up sleeping in trees during the day.

Skeletal remains varied in two physical ways correlating with stages in nesting. Bones collected from 14 May until early November were individual elements; femora, vertebrae, jaws, and skulls usually with damaged or segmented craniums. This reflected the adults' manner of feeding on a carcass. Remains from late November through 5 April included complete spines with skull and limbs sometimes attached. Several items were draped with dry skin. These reflected the weaker, less experienced techniques of the juvenile in feeding on a carcass.

Between 26 March and 21 May 1973 in Surinam, we discovered hair and bones of two-toed sloths and prehensile-tailed porcupines (*Coendou prehensilis*) captured by Harpy Eagles. The remains were scattered on the tops of fallen tree trunks, which suggested that kills, especially large prey, were more easily handled and eaten near the ground. In one case, different species remains were found on the same log indicating that the eagle fed more than once at that location.

To film a hunting sequence, we placed a 2.7-kg three-toed sloth in a tree near the nest site. We observed and photographed the remarkable maneuvers of the female when she captured the sloth. From 135 m away, she dropped from the perch, gained a speed of about 80 km/h with strong flapping flight, and about 2.5 m from the sloth turned sideways and thrust her talons fully forward to snatch it from the tree. Her flight carrying the sloth was somewhat labored, but she easily controlled it when she landed a short distance away. Because of her ability to fly with this animal and because of the weights of prey remains brought to the nest, we believe that the female could fly with prey or parts of prey weighing up to 4.0 kg.

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