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First breeding survey of the endemic Madagascar Red Fody *Foudia madagascariensis* and Forest Fody *Foudia omissa* at Ranomafana National Park, Madagascar

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Abstract

An intensive study of the breeding biology of *Foudia madagascariensis* and *Foudia omissa* in the family Ploceidae was first conducted in Ranomafana National Park from November 2003 to April 2004. During the survey, 368 nests of *Foudia madagascariensis* and 7 nests of *Foudia omissa* were found. Nest building of *F. madagascariensis* can be divided into four stages. The male builds the nest up to stage 2. Then the female partner finishes construction of the nest until stage 4. In both species incubation lasts 13 to 17 days and the number of eggs varies from 1 to 5 per brood for *F. madagascariensis* and 1 to 3 for *F. omissa*. Males of both species occupied more than one nest in their territory and had at least three different partners, thus are apparently polygamous. They defend their territory and rarely feed their chicks or engage in parental care at all. The females ensure incubation of the eggs, clean the nest and rear the chicks. The nestlings first flew out after 13 to 15 days and were consecutively led by the parents. During the study period a cyclone and especially anthropogenic nest destruction contributed to 26% of nest failures.

Key words

Foudia madagascariensis, *Foudia omissa*, breeding, behaviour, Ranomafana, Madagascar.

Introduction

Among the 119 species of the family Ploceidae in the world (Dickinson, 2003), four species are endemic to Madagascar: *Foudia madagascariensis, Foudia omissa, Ploceus nelicourvi and Ploceus sakalava*. *Foudia* is a distinctive genus endemic to the islands of the tropical western Indian Ocean (Moreau, 1960; Safford, 1997a). Until now, Malagasy fody species have received relatively little attention, some information is available about their reproductive biology and about effects of the invasion of *F. madagascariensis* on the harvest of rice paddy (Andriatsilavo, 1997; Sama, 1999). A biometric survey of *F. madagascariensis* in the non-breeding period has been conducted by Koenig in 2005. A molecular survey based on cytochrome-*b* sequences (Craig, 1999) revealed that *F. madagascariensis* is closely related to *F. eminentissima*. However research on the breeding biology of Malagasy fody species is still limited. No information on different stages of nest construction and on parental care existed before the current study.

The distribution areas and abundance of the two study species in Madagascar differ in some aspects. *F. madagascariensis* occurs commonly in Madagascar and its neighbouring islands such as: Mauritius, La Réunion, Rodrigues, Seychelles and the four islands of

Comoros (Sinclair & Langrand, 2003). It is the most well-known bird in Madagascar, called "Fodilahimena". On the other hand, *F. omissa* is only found in the eastern part of the island and is not well studied in its distribution area. We chose the National Park of Ranomafana as a site of survey because there the two species live in sympatry and can be frequently observed.

In this study we aimed to improve the knowledge of the species' breeding biology especially the process of nest building, the mating system and the parental care.

Study area

The presence of secondary forest, extensive rice fields and abundant nests were the main criteria of our survey site choice at Ranomafana National Park, located between 47° 18′–47° 37′ E and 21° 02′–21° 35′ S in South Eastern part of Madagascar. Elevation varies from 900 m to 1200 m (Wright, 1997). Vohiparara and Sahamalaotra were chosen among the six sites visited around this park. In the mean, it rains during 200 days per year and the annual precipitation reaches 2600 mm. The annual average temperature varies between 14°C and 20°C, with minimum of 3°C and a maximum of 37°C (Wright, 1997).

Methods

Nest monitoring

An active search for nests began on 2nd December 2003 and lasted until 5th April 2004. Nests were searched for systematically inside the bushes or secondary forest at the edge of the rice fields and were also found by careful observation of males in their own territories. All nests found were numbered, tagged, and recorded by GPS receiver. The presence of fresh green grasses, the stage of construction and the presence of eggs or fledglings were daily recorded for each nest. Each observation normally lasted from the discovery of the nest until the 1st take-off of the nestlings but was eventually stopped if unexpected destruction of the nest or plundering of the eggs and fledglings was caused by the villagers.

At the time of the observation, the camouflaged observer sat at least 5 m from the nest and recorded the detailed activities of the pair during nest building, incubation and chicks rearing with the aid of binoculars and telescopes. Nail polish was used to colour the nail of the left or right claws of the chicks aged of 1 to 4 days. However, one aluminium ring and two plastic rings were put on a fledgling's tarsus from day 6 on in order to identify them. From the 9th day on, the fledglings became robust and ready to fly. For this reason, the duration of observation could not go beyond 8 days to avoid the risk of the first unexpected flights of the nestlings.

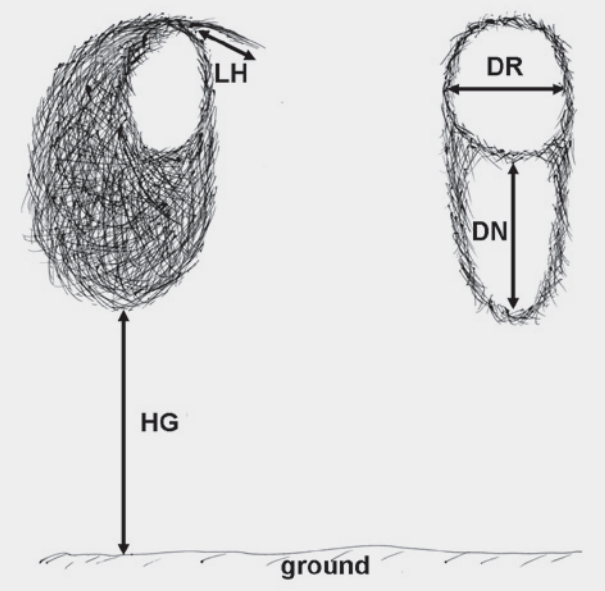

Fig. 1. Shape of the nest showing all the measurements taken, depth of the nest (DN), diameter of the ring (DR), height from the ground (HG), length of hat (LH).

Capture and ringing of the parents

When the age of the fledglings had reached at least 10 days, a mist net 8 m long and 2.5 m high was installed at more than 10 m in the direction of flights which has been previously detected during the nest monitoring in the territory of the pair. After the measurements, each individual was marked on their tarsus by three coloured plastic rings (red, green, purple, orange, yellow and white) and numbered Aluminium rings. This system facilitated their identification and helps to know the case of potential other helpers at the nest and the mating system.

Results

Description of nests

In total, 368 nests of *F. madagascariensis* and only 7 nests of *F. omissa* were found during 54 days of intensive research. All *F. omissa* nests were located around the cultivated area and about 400 m from the rice field. Amongst *F. madagascariensis* nests, 62% were around the rice field, 10% were along the stream, 21% were in cultivated area and 7% were located in secondary forest. These nests were classified according to the stage of their manufacture and the presence of eggs or nestlings (Table 1). All the nests found were built and located in the territory occupied by the male.

Fig. 2. Pictures of the four stages of *F. madagascariensis* nest; **A**) nest in stage 1, **B**) stage 2, **C**) stage 3 and **D**) stage 4; all pictures taken at Ranomafana, February 2004.

Due to the frequent destruction and abandonment of nests, the evaluation of duration of nest construction in both species from the beginning to the end (in particular for *F. omissa*) was difficult. Furthermore, no measurements could be taken from the nests of *F. omissa*, since the nesting sites in the spiny bushes were inaccessible for observation. The size of the stitches in every nest of *F. madagascariensis* varied according to the stage of manufacture. The process of nest building was thus divided into 4 stages (Figs 1, 2A, B, C and D).

Stage 1 (Fig. 2A). The nest was not yet well shaped, only the ring or site entrance and the roof were weaved. The size of the stitches ranged from 2 to 3 cm.

During this survey, a total of 74 first nest records of *F. madagascariensis* were nests of stage 1: Of these, 20 (25.6%) were abandoned at stage 1, 12 (15.4%) reached stage 2 and 7 (9.0%) developed through stage 3. Only two (2.6%) nests reached stage 4 but they were abandoned later on. Further 33 nests were destroyed.

During construction of nest No. 307 the male initially carried some items in his bill such as the twigs to weave the ring that is going to serve as the nest entrance. Meanwhile, he showed some courtship behaviour of "chew" call display and approached the females passing through his territory. He also suddenly tried to chase a female and change the direction of flight toward his nest in construction as a nest invitation. The lack of nest visits by females and the dryness of the nest at stage 1 were possibly the main causes of nest abandonment by males.

Stage 2 (Fig. 2B). The size of the stitches was 1–2 cm, the nest had a U-shape and a nest chamber.

In total, 98 nests of *F. madagascariensis* were first found in stage 2 of which, 60 (61.2%) were abandoned and 33 (33.7%) destroyed. Five (3.1%) nests reached stage 4 and contained 3 eggs. Of the latter five nests, three were destroyed, the eggs in two nests hatched. Only the fledglings of one nest survived and flew out.

Three nests were intensely surveyed at this stage, (nest No. 80, 96 and 396). The males of each nest continued working and increased their activity around their territories. They brought nesting material in the bill 28 times. This transportation only represents about 5% of their activity, because more than 90% was spent in surveillance of their nest or flying around their territory. Meanwhile, the males always showed courtship display

Table 1. Detailed list of *F. madagascariensis* and *F. omissa* nests.

		F. madagascariensis	***F. omissa***
Abandoned nests		185 (50.3%)	1 (14.3%)
Destroyed nests		91 (24.7%)	1 (14.3%)
Nests with eggs	abandoned	3 (0.8%)	—
	Disapeared	50 (13.6%)	2 (28.6%)
Nests with chicks	Dead	10 (2.7%)	1 (14.3%)
	Disapeared	11 (3.0%)	—
	1st flight	18 (4.9%)	2 (28.6%)
	Total	368	7

Table 2. Dimensions of the *F. madagascariensis* nests; length in cm including standard deviation.

Nest No.	Diameter of the ring	Depth of the nest	Height from the ground	Length of hat
137	6.1	4.6	13.8	5.6
287	5.7	5.7	17.8	6
13	5.5	7.7	14.3	6.4
68	5.4	5.4	14.5	destroyed
329	5.8	4.7	12.3	6.2
Mean	5.7 ± 0.3	5.6 ± 1.32	14.5 ± 2.0	6.0 ± 0.3

Table 3. Number of eggs per brood inside the nests of *F. madagascariensis* and *F. omissa.*

Egg number per clutch	**Nest of *F. madagascariensis***		**Nest of *F. omissa***	
	Number	%	Number	%
1	7	8.5	1	25
2	14	17.1	1	25
3	52	63.4	2	50
4	8	9.8	—	—
5	1	1.2	—	—
Total	82	100	4	100

by singing and by chasing the females passing through their territories. This approach often ended by one visit of the females to his nest. Nest abandonment by the males occurred when females did not reply to their courtship.

Stage 3 (Fig. 2C). The size of the stitches was 1 – 0.5 cm, the shape of the nest was complete.

During the survey, 82 *F. madagascariensis* nests were first recorded in stage 3: of these, 69 (84.1%) were abandoned and 5 (6.1%) were destroyed after this stage. Eight nests developed to stage 4 and contained 5 eggs and 3 nestlings. Only one nestling survived until its first flight.

Nine nests No. 38, 80, 81, 98, 156, 191, 276, 281 and 283 were intensely surveyed at this stage. After the nest visit, the females replaced their partners and continued the nest to the stage 3. They carried some herbs and grasses 120 times and continued weaving the nests. The involvement of the males in nest construction of the nests at this stage was short, they just brought nesting material 7 times.

Stage 4 (Fig. 2D). The size of the stitches of the nest was smaller than 0.5 cm; the shape was complete.

Overall, 116 *F. madagascariensis* nests were first recorded at stage 4 during the intense nest search. Of these, 20 (17.2%) had already been abandoned, 13 (11.2%) were empty at the first day of record but contained eggs afterwards, 83 (71.6%) were found with eggs at the first day of discovery. Of the latter 83 clutches, 56 were abandoned after plundering of eggs and 27 contained hatching eggs. Later, 6 of the latter nests contained dead nestlings and 10 nests with fledglings were plundered.

Six nests in stage 4 No. 38, 80, 107, 124, 190 and 270 were intensely surveyed, the females transported herbs fifteen times. On the other hand, the males kept watching longer around their territories, and transported nest material 2 times only. They did not make any repairs. The females finished the manufacture of the nests while the males defended the nesting site.

The nests of *F. madagascariensis* had a bowl shape. The roof of the nest ended with a hat to the upper part; these nests were all attached to branches or concealed in

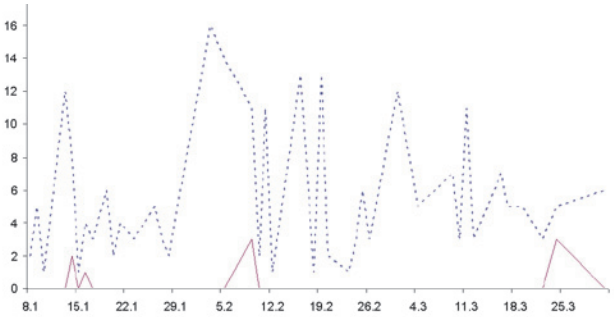

Fig. 3. Diagram of the total of eggs laid per day by *F. madagascariensis* (blue dashed line) and *F. omissa* (red line) found in 2004.

a tuft of herbs. The size of 5 nests in stage 4 is given in Table 2 and all measurements are illustrated in Fig. 1.

Breeding behaviour

Mating

Two attempts of mating were intensely observed for *F. madagascariensis*. The owner of the nest No. 166 was found copulating twice for 4 and 9 seconds with another female passing through his territory while his mated female was incubating. Another couple from a nest at stage 4 of construction to the No. 283 mated three times during 5 to 7 seconds. Both males approached and displayed "chew" calls towards their partners and adopted a drooped wings posture. No mating of *F. omissa* could be observed during this survey.

The observations confirmed that males can have at least two different female partners. What may explain this fact was the availability of food provided by the rice paddy which should be their main food. Furthermore, many males of *F. madagascariensis* were observed having apparently more than one partner, but since the capture of them was difficult only 3 cases were definitely proven: 2 nests of one *F. madagascariensis* male with 3 different partners represented by nest No. 23 and 24; a second male with three different partners of nests No. 28, 105, and 152; a third male with 5 different partners of nests No. 62, 63, 75, 114, and 115. Besides, four females have been found being partners of the same male of *F. omissa* in his territory (nest No. 7, 8, 132, 247 and 350).

Number of eggs per brood

The clutch size varied from 1 to 5 with a mean of 2.8 ± 0.8 (N = 82) for *F. madagascariensis* and 1 to 3 for *F. omissa* with a mean of 2.2 ± 0.9 (N=4). More than half of the *F. madagascariensis* nests observed contained 2 or 3 eggs (Table 3). Apart from these, one nest only had 5 eggs and 8 nests contained 4 eggs.

Incubation

Overall 224 eggs of *F. madagascariensis* were found from January to April 2004 in a total of 82 nests, with 44.3% of incubation success, 7.4% abandoned, 4.9% destroyed, 26.5% disappeared, 10.5% plundered. A total of 9 eggs were found in 4 nests of *F. omissa*. The length of incubation of *F. madagascariensis* and *F. omissa* is about 13 to 17 days (mean values: 15 days). The peak of the egg laying for *F. madagascariensis* during these four months was in early February 2004 (Fig. 3). However such a peak could not clearly be described for *F. omissa* due to the low number of nests found (Fig. 3). The latest clutch of *F. madagascariensis* was found at the end of March.

The survey of 25 nests of *F. madagascariensis* clearly showed that the males of this species did not participate in the incubation. The same was found in males of *F. omissa*. Four out of seven males of *F. madagascariensis* and one male of *F. omissa* began to build a new nest and got a new female partner while their first partner was incubating. This is why nests with eggs or fledglings were recorded alongside with a nest in construction in a male's territory.

As an example one *F. madagascariensis* male initiated the construction of nest No. 32 for his second partner before January 9th, 2004 when his first partner sat in the nest No. 24. Then he manufactured another nest (No. 23) for his third partner on January 29th, 2004. The same procedure was recorded for the male owner of the nests No. 62, 63, 75, 114 and 115 with four different partners.

In contrast, females were always sedentary on their nests only leaving the nest to get fresh supplies or when disrupted. Besides, one female ejected the remnants of egg shells outside of the nest when chicks had newly hatched (nest No. 341 April 27th, 2004). The females would feed the first nestling at the nest entrance and got inside the nest to continue the incubation of the remaining eggs (nests No. 65, 117, 231 and 341).

Chick rearing

The chicks in nest No. 341 hatched at different time, the second chick hatched at least 2 hours after the first. Hatching could go on for more than one day (nest No. 245 March 7th, 2004. hatching of the first two chicks, then March 8th, 2004, hatching of the third chick).

Overall, 121 nestlings of *F. madagascariensis* (38.6% of them died, 7.8% had been predated, and 53.6% flew out from the nests) and 6 nestlings of *F. omissa* (50% died and 50% did their first flight) were found. 29 nests with nestlings were observed for a time period of about 205h. During this time, males just fed the nestlings (nest No. 149, 210, 215 and 271) on 12 occasions while perching on the site entrance and left afterwards. On the other hand females fed 353 times in all nests monitored. They also perched on the border of site entrance and fed the fledglings while regurgitating the food bowls inside the

open beaks of fledglings. The females then entered their nests and they sometimes sang inside to communicate with the male partner outside. The female also regularly removed from the nest the faecal sacs of fledglings. Two nests of *F. madagascariensis* No. 181 and 333 respectively were monitored for about 4h when the parents helped the young to leave the nest during first attempts of flight. The behaviour of the nestlings changed from the 10th day after hatching. They often put their heads out of the nest and tried to leave.

Threats and anthropogenic pressure

Fodies are considered to be harmful birds, as their colonies and feeding do considerable damage to agriculture, especially during the harvest time of rice. It was observed that villagers purposely destroyed the nests and even stole the eggs or nestlings in order to ban the whole population.

The violent passage of the two cyclones Elita (31/01/04 until 02/02/04) and Gafilo (7/03/04 until 10/03/04) in this region brought violent winds and some heavy rains and flooded 7 nests around the rice fields (nests No. 43, 62, 243, 248, 249, 287 and 289). Moreover, the quasi daily fall of rains damaged the nests and incited the birds to abandon their nests and to re-nest at another nesting site. One of the three eggs inside the nest of *F. madagascariensis* No. 48 had been washed away by flood (February 3rd and 4th 2004) but it was replaced after seven days (February 11th 2004) and the eggs number got back to three.

Three predators have been recorded: *Centropus toulou* with 15 broken eggs, *Rattus rattus* with 7 broken eggs and one nestling predated and one case of *Microcebus sp*. shelling one egg and squatting the nest in stage 3 and 4 as their dormitory. The latter nest with *Microcebus* was filled with dry leaves after it had been abandoned by the bird.

Discussion

Overall, 368 nests of *F. madagascariensis* and 7 nest of *F. omissa* were found in the study area between November and April. This big difference between the number of nests of *F. madagascariensis* and *F. omissa* may imply two explanations:

1. Various authors found the Forest Fody slightly secretive, interior forest dependent and more uncommon within its range (Langrand, 1990; Sinclair & Langrand, 1998; Andrianarimisa *et al.*, 2000). The nests of *F. omissa* were very rare even though an intensive search for *F. omissa* nests was carried out which could imply that the place inspected would not be their common territory.

2. The breeding season of *F. omissa* may not largely overlap with that of *F. madagascariensis*. Establishment of territory and pair formation in the two species seem to take place within the period between November and April in Ranomafana. Both species are vocally active and males develop their breeding plumages during that period. Goodman *et al.* (1997) suggested a protracted breeding season that extends from September to May for *F. madagascariensis*. Some studies suspect hybridization between the two species in an area where the ranges have been brought into contact as a result of habitat destruction (Benson *et al.*, 1977) and genetic studies have confirmed a historical hybridization scenario including mitochondrial capture due to unidirectional introgression (Warren *et al.,* 2012). These findings corroborate the overlapping of the breeding season, and the current information from Ranomafana is not exceptional compared to elsewhere. In fact, the presence of hybrid specimens as reported by Benson *et al.* (1977) would not be possible without an overlapping of the species' breeding period. However, the insufficient data of *F. omissa* nests collected did not allow for confirming a presumed synchronisation of the breeding period in Ranomafana.

Role of male and female

Male and female behaviour of *F. madagascariensis* during the breeding season is remarkably different. The male begins the nest construction, defends the territories and is only little involved in parental care. The female assures the incubation, plays the major role in chicks rearing and parental care.

The observations of *F. madagascariensis* nest during the stage 1 and 2 did not confirm any involvement of the females in nest construction. The observation made by Rand (1936) on a nest of *F. madagascariensis* suggesting the involvement of the female since the first construction of the nest is not supported by the present survey. According to our field data the involvement of the female from the onset of the nest construction could be not common.

The role of the female during incubation is similar to other fody species. For instance, Safford (1997b) found that only female Mauritius fodies incubate and they leave the nest unattended at maximum periods of around 20 minutes for feeding. Similarly Craig (2003) reported only *F. madagascariensis* female incubate while the male perches nearby. The findings during the current research on incubation, nest construction would then be common to both *Foudia* species.

Our observations furthermore suggest successive polygyny as the mating system of *F. madagascarienis* in our study area. Hence, the observation made by Craig in 2003 who defined the species *F. madagascariensis* as monogamist is at least put to question by the results of our field survey. Observations made on captive breeding birds also revealed the construction of more than one nest by each male (Kleefisch, 1981). These nests could serve to attract different females and would indicate a polygamous breeding behaviour. For further studies, genetic

analysis of the nestlings is recommended to determine the fatherhood of the fledglings and to know about the abundance of possible extra-pair copulations of females. This analysis would also permit to confirm possible polyandry of females in these two species.

Clutch size and incubation success

A clutch size of 2 to 4 for *F. madagascariensis* found by Craig (2003) and 3 to 4 by Langrand (1990) was confirmed by the current study (2.76 ± 0.79, N = 82). Since no previous information is available for *F. omissa* (Langrand, 1990) the current study is the first known estimate for the clutch size of this species with 1 up to 3 eggs (N = 4). However, the low number of nests found of the latter could not allow drawing a definite conclusion. For other species of the genus Moreau (1960) reported 1 and often 2 eggs per nest from 28 nests of *F. seychellarum* on Fregate Island. Similarly *F. aldabrana* was found to have 4 eggs (Ridley, 1958), and it is the maximum number for *F. rubra* (Cristinacce, 2008).

Craig (2003) reported that in captivity the incubation period of *F. madagascariensis* lasted 11 to 14 days. Compared to these data, in Ranomafana, the incubation period varied between 13 to 17 days for both species (*F. madagascariensis* and *F. omissa*). *F. rubra* incubation period was estimated 14 days (Cristinacce, 2008). Incubation success of 44% of 224 eggs seems to be quite high for *F. madagascariensis* in our study area where anthropogenic disturbance and even destruction of habitat and nests exists. Incubation success was accounted about 35% for *F. rubra* (Cristinacce, 2008), and it could be naturally increased in some areas with exotic trees (Safford, 1997c). Given the above findings, *F. madagascariensis* might have even higher incubation success in areas with less anthropogenic impact. In fact, most nesting failure in our survey area was from anthropogenic pressure and spontaneous abandonment. Fodies like most weavers might abandon many nests when only partly-built (Safford, 1997a) especially at stage 2 for the male and stage 3 for the female of *F. madagascariensis*. However, natural predation plays an important role, too. *Centropus toulou*, *Microcebus sp.*, and *Rattus rattus* were the predators of *F. madagascariensis* nests found during the study. There was strong evidence that predation occurred in 41% (11/27) of failures after the start of incubation for the Mauritius Fody *F. rubra* (Cristinacce, 2008). In fact, *F. rubra* population has declined rapidly between 1975 and 1993 due to habitat destruction and nest predation by introduced rats and monkeys (Cristinacce, 2008). In Madagascar, human persecution seems to be the strongest close to anthropogenic areas (Sama, 1999). However, due to its status as the most common and widespread bird on Madagascar (Craig, 2003), *F. madagascariensis* condition is far from giving cause for conservational concern. In contrast, the lack of information on *F. omissa*, its habit to be adapted to forest areas, and the evidence of hybridization with *F. madagascariensis* would need more precaution and accord priority for future investigation regards to Madagascar weavers.

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