CORELLA
Journal of the Australian Bird Study Association

Volume 33 Number 1 March 2009

Corella, 2009, 33(1): 1-6

THE BREEDING BIOLOGY OF THE WHITE-RUMPED SWIFTLET *Aerodramus spodiopygius spodiopygius* IN SAMOA

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Received: 2 August 2004

In the lava-tube caves of Samoa the White-rumped Swiftlet *Aerodramus s. spodiopygius* has a protracted breeding season, laying eggs every month of the year. It builds nests of vegetation and saliva that average 44.7 × 43.7 × 11.8 millimetres in size, 5.1 metres from the cave floor and 5.2 metres from their nearest neighbour. These nests took 19 days to three months to build and usually contained a single egg weighing 1.6 grams and 18.2 × 12.3 millimetres in size. The nests lasted an average of 9.4 months and were used to raise up to three broods. The eggs took 25 or 26 days to hatch and the nestlings fledged in 47–57 days. Nesting success was 72 per cent in the Tafatafa colony and 45 per cent in the Falemauga Small Cave colony. The 72 per cent success rate is the highest for any swiftlet studied to date. The 45 per cent rate was probably a result of a combination of low placement of some nests, infertility, predation by rats or disturbance by observers.

INTRODUCTION

It was previously thought that in Samoa White-rumped Swiftlets *Aerodramus s. spodiopygius* laid a single egg (data from only five clutches held in the American Museum of Natural History – but these lacked clear field notes). It was also thought that the climate was distinctly seasonal (Cumberland 1968), which led to the possibility that the Samoan subspecies might utilise nestling incubation. Whitmee's (1875) suggestion that the White-rumped Swiftlet in Samoa had a synchronised breeding season also added weight to the premise of a short breeding season with accompanying strategies.

Studies of White-rumped Swiftlets in Fiji and Queensland (Tarburton 1986, 1987a, 1987b, 1988) revealed very different breeding strategies so this study was initiated to determine if the Samoan subspecies used similar or different breeding strategies. In Queensland White-rumped Swiftlets have a contracted breeding season in which they produce two single-egg clutches with timing such that the first nestling incubates the second egg (Tarburton and Minot 1987; Tarburton 1988). In Fiji, where its prey is a little more abundant and its breeding season a little longer, it produces a clutch of two (Tarburton 1986). Its very close relative, the Atiu Swiftlet *A. sawtelli* on Atiu (Cook Islands) also produces a two-egg clutch but instead of clumping its nests it scatters them widely throughout the colony to avoid depredation by the two species of crabs that predate them (Tarburton 1990).

METHODS

The location and size of the breeding colonies providing data for this study are given in Tarburton (in press). Much of these data were collected during 1994–97 inclusive, from 50 one-off visits to 38 caves on the islands of Upolu and Savai'i. Individual nests and their contents were examined closely in only two of those caves. These were Tafatafa Cave and Falemauga Small Cave, both on Upolu Island. In these caves nests were identified by securing uniquely numbered tags to each with an electrician's nylon cable strap. Numbers were printed on thin laminated card 3 x 3 centimetres in size. In assessing the number of breeding attempts made by a pair it was assumed that pairs remained together at the same nest as long as that nest lasted. At the time of daily visits, Tafatafa contained ten nests and Falemauga Small Cave held 23 nests. The former was visited six days a week during June and July 1994 and the latter during September to November 1994. The time taken to replace lost clutches and broods is not particularly accurate due to visits to these two caves over the four years being a mixture of daily (n = 40), weekly (n = 3), and monthly (n = 15) censuses.

Eggs and nestlings were weighed on Pesola 5, 10 and 30-gram spring balances; eggs and nests were measured with Bergeon dial callipers and flattened wing chord measured on a chocked BOU metal ruler. Distances were measured to each nest's nearest neighbour within a cave. The measures of nest duration (period from construction to abandonment) should be taken as minimal for some may have lasted up to two months longer without detection of their demise. The time of abandonment of a nest was determined by its falling from the wall or roof, or the cessation of white excrement appearing on the floor below an existing nest. It was determined that the white part of the swiftlets excrement lasted on the floor between one and two weeks. This was not only useful for locating new nests but also for determining when a nest was no longer used. Nest length, breadth, depth and external height of the nest were

measured. Nests were recorded as being in the twilight zone or in the totally dark zone of each cave. The latter is defined as where light from the cave entrance cannot be seen after an hour of the observer's visual accommodation.

Rainfall data were collected from the Meteorological Office in Apia and their recording methods were assessed by comparing their daily records with their monthly and annual summaries. Humidity in the caves was determined by taking readings on wet and dry bulb thermometers and then read from a standard chart. Ambient temperature was recorded in three caves.

RESULTS

Nests and nest sites

All nests were made of plant material, which was held together and to the wall with varying amounts of saliva. Most nests were placed on ledges and only a few were placed on the wall using the bracket and cup construction typical of swiftlets (Medway 1966). The identity and frequency of the plants used in the nests is shown in Table 1**.** The nest composition varied seasonally and varied even more with location. For example, 80–90 per cent of nests in the Falealupo South caves (Savai'i Island) were composed of Mile-a-minute *Mikania micrantha* and only 10–20 per cent were composed of mosses. In contrast it was rare to find any Mile-a-minute strands in the moss nests of Tiapapata Cave (Upolu Island). The moss in the rim of these nests was often living, even in locations that were in, what appeared to be, totally dark locations. The linear frond of the

TABLE 1

Plant composition of White-rumped Swiftlet nests in Samoa.

Plant Species	Number (n = 84)	Percentage
Moss bases with Mile-a-minute rims	33	39
Moss and lichen	13	16
Mile-a-minute *Mikania micrantha*	13	16
Moss (mostly branching types)	11	13
Grass (unidentified)	5	6
Fern *Vaginularia angustissima*	3	4
Lichen	2	2
Fern and lichen	1	1
Coconut-crown sheath fibre *(Cocos nucifera)*	1	1
Moss base with Elephant Grass *(Pennisetum purpureum)* rim	1	1
Couch-type grass	1	1

TABLE 2

Distances between nests for a sample of cave colonies in Samoa.

Cave	Date	Mean	*sd*	min	max	*n*
Satalo	15.09.1994	1.2	0.99	0.3	4.2	36
Falemauga sm	25.10.1994	2.1	1.4	0.35	6.2	28
Samatau	12.12.1994	1.8	1.21	0.4	3.4	8
Vaitoamuli	11.02.1995	1.7	1.71	0.09	6	34
Asau #1	11.02.1995	3.7	1.91	2.3	5	2
Asau #2	11.02.1995	2.5	2.08	0.5	6.3	9
Asau #3	11.02.1995	1.8	0.98	0.6	3.5	9
Saleaula	10.07.1994	2.4	2.01	1.2	5.4	4
Lano	08.08.1996	3.8	2.49	0	7.8	26
Salamumu #3	04.11.1996	3	1.52	1.2	6	12
Apolima Uta L	12.11.1996	2.2	1.5	0.35	3.6	5
Apolima Uta S	12.11.1996	65				2
Anaseuao	25.11.1996	13.1	20.88	1	58	11
Samatau-i-uta	04.10.1997	16.7	10.6	7	28	3
Satuiatua	03.10.1997	8.8	6.99	0.5	23	12
Falealupo Sch	04.10.1997	7.9	11.38	2.3	31	6
Mago	04.10.1997	20.2	25.21	1	85	16
Falealupo 400S	04.10.1997	11.3	12.73	1	45	14
Manunu	24.11.1997	1.3	0.98	0.35	3	15

TABLE 3

Height of White-rumped Swiftlet nests above the cave floor in Samoan caves.

Cave	Date	Mean	*sd*	min	max	Number of nests
Satalo	15.09.1994	4.2	2.46	1.6	10.2	52
Lalonea	30.09.1994	2	0.69	1	3.7	28
Samatau	12.12.1994	2.2	0.29	1.6	2.6	8
Vaitoamuli	11.02.1995	2.9	0.97	1.3	5	31
Asau #1	11.02.1995	2.1	0.25	1.9	2.4	3
Asau #2	11.02.1995	3.6	1.06	2.1	5.5	19
Asau #3	11.02.1995	2	0.28	1.6	2.4	10
Letui	12.02.1995	2.4	0.29	2	2.8	6
Saleaula	10.07.1994	2	0.66	1	3	9
Lano	08.08.1996	8.8	1.25	7.2	11	27
Salamumu #3	04.11.1996	4.8	0.72	4	6	12
Apolima Uta S	12.11.1996	2.8		2.7	2.9	2
Apolima Uta L	12.11.1996	4.6	0.27	4.2	5	8
Anaseuao	25.11.1996	3.2	0.78	2.4	4.5	13
Satuiatua	03.10.1997	5.7	1.54	3	8	16
Falealupo	04.10.1997	3.5	1.13	1.44	4.8	7
Samata-I-uta	04.10.1997	1.3	0.25	1	1.44	3
Falealupo Sch	04.10.1997	1.3	0.25	1.01	1.5	3
Mago	04.10.1997	4.1	1.87	1.3	8.2	17
Falealupo 400mS	04.10.1997	5.4	1.95	2.3	9	15
Falealupo 400mN	04.10.1997	29.6	9.21	2	35	14
Manunu	24.11.1997	3.3	0.56	2.3	4.2	20

small epiphytic fern *Vaginularia angustissima* was used in four per cent of nests, particularly in caves near mature forests. The swiftlet's own flight and body feathers were often incorporated into the nest structure in low proportions.

Nests averaged 5.2 metres (range 0–85 m; *sd* = 10.73; *n* = 252; see Table 2 for sample of colonies) from their nearest neighbour. Most of these colonies were not closely packed compared to nests in Fiji and Queensland, probably because it was just four to eight years after cyclones had drastically reduced their populations. Further evidence for this being the reason for low-density nesting is given in Tarburton (in press).

Most nests were placed in total darkness, though in some caves a small percentage was in the twilight zone. The average height of nests above the cave floor was 5.1 metres (*sd* = 5.98) ranging from 1–35 metres (*n* = 323) – see Table 3. In some caves nests could be reached without the use of a ladder, but as the average height indicates, most nests could only be reached utilising a ladder. Nests had the dimensions shown in Table 4, which gave an average internal volume index ($l \times b \times d$) of 23.2 cubic centimetres. Nests generally took one to three months (± 1 week) to build though nest number 23 (Falemaunga Small Cave) was built in 19 days, but in that case it was 30 days before an egg appeared in the nest.

The duration of nests varied from two to 31 months averaging 9.4 ± 7.7 months (mean ± *sd*; *n* = 21). Some of the short-lived ones were built during dry spells in normally very moist sites and could not hold together when water flowed almost continuously over them. Other nests were destroyed apparently by rats but those that lasted the longest were in dry locations out of reach of rats and were periodically repaired by the addition of vegetation and saliva.

TABLE 4

Nest dimensions of White-rumped Swiftlets in Samoa.

	Length	Breadth	Depth	External Height
Mean	44.7	43.7	11.8	35.1
sd	5.5	6.2	4	21.7
Min	31	33	5	12
Max	55	59	19	150
Number of nests	42	42	42	45

Nests contained few parasites compared to those seen on swiftlet nests in Queensland (Tarburton 1988) and West Papua (Tarburton 2003). Ectoparasites included an unnamed Hippoboscid or louse fly *Myophthiria* spp, (Maa 1980), probably several species of feather lice and the head louse *Dennyus tarburtoni* (Clayton *et al.* 1996).

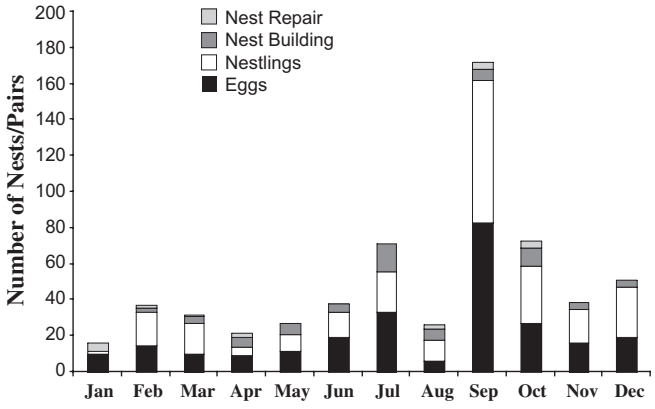

Figure 1. *Breeding season of the White-rumped Swiftlet in Samoa, showing nest construction and repair, and numbers of eggs and nestlings observed for each month.*

Nesting season

Eggs are white, without gloss and elliptical to long elliptical in shape and were laid in all 12 months of the year with an obvious peak in the Austral Spring (Fig. 1). The building of new nests and the repair of old nests also occurred in all months but peaked just prior to the peak in egg laying. This lack of a constricted breeding season did not fit the published climate data, which indicated considerable variability within a year and between years. A closer look at the meteorological data showed many gaps in the records, as well as inclusion of incomplete monthly and annual records in determining averages. This produced greater variability than when these incomplete data were omitted from average monthly rainfall calculations.

Clutch size is normally one egg (n = 30). In addition to these data from Falemaunga Small Cave where records were made daily for two weeks, another 313 single clutches were recorded from less frequent visits to this and other caves. These infrequent visits also detected 12 clutches of two eggs. In one of these nests one egg was milky and in another one was blood red when inspected by candling. In a third the first egg had remained in the nest for five months, so the second egg was probably a replacement egg in these three cases. The other nine clutches were not examined thoroughly or often enough to make a similar judgment. Of this latter group two nests were later observed with two nestlings in them, but whether these were produced by one or two females is unknown.

The average mass was 1.6 grams (range = 1.2–1.98 g; sd = 0.13; n = 70); average length was 18.2 millimetres (range = 16.7–20.1 mm; sd = 0.69; n = 113) and average breadth of the same 113 eggs was 12.3 millimetres (range = 11.2–13.7 mm; sd = 0.35).

The incubation period for an egg in Tafatafa Cave in June 1974 was 25 days (± 1 day). Another egg in the Falemauga Small Cave hatched in 26 days (± 1 day).

As the ambient temperature has been shown to affect the incubation period, temperatures were taken in three of the caves near the nests. One temperature reading taken in the open chamber of Tafatafa was two degrees cooler than at the nest site that was measured each trip. The average temperature in Tafatafa was 27.96 ± 1.01°C with a range of 26.2–29.5°C (n = 16). The average temperature in Falemauga Small Cave was 26.47 ± 1.5°C with a range of 24.3–29°C (n = 33). A single temperature taken near the nests in Satalo cave was 24°C. High humidity is normal in tropical caves and the Samoan caves are no exception. Readings taken each month of the year in Falemauga Small Cave ranged between 95–98 per cent.

Moult

The majority of birds do not moult and breed simultaneously but swiftlets are exceptions to this trend. All birds caught diurnally in the caves are presumed to be breeding (proven in most cases). Their moult does not show a distinct seasonality (Table 5). Moult was initiated in five different months and completed in eight different months in a year. The duration of moult in any individual was not determined.

Nestling Development

The mass of three newly hatched nestlings was 1.2, 1.22 and 1.3 grams. The growth in mass per day is shown in Figure 2 and the increase in wing length in Figure 3. Hatchlings were naked and developed no down before the emergence of adult feathers. Primary pins were the first flight feathers to appear and they broke through the skin on day 14 (n = 1) and erupted from their sheath between day 17 and day 21 (n = 2).

The average adult mass of 9.03 (sd = 0.93g; n = 170) was reached on day 18 by a Tafatafa individual and between an estimated 22 and 37 days in the Falemauga Small Cave colony (n = 4). Nestling mass peaked at 10.3 grams on day 41 in the Tafatafa individual and between 9.2–10.1 grams between days 40 and 54 in the Falemauga colony (n = 4). Average adult wing length (119.3 ± 2.54 mm - mean ± sd; n = 165) was not reached by any of the nestlings before they fledged. Minimum adult wing length was 111 millimetres and this measure was exceeded by four birds from the Falemauga Small Cave colony reaching 112, 113, 116 and 118 millimetres prior to fledging. A fifth bird had a wing of 109 millimetres when its nest fell from the ledge and it was not seen again. The age of the four fledglings at their departure was estimated to have been 47, 48, 54 and 57 days.

Nesting success and nestling mortality

The hatching rates in the two caves visited daily were significantly different (χ^2 = 3.9, P<0.05), but the fledging rates were not significantly different (χ^2 = 2.1, P>0.1). In Tafatafa Cave 15 of 18 eggs hatched (83%) whereas in Falemauga Small Cave only 31 of 59 eggs hatched (52.5%). The fledging rate in Tafatafa Cave was 87 per cent (n = 18) and in Falemauga Small Cave it was 86 per cent (n = 36). This means that in Tafatafa Cave 72 per cent of the eggs laid produced fledglings, whereas in Falemauga Small Cave only 45 per cent of the eggs laid matured to the fledgling stage.

Rat *Rattus* spp footprints were seen near the nests in Falemauga Small Cave and observations of the remains of dead adults and nestlings were consistent with rat predation, rather than cat or raptor. Numerous rat footprints were seen in the nearby Falemauga Large Cave where a large pile of bird remains gave evidence of their predation of the swiftlets. Rats were also seen in Tiapapata Cave. An Eastern Barn Owl *Tyto javanica* was the likely predator in Satuiatua Cave on Savai'i, as eggs disappeared and fell from nests rats could not reach, and the locals reported seeing Lulus (Barn Owl) in that cave.

TABLE 5

Progress of moult in the primary (P) flight feathers of White-rumped Swiftlets in Samoa.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Number of birds sampled	1	17	51	8	8	0	20	14	14	32	15	6
Number in moult												
P1	-	-	2	-	-	-	-	1	1	3	1	-
P2	-	1	-	1	-	-	-	-	2	2	2	-
P3	-	-	-	-	-	-	1	-	3	2	1	-
P4	-	-	1	-	-	-	1	-	2	1	2	1
P5	-	1	1	-	-	-	-	1	-	4	-	2
P6	-	1	1	-	-	-	-	-	1	4	1	1
P7	-	5	2	-	-	-	1	-	-	2	1	-
P8	1	4	6	1	-	-	-	-	-	-	3	-
P9	-	-	8	-	1	-	-	1	-	-	-	-
P10	-	-	11	1	5	-	2	2	1	2	-	1
Number not in moult	-	5	19	5	2	-	15	9	4	12	4	1

DISCUSSION

Nests

The average nest size (volume index = 45.3 ± 0.6 cm^3) is interesting in that its cavity volume is closer to that of the nests of the Atiu Swiftlet (41.9 ± 0.6 cm^3 – Tarburton 1990) in the Cook Islands and the White-rumped Swiftlet *A. spodiopygius assimilis* in Fiji (52.0 ± 0.5 cm^3 – Tarburton 1986) which contain two nestlings, rather than the White-rumped Swiftlet *A. s. chillagoensis* nests in Queensland (25.0 ± 0.5 cm^3 – Tarburton 1988) which contain one nestling.

Tarburton (1986) tentatively concluded that the nests of White-rumped Swiftlet in Fiji and those from Samoa were very similar, even though it was clear that Medway (1966) had confused the origins of some of the nests he was studying in British and American Museums. This assumption was incorrect as almost all Fijian nests are self-supporting whereas almost all Samoan nests are built on a ledge or protrusion from the wall. Fijian nests have very thin walls whereas Samoan nests have much thicker walls and may be built to quite some height (<17cm) over a year or two. The exception was a cave on Cicobia-I-Lau where photographed Fijian nests were resting on ledges (Tarburton 1986) and also had very thick walls (pers. obs.). It thus appears that in this species thin-walled nests are a result of having only vertical or overhanging surfaces on which to build, and bulkier nests are the norm where supports are available. The Atiu Swiftlet builds both types of nests in the same cave and the bracket-type self-supporting nests have thin walls while the ledge-supporting nests have thick walls (Tarburton 1990).

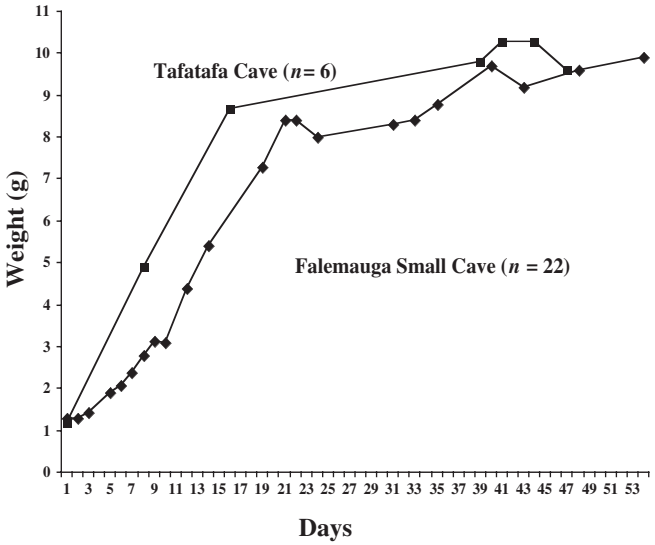

Figure 2. *Body mass increase in nestling White-rumped Swiftlets.*

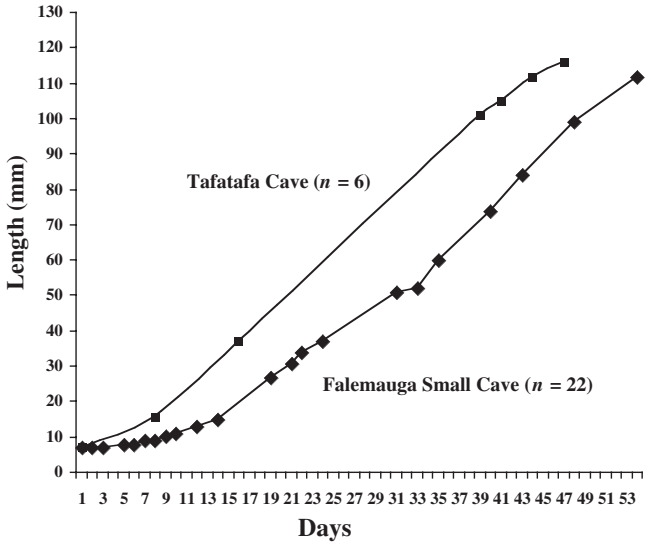

Figure 3. *White-rumped Swiftlet nestling wing growth.*

Clearly the choice of building materials birds have to build their nests, as well as the type of sites offered in available caves do have some controls on the nest that is produced. While this environmental imposition obviates the suggestion (Sims 1961; Medway 1966, 1975) that nest structure in swiftlets can be used to help define their taxonomy it supports the findings of Lee *et al.* (1996) that no character of *Aerodramus* nests showed a statistically significant fit to the molecular phylogeny using cytochrome *b* mitochondrial DNA sequences.

Nesting season

While data in Figure 1 clearly show that eggs were laid in all 12 months of the year the marked mode for September is probably in reality not as prominent as indicated. This is because sample sizes for months like June and August were very small by comparison to September.

Nesting

The White-rumped Swiftlet in Samoa does not lay a second egg in time for the first nestling to incubate, but because rainfall in most parts is reliable throughout the year, making insect prey available throughout the year, this subspecies breeds in every month of the year and has no need for the rare strategy of sibling incubation used by the Australian sub-species in order to raise more than one offspring per year.

Whitmee (1875) was incorrect in suggesting that the White-rumped Swiftlet in Samoa had a synchronised breeding season. Although Armstrong (1932) disagreed with Whitmee regarding the synchronisation, he also was incorrect in concluding that these swiftlets had a single discreet breeding season. However, in dry years the small colony near Letui on Savai'i does have a non-breeding period in the dry season (pers. obs.), which only that part of Samoa appears to experience. Previously there was a full range of nesting activities in one cave or another in any month of the year, and once the effects of the cyclone have passed these smaller colonies are expected to have all stages of breeding occurring in any given months, just as the larger colonies did during the years of this study.

Nestling growth

With nestling periods of 47 to 57 days the Samoan Swiftlets fit well within the range of 38.5 to 60 days recorded for five swiftlet species (all cited in Tarburton 1986; plus repeat experiments by Lee and Kang 1994). The nestling periods are also close to those of other White-rumped Swiftlets. Those at Chillagoe spent an average of 46 days in good (wet) years and 51 days in dry years (Tarburton 1988), and the Atiu Swiftlet spent an average of 53.3 days in the nest (Tarburton 1990).

Nesting success

The 72 per cent nesting success for Tafatafa Cave is higher than that of Falemauga Cave and all other previously studied swiftlet colonies (data and references cited in Tarburton 2003), except for that of the Black-nest Swiftlet *Aerodramus maximus*, which in Vietnam had a 73 per cent nesting success rate (Lee and Kang 1994). Predation, infertility and disturbance by the observer are likely to be the three main factors contributing to a lower success rate in the Falemauga Cave as nests in Tafatafa Cave were less prone to predation and visited less frequently than those of Falemauga Cave.

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