Observations on the breeding biology of the Seychelles Fody on Cousine Island

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The Seychelles Fody, Foudia sechellarum, is a ploceid weaver occurring naturally on three islands in the Seychelles group in the Indian Ocean. The population on Cousine Island was studied between 30 June and 25 August 1997. The size of the population on the island was estimated at 458–614 individuals and densities varied in different habitat types. As Seychelles Fodies in non-breeding plumage are difficult to sex, we provide sexing criteria based on wing length. Breeding pairs form small, probably temporary, territories that are defended by both partners against other fodies, including the introduced Madagascar Fody, Foudia madagascariensis. The Seychelles Fody often breeds semi-colonially and we observed up to five nests close together. The birds are socially monogamous and both sexes share responsibilities in the young. Only females incubate. Many nests were deserted before eggs were laid, including some that had been accepted by the female. Additional males and females were sometimes seen helping provide the young, but this cooperative breeding behaviour appeared to be uncommon. Non-breeding individuals congregate in large flocks, sometimes joined by breeding birds.

Introduction

The Seychelles Fody (or Toc-toc), Foudia sechellarum, belongs to a genus of Ploceidae that is confined to the western Indian Ocean (Moreau 1960) and is one of six bird species endemic to the Seychelles Islands (Penny 1974). The species occurs on the islands of Frégate (220ha), Cousin (29ha) and Cousine (25ha) (Figure 1, areas from Losos 1986). In 1965, five individuals from Cousin were introduced to D’Arros Island in the Amirantes group (Gaymer et al. 1969) and the species currently persists there in small numbers (c. 125 individuals recorded in 1990, Skerrett pers. comm.). Historically, the species was reported from at least four other islands, all located in the central Seychelles: Marianne, Praslin, La Digue and Aride (Diamond 1984). However, the records from La Digue and Aride have been questioned (Gaymer et al. 1969) and so have the specimen records from Praslin (Collar and Stuart 1985), although Crook (1961) quotes Goodwin saying that ‘there is no valid reason to doubt these [latter] records’. During the 1950’s the total population of Seychelles Fodies was estimated at only 200 individuals (Savy, in Moreau 1960). In 1960 the population was estimated at 435–485 birds (Crook, in Gaymer et al. 1969), while five years later Gaymer et al. (1969) counted between 750 and 1 100 individuals. Subsequently, regeneration of native vegetation on Cousine Island has led the population there to increase to about 1 300 individuals by the late 1970’s (Brooke 1985). The population on Cousine was estimated at 100–150 birds in 1964, when coconut palms covered most of the island (Gaymer et al. 1969). Recently, the population on Cousine was estimated at 518 (±85) birds (Rocamora 1997). We know of no recent population estimates for Frégate. The species is listed as rare in the 2000 IUCN Red List of Threatened Species (www.redlist.org).

Throughout its natural range, the Seychelles Fody occurs together with the Madagascar Fody, Foudia madagascariensis, which was introduced to the Seychelles in the late 19th century (Crook 1961). The two species appear to be reproductively isolated, although there has been one documented record of a hybrid pair successfully raising offspring (Lucking 1997). Direct competition between the two species seems to be limited. The Seychelles Fody is an opportunistic feeder, whose diet consists mainly of insects, nectar and to a lesser extend fruits, seeds, bird eggs and fish remains (Prýṣ-Jones and Diamond 1984). The Madagascar Fody feeds mainly on seeds and flowers, but not on insects (Prýṣ-Jones and Diamond 1984).

Unlike many of its relatives, the Seychelles Fody is dull brown. Its only ornaments are yellow patches on the forehead and throat of the breeding male. During the non-breeding season the males resemble females. The breeding behaviour of the Seychelles Fody has previously been studied on Frégate (Crook 1961) and Cousin (Brooke 1985, Prýṣ-Jones and Diamond 1984). Both partners participate in territorial defense and provisioning of the young (Crook 1961) and only females attain a brood patch (Brooke 1985). Brooke (1985) further suggested that fledglings are mainly fed by the female. Parental roles in nest-building are unknown. None of these studies involved colour-banded populations and detailed knowledge of parental care is lacking.

Although not endangered at present, the Seychelles Fody has a restricted range and estimates of its population size and knowledge of its breeding ecology will benefit its future conservation. Here we report on observations on aspects of the breeding behaviour of the Seychelles Fody,
conducted on Cousine Island during a single breeding season. Some of our findings point to peculiarities that were previously unknown and warrant further study. We also made an estimate of population size on the island and provide sexing criteria that may be of use to future researchers.

Methods

Study site

The study was conducted on Cousine Island, which is one of the smallest islands inhabited by humans in the Seychelles. The island is privately owned and management is focused on conservation and restoration of the natural vegetation. Most of the island is covered by forest dominated by Pisonia grandis and Ficus reflexa. Madagascar Fodies were first seen on the island in 1958 (Lalanne, in Crook 1961) and are now common, although not as numerous as Seychelles Fodies and mainly confined to the coastal plateau (pers. obs.).

Study species

The study was conducted between 30 June and 25 August 1997, during the main breeding season, which lasts from May to September (Brooke 1985), although breeding may continue into December (Prýs-Jones and Diamond 1984). Unusually heavy rain at the end of the study period reduced insect numbers and caused almost total failure of the breeding season of Seychelles Warblers, Acrocephalus seychellensis, on Cousine (Kraaijeveld 1997). Numbers of seabirds were low compared with other years (P Hitchins pers. comm.). As islands with seabird colonies are known to support twice the arthropod numbers of islands without seabirds (Polis and Hurd 1996), this may have led to a secondary decrease in terrestrial arthropod abundance. For these reasons, the breeding season for Seychelles Fodies cannot be assumed to have been representative of the normal situation. Parameters such as breeding success and recruitment rate are thus likely to be misleading and are not reported. However, as all behavioural observations were conducted prior to the onset of the rains, these are unlikely to have been affected by subsequent bad weather.

A number of Seychelles Fodies on Cousine had been individually colour-banded during previous work (45 during March 1995 and a further 85 during May–July 1996). Subsequently, a total of 249 Seychelles Fodies were colour-banded during a banding exercise in July 1996 (Rocamora 1997).

During the study period, all banded birds seen in the field were mapped. A random point count (Bibby et al. 1992) was conducted to determine relative densities of Seychelles Fodies over the island. All birds seen or heard within 20 m from the observer while standing for 5 min at each of 30 randomly chosen points were counted. This was done twice (8 and 19 August) and observed numbers were averaged. Using a simplified version of the vegetation map of Cousine (Bourquin 1997), the available habitat on the island was divided into ten types (Figure 2). Each of the 30 random points was then categorised according to these types. The distribution of the 30 random points represented the habitat types well, since the number of points per habitat type was correlated closely with the area of that habitat type on the island ($r^2 = 0.7$, $n = 10$, $P < 0.01$). For each habitat-type the relative density of Seychelles Fodies was then determined from the point-count. Densities ($x$) were expressed as the average number of birds seen or heard during 5 min at each counting point, and were categorised as high ($x > 10$), medium ($5 < x < 10$) and low ($x < 5$). Over-estimation due to birds following the observer was minimised by visiting adjacent points at different times of day. The order in which points were visited was changed between the two days to minimise the effect of birds using different habitats at different times of day.

Adults were caught in mistnets and unbanded birds were individually colour-banded. The following measurements were taken: maximum wing chord (to the nearest 1 mm, using a butt-ended ruler), tarsus length (to the nearest 0.1 mm using callipers), bill height at the distal end of the nostril (to the nearest 0.1 mm using callipers), bill length (from base of feathering to the tip of the bill, to the nearest 0.1 mm using callipers) and mass (to the nearest 0.1 g, using a spring balance). The birds were caught opportunistically over the whole island. Biometric data were obtained during previous work in March 1995 ($n = 45$) and May–July 1996 ($n = 85$), as well as this study. Male Seychelles Fodies in non-breeding plumage closely resemble females and birds in brown plumage in the hand can thus be sexed unequivocally only as female when they have a brood patch (Brooke 1985), which was not recorded in our study. Therefore, sex was determined only for males in breeding plumage and birds that were sexed by their behaviour in the field. ‘Upright wing beating’ is a common nest-advertisement behaviour by males in forest-living weaver birds (Crook 1964) and therefore a bird in brown plumage performing such a display to another brown bird was considered a male. When only two birds were observed at a nest, the brown individual was con-
considered to be a female. When more than one brown individuals were observed at a nest, we did not assign sex. We developed univariate sexing criteria using software developed for this purpose (Rogers 1995). Briefly, the means and standard deviations were calculated for the two normal distributions underlying the bimodal histogram of the complete dataset for one measurement. From these upper and lower limits for each sex were calculated at different levels of confidence (Rogers 1995).

Breeding

Nests were searched for over the whole island. Every forested section of the island was visited at least once a week. For each nest we recorded the height (estimated to the nearest 0.5m), the tree species in which nest was built and the position of the nest in the tree. This was compared to the relative abundance of each tree species on the island as calculated from data in Bourquin (1997), who determined the abundance of each species in each of 14 plant communities. We used the area covered by these communities to calculate the relative abundance of the tree species on the entire island. The contents of nests that were within reach were checked weekly after discovery. When found, nests were observed for one hour during nest-building, incubation and provisioning of nestling and fledgling. One observation of cooperative breeding made during July 1996 is included. Data on breeding activity were compiled for nests at which all members of the breeding group were banded (see Table 1). Incubation was recorded as time spent in the nest and nest-guarding as the time spent within 10m of the nest. Nest guarding was defined thus, because Seychelles Fodies respond aggressively to decoy males only if they are placed within 10m of the nest (see section Territoriality under Results and Discussion). Nest-building and provisioning were expressed as the number of instances per hour. All colour-banded individuals that approached the nest or fledgling under observation to within 20m were identified.

Territoriality

A conspecific male in breeding plumage was placed in a chicken wire cage (50cm x 20cm x 20cm, open on all sides) at six positions relative to the nest and this was repeated for 15 pairs. Two additional trials were conducted using a male Madagascar Fody. The response of the breeding birds to the decoy was scored on a scale from 0–4 of increasing intensity, where: 0 = no reaction, 1 = approaching the cage within 2–5m, 2 = approaching the cage within 2–5m and giving alarm calls, 3 = approaching the cage within 2m and often displaying aggression, 4 = sitting on the cage and pecking at the decoy male. The starting position for each trial was chosen randomly and cages were subsequently moved towards or away from the nest at 5m intervals. Cages were left at each position for 3min.

Analysis

Means are given ± standard deviation. Biometric data did not deviate significantly from normality and were therefore analysed using unpaired, two-tailed t-tests. Non-parametric tests were used for all other data.

Results and discussion

Population census

Our banding data allow the population size of Seychelles Fodies on Cousine to be calculated in two ways. First, of the 106 birds we caught, 43 were recaptures of birds banded by
Rocamora a year prior to our study \( (n = 249) \), which includes some birds banded previously by others; Rocamora 1997). Using a Lincoln Index (Bibby et al. 1992), the total population can be calculated as: \( (106 \times 249)/43 = 614 \) birds. Second, a total of 185 previously banded individuals was seen on Cousine. The percentage of banded birds among adults in the captures was 40.4%. Assuming that the percentage of banded birds in the catches corresponds to the real percentage on the island, the minimum population of Seychelles Fodies on Cousine was estimated at \( 185/0.404 = 458 \) birds. As both observation and catching efforts covered the entire island, we feel confident this assumption was met. However, as it is unlikely that we recorded all colour-banded birds present on Cousine, the latter figure is an underestimate. In conclusion, we estimate the population of Seychelles Fodies on Cousine to comprise 458–614 birds. This figure corresponds well to the estimate of 518 obtained by Rocamora (1997). The latter estimate was also calculated using a mark-resighting method, although the interval between marking and resighting was much shorter than during our study. Brooke (1985) also used a Lincoln Index to obtain his population estimate of 1300 birds for Cousin, although during that study birds were caught in only a small part of the island.

Using our first population estimate of 614 individuals of which 40.4% were banded, the total number of banded individuals on the island in 1997 was estimated at 248. The total number of birds banded in 1996 was 249 + 85 = 334, which included an unknown number of individuals that had already been banded in 1995. Annual survival between 1996 and 1997 was thus estimated at \( (248/334) \times 100 = 74\% \). This is slightly lower than the 79–83% estimated for Cousin (Brooke 1985).

Densities of Seychelles Fodies varied over the island (Table 2, Figure 2). The highest concentration of fodies was found in the gardens (habitat type 2), while plateau area (habitat type 1) and the forest (habitat types 5, 7, 8, 9, 10) held medium numbers. Concentrations were lowest on the sparsely vegetated west and south coasts of the island (habitat types 3 and 4) and in Pandanus woodland (habitat type 6). Although the sample sizes for these estimates are small, the repeatability of the counts is reasonable (Spearman rho = 0.41, \( P < 0.05 \)).

### Biometrics

The biometrics of Seychelles Fodies caught during this study are summarised in Table 3. Sexing was difficult, apart from males in breeding plumage. One bird in male plumage, which was caught in July, had previously been banded in female-type plumage in June 1996. Twenty-six individuals were identified as female based on their associations with breeding males. For nine of these, biometric data were available. Females had a significantly shorter wing chord and tarsus length than males (Table 3). However, we found no intersexual differences in bill length, bill height and weight. Wing length was found to be the only measurement for which the histogram showed two sufficiently distinct peaks for univariate sexing criteria to be calculated. These are summarised in Table 4 and may be useful when attempting to sex Seychelles Fodies in female-type plumage. Using the criteria at 90% confidence, 78% of 76 known males would have been correctly identified as males, while 2% would have

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<th>Density ± SD 8/8/1997</th>
<th>Density ± SD 19/8/1997</th>
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<td>2</td>
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<tr>
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<td>6.3 ± 2.5</td>
<td>4 ± 2</td>
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### Table 2: Mean number of Seychelles Fodies counted during random point count for each habitat type. See Figure 2 for description of habitat types

### Table 3: Biometrics (in mm) of Seychelles Fodies caught on Cousine during March 1995 \( (n = 45) \), May–July 1996 \( (n = 85) \) and July–August 1997 \( (n = 75) \) and sexed on plumage or behaviour

<table>
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<th></th>
<th>Males</th>
<th>Females</th>
<th>Unsexed</th>
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<tr>
<td>Wing chord</td>
<td>74.5 ± 1.6 ( (n = 76) )*</td>
<td>69.3 ± 1.4 ( (n = 9) )</td>
<td>70.3 ± 2.1 ( (n = 94) )</td>
</tr>
<tr>
<td>Tarsus</td>
<td>20.6 ± 7.1 ( (n = 77) )*</td>
<td>19.8 ± 11.1 ( (n = 9) )</td>
<td>20.0 ± 6.9 ( (n = 98) )</td>
</tr>
<tr>
<td>Bill length</td>
<td>15.3 ± 5.8 ( (n = 22) )</td>
<td>15.2 ± 8.7 ( (n = 3) )</td>
<td>15.3 ± 7.3 ( (n = 34) )</td>
</tr>
<tr>
<td>Bill height</td>
<td>6.5 ± 2.5 ( (n = 22) )</td>
<td>6.7 ± 1.7 ( (n = 3) )</td>
<td>6.4 ± 2.5 ( (n = 34) )</td>
</tr>
<tr>
<td>Mass</td>
<td>19.1 ± 11.9 ( (n = 54) )</td>
<td>18.1 ± 13.9 ( (n = 8) )</td>
<td>18.5 ± 13.6( (n = 70) )</td>
</tr>
</tbody>
</table>

* Significantly different from the values for females \( (P < 0.001) \) and unsexed \( (P < 0.001) \)

* Significantly different from the values for females \( (P < 0.005) \) and unsexed \( (P < 0.001) \)

All other comparisons are not significant
been wrongly sexed as female. The remaining 20% would have remained unsexed. All wing measurements of nine known females were within the 90% confidence limits for females. Using these limits, 70 (74%) of the 94 unsexed birds were female, eight (9%) were male and 16 (17%) were of unknown sex. In summary, the overall sex ratio in the sample for which wing length was measured would have been estimated at 67 males, 81 females and 31 unsexed birds using these criteria.

Breeding
The characteristics of 31 nests, of which 26 were active and five were old, were described. The height at which these were built in the trees ranged from 0.2–10m (mean = 3.4 ± 2.0). The majority of nests (67.7%) were suspended from the ends of branches, while the remaining nests were located close to the trunk. A wide range of tree types was used (Figure 3). Citrus bushes were used significantly more often than expected on the basis of their abundance on the island. A similar preference for dense citrus bushes for nesting was reported for Frégate (Crook 1961). Euphorbia pyrifolia was used less often than expected, presumably because of its relatively open foliage. Usage of the other tree species did not differ significantly from random (Figure 3).

Since all parts of the island were searched with equal intensity and visibility of nests did not vary greatly between habitats, Figure 2 is representative of the nesting densities. Six congregations of two to five nests in close proximity (within a 20m radius) were found (see Figure 2). The remaining nests were distributed fairly evenly over the island. No clustering of nests was found on Frégate (Crook 1961). In total, 41 nests and four fledglings were found. Of these nests, 28 were active and all except one were accessible enough to allow monitoring of the contents (Table 1). Most (94%, n = 17) nests were deserted before egg-laying and in 41% of these cases, the nests were deserted before nest-building was complete (Table 1). One pair abandoned a nest and started another 50m away, indicating that at least some of the abandoned nests had been accepted by a female. This curious behaviour has also been reported for the Mauritius Fody, Foudia rubra (Safford 1997). Of five nests where observations of nestbuilding were made, both sexes were seen building at three nests, only the male at one nest and only the female at one nest. All other conspecifics were chased away. Both sexes were seen to build at nests in very early stages of construction. Nestbuilding intensity varied from 1–8 instances per hour. The nest can take 27 days to complete (n = 1).

Two males were seen to display to females using 'upright wing beating' (Figure 4). In both cases the female responded by crouching along the branch, facing the male with her bill opened and pointed upward. This response, depicted in Figure 4, is different from the copulation solicitation behaviour described by Crook (1961), in which the female spreads her wings and faces away from the male. One male observed performing this display was in breeding plumage and building a nest nearby. The other individual seen to display to a female was in female-type plumage. Neither of these displays resulted in copulation, although the latter bird unsuccessfully attempted to mount the female. The function of the 'upright wing beating' display is unclear. The first of the two cases described here appears to be consistent with nest advertisement behaviour common to many weavers (Crook 1964). However, females were seen building at very incomplete nest structures and one pair moved to a new nest together. Crook (1961) suggested that Seychelles Fodies, in contrast to many other species of weaver, have no nest invitation. The same appears to be true for the Mauritian Fody (Safford 1997). Our observations on Seychelles Fodies are contradictory.

Only females incubated eggs (n = 6), at a mean rate of 22.7 ± 12.3min/hr. Of the five clutches that could be inspected, four had two eggs and one had one egg. Eggs were completely white and measured 13.8 ± 0.4mm by 20.3 ± 0.6mm (n = 4). During incubation males spent a lot of time guarding the nest (21.3 ± 12.9min/hr; n = 6 nests). Males were typically away from the nest while females were incubating, suggesting that they guard the eggs, rather than the females. During nest guarding, males chased away other Seychelles Fodies on five occasions (mean 0.8 ± 1.3 times per hour). At one nest both partners attacked and successfully chased a Wright’s skink Mabuya wrightii, an egg predator (Komdeur and Kats 1999), which was on the branch in which the nest was built. We did not observe courtship feeding during any stage of the breeding cycle.

Observations during the nesting phase were conducted at six nests. Both males and females fed nestlings by regurgitation. Females tended to feed more than males (1.8 ± 1.3 and 0.4 ± 0.9 attempts per hour, respectively, n = 5; Wilcoxon Z = 1.8, P = 0.07). Males spent a similar amount of time guarding the nest as during incubation (14.0 ± 5.4min/hr, n = 4; Mann-Whitney U = 16, P > 0.5). At a single nest observed in July 1996, only the resident pair was seen during incubation. However, three different female-plumaged birds and one male were subsequently seen feeding the nestling.

Seven fledglings were found during the study period (Table 1). Provisioning efforts to three fledglings were observed inside their natal territory just after fledging, while their flight abilities were still poor. Two of these were fed exclusively by the male (three and five times per hour). The

<table>
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<th>Confidence level</th>
<th>Upper limit for females</th>
<th>Lower limit for males</th>
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<th>Unsexed</th>
<th>Incorrect</th>
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<td>64%</td>
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Table 4: Univariate sexing criteria for Seychelles Fodies based on wing chord measurements (in mm). Theoretical percentages of birds sexed correctly and incorrectly at the given confidence levels are included. Method follows Rogers (1995)
nests from which these birds had fledged were not found and it was therefore not known if they had siblings. However, a brief observation of another fledgling, being fed by a female within 20m of one of these two, suggests that when two young fledge, the parents may split up and take care of one fledgling each. The third fledgling at which a provisioning observation was conducted was fed by the male, the female and a male and a female-plumaged helper. The sibling of this fledgling had died just before fledging. Unfortunately, no provisioning data were collected for this group while the young were still in the nest. Three hours observation of this group yielded the following mean feeding efforts per hour; male = 1.7 ± 0.6, female = 1.3 ± 0.6, helper male = 0.3 ± 0.6 and helper ‘female’ = 0.3 ± 0.6. This group was located in the area on the island which has the highest density of Seychelles Fodies (Figure 2) and the nest was within 20m of another nest.

After 21–26 days (n = 2) fledglings started making trips out of the territory. These fledglings were both accompanied by the female only. Distances covered were relatively large; fledglings were seen about 300m away from their territory of origin. Food items delivered to the fledglings included banana and paw-paw, but most were unidentifiable. Fledglings did not achieve independence for a considerable period and one bird was still begging for food after 44 days.

In a study by Brooke (1985), 31 juveniles were fed by a female, while only one juvenile received food from a male. Brooke (1985) suggested that males feed only when two young fledge from a nest, but no prolonged provisioning watches were performed during his study. Although we did observe one possible case of brood partitioning, our observation that both parents feed the nestlings and at least some fledglings, suggests that brood partitioning is unlikely to be frequent.

In summary, the species exhibits a socially monogamous mating system, in which both sexes share most parental duties. This is typical for forest-living weaverbirds (Crook 1964). Whether the pair-bonds are sustained for multiple breeding seasons, as suspected by Crook (1961), remains to be determined. Our study is the first to report cooperative breeding in the Seychelles Fody. We had no data on the relatedness between the cooperating individuals in any of the groups. Both cases of helping were in clusters of nests in close proximity (four and two nests). Cooperative breeding is rare in Ploceidae, and has been recorded in only four out of 144 members of this family (Brown 1987), none of which are in the subfamily Ploceinae to which the Seychelles Fody belongs. Although twelve nests were observed closely on Frégate by Crook (1961), no cooperative breeding was recorded. However, very few birds were banded during Crook’s study, so cooperative breeding would have been hard to detect.

Seychelles Fodies form foraging groups, consisting mainly of non-breeding individuals. Thirty-five such groups were described and ranged in size from 3–18 individuals (mean = 6.7 ± 4.1). These groups usually contained more birds in female-type plumage than males in breeding plumage. The mean percentage of males in breeding plumage in the groups was 34% (range 0–66.7%), while the
percentage of female-type birds ranged from 33%–100% (mean = 66%). The number of males per group did not increase significantly with group size (linear regression $r^2 = 0.05$, $n = 35$, $P > 0.19$), and large groups contained mainly females and/or males in eclipse plumage. Foraging group size did not decrease as the breeding season progressed (linear regression group size = -0.02x + 7.7; $r^2 = 0.0004$; $n = 4$, $P > 0.8$). These groups tended to remain in the same area, although individuals left and rejoined them freely. On 12 occasions the same individuals were seen in different groups located elsewhere on the island. Breeding individuals sometimes also joined these aggregations, probably while foraging. On only two occasions two members of the same breeding unit were seen in the same feeding flock. In contrast, breeding birds were seen associated with birds from other breeding groups four times. Twice two birds from the same breeding group were seen in different feeding flocks. Seychelles Fodies on Frégate typically moved around in pairs or small family groups (Crook 1961), rather than in the large flocks we observed during our study. The dynamic nature of these groups and the observation that birds from the same breeding units associated with different flocks seems to argue against a family-based group composition on Cousine.

**Territoriality**
The results of the intrusion-experiment are presented in Figure 5. In all cases, the male and the female responded to the decoy male with equal intensity. The pairs were more likely to respond to the experimentally intruding male at the nest during incubation than during the other stages of the breeding cycle (Figure 5a; $\chi^2_3 = 13$, $P < 0.01$). The intensity scores were also higher during incubation than during other stage (Kruskal-Wallis H = 9.8, $P < 0.02$). This also appeared to be true within pairs. One pair was tested during two stages, and responded much more intensely during incubation (response 4) than during nestbuilding (response 1). The pairs were also significantly more likely to respond when the decoy male was closer to the nest (during incubation see Figure 5b; $\chi^2_3 = 19$, $P < 0.01$). The intensity of the responses was higher when the decoy was closer to the nest (Kruskal-Wallis H = 17.3, $P < 0.01$). Nests were not defended when the decoy male was more than 20m away. On Frégate pairs were found to defend territories up to 50m from the nest, more than twice the size of the territories on Cousine (Crook 1961). Fledglings were often not defended at all, which resulted in significant harassment of the fledglings. One fledgling, which was being fed by four different Seychelles Fodies, was repeatedly attacked by a pair of Seychelles Warblers, without interference from the parents or helpers. An intruding male attempted to copulate with another fledgling, which was fed only by the male parent, no less than 11 times when the parent was away gathering food.

The intrusion experiments show that both partners actively defend the nest against other Seychelles Fodies. Observations showed that the nests are guarded by the males during the incubation and nestling stage, although the response to the experimental Seychelles Fody was strongest during incubation. As Seychelles Fodies prey on eggs of other birds, including seabirds and Seychelles Warblers (Komdeur and Kats 1999), predation on eggs of other fodies may also occur. However, we have no records of this. Nestlings and fledglings are probably safe from other fodies. Both eggs and small nestlings are probably vulnerable to predation by Wright’s Skinks, which are very common on Cousine (538 adults/ha in the wooded areas, S LeMaitre pers. comm.), and known to prey upon eggs and nestlings of Seychelles Warblers (Komdeur and Kats 1999).

Another possible nest predator, the Common Myna, *Acridotheres tristis*, which is known to take fody eggs (AW Diamond in litt.), occurs on Cousine infrequently and in small numbers.

A male Madagascar Fody was introduced at two pairs and results were similar to those obtained with a male Seychelles Fody at the same nests (both incubating: Madagascar Fody response 4 and 3, Seychelles Fody response 4 and 4, respectively). The aggression Seychelles Fodies display towards the introduced and closely related Madagascar Fody, which does not eat eggs, might be a defense against the stealing of nest material, which the latter has been seen to do on Cousin (Komdeur unpublished).

**Conclusion**
As pointed out above, some of the behaviour displayed by the Seychelles Fodies on Cousine differs from that reported from Frégate (Crook 1961). Breeding territories on Cousine

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**Figure 5:** The percentage of breeding Seychelles Fody pairs responding to an experimental intruding male (a) during different stages of the breeding cycle within 20m of the nest ($n$ is indicated above the bars), and (b) at increasing distances from the nest during incubation ($n = 5$)
are smaller, while feeding flocks are larger than those report-
ed by Crook (1961). Furthermore, Crook (1961) observed no
cooperative breeding or clustering of nests. Interestingly,
similar differences seem to exist between the Seychelles
Fodies on Cousine and the endangered Mauritius Fody,
which inhabits remnant native forest on Mauritius (Safford
1997). Like the Seychelles Fody, the Mauritius Fody exhibits
social monogamy and biparental care, but territories are
substantially larger than those found in our study and are
maintained all year round (Safford 1997). Pairbonds in this
species are thought to be long-term (Safford 1997). Both the
Mauritius Fody and the Seychelles Fody on Frégate at the
time of Crook’s (1961) study occurred at much lower popu-
lation densities than the Seychelles Fody on Cousine
(Safford 1997, Gaymer et al. 1969). It would therefore seem
that the high densities of Seychelles Fodies on Cousine
have led to small territories, semi-coloniality, large flocks
of non-breeding birds and cooperative breeding.

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References


Island Report, unpublished

Brooke M de L 1985. The annual cycle of the Toc-toc Foudia
sechellarum on Cousin Island, Seychelles. Ibis 127: 7–15


Collar NJ and Stuart SN 1985. Threatened Birds of Africa and
Related Islands. The ICBP/IUCN Red Data Book Part I.
ICBP/IUCN, Cambridge

Crook JH 1961. The Fodies (Ploceinae) of the Seychelles islands.
Ibis 103a: 517–548

Crook JH 1964. The evolution of social organization and visual
communication in the weaver birds (Ploceinae). Behaviour
Supplement 10

Diamond AW 1984. Biogeography of Seychelles land birds. In:
Stoddart DR (ed) Biogeography and Ecology of the Seychelles

Gaymer R, Blackman RAA, Davidson PG, Penny M and Penny
CM 1969. The endemic birds of the Seychelles. Ibis 111:
157–176

between nest guarding and foraging in Seychelles Warblers.
Behavioural Ecology 10: 648–658

Kraaijeveld K 1997. The Cousine Seychelles warbler population:

Losos JB 1986. Island biogeography of Day Geckos (Phelsuma) in
the Indian Ocean. Oecologia 68: 338–343

Foudia madagascariensis and Seychelles fody Foudia sechel-
larum on Aride Island, Seychelles. Bird Conservation
International 7: 1–16

Moreau RE 1960. The Ploceine weavers of the Indian Ocean
Islands. Journal für Ornithologie 101: 29–49


Polis GA and Hurd SD 1996. Linking marine and terrestrial food
webs: allochthonous input from the ocean supports high second-
ary productivity on small islands and coastal land communities.
American Naturalist 147: 396–423

on the granitic and coraline islands of the Seychelles, with par-
ticular reference to Cousin Island and Aldabra Atoll. In: Stoddart
DR (ed) Biogeography and Ecology of the Seychelles Islands. pp
529–558. Dr W Junk Publishers, The Hague

Rocamora G 1997. Rare and threatened species, sites and habitats
monitoring program in the granitic Seychelles. Report Ministry of
Environment Seychelles/Birdlife International EU

Rogers KG 1995. Computer programs for sexing birds on measure-
ments using univariate data. Corella 19: 25–34

Safford RJ 1997. The annual cycle and breeding behaviour of the

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