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NESTING BIOLOGY AND BEHAVIOR OF THE MADAGASCAR HARRIER-HAWK (*POLYBOROIDES RADIATUS*) IN NORTHEASTERN MADAGASCAR

RUSSELL THORSTROM
The Peregrine Fund, 566 West Flying Hawk Lane, Boise, ID 83709 U.S.A.

GIUSEPPE LA MARCA
Via Plinio, 9, 20129-Milano, Italy

ABSTRACT.—We studied the endemic Madagascar Harrier-Hawk (*Polyboroides radiatus*) during the 1998 breeding season on Masoala Peninsula, northeastern Madagascar. One nesting pair was observed from courtship to 1 wk into the post-fledging period (September–January). Copulations started 25 d prior to egg laying and peaked 7 d before egg laying. Two eggs were laid and the female and male incubated for 61.6% and 35.5% of 189.8 hr of nest observations, respectively. Incubation lasted 39 d from laying to hatching of the first egg. Both eggs hatched but the second-hatched young died from siblicide at 7 d of age. The surviving young fledged at 50 d of age. Frogs (*Boophis* and *Platypelis* spp.), geckos (*Uroplatus* and *Homopholis* spp.) and nestling birds were the most numerous prey taken, representing 82% of 160 identified prey items.

KEY WORDS: *Madagascar Harrier-Hawk*; Polyboroides radiatus; *nesting biology*; *behavior*; *siblicide*; *food habits.*

Biologia de anidación y comportamiento de *Polyboroides radiatus* en el noreste de Madagascar

RESUMEN.—Estudiamos al endémico *Polyboroides radiatus* durante la estación reproductiva de 1998 en la Península de Masoala, noreste de Madagascar. Una pareja en anidación fue observada desde el cortejo hasta una semana después de que los pichones pudieron volar (Septiembre–Enero). Las cópulas comenzaron 25 días antes de la postura de huevos y su pico ocurrió 7 días antes de la postura. La nidada fue de dos huevos, la hembra y el macho incubaron el 61.6% y el 35.5% respectivamente de las 189.8 horas de observación en el nido. La incubación tuvo una duración de 39 días desde la postura hasta la eclosión del primer huevo. Los dos huevos eclosionaron, el segundo pichón fue eliminado por su hermano a los siete días de edad. El pichón sobreviviente pudo volar a los 50 dias de edad. Las ranas (*Boophis* y *Platypelis spp.*) geckos (*Uroplatus* y *Homopholis spp*) y pichones de aves fueron las presas mas abundantes representando el 82% de las 160 presas identificadas.

[Traducción de César Márquez]

Our knowledge of African tropical raptors, mainly from the southern subtropics, has increased in recent years but the raptors endemic to the western Indian Ocean islands are still poorly known (Virani and Watson 1998). During the last decade several studies have focused on Malagasy raptors (Thorstrom et al. 1995, René de Roland et al. 1996, Berkelman 1996, René de Roland in press, Thorstrom 1999, Thorstrom and René de Roland in press). The genus *Polyboroides* contains two species, the Africa Harrier-Hawk (*P. typhus*) which is confined to mainland Africa and the Madagascar Harrier-Hawk (*P. radiatus*) which occurs only on Madagascar. The latter species is common throughout Madagascar but has been little studied (Dee 1986, Langrand 1990, del Hoyo et al. 1994). Existing information comes mainly from incidental and anecdotal observations (Dee 1986, Milon et al. 1973) and data on food habits (Goodman and Pidgeon 1991, Karpanty and Goodman 1999), but little is known of its breeding biology (Langrand 1990, del Hoyo et al. 1994). Here, we report on the nesting biology of the Madagascar Harrier-Hawk in an undisturbed lowland tropical forest of northeastern Madagascar.

STUDY AREA AND METHODS

The west coast of the Masoala Peninsula is roadless and composed of a mosaic of slash-and-burn clearings, secondary growth and primary rain forests. The mature lowland rain forest of the Masoala Peninsula has a canopy

height near 30 m with emergent trees, high floristic diversity and steep mountainous topography (Guillaumet 1984). Elevations range from 0–1200 m. Average annual rainfall recorded at Andranobe Field Station (AFS) was 6049 mm from 1991–96 (range = 4468–7002 mm) (Thorstrom et al. 1997). Monsoon rains and cyclones occur between December and March, but rain falls steadily between April and August. September to November are the driest months receiving, on average, 481 mm (8%) of the annual rainfall recorded during 1991–96 (Thorstrom et al. 1997).

Daily observations were made at a harrier-hawk nest from 0500–1700 H, initially from the ground and later from a tree hide, with 10× binoculars from distances of 25–45 m. Observations from the hide were also made using a 16–48× spotting scope. Data collected included notes on adult and nestling behavior, nest attendance and identification of prey and provisioning rates. The length, breadth and depth of the nest were measured with a metric tape and nest height was measured with a plumb line from the nest to the ground. Nest tree height was estimated in meters above the nest height.

Egg volume was estimated from the equation $V = 0.51LB^2$, where L is the length and B the breadth of the egg (Hoyt 1979). The equation $(V_{largest} - V_{smallest}/V_{smallest})$ was used to calculate the percent difference in volume between the two eggs in the nest (Edwards and Collopy 1983).

RESULTS

The pair of Madagascar Harrier-Hawks nested in a tree near one of the main research trails, approximately 2.0 km north of AFS, from 1991–98 (Borge 1992). The nest was a large, stick structure approximately 18 m above the ground within the canopy and slightly below a ridge on a north facing slope. The pair fledged one young every year the nest was observed. In 1995, the nest tree fell down and the pair constructed a new nest 50 m northeast of the old nest site. In 1996, this nest measured 76 × 72 cm, with 7 cm interior and 47 cm exterior depths. Two other nests were located in 1998 25–30 km to the east of AFS. They had lengths and widths measuring 85 × 50 cm and 90 × 70 cm and interior depths of 5 and 9 cm and exterior depths of 45 and 46 cm. Nest heights were 30.8 and 31.9 m and nest tree heights were 33 and 36 m.

In 1998, we made observations totaling 677 hr from courtship (September) to the post-fledging period (January) at the nest nearest to AFS. We observed 203 items of nesting material delivered to the nest throughout the nesting period. Of them, 90 (44.3%) were delivered during courtship, 31 (15.3%) during incubation, 81 (39.9%) during the nestling period and 1 (0.5%) during the post-fledgling period. Green branches made up 89.7% (182) of the greenery delivered during the nesting period with dry branches making up the remaining 10.3% (21). The female contributed 79.8% (162) and the male 20.2% (41) of the greenery throughout the breeding period. Both the male and female were observed constructing the nest during all daylight hours (0500–1700 H), but most of the construction took place in the morning hours between 0600–1100 H; 82% of the nesting material was added to the nest before 1200 H. The female made the last delivery of greenery to the nest on 7 January 1999, two days after the young fledged from the nest tree.

We observed 167 prey items delivered by the male and female to the nest from courtship to the post-fledging period. The harrier-hawks had a broad diet delivering at least 15 different taxa during the nesting period. Prey was always carried and exchanged at the foot of the nest by the male to the female. Of these, 160 were identified at least to class level. Frogs (*Boophis* and *Platypelis* spp.) totaled 31.3% (50), lizards (*Uroplatus* and *Homopholis* spp.) 23.8% (38), birds (*Otus rutilus and Coua spp.*), mainly nestlings (*Phyllastrephus* spp. and *Coua* spp.), 26.9% (43), and rodents (*Eliurus* spp. and *Rattus* spp.) and lemurs (*Lepilemur mustelinus* and *Microcebus* spp.) 17.5% (28) of the identified prey items. Of interest was the occurrence of 7 lemurs delivered during the nestling period by both the male and female. Nestling birds accounted for 86% of the 43 avian prey items delivered during the nestling period. The male delivered 131 prey items from courtship to the post-fledging period and the female delivered 36 prey items from the beginning of incubation to the post-fledging period.

We observed the pair for 152.4 hr during the courtship period which lasted from the first week of September to 7 October 1998. During this period, the female made 64 deliveries of nesting material consisting of 57 green sprigs and 7 dead branches. The male delivered 24 green sprigs and 3 dead branches. We observed 80 copulations during the 4-wk courtship period. The earliest copulation was on 13 September 1998, 25 d before egg laying, and copulations were most frequent 7 d before egg laying on 1 October 1998. On that day, we observed the pair copulate eight times during a 10.5 hr nest observation period. A total of 76 copulations totaling 1634 sec was observed for an average copulation time of 21.5 sec (range = 10.5–34.0 sec). The duration of copulations gradually increased from 13.0 sec 25 d prior to egg laying to

34.0 sec 5 d prior to egg laying and subsequently tapered off with no copulations were observed after the first egg was laid. Copulations occurred at the nest and on perches of the nest tree and nearby trees. During copulations both sexes exhibited the red facial flushing described by Thurow and Black (1981) for the African Harrier-Hawk. Both sexes gave a high, shrill call during copulations. We observed the male feed the female 24 prey items. Fifty percent (12) were frogs, 12.5% (3) lizards, 12.5% (3) rodents, 8.33% (2) birds, 4.17% (1) snake and 12.5% (3) unidentified items.

In 1994 and 1996, 2 two-egg clutches were measured and weighed. In 1994, the first egg weighed 46.0 g and measured 57.0 × 42.3 mm and the second egg weighed 47.0 g and measured 54.4 × 41.2 mm. In 1996, the first egg weighed 48.0 g and measured 49.6 × 38.8 and the second egg weighed 59.0 g and measured 54.5 × 41.6 mm. The percent difference in volume between the two eggs in 1994 was 10.5% and in 1996 was 26.1% ($\bar{x}$ = 18.4% ± 0.05, ±1SE). The eggs were buff, marbled and spotted with reddish-brown

Nest observations totaled 189.8 hr during incubation, from 8 October–16 November. One egg was laid on 8 October and the second egg was laid between 10–12 October. The female delivered greenery to the nest 18 times (17 green and 1 dry) and the male 13 times (all green branches) during the incubation period. During incubation, the male delivered 23 prey items to the female, of which 82.6% (19) were frogs. The female also brought a lizard to the nest that she ate herself after an incubation exchange with the male. The total incubation time for the female and male was 116.8 (61.5%) and 67.6 (35.6%) hr, respectively and both adults were absent from the nest for only 2.9% (5.3 hr) of the time during incubation. The incubation period from laying to hatching of the first-laid egg was 39 d.

Nest observations totaled 294.7 hr during the nestling period from 16 November 1998, when we observed the first hatched nestling at 0719 H, to 5 January 1999. We documented asynchronous hatching with at least a 2-d interval between hatching of the first and second eggs. The second egg hatched on 18 November 1998. From 18–25 November, we observed the oldest young strike the younger nestling 822 times with its beak, eventually leading to its death on 25 November at 7 d of age. During the one week period of 18–25 November, the female was observed feeding the oldest young 519 pieces of food while the younger nestling received only 59 pieces. After the younger nestling died in the nest, the female ate most of it and fed some to the surviving nestling.

The female was the sole attendant at the nest during the nestling period and she brooded the nestling, fed it and delivered greenery 76 times (66 green sprigs and 10 dry branches). The female also delivered 28 prey items consisting of 14 (50%) geckos (*Uroplatus* spp. and *Homopholis* spp.), 5 (18%) birds, 4 (14%) frogs, 3 (11%) lemurs and 2 (7%) rats. During this period, the male only delivered prey to the female and nestling. The female always vocalized a high "pe-ee-ee-ee" (Langrand 1990) at the nest or near the nest as the male arrived with food. The male delivered greenery only once. The male delivered 80 prey items that consisted of 33 (41%) birds, 15 (19%) rodents, 14 (18%) lizards, 12 (15%) frogs, 4 (5%) lemurs and 2 (2.5%) unidentified items. The young fledged on 5 January 1999, at 50 d of age.

We observed the young for 40.4 hr during the post-fledging period from 6–14 January. During this period, the female delivered 1 green branch and spent 2.9% of the time at the nest. The female delivered 7 prey items consisting of 5 geckos, 1 frog and 1 unidentified item. The male delivered 2 frogs, 1 gecko and 1 unidentified item during this period.

DISCUSSION

The Madagascar Harrier-Hawk occurs throughout Madagascar, except on the high plateau. Despite the fact that it is the fourth most common raptor on the island (Langrand and Meyburg 1984), it has not been studied in great detail. Thorstrom and Watson (1997) found the Madagascar Harrier-Hawk at seven of eight avian inventory sites throughout the Masoala Peninsula confirming its widespread occurrence in the rainforest of this region.

For diurnal raptors in general, nest building takes place in the morning and males are mainly responsible for nest construction (Newton 1979). Our results showed that harrier-hawks added most nesting material to the nest before 1200 H but the female was the main nest builder.

Thurow and Black (1981) reported that breeding activity of African Harrier-Hawks in South Africa begins in late spring before summer rains begin. Tarboton and Allan (1984) were more specific indicating that hatching coincides with peak pro-

duction of passerine nestlings from October to December. Breeding activity of the Madagascar Harrier-Hawk was similar beginning in August and ending in January (Tarboton 1978). Nestlings hatched during November when conditions were at their driest and most passerines were breeding, and fledging occurred during January when the rainy season had begun.

The three nests of the Madagascar Harrier-Hawk we studied were similar but averaged slightly larger (75 cm in diameter × 20 cm wide) and higher (10.3 m) than nests described by Tarboton and Allan (1984) for the African Harrier-Hawk. Similar to the Transvaal region where many nests were used in consecutive years, the pair of harrier-hawks we observed occupied one nest site from 1991–95 and a newly constructed site from 1996–98.

Madagascar Harrier-Hawks broke off branches within a 20–50 m radius of the nest tree. After delivering greenery to the nest, they frequently cut off the leaves and placed them in the nest bowl and then positioned the leafless branch to the exterior to form a nest rim. Green branches appeared to be preferred over dry branches, perhaps because they offered both material for constructing the nest and fresh leaves for lining the nest bowl. Perhaps, the greenery provides insulation and protection for eggs and nestlings, and positioning of twigs in a nest rim creates a border for maintaining them in the center of the nest.

At 7 d before egg laying, we observed the highest frequency (8 times) of copulations during a nest observation period and the average copulation time gradually increased to the longest duration 5 d prior to egg laying. Based on our observations, we suspect that the optimum time for insemination of harrier-hawks occurs from 5–7 d before egg laying. Optimum inseminations for a captive Northern Goshawk (*Accipiter gentilis*) via artificial insemination occurred 4 d before the first egg (Berry 1972). Thurow and Black (1981) observed one pair still copulating after egg laying and until the nestling was 8 d of age. In this pair of Madagascar Harrier-Hawks, no copulations were observed after egg laying.

Siblicide has been documented for some marine birds (Proctor 1975, Anderson 1990) and large eagles, including the Madagascar Fish Eagle (*Haliaeetus vociferoides*), with a clutch size of two eggs (Meyburg 1974, Edwards and Collopy 1983, Gargett 1993, Watson et al. 1996). It has been documented for only a few smaller birds of prey that lay two eggs, e.g., the American Swallow-tailed Kite (*Elanoides forficatus*) in the northern Neotropics (Gerhardt et al. 1997), the Augur Buzzard (*Buteo augur*) in mainland Africa (Gargett 1970) and the African Harrier-Hawk (Tarboton et al. 1990, del Hoyo et al. 1994). Tarboton and Allan (1984) recorded 10 2-egg clutches of the African Harrier-Hawk in Transvaal but seven nests contained only one young. A 2-egg clutch was documented at the study nest of the harrier-hawk and we suspected that siblicide occurred at 8 other harrier-hawk nests observed from 1991–98.

Edwards and Collopy (1983) described two types of siblicide, obligate and facultative, in large eagles with asychronous hatching and a high percentage of volume difference within two-egg clutches (>10%). In a species with obligate siblicide, the second young to hatch always dies, e.g., *Aquila pomarina, A. verreauxii* and *Stephanoaetus coronatus* (Edwards and Collopy 1983). In facultative siblicide species, the second-hatched young sometimes dies, usually during food restriction, and egg volume difference is <10%, e.g, *A. chrysaetos, A. audax, A. rapax, A. clanga, Hieraaetus fasciatus, H. pennatus,* and *Haliaeetus leucocephalus.* The African Harrier-Hawk appears to exhibit faculative siblicide (Tarboton et al. 1990). We feel that the Madagascar Harrier-Hawk may be more like the Swallow-tailed Kite (Gerhardt et al. 1997) and Augur Buzzard (Gargett 1970) and has obligate sublicide. The mean egg volume of 18.4% for the Madagascar Harrier-Hawk fell into the category associated with the large obligate siblicide eagles (Edwards and Collopy 1983).

We found the Madagascar Harrier-Hawk to have similar reproductive parameters to the African Harrier-Hawk, with an incubation period of 39 d compared to 35–36 d, a nestling period of 50 d compared to 45–55 d and occurrence of siblicide, though two young may sometimes fledge (Tarboton and Allan 1984, Tarboton et al. 1990, and del Hoyo et al. 1994).

Previous information reported on food habits of the Madagascar Harrier-Hawk comes from Rand (1936), who found carrion (*Tenrec ecaudatus*), spider, insects, locusts, frog, lizards, snake and a small mammal (*Mus musculus*) in the diet. Recently, in the dry climate of extreme southeastern Madagascar, Goodman and Pidgeon (1991) documented the harrier-hawk preying on flying foxes (*Pteropus rufus*) and Karpanty and Goodman (1999) documented it feeding on adult and infant Verreaux's

Sifaka (*Propithecus verreauxi*) during the courtship period. In the courtship period of September 1997, we observed one partially eaten dwarf lemur (*Cheirogaleus major*) lying at the base of the nest tree and, during nest observations, we documented lemurs (*Microcebus* and *Lepilemur*) in the diet only in the nestling period. Frogs were the predominant prey type during the courtship and incubation periods while nestling birds were the major prey types taken during the nestling period. In 85 prey items of the African Harrier-Hawk, nestling birds composed 31% of them (Thurow and Black 1981).

The high percentage of nestling birds, Scops Owls (*Otus rutilus*), nocturnal geckos and frogs in the diet may be explained by the unique foraging strategy used by Madagascar Harrier-Hawks. They have an unusual morphological adaptation, an intertarsal joint that permits them to flex their legs backward, as well as forward (Burton 1978), which allows them to use their feet to probe and extract prey from crevices, holes in trees, rotting trunks and epiphytes. Such an adaptation may enable harrier-hawks to extract nestling birds from difficult-to-reach places. We had only one piece of evidence indicating that these harrier-hawks robbed bird nests. It occurred when the male arrived at the nest with a very small nestling bird and egg shell fragments stuck to its face. Further evidence on nestling predation occurred when René de Roland et al. (1996) observed Madagascar Harrier-Hawks feeding on nestling Henst's Goshawks (*Accipiter henstii*) on two occasions.

In the dry southeastern part of Madagascar, Karpanty and Goodman (1999) found two pairs of harrier-hawks feeding mainly on mammals and birds, thus differing from our observations in the rainforest where they fed predominately on frogs and birds. Our study occurred in the wettest region of Madagascar, the northeastern coastal rainforest, and although it was based on observations at only one nest, it concurred with Karpanty and Goodman (1999) in showing that the Madagascar Harrier-Hawk is a generalist and its diet can vary between regions within Madagascar.

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