Breeding ecology of the Tylas Vanga *Tylas eduardi* in southeastern Madagascar

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Abstract Although the family Vangidae provides one of the most striking examples of adaptive radiation in the avifauna of Madagascar, basic information on the breeding biology of each species is lacking. To examine the breeding system of the Tylas Vanga *Tylas eduardi*, a species endemic to Madagascar, we studied the contributions made by males and females of two pairs (involving four nests) to nest building, incubating, brooding, and feeding the young. The study was conducted from October 2007 to January 2008 at Ranomafana National Park, situated in southeastern Madagascar. Males had dispersed territories and paired with single females. Copulation took place between females and males on whose territories they nested. During the nest-building stage, males and females provided nest materials. We observed parental care at two nests. Both sexes participated in incubating and brooding at one nest, whereas only the female incubated and brooded at another nest. During the nestling period, both sexes delivered food (mainly caterpillars, moths, butterflies and crickets) to the nestlings and no helpers were observed. These results suggest that the Tylas Vanga is socially monogamous. We discuss the sex determination based on plumage color and mating system of Tylas Vanga.

**Key words** Biparental care, Diet, Madagascar, Monogamy, Plumage color
type of their breeding system by evaluating the parental investment of males and females throughout the reproductive cycle.

**STUDY AREA AND METHODS**

This study was conducted in the Sahamalaotra area (21°13’S, 47°23’E; 1,141 m above sea level) of Ranomafana National Park, southeastern Madagascar, from October 2007 to January 2008. The period from May to October is the dry season, and from November to April is the rainy season in the park. This montane tropical rainforest is composed of primary forest with a high floristic diversity and secondary growth consisting mainly of the introduced *Psidium cattleianum*. The understory is very diverse with many shrubs. *T. e. eduardi* is common in Ranomafana National Park (Langrand 1990).

To examine home ranges, we walked along trails at random from 0500 to 1000 almost every day during November 2007. When we located individuals, we recorded their positions and behaviors on a map. Home ranges were delineated with curved lines connecting the outermost observation points of each individual.

During the study, we found a total of 12 individuals, identified six home ranges, and found four nests. We were able to classify the 12 individuals as belonging to two color types: one with a black head, nape, and chin, and white underparts (Fig. 1a), one with a black head, nape, and chin, a white band across the upper chest, and orange underparts (Fig. 1b). We consider the six birds with white underparts to be males and the six birds with orange underparts to be females based on an observation of copulation in which a white-bellied bird mounted an orange-bellied bird. We were able to recognize four individuals attending their nests based on variation in their plumage color (color of throat, cheek and tail tip) and the shape of the bill tip.

Four nests (A to D) were found and their heights above ground were measured. We identified the scientific name of the nesting trees. The diameter at breast height (DBH) of each of the nest trees was also measured. To examine the relative contributions of the sexes to reproductive efforts, we studied the following activities: (1) nest building, (2) egg laying, (3) time budgets of incubation (percentage of time that individuals spent incubating), (4) time budgets of brooding (percentage of time that individuals spent brooding), (5) feeding frequency (times/h/brood) and (6) prey items delivered to nestlings. An incubation session was defined as having started when a focal individual began incubating eggs, and was considered to have ended when that individual left the nest. Similarly, a brooding session was defined as having started when a focal individual began brooding the nestlings, and was considered to have ended when that individual left the nest. If a parent stayed for more than two minutes in the nest with its hatched young, we defined this behavior as brooding.

Nests were visited at two-day intervals to examine their status. Direct observations (for a total of 186 h) were made using a 20× spotting scope, and indirect observations (for a total of 253 h) were made with a SONY video Hi8 camera (CCD–TRV96), from a vantage point that allowed a good view of the nest (5–15 m). Direct and indirect observations were usually made between 0600 and 1200, sometimes from 0600 to 1800. Data from both direct and indirect observations were combined for the analysis.
Calls were recorded at three vanga territories during the study period. All recordings were taken from a distance of 5–10 m using a Sony TCM-500 cassette tape recorder and a Victor MZ-200 shotgun microphone. We digitized recordings using Roland R-09HR recorder (sampling rate 44.1 kHz and sample size 16 bits). Sound files were analyzed using Raven 1.2 (Cornell Laboratory of Ornithology 2004, Ithaca, NY, US). Analysis was conducted on a spectrogram display type ‘Hann’ (filter bandwidth: 124 Hz; size: 512 samples, time grid: overlap: 50%; grid resolution: 5.8 ms, 86.1 Hz, DFT 512 samples). We chose the best example of each call type (i.e. the least degraded recording with the least background noise) to measure in our study. We calculated the time budgets of song (percentage of time that individuals spent singing).

Statistical analyses were performed with StatView 5.0 (SAS 1998). We used a significance level of 0.05 and, unless otherwise stated, the reported P-values are based on two-tailed tests. In cases, when data were not normally distributed, we used nonparametric tests. Mean values in the text are reported with standard errors (±SE).

RESULTS

1) Vocalizations

Tylas Vanagas gave four different types of calls during the breeding season. The first call type was a territorial call usually consisting of three (sometimes two) whistled notes (Fig. 2a), diminishing in volume. The second call, a contact call (type A), was a quiet ‘mobiru mobiru mobiru’ (Fig. 2b), given while the pair moved through the forest. The third call, also a contact call (type B), was a whistled ‘phu’ (Fig. 2c), sometimes a double ‘phu phu’, given by both sexes when changing over at the nest for incubation. The fourth call, a quiet ‘fifiifi’, was an alarm call (Fig. 2d) repeated by both sexes.

2) Space use

We found six home ranges along the trails (Fig. 3), each of which was shared by one male and one female. None of the home ranges overlapped (Fig. 3). Seven confrontations were observed at the peripheries of the home ranges (Fig. 3). All confrontations involved males chasing males.

We found four nests (nests, A, B, C and D). One pair built nests A, C and D in a home range (Fig. 3), but failed their breeding attempt at nests A and C.
Another pair built nests B in a home range (Fig. 3). We could not find the nest in other home ranges although pair seemed to breed.

When other bird species (Ashy Cuckoo-shrike *Coracina cinerea*, Long-billed Green Sunbird *Nectarinia notata*, Madagascar Bulbul *Hypsipetes madagascariensis*, Long-billed Greenbul *Phyllastrephus madagascariensis*, Madagascar Magpie-Robin *Copsychus albospectus* and Nellicourivi Weaver *Ploceus nelicourvi*) approached the nest, the pair chased them away using alarm calls.

A Pollen’s Vanga *Xenopirostis polleni* visited nest B at 0753 on 7 November and sat on the nest. The bird (probably a female) crouched on the nest, fluffed her body feathers, and fluttered her wings and tail, in a manner resembling the begging behavior of the young of Pollen’s Vanga. She continued to flutter her wings while sitting on the nest, but flew away at 0755. We did not know why the Pollen’s Vanga did this.

3) Nest

The nests were cup-shaped, and each was built in the fork of a tree (see Fig. 1), usually located 4.2–6.5 m above the ground (Table 1). Nests A and C were blown down by strong winds, so these were collected. The exterior nest diameter of both nests was 95 mm. The interior diameter of nest A was 75 mm and that of nest C was 70 mm. The exterior depth of nest A was 60 mm, while that of nest C was 50 mm. The interior depth at the center of both nests was 45 mm.

Nest material consisted mainly (about 90%) of the petioles of dead leaves, but also included hairs from *Palmae* leaves, and *Asparagus* sp. leaves. The exteriors of the nests were composed of spider webs and mosses (*Muscinees*), while the interiors were lined with the inflorescences of *Panicum* sp.

4) Nest building

During 119 h of observations, we noted nesting materials being brought by both males and females to nests A, B and C. At nest A, the female brought material on 19 (70%) occasions, whereas the male brought material on eight (30%) occasions within 32 h (data pooled over four days). At nest B, the female delivered material on 96 (74%) occasions, whereas the male brought material on 34 (26%) occasions, within 29 h (data pooled over three days). At nest C, the female brought material on 243 (86%) occasions, whereas the male brought material on 63 (14%) occasions, within 58 h (data pooled over eight days). At nests B and C where the sample sizes were large, the female was more engaged in nest building than the male: assuming that male and female brought nesting material in equal proportion, there was a significant bias towards the activities of the female at nests B and C (nest B: G=15.9, P<0.0001, nest C: G=59.3, P<0.0001).

We have no precise data on the duration of nest building. Construction of nest B had already begun by 5 November and the pair completed building the nest on 12 November. Construction of nest C had already begun by 10 November and the pair completed building the nest on 20 November. Thus, they spent at least 8–11 days constructing their nests.

During the nest building stage, male Tylas Vangas sang, and repeated territorial calls several times at regular intervals from established song posts (Fig. 4). However, they stopped singing when their females began incubating their eggs (Fig. 4).

5) Copulation and courtship display

At 1002 on 14 November, during the nest-building

![Table 1. Summary of nest tree (scientific name), nest height (m above the ground), DBH (diameter at breast height) at four nests in Tylas Vangas.](chart)

<table>
<thead>
<tr>
<th>Name of nest</th>
<th>Nest tree</th>
<th>Height (m)</th>
<th>DBH (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td><em>Mascarenhasia arborensis</em></td>
<td>5.3</td>
<td>4.1</td>
</tr>
<tr>
<td>B</td>
<td><em>Mascarenhasia arborensis</em></td>
<td>4.2</td>
<td>4.3</td>
</tr>
<tr>
<td>C</td>
<td><em>Mascarenhasia arborensis</em></td>
<td>4.5</td>
<td>2.5</td>
</tr>
<tr>
<td>D</td>
<td><em>Mascarenhasia arborensis</em></td>
<td>6.5</td>
<td>7.5</td>
</tr>
</tbody>
</table>

![Fig. 4. Song time budgets of male Tylas Vanga at three nests.](chart)
period, we observed one copulation near nest C involving the nesting female and her mate. At first, the female courted the male by crouching on a branch near her nest, fluffing her body feathers, and fluttering her wings and tails in a posture resembling the begging behavior of the young, however, she was silent. The male was not observed to perform any sexual display, but rather appeared simply to watch the soliciting female, then approach her from the side and mounted her. No courtship feeding was observed.

During the nest-building period, both males and females were seen giving the soliciting display (fluttering wings extended). At nest A, the male once and the female twice. At nest B, the male gave the fluttering display, twice and the female once. At nest C, the male gave the fluttering display four times and the female twice. Both males and females performed the fluttering display at the nest or on a branch near the nest. The display occurred when they changed over during nest-building.

6) Egg laying and clutch size

During the egg-laying period, only the females brought nesting materials at nests B and D. When their females approached the nest with nesting materials, the males associated closely with them.

We photographed the contents of nests B and D with a camera mounted on an extendible pole. Nests B and D contained two eggs. The eggs were pale blue, with small black spots. Assuming that interior diameter of nests B and D was 72.5 mm, the major and minor axes of the eggs were 24.7–25.6 mm and 17.4–17.7 mm, respectively. We were unable to determine the clutch sizes of nests A and C because the pairs abandoned their nests before the female laid her eggs (nest A) and just after the female incubated eggs (nest C).

7) Incubation

At nest B, only the female incubated the eggs, spending a total of 69.2±2.3% of her time incubating (N=5 days; Fig. 5). The mean incubation session was 27.9±1.8 min (N=57). Males did not bring food to the incubating female, but perched near the nest and watched the eggs during the female’s incubation breaks (16 out of 57 incubation sessions).

At nest D, both the male and the female took turns incubating, spending a total of 70.5±4.3% of their time incubating (N=10 days; Fig. 5). The female had significantly longer incubation sessions (32.8±2.1 min, N=64) than males (13.4±2.0 min, N=16,

z=4.86, P<0.0001). The male did not give food to the incubating female. At nest D, we observed the pair change over at the nest during incubation 105 times. On 16 of these 105 occasions, the change over was preceded by contact calls (type B) given by the arriving or the leaving adult, nine times by the male and seven times by the female.

We observed the fluttering display when birds changed over during incubation at nest D. Out of 105 change overs the male performed the display seven times and the female 13 times. Both male and female performed the display only when their mate was near the nest. The display lasted 10.1±6.8 s (male; N=10) and 11.0±4.4 s (female; N=13); the difference between the length of displays by males and females was not significant (z=1.78, P=0.07).

We did not observe the fluttering display at nest B, and did not observe courtship feeding at either nest B or nest D.

The female at nest B began incubating on 13 November and the pair was observed delivering food to their nestlings on 29 November. Thus, their incubation period lasted for at least 16 days. The pair at nest D began to incubate on 3 December and was first observed delivering food to their nestlings on 21 December. Thus, their incubation period lasted for at least 18 days.

8) Brooding

Nests B and D contained two nestlings. At nest B, the nestlings were brooded only by the female (Fig. 6), and both nestlings were found to be out of the nest on 9 December (when the chick was 11 days old). At nest D, the male brooded the nestling on just one day (Fig. 6). Females spent less time brooding their
young as the nestlings grew (Fig. 6).

We observed the fluttering display four times at nest D, but not at nest B. The male performed this display three times on 21 December (when the chick was one day old, see Fig. 6). Before he delivered food to the nestlings, the male perched on the nest and performed the fluttering display. After the female finished brooding, she performed the display on the nest on 23 December (when the chick was three days old, see Fig. 6). Whenever a bird performed this display, its mate was also near the nest. We did not observe this display after the chicks had reached five days old.

9) Feeding frequency

Both members of each pair brought food to their nestlings during the nestling period (Fig. 7). The feeding frequency of females was lower than that of males early during the nestling period (Fig. 7). This was because the female brooded the nestlings during this period (Fig. 6). When the female was brooding the nestlings, the male did not deliver food directly to the nestlings but gave food to the brooding female who then either fed herself or gave the food to the nestlings. Males sometimes gave food to brooding females. The feeding frequency increased with nestling age but decreased after the chicks had reached 11 days old (Fig. 7).

The brooding female at nest D was observed picking up an eggshell on 21 December 2007 and all of the nestlings left the nest on 5 January 2008. Thus, the nestling period lasted at least 15 days.

Table 2. List of prey items of male and female Tylas Vanga. Prey items were recorded during the nestling period at two nests (nests B and D). Figures indicate the sample size, with percentages in parentheses.

<table>
<thead>
<tr>
<th>Prey</th>
<th>Male</th>
<th>Female</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spider</td>
<td>7 (3.7)</td>
<td>4 (4.4)</td>
<td>11 (4.0)</td>
</tr>
<tr>
<td>Cockroach</td>
<td>7 (3.7)</td>
<td>2 (2.2)</td>
<td>9 (3.2)</td>
</tr>
<tr>
<td>Cicada</td>
<td>8 (4.3)</td>
<td>4 (4.4)</td>
<td>12 (4.3)</td>
</tr>
<tr>
<td>Cricket</td>
<td>13 (7.0)</td>
<td>4 (4.4)</td>
<td>17 (6.1)</td>
</tr>
<tr>
<td>Grasshopper</td>
<td>1 (0.5)</td>
<td>1 (1.1)</td>
<td>2 (0.7)</td>
</tr>
<tr>
<td>Dragonfly</td>
<td>1 (0.5)</td>
<td>1 (1.1)</td>
<td>2 (0.7)</td>
</tr>
<tr>
<td>Mayfly</td>
<td>1 (0.5)</td>
<td>0 (0.0)</td>
<td>1 (0.4)</td>
</tr>
<tr>
<td>Fly</td>
<td>7 (3.7)</td>
<td>3 (3.3)</td>
<td>10 (3.6)</td>
</tr>
<tr>
<td>Horsefly</td>
<td>6 (3.2)</td>
<td>3 (3.3)</td>
<td>9 (3.2)</td>
</tr>
<tr>
<td>Moth/Butterfly</td>
<td>14 (7.6)</td>
<td>7 (7.7)</td>
<td>21 (7.6)</td>
</tr>
<tr>
<td>Caterpillar</td>
<td>38 (20.4)</td>
<td>15 (16.5)</td>
<td>53 (19.1)</td>
</tr>
<tr>
<td>Snail</td>
<td>1 (0.5)</td>
<td>0 (0.0)</td>
<td>1 (0.4)</td>
</tr>
<tr>
<td>Frog</td>
<td>1 (0.5)</td>
<td>0 (0.0)</td>
<td>1 (0.4)</td>
</tr>
<tr>
<td>Unidentified prey</td>
<td>82 (43.9)</td>
<td>47 (51.6)</td>
<td>129 (46.4)</td>
</tr>
<tr>
<td>Total</td>
<td>187 (100.0)</td>
<td>91 (100.0)</td>
<td>278 (100.0)</td>
</tr>
</tbody>
</table>

10) Nestling diet

Throughout 72 h of observation at nests B and D, we observed 278 prey items being fed to nestlings (Table 2). It was difficult to identify food items especially during the early nestling period, because the parents usually masticated the food before offering it to their nestlings, and because feeding was very rapid. However, we were able to identify 149 (53.6%)
DISCUSSION

1) Plumage color of male and female Tylas Vanga

Langrand (1990) reported that the eastern nominate Tylas Vanga is sexually dimorphic in plumage coloration; with the male having a black head, nape and chin, and the female a dark gray forehead and front of the head and a whitish chin (see Plate 38 in Langrand 1990). He also reported that the male has gray-green upperparts and orange underparts with a white band across the upper chest extending up the sides of neck. Sinclair and Langrand (2003) described males of the eastern race as having orange underparts. They also reported that some individuals are almost entirely white on the underparts, with only a faint tinge of orange. In contrast, Morris and Hawkins (1998) did not describe the plumage color of both sexes in their photographic guide, although they inserted a color picture of Tylas Vanga.

In our study, the plumages of both male and female Tylas Vanga (see Fig. 1) differed from those previously described by Langrand (1990), and by Sinclair and Langrand (2003). The plumage of the males in our study was similar to that described for the western race T. e. albigularis by Langrand (1990) and by Sinclair and Langrand (2003); i.e. with a black crown, cheeks, and nape, a white band across the upper chest extending up the sides of the neck, and white underparts. The plumage of the females in our study was the same as that described for males by Langrand (1990) and by Sinclair and Langrand (2003).

In this study, we were able to confirm, by observation of copulation, that the male (mounting) has white underparts and the female (mounted) has orange underparts. Based on our observations, the bird most active in nest building, incubating and brooding was the female (Figs 5 & 6), which is to be expected. It appears that Langrand (1990) and Sinclair and Langrand (2003) mistakenly described the sexes of Tylas Vanga. However, since there is individual variation in plumage color and as plumage varies with age in birds (Dale 2006), further study is required to confirm our observations.

2) Breeding system

The dispersion pattern of individuals is a factor in determining the mating system of a given species, and monogamous birds usually hold a territory that is shared by both sexes (Davies 1991; Ligon 1999). Tylas Vangas were found to occupy home ranges, to have individual males paired with single females, and the single copulation that we observed, occurred between a male and a female in their home range. The home ranges of the six pairs that we observed did not overlap, and confrontations between males were observed only at the peripheries of their home ranges (Fig. 3). Thus, we interpreted the home ranges as being territories and these territories appeared to be defended mainly by males, who responded to the songs of other males.

Our results suggest that male and female Tylas Vangas did not contribute equally to overall breeding activity. During the nest-building stage, both males and females provided nest materials. Both sexes participated in incubating and brooding at one nest (Figs. 5 & 6), however, females more frequently engaged in parental task (Figs 5 & 6). Both sexes delivered food to the nestlings (Fig. 7).

The degree of investment by each parent differs considerably between social mating systems such as monogamy, polygyny, and polyandry (Clutton-Brock 1991; Davies 1991; Ligon 1999). In monogamous birds, biparental care is common, and males are more active in territorial defense (Clutton-Brock 1991). In most socially monogamous bird species, females take the larger share of brood care by doing most of the incubation and brooding of the young (Clutton-Brock 1991). Our results fulfilled these conditions. In both the Rufous Vanga (Yamagishi et al. 1995; Eguchi 2002 et al.) and the White-headed Vanga (Nakamura et al. 2001), both also endemic to Madagascar, helpers have been observed at the nest. However, during our study of Tylas Vanga we did not observe helpers, thus, we conclude that its mating system is best described as socially monogamous, like the Helmet Vanga (Rakotomanana et al. 2000; Marca & Thorstrom 2000), the Hook-billed Vanga (Rakotomanana et al. 2001) and the Van Dam’s Vanga (Mizuta et al. 2001). However, two questions remain: why do both sexes perform the fluttering display from the nest building to the nestling periods and why do males sing during the nest building period, even after they have acquired a mate? Further nest observations are necessary in order to more fully describe the social structure of Tylas Vanga.
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REFERENCES