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Breeding and foraging behaviour and habitat characteristics of the Scaly Ground-roller *Geobiastes squamigerus* in Madagascar

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The endemic Scaly Ground-roller *Geobiastes squamigerus* was studied during two breeding seasons from October 1997 to January 1999 in Masoala National Park, Madagascar. Several vocalisations were associated with territorial defence, contact, excitement, and aggressiveness towards intruding conspecifics. Of the 269 prey items observed, 71.5% were invertebrates, 7.5% vertebrates, and 21.0% unidentified. Earthworms and centipedes represented the most numerous prey-types taken, representing 55% and 21% of the identified prey, respectively. Three nests were located in valleys and near streams. Nests were placed in ground burrows with tunnels that measured less than 10cm in diameter and less than 1m in depth. A single egg clutch was laid in each nest, and incubation and the nestling periods lasted 18 days and 24 days, respectively. Nesting began in late October, and one young from each nest successfully fledged in mid-December. Only the female incubated and brooded the young. Both male and female provided food for the nestling, and feeding rates did not differ between the sexes. Nesting habitat differed significantly from random plots sampled. Herbaceous coverage density was higher in nesting areas than random plots.

Introduction

The Scaly Ground-roller *Geobiastes squamigerus* (*sensu* Kirchman *et al.* 2001) is a burrow-nesting species (Benson *et al.* 1976, Goodman 1994) whose range extends from the north to the centre of the eastern rain forest of Madagascar (Langrand 1990). It belongs to the endemic family of Brachypteraciidae and was formerly placed in the genus *Brachypteracias* until a recent phylogenetic study of the family (Kirchman *et al.* 2001). The Scaly Ground-roller is categorised as vulnerable (a taxon facing a high risk of extinction in the wild in the medium-term future) in the recently updated Red Data List (Collar *et al.* 1994). The species is known to inhabit undisturbed evergreen primary rain forest with a preference for relatively dark undergrowth that offers fairly low herbaceous vegetation and a carpet of dead leaves and branches (Langrand 1990). Little information is available on its behavioural ecology and breeding biology and this paper presents the first systematic study of this species.

Methods and study area

Scaly Ground-rollers were studied during two breeding seasons, covering the periods October 1997 to January 1998 and October 1998 to January 1999, in the Masoala National Park, northeastern Madagascar. The study was conducted at two sites, both below 600m above sea-level. The first site was situated near Andranobe Field Station (AFS) on the west coast of the Masoala Peninsula (15°41'S, 49°57'E). The second site, also on the peninsula, was 3km east and up slope from the village of Ambanizana, 7km north of the AFS. The peninsula is road less and composed of a mosaic of slash-and-burn clearings, secondary growth, and largely intact forests. The mature lowland rain forest of the Masoala Peninsula has a canopy height less than 30m with few emergent trees, high floristic diversity, and steep mountainous topography (Guillaumet 1984), and elevations range from 0–1 200m. Average rainfall recorded at AFS from 1992–1996 was 6 049mm (Thorstrom *et al.* 1997), making it one of the wettest regions on the island. Monsoon rains and cyclones occur between December and April (Donque 1972). September through November is normally the driest period of the year. Annual temperatures vary from a low of 18°C to a high of 33°C.

We located Scaly Ground-rollers by their calls. Vocalisations were recorded and analysed with Spectrogram 3.2.1 software (Horne 1994). Behaviours associated with the call were noted for further identification of each call type. We captured adults with mist nets (2.6m x 12.2m, 36mm mesh) installed near nests or where pairs had often been encountered. Captured ground-rollers were measured with vernier calipers (nearest 1.0mm), weighed with Pesola 300g spring scale (nearest 1.0g), and fitted with coloured plastic rings. Morphological measurements include bill length taken from the end of feathering on the top mid-line to the tip (Palmer 1962); unflattened wing chord taken from the front of the folded wrist to the tip of the longest primary (Biggs *et al.* 1978); tarsus length taken from the posterior centre of the tibiotarsal-tarsometatarsal joint to the dorsal base of the centre toe (Biggs *et al.* 1978); and tail length taken from the point of insertion of the central feather to the tip.

Scaly Ground-roller nests were located in two ways.

First, in order to solicit response from breeding adults, we played tape recordings of their calls. We followed adults to the presumed nest areas and searched for potential nest sites. We then monitored potential burrows and recorded observations of Scaly Ground-roller nesting activities at these sites. Second, we attached a 2.1g back-mounted transmitter (Holohil Systems Ltd, Canada) to a captured adult and monitored its movements and behaviours prior to the nesting activities. The transmitter weighed less than 3% of the weight of the individual and lasted two weeks. The nesting behaviour of Scaly Ground-rollers was observed from blinds or other camouflaged locations at about 30m from nest. Observations were made using 10 x 40 binoculars and data were recorded in a continuous written log that included the time of day, frequency, and duration of their nesting activities at and around nest sites.

We recorded data for each pair using the coloured plastic rings and assigned sex based on behaviour during the nesting period. As only one individual was seen to perform all the incubation duties and brooding in each pair, we assumed that individual was the female.

For nesting phenology, egg laying was assumed to have occurred and incubation began when the female started to spend more than three hours a day in the nest. Hatching was assumed to have occurred inside and brooding begun when the male started to deliver prey to the nest while the female remained inside. Nests were checked about every 10 days to follow the development of the young. Prey items fed to the nestling by adults were visually identified and sizes estimated. Nest chambers were excavated and measured the following breeding season after confirmation that they had been abandoned.

Several parameters were considered within an area of 100m^2 around the nest to characterise the site. Saplings and herbaceous coverage were categorised into ranges of size. Data recorded included herbaceous coverage density, tree density, and distance from water, slope, and canopy density. The same parameters were measured on 10 randomly sampled plots of 100m^2 within the same forest blocks. Location of the plots (distance from the nest, direction and angle) was determined by randomly drawing numbers in a bag containing numbered papers. We then compared nest sites with random plots in order to detect any unique characteristics of the nest site.

Data referring to nest site characteristics were first tested for normality using the Shapiro-Wilk test (Shapiro and Wilk 1965). All variables except number of tree species, distance from water, and distance from valley bottom were normally distributed. The Student's t-test was used to compare nest sites and random plots for herbaceous vegetation, sapling density, tree density, slope of the nest, slope of the site, number of liana, ferns, tree height, tree diameter at breast height (dbh), and foliage density. The Wilcoxon two sample test (Sokal and Rohlf 1995) was used for number of tree species, distance from water, and distance from valley. We used the sequential Bonferonni correction (Sokal and Rohlf 1995) to adjust the rejection criteria of the analyses in order to decrease the probability of making a type I error, as some of the comparisons were not totally independent. All the analyses were done with the SAS package (SAS 2001).

Results

We located three nests for which observation time totalled 483h, with an average of 10h ± SD of 1.8h per day in 1997 (n = 22 days), and 7h ± SD of 1.3h per day in 1998 (n = 39 days).

Vocalisations

Several vocalisations were identified. These calls were associated with different behaviours. Territorial calls were represented by a sequence of '*whoop*' notes that were uttered with various frequencies according to circumstances. Frequency of notes (number of notes per time unit) was seen to increase when two neighbouring birds were in close proximity to each other while defending their respective territories (from 7–10 call min^{-1}, duration = 22min). Most territorial calls were given early in the morning (05h00–06h00) and late in the afternoon (16h00–17h00) (Figure 1). Territorial calls were broadcast from perches with an average height of 1.2m (range 0.8–2m) and diameter of 2.5cm (range 1–4cm, n = 5 perches).

A second type of vocalisation, the contact call, was associated with communication between a pair as they moved through the forest. The call consisted of a hollow single and deep '*whoop*' note similar to the territorial call. Spectrogram analyses of the territorial and contact calls showed a difference between them in frequency and duration of notes. Territorial call notes had a seemingly higher frequency (mean = 43.23kHz, SD = 0.04kHz, n = 10 notes) and lasted a shorter period of time (mean = 312.9ms, SD = 67.8ms, n = 10 notes) than the contact call (25.73kHz, 372ms, n = 1 call).

A third type of vocalisation, a sharp, harsh '*kwek*' alarm call was made when the bird became excited (e.g. during prey capture) or when threatened (e.g. when trapped in mist

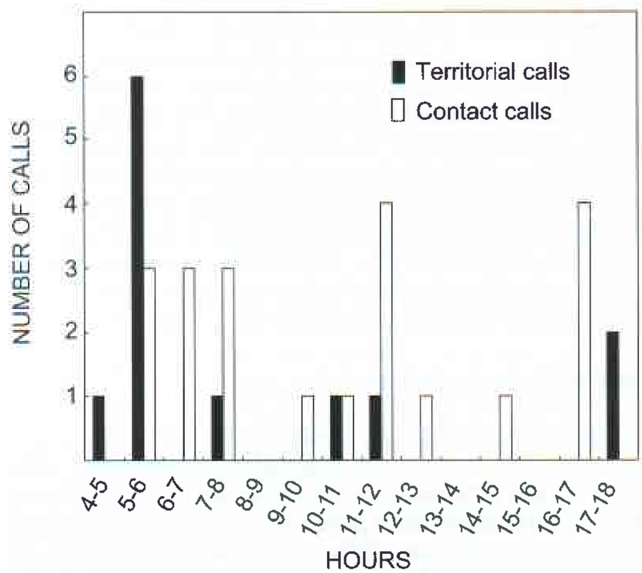

Figure 1: Periodicity of two call types made by Scaly Ground-rollers during two breeding seasons on the Masoala Peninsula, Madagascar

nets). This call is similar to that described by Langrand (1990). A fourth type of call was made when the bird was threatened and consisted of a sharp raspy hissing *kwish-sh* accompanied by spreading its tail, fluffing its feathers and facing the observer. This call was made when the bird was upset (e.g. in the presence of a human in close proximity) or startled (e.g. during an encounter when a pair of birds were with their young) and was presumably intended to intimidate or distract the intruder.

Measurements

Six individuals were trapped, measured and weighted (Table 1). Trapped paired birds appeared to be sexually dimorphic with males being larger than females (mean wing length: male 125.5mm, female 118.5mm; mean weight: male 155g, female 137.5g, n = 2 males and 2 females). For the third pair, the sex of each individual could not be determined because nesting behaviour was not observed due to the late discovery of the nest.

Feeding and foraging behaviour

We made 483h of observations during the period when nestlings were being fed at three nests. There was no significant difference in feeding rates of nestling by adult males and females of each pair (t-test, P = 0.35, n = 18 days for pair 1; P = 0.16, n = 16 days for pair 2). Of the 269 prey items observed, 71.5% were invertebrates, 7.5% vertebrates, and 21.0% unidentified. Disregarding the unidentified prey category, earthworms (*Pheretima* sp.) (54.7%) and centipedes (*Scolopendra morsitons*) (20.9%) made up the most numerous prey taken (Table 2). An average of 12 prey items per day (range 9–20, n = 34 days) was delivered to the nestling in each nest. Prey items had a mean length of 6cm (range 2–30cm, n = 269). Prey taken exclusively on the ground represents 80.3% of the items observed. Scaly Ground-rollers use their beak to dig and overturn leaf litter when searching for food. While digging, they use their beak to toss the soil and ground cover debris aside and pick up the food items. Foraging strategies seemed to be based mainly on the detection of noise and movement. A foraging ground-roller would remain in one place for some seconds slightly inclining its head, listening and checking carefully for movement. Upon location of a prey item, the bird would quickly hop forward, cocking the head for capture, and would dispatch the prey with a flick of the head if the latter tried to resist.

Habitat use

Scaly Ground-rollers were observed on the ground during nearly all of its main activities and occasionally on low perches while calling or resting. On several occasions, the study pairs were seen foraging in valley bottoms with creek drainages and from time to time on valley ridges. No intensive use of trees was recorded during this study. Trees were used only as roosts (n = 2 observations), as perches from which territorial calls were vocalised (n = 7 observations), and finally as resting perches (n = 5 observations).

The radio tagged individual was located twice at two different night roost sites that were above the ground. The first roost was a small and slightly inclined branch (15° from horizontal) situated 0.27m from the centre of the tree, 2.5cm in diameter, and 3.13m above the ground. The roost site was a

Table 1: Measurements of six individuals of Scaly Ground-rollers from this study

		Bill length (mm)	Wing length (mm)	Tarsus length (mm)	Tail length (mm)	Mass (g)
Pair 1	male	31.2	124	47.4	120	165
	female	30	120	49.6	90.2	140
Pair 2	male	34.2	124	51	98.2	145
	female	29.6	116	49	93.5	135
Pair 3	Unknown	31.3	118.7	45.1	95.2	158
	Unknown	28	115	48.2	95	128

Table 2: Prey observed delivered to nests by Scaly Ground-rollers from 1997 to 1999 (n = 269 prey items, n = 3 pairs)

Prey type (Class, Order, Family or Genus)	1997 Number (%)	1998 Number (%)	Average Number (%)	Mean Size (cm)	Others (prey capture location, proportion)
Earthworm (*Pheretima* sp., Megascoleidae)	34 (32.6)	83 (76.8)	117 (55.4)	7.5	Ground
Centipede (*Scolopendra morsitons*, Myriapodes)	37 (35.5)	7 (6.3)	44 (20.8)	7.0	Ground
Insects	16 (15.5)	9 (8.3)	25 (11.8)	3.0	25% Coleoptera 19% Hymenoptera 19% Lepidoptera 37% Unidentified
Larva	4 (3.8)	4 (3.7)	8 (3.7)	2.5	Ground or rotten tree trunk
Frog	3 (2.8)	4 (3.7)	7 (3.2)	5.0	Ground
Spider	4 (3.8)	0 (0)	4 (1.9)	2.0	Between branches
Lizard (*Zonosaurus* sp., *Phelsuma* sp.)	3 (2.8)	0 (0)	3 (1.4)	3.5	Tree trunk or ground
Millipede (Diplopoda)	1 (0.9)	1 (0,9)	1 (0.9)	4.5	Ground
Shrew tenrec (*Microgale* sp., Tenrecidae)	1 (0.9)	0 (0)	1 (0.4)	6.5	Ground
Snail (*Sphaeroterium* sp., Gastropoda)	1 (0.9)	0 (0)	1 (0.4)	2 (diameter)	Tree trunk or ground

small tree of 6cm dbh, 70% foliage density, and 4.2m in height. The second roost site was a liana situated 6.5m off ground. Both roost sites were located near valley bottoms and within 20m of water on a slightly inclined slope.

Breeding cycle

Courtship behaviour and nest building

Courtship feedings were observed. On one occasion, the male caught a 7cm earthworm and gave a contact call. The female responded three times with the same call, then approached, and took the prey from the male's beak. The male allopreened the female's head for a few seconds, and then they separated.

We did not observe any nest excavation or indication of reuse of other animal burrows for nest during this study. During incidental encounters, an individual accompanied by its mate was seen carrying dead leaves, probably to its nest, which suggested that both sexes participated in the preparation of the nest. Dead leaves were a major component of the nest lining. Neither dust nor piles of dirt were seen around the nest entrance before the nesting period.

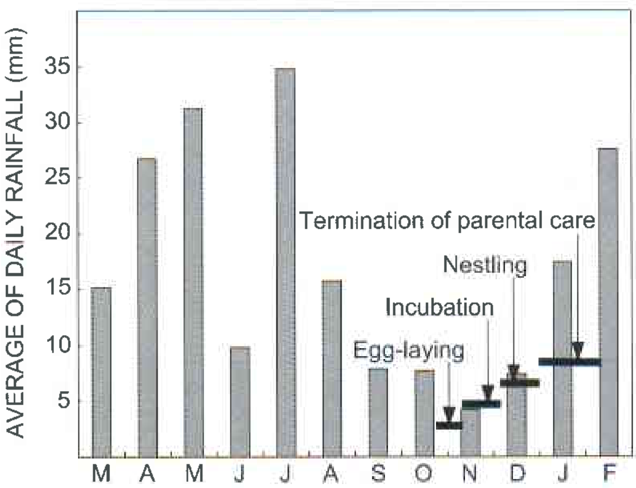

Figure 2: Breeding phenology of the study pairs of Scaly Ground-rollers plotted with average daily rainfall data obtained from 1997 to 1998 in AFS, Masoala Peninsula

Nest description

Nest burrows were located in the ground, in close proximity to water, on either flat or inclined valley bottoms. Nests consisted of tunnels that measured 8.8cm in diameter (range 6.5–10cm) and 62.5cm in depth (range 57–77cm, n = 3) (Table 3). The entrance tunnels were angled and it was impossible to see into the nesting cavity from outside the entrance. The posterior end of the tunnel was wide and formed the nesting chamber. Distance between two neighbouring nests was 230m and distance between nests that belonged to the same pair during two successive breeding seasons was 50m (n = 1 pair).

Egg-laying, incubation, and hatching

Egg-laying occurred from mid-October to early November (Figure 2). On one occasion, a distinct behaviour was observed when both the male and female remained within 40m of the nest and vocalised excitedly. Shortly afterwards, they moved towards the nest, and the female entered the nest (duration: 12min) while the male remained nearby and continued to call almost continuously. Both individuals then left the nesting area and moved towards their roosting site. The complete behavioural sequence commenced at 15h00 and lasted 25min. This behaviour might be associated with egg laying given its date of occurrence and circumstances.

Only a single whitish egg was observed in each nest. Reconstitution of a Scaly Ground-roller eggshell showed that egg dimensions were 45mm x 30mm.

We made 128h of observation during the incubation periods that lasted 18 days. Based on our observations, the females performed all the incubation duties and spent the night in the nest. No prey deliveries were observed during the incubation period.

Hatching occurred around mid-November (Figure 2). The female stayed in the nest almost all the time during the brooding period, which lasted 7 days. However, on one occasion, the female was observed to leave the nest during the fifth day of the brooding period (duration female-off nest: 2h 10min) and brought food to the nestling. During the brooding period, the male would visit the nest and bring food at an average rate of 21 prey items a day (range 16–23, n = 4 days). Prey deliveries recorded during the nestling period (day 7 post-hatching to fledgling) averaged 12 items a day (n = 15 days). Disparity in prey delivery rates recorded dur-

Table 3: Nest and nest site characteristics of three breeding pairs of Scaly Ground-rollers from 1997 to 1999

Parameters		Pair 1	Pair 2	Pair 3	Mean
Nest entrance diameter (cm)		10.00	10.00	6.50	8.80
Depth from nest entrance (cm)		68.00	57.00	77.00	62.50
Vertical distance between nest entrance and receptacle (cm)		42.00	37.50	55.00	44.80
Receptacle Dimensions	Height (cm)	12.00	11.00	11.50	11.50
	Length (cm)	26.00	23.00	22.00	23.70
	Width (cm)	22.00	20.00	17.50	19.80
Slope of the ground (°)		38.00	59.00	45.00	47.30
Slope at the nest entrance (°)		8.00	6.00	12.00	8.70
Foliage density (%)		32.00	67.00	93.24	64.10
Distance from the flat valley bottoms (m)		20.00	0.00	63.00	27.70
Distance from water (m)		53.00	49.00	61.00	54.30
Distance from the nearest human disturbance (km)		1.73	1.50	1.78	1.67

Table 4: Statistical comparisons conducted on nest sites and random plots

Parameters	Statistical tests	Results	Significance ($\alpha' = 0.05/k_i$)
Herbaceous coverage density (height ≤50cm)	Student t-test	P = 0.0023	*** ($\alpha' = 0.0055$)
Saplings density (height >50cm and dbh <2.5cm)	Student t-test	P = 0.0008	*** ($\alpha' = 0.0041$)
Tree density	Student t-test	P = 0.30	Non-significant
Number of species	Wilcoxon two sample test	P = 0.10	Non-significant
Tree height	Student t-test	P = 0.89	Non-significant
dbh	Student t-test	P = 0.64	Non-significant
Foliage density	Student t-test	P = 0.0020	*** ($\alpha' = 0.0045$)
Slope/nest	Student t-test	P = 0.0001	**** ($\alpha' = 0.0038$)
Slope/ground	Student t-test	P = 0.026	Non-significant
Distance from water	Wilcoxon two sample test	P = 0.01	Non-significant ($\alpha' = 0.0062$)
Distance from valley bottoms	Wilcoxon two sample test	P = 0.30	Non-significant
Number of liana	Student t-test	P = 0.09	Non-significant
Number of ferns	Student t-test	P = 0.41	Non-significant

* Level of significance

Figure 3: Photo of a nestling at 21 days old (three days before fledgling). The nestling travelled up to the nest entrance gaping for food after we imitated the female's call

ing brooding and nestling periods probably relates to the provisioning of the female during the brooding period.

Development of young and fledgling period

At the end of the brooding period, nestlings had almost acquired their full subadult plumage and were able to move to the nest entrance to receive food. Young fledged 24 days after the date of hatching and definitely left the nest (Figure 3). Thereafter, the nest site entrance was covered, filled, and hidden with dead leaves and sticks (n = 3 nests).

The female always stayed with the young during the first post-fledgling week whereas the male often left the family group for a variable amount of time (mean duration: 25min, range 15–40min, n = 3). Parental care of fledglings appeared to cease at 60 days of age.

Nest sites' characteristics

Statistical analyses showed that nest sites are mainly characterised by a higher herbaceous cover and sapling density, a lower foliage density, and a less inclined slope at the nest entrance as compared to randomly placed study plots (Table 4). However, herbaceous cover was not uniformly distributed within the nest site, as at least 16m^2 around each nest entrance had open understory (n = 3 nests).

Discussion

The Scaly Ground-roller appeared to be very common in the study sites located below 600m above sea level. Eight pairs were located within an area of approximately 100ha around AFS, and four pairs in Ambanizana. Thorstrom and Watson (1997) reported that the species was detected in all but one of the eight sites visited in Masoala Peninsula. The site where it was not detected was in Ambohitsitondroina Ambanizana (15°34'S, 50°00'E), located to the east of the village of Ambanizana. In contrast to other areas surveyed, Ambohitsitondroina is an area characterised by mid to high-elevation moist montane forest (600–1 000m). These observations suggested the species might be more common in sites at lower elevations. Such sites would have a certain level of human disturbance due to their easy accessibility. But as shown by this study, Scaly Ground-rollers may not require completely intact forests because trees were used only for roosting and perching; nests were on the ground, and prey items taken on tree trunks represented only 2% of the prey captures observed. Moreover, we had incidental observations of the species from *tavy* (cleared areas for swidden agriculture) and secondary growth. Therefore, the Scaly Ground-roller is not restricted to primary forests, and this species may be more adaptable to or tolerant of forest degradation and alteration than previously suspected.

The exact dates of nest building (excavation) and reuse of nests need further study. Although the study pairs were not observed in nest building activities, nest dimensions suggest this activity could last several weeks. Observations in Mananara (pers. obs.), a site located about 50km south of AFS, suggested nest building may even occur several months before the breeding season as a pair was seen twice on 14 and 16 March 1999 digging a fresh hole, probably its nest for the upcoming breeding season. Another suggestion is that the species may use pre-existing animals' ground burrows that need only to be enlarged. Such burrows are very common in the study sites and are made by terrestrial crabs (*Sesarma* sp.). The case of cohabitation between the rodent *Eliurus webbi* (Nesomyinae) and Scaly Ground-roller in a ground burrow reported by Goodman (1994) supports this hypothesis. Nest entrances were always covered and filled with dead leaves and sticks at the end of the nesting period. This behaviour was intended to hide the burrow entrance and possibly retain the nesting site for the following breeding season. However, no nest reuse was observed during this study. Moreover, dead leaves that had been brought into the nest to protect the egg and insulate the nestling probably decayed the following year and may have prevented any nest reuse. Further investigations based on a long-term study and a larger sample size is needed to verify these observations.

The Scaly Ground-roller is a terrestrial species that feeds chiefly on earthworms and centipedes. Prey items observed in this study were based mainly on food delivered to the nestlings. This study and previous findings (Langrand 1990, Thompson and Evans 1992, Thorstrom and Watson 1997) suggest the ground-roller might show a preference for earthworms. Langrand (1990) reported the species feeds rarely on vertebrates. However, our observations showed a relatively important proportion of vertebrate prey items (9.1%) taken by the species. It was seen feeding on a large shrew tenrec, perhaps *Microgale talazaci*, plated-lizard *Zonosaurus* sp., and the day gecko *Phelsuma* sp.

Observations in other sites of the Masoala Peninsula indicated the Scaly Ground-roller was observed on several occasions feeding on dwarf chameleons *Brookesia* sp. (Thorstrom and Watson 1997). Powzyk (1995) also reported that the species was seen feeding on a baby *Rattus* sp. in Mantadia.

All foraging was from the ground. This species rarely flew. Occasional flights were associated with river and creek crossings and entering and exiting the nest sites, which may have been to avoid leading potential predators to the nest sites. Flights were short in duration, low, and noisy (mean distance 11m ranging from 7–18m, n = 16).

No territorial calls were made around the immediate nest vicinity though pairs were extremely vocal shortly before the beginning of their nesting activities. This lack of activity near the nest was probably to avoid attracting predators. No case of egg or nestling predation in the nest was recorded during this study. Potential predators would include the Ring-tailed Mongoose *Galidia elegans* and the Brown-tailed Mongoose *Salanoia concolor*, which are common in the area.

Scaly Ground-roller and Short-legged Ground-roller *Brachypteracias leptosomus* are two sympatric species that belong to the family of Brachypteraciidae and are found in the Masoala Peninsula. The Short-legged Ground-roller is an arboreal species that nests in tall trees and forages mainly under the canopy level with an average height above ground for prey capture of 6.1m + 4.0 (range 0–18, n = 69) (Thorstrom and Lind 1999). On the other hand, the Scaly Ground-roller is a terrestrial species that nests and forages mainly on the ground (80.3% of prey were taken from this substrate). Consequently, difference in vertical use of the same habitat allows these two sympatric species to coexist and to avoid competition, an adaptation that would allow the coexistence of morphologically similar birds (e.g. Pimm and Pimm 1982, Nudds *et al.* 1994). Further, the lack of intensive use of trees by Scaly Ground-rollers allows the latter to tolerate a certain level of human habitat disturbance.

Rainfall was the most influential factor to explain the start of the nesting season. Nest site characteristics such as foliage density at and above the nest entrance made burrows more exposed to flooding during heavy rains. September through November are the driest months in this region and nesting activities coincide with this dry period. Low rainfall during this period would facilitate finding dry and dead leaves for the incubation, and food for the nestling assuming that a high rainfall might decrease their foraging efficiency.

Herbaceous cover and sapling density, foliage density, and slope at nest entrance are the variables that differed between nest sites and the random plots. However, previous observations reported the species has been seen in habitat with dense herbaceous cover (Langrand 1990, Thompson and Evans 1992, Evans *et al.* 1992). Dense herbaceous cover would play two key roles: at the nest sites it would make the nest more difficult to find and within the habitat it would help individuals escape from predators.

The slope at the nest entrance was less inclined than those of the random plots. This slope difference probably prevented nest flooding during heavy rains and water runoff. Nests were located near streams and in valleys similar to the species preference for humid habitat as reported by Thompson and Evans (1992). The existence of a permanently humid soil, associated with a relatively high annual temperature probably contributes to the density or availability of prey (e.g. earthworms) in the study sites. Consequently, climatic factors would be the main factors that limit the distribution of this species by playing a key role in the distribution of the preferred prey species.

Habitat loss is the main threat for this species. Deforestation occurs mostly in the low and mid-elevation area of the eastern rain forest due to its relatively easy accessibility to humans (Green and Sussman 1990). Despite its tolerance to habitat degradation suggested by this study, Andriamasimanana *et al.* (2001) classified the Scaly Ground-roller among the most vulnerable species associated with habitat fragmentation and loss based on their presence in the seven forest fragments they studied. The apparent tolerance to habitat degradation contrasted by its vulnerability to habitat loss and fragmentation suggests that its susceptibility might be due to a patchy distribution that causes sampling effects. The species might be locally common but regionally rare. Due to the rapid pace at which habitat loss and degradation is occurring in eastern Madagascar and the lack of detailed biological data on the range of forest dependent species, conservation efforts often rely on area size as the main criteria for selecting and designing reserves. However, this study suggests that additional factors, such as microhabitat patterns play a key role in designing an effective reserve network. Conservation of species that have patchy distributions requires protection of specific sites where the species are locally common. Therefore, further studies of species distributions are among the priorities for effective conservation of the entire avifauna of the eastern rainforest of Madagascar.

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Food niche segregation between the Malachite Kingfisher, *Alcedo cristata*, and the Pied Kingfisher, *Ceryle rudis*, at Lake Nokoué, Bénin

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Several species of kingfisher occur on Lake Nokoué, southern Bénin, including Malachite (*Alcedo cristata*) and Pied Kingfishers (*Ceryle rudis*). Here, we compare their diet and estimate the degree of overlap in food niche by analysing contents of regurgitated pellets collected near nesting sites of Pied Kingfishers or inside the nest chambers of Malachite Kingfishers. Characteristic fish skull bones were identified using a reference collection of local fish skeletons. Malachite Kingfishers feed most frequently on fish that occur around floating vegetation, mainly *Kribia* sp. (56%), *Hemichromis fasciatus* (28%) and *Sarotherodon melanotheron* (8%). Important differences were found between different pairs, and between adults and nestlings, the latter being fed almost exclusively on *Kribia* sp. Larger fish are fed to nestlings than are eaten by the adults. Pied Kingfishers prey upon 14 different fish species, some of them being caught in the pelagic region of the lake, particularly clupeids taken by hovering. By comparison with Malachite Kingfishers, Pied Kingfishers feed on a wider diversity of prey, and take larger fish, so that the dietary overlap between the species is relatively low (O = 0.181).

Introduction

The Malachite Kingfisher (*Alcedo cristata*) is one of the most common kingfishers in Africa, and is abundant in lowland equatorial and subtropical savannas, where it inhabits reeds or papyrus fringes and the bank vegetation of ponds, lakes and rivers (Bannerman 1953, Fry *et al*. 1992). Throughout its large distribution area — almost the largest among African kingfishers — it is easily observed, hunting for prey from a low perch on small branches or emergent rocks. However, its feeding habits have been rarely studied. Bannerman (1953) and Bouet (1961) mention small fish and freshwater crustaceans (crabs and prawns) as its main food. Van Someren (1956) and Newman (1974) found the diet dominated by aquatic insects, mainly damselflies and dragonflies (nymphs and adults) as well as water beetles (Dytiscidae) and water boatmen (Notonectidae) but also including small fish (e.g. *Barbus* sp., *Tilapia* sp.), frogs, tadpoles and occasionally small lizards and terrestrial insects such as grasshoppers and mantises. On a polluted river where there were no fish, Meadows (1977) observed an individual feeding exclusively on insects (water beetles, water boatmen and adult Odonata) during a period of at least 47 days. Reyer (in Fry *et al*. 1988) reported an exclusive consumption of fish (*Tilapia grahami*) and estimated the daily requirements at 15–20 small fish, 30–40 when nesting, and 60 or more fed daily to five nestlings.

Many fish-eating birds occur on the lagoons and associated swamps of southern Bénin, including cormorants, egrets, herons, terns and five kingfishers; Pied (*Ceryle rudis*), Woodland (*Halcyon senegalensis*), Giant (*Megaceryle maxima*), Malachite and African Pygmy-kingfisher (*Ispidina picta*) (Schockert 1998). Among these potential competitors, the Pied Kingfisher is probably the most numerous, the most widespread and the most likely to compete with the Malachite Kingfisher, as observed by Reyer *et al*. (1988). It therefore seems of interest to compare the composition of the diet of both species in the same habitat and to analyse the extent of overlap in their respective food niches.

In this paper we report on variations in the food of Malachite Kingfishers in relation to localities of nest sites and the age of nestlings. Detailed results of analyses of the food of Pied Kingfishers are discussed elsewhere (Laudelout and Libois 2003).

Study area

Southern Bénin is in a subequatorial climate zone (Figure 1), with a high relative humidity (77–93%) and a high mean monthly temperature, ranging from 22.4–32.9°C. Annual rainfall is about 1 000mm distributed over a long rainy season from March/April to July and a short rainy season from September to mid-October (Pliya 1980).

Lake Nokoué (6°23'–6°28'N, 2°22'–2°33'E) is a shallow lagoon not exceeding 2.50m in depth. In 1990 and 1991, its mean depth ranged from 1.07m at the end of the dry season (April) to 1.72m during the floods (September). Its waters are relatively turbid, especially during the floods: Secchi depth varies between 50–120cm in Véki, in the vicinity of the study sites. Salinity also fluctuates widely: from 25–30mg l^{-1} in April–June to 0–5mg l^{-1} in August–November (Laleye 1995). Its north-western edges correspond to the delta of the River Sô, occupied by villages built on piles, cultivated fields and *Paspalum vaginatum* meadows.

The fish community comprises at least 78 species from