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SWIFTLET BEHAVIOUR RESPONSES TO PREDATORS IN PROXIMITY TO THEIR NESTS

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When they have the opportunity, swiftlets nest in totally dark parts of caves. This prevents most predation on eggs, young and incubating adults. However, a few predators are able to either reach the nests or prey on birds flying to and from nests. In response, swiftlets have developed anti-predatory behaviour. To reduce predation, adult birds enter and exit caves in groups, increase flight speed at the entrance (where most predators attack), and feed their young less frequently than comparable species that do not nest in caves. Where there have not been predators consistently at entrances the birds do not form groups but fly singly and slowly. In most colonies a few birds use alternative entrances. Predation at the nest is reduced by adults clumping their nests on high, smooth, overhanging rock surfaces. When such safe surfaces are not available or predators are able to climb the walls, swiftlets respond by spacing nests widely, reducing the chance that a predator will find them.

INTRODUCTION

Both adult and nestling birds are at high risk from predation during breeding and both have been shown to have their predation rates reduced in species that nest in holes (Lack 1968). Caves may offer similar protection as do nest holes and might help explain why cave-nesting swiftlets have lower mortality than the ecologically similar swallows, which nest in exposed areas (Tarburton 1986c).

All swiftlets in the genus *Aerodramus* have the ability to echolocate (Brooke 1972) and tend to nest in totally dark sections more frequently than lit areas of caves or in ravines (Collins and Murphy 1994; Francis 1987; Medway and Pye 1977; Tarburton 1986b, 1988a, 1990).

Birds that have a low mortality usually have a low reproductive rate. This is true for all swiftlets, which characteristically inhabit tropical rain forests. It has been proposed that birds nesting in stable environments such as tropical rainforests would have little need to increase their reproductive rates and would profit more by placing greater energy into *K*- selected activities that would prolong their own life (Cody 1966; Ricklefs 1980). Such activities would include the taking of shortcuts in the reproductive process in years of little food, and predator avoidance. It has been shown that the Australian Swiftlets at Chillagoe place less saliva in their nests in years of poor food supply and that this results in fewer fledged offspring (Tarburton 1988a).

In the mid- and late 1960s the Sydney Speleological Society and Chillagoe Caving Club (respectively) started to explore and document caves in the Chillagoe-Mungana district. Many of these limestone caves extended into totally dark zones and it was not long before members started to discover Australian Swiftlets *Aerodramus terraereginae* nesting in some of them. Smyth *et al.* (1980) visited four of these colonies and saw nests in total darkness. The Chillagoe Caving Club (1982) reported 21 caves with swiftlet colonies in them. The ones that actually did hold colonies breeding in total darkness are part of this study.

Nesting in caves has advantages, but reaching and using these sites is not without risk. This paper looks at these risks and how the birds behave to reduce their effects.

Nomenclature as outlined in Christidis and Boles (2008) is used in this paper but many taxonomic issues within *Aerodramus* have yet to be resolved.

METHODS

The White-rumped Swiftlet *Aerodramus spodiopygius* is distributed throughout most of Melanesia and western Polynesia, with close relatives in eastern Polynesia. *A. s. assimilis* was studied at five colonies in Fiji during all seasons of 1974–1976 and during the breeding seasons of 1981 and 1983. Waterfall Cave was visited 77 times; Dry Cave, 70 times; Ono cave ten times and the other two caves once each.

In Samoa, *A. s. spodiopygius* was studied during the years 1994 to 1997. On New Ireland the *A. s. eichhorni* colony in the cave at Dalom was visited twice in 2000. The closely related Atiu Swiftlet *Aerodramus sawtelli* was studied for two months in the breeding season of 1986 at both of its known colonies on Atiu in the Cook Islands. On Atiu, Tupuranga Cave was visited 35 times and Takitaki Cave was visited three times.

The Australian form (Australian Swiftlet), which has been distinguished from *A. spodiopygius* and split (Pecotich 1982; Christidis and Boles 2008) into *A. terraereginae chillagoensis* (coastal north and central Queensland) and *A. t. terraereginae* (inland north Queensland), was studied at 34 colonies in Queensland during the breeding seasons of 1985, 1986, 1988, 1989, 1991,1993, 1999, 2001, 2006 and 2007. Two of the Queensland colonies (Gordale Scar Pot and Guano Pot) were visited 98 times each and the other 32 colonies were visited only once each season.

Visits to all caves lasted two to 14 hours, except those Queensland caves visited only once each season, where a one-hour visit was normal. High beam on an Oldham miner's cap lamp was used to count nests. Low beam was used at the frequently visited colonies while recording other data apart from census collection. Three 14-hour periods were spent in a concealed manner, watching and listening, both inside and outside cave entrances to make sure that observed behaviour was not being affected by my presence. During one of the days spent inside the cave, the only light used was an ultra-violet light, which was utilised to illuminate part of the nesting area nearest the entrance. A night viewascope was used to view bird behaviour in this light, which I believe was either undetected by the birds or at least did not affect their behaviour. For example, they flew in to feed their nestlings more readily than when a dull white light lit the area. Adults of those nests were marked with individually recognisable ultra-violet reflective marks to determine if both parents were sharing the risks involved in entering the cave to feed their young.

The flight speed of swiftlets was determined by timing them with a stopwatch over a measured ten-metre interval. Measurements are given in the form of $\bar{x} \pm sd$.

RESULTS AND DISCUSSION

Light Intensity and Nesting Sites

Although Queensland coastal and island colonies nest in granite boulder-roofed caves they still use the darkest parts for their nest sites. These sites are dark enough for much of the day to require the birds to use their echolocation to find nests and avoid obstacles.

The Chillagoe-Mungana and Mitchell-Palmer karst districts contain more than 800 caves, most of which are long enough to have totally dark sections. Australian Swiftlets do not nest in most of these caves probably because they do not possess smooth overhanging roofs suitable for protection against predators that can overcome the darkness barrier.

Total darkness stops many predators from taking young or adults while they sleep on their nests. Cats, quolls, sparrowhawks, falcons and Eastern Barn Owls *Tyto javanica* have been found preying on birds near entrances or in the twilight zone of caves but none have been observed near nests placed in total darkness. Only pythons and rats have been seen or have left evidence showing their predatory activities at colonies placed in total darkness. The advantage appears worthwhile as in almost all 38 colonies I visited at Chillagoe, nests were in totally dark zones of the caves. Many caves with suitable overhanging rock surfaces in twilight zones are unused by swiftlets in the Chillagoe-Mungana cave region.

Entering and Departing Caves

In Fiji and Queensland, avian, reptilian, and mammalian predators preyed on swiftlets at suitable cave entrances or, in the case of reptiles, at narrow constrictions inside the cave. Swiftlets in both Queensland and Fiji were found to be conscious of these predators and circled above the entrances waiting for others to arrive before the group made high-speed passage into the cave. On Atiu, Samoa and New Ireland where predators did not operate at cave entrances, the swiftlets did not form groups but entered as soon as they arrived, usually singly, though sometimes in pairs. Birds returning from foraging trips in Queensland typically circled above their cave entrance(s) for one to six minutes (n = 51). During this time numbers built up until many of the group entered in rapid succession.

TABLE 1

Swiftlet *(Aerodramus spp.)* flock sizes (number of individuals) by location and intention.

Parameter	Group Size - Queensland			Group Size – New Ireland and Atiu
	Exiting Flocks	Entering Flocks	Circling Flocks	Entering "Flocks"
Mean	6.72	6.56	28.32	1.03
sd	18.4	8.6	55.14	0.17
n	111	172	69	200

Departing birds were usually observed circling just inside the entrances prior to taking part in a group exit. Once outside these birds did one of two things. They either flew away as a group or mixed for one to nine minutes (n = 45) with those waiting for entry before flying away to feed. Because outgoing as well as incoming birds usually circled together above the entrance those groups were larger than groups entering or leaving the cave entrances. Swiftlets entering caves did not join those circling inside but normally flew directly to the area of their nest or to the nest itself (Table 1).

Nestlings tended to take their first flight when adults or older fledglings were leaving nearby nests. This behaviour may help them find their way to the entrance as well as providing protection against predators operating at or near the cave entrance.

Flight Speed Through Entrances

At Fiji and Queensland sites birds increased their speed to averages of 47.3 ± 14.7 kilometres per hour at Waterfall Cave in Fiji (Tarburton 1986b) and 37 ± 16.5 kilometres per hour at Tarby's Swiftlet Pot at Chillagoe, Queensland (Tarburton 1988b). The slowest of the 92 birds timed in Fiji was travelling at 24 kilometres per hour and the fastest, 106 kilometres per hour. The slowest of the 32 Queensland birds was travelling at 23 kilometres per hour and the fastest, 111 kilometres per hour.

At Atiu the swiftlets did not increase their speed at the entrances of the two caves in which they were nesting. The average speed of entry at Takitaki Cave was 22 ± 3.6 kilometres per hour. This is significantly less than the entry speed in both Fiji ($P < 0.001$, $t_{130} = 15.1$) and Queensland ($P < 0.001$, $t_{72} = 5.1$).

That it is the presence of predators at the cave entrance that causes the increase in swiftlet flight speed is further confirmed from similar behaviour at a swift colony in Rhodesia. There, a small colony (14 nests) of Mottled Swifts *Apus aequatorialis* was nesting in a cave with its entrance patrolled by a pair of Lanner Falcons *Falco biarmicus* and when exiting, the swifts dived "at very high speed" from the cave into the valley below (Cooke 1965).

Using Multiple Cave Entrances

An individual predator can only wait at one entrance suitable for their operations and if swiftlets use more than one entrance it is going to be harder for all of them to fall prey to a predator. Cats cannot operate at large entrances, particularly those that open to the sky and avian predators generally cannot operate at low winding entrances. With the small colony sizes at Chillagoe-Mungana there appears to be insufficient prey for more than one predator to operate. Neither National Parks staff, caving club members nor myself have ever seen more than one predator operate at the same colony. I have found swiftlets using more than one entrance at most caves (Swiftlet Cavern, Gordale Scar Pot, Guano Pot, September Cave, Hercules Cave and Golgotha Cave) thus reducing the likelihood of being captured.

Feeding Frequency

As in all swifts, White-rumped and Australian Swiftlets carry their prey in their throats, using adhesive saliva to hold the prey together in a bolus. There may be more than 700 invertebrates in a bolus (Tarburton 1986a). Storing food in a bolus reduces the number of feeding trips adults have to make and as the nestlings are adapted to survive infrequent feeding (Collins 1973), parents obtain the additional advantage of spending less time in the vulnerable activity of entering and leaving caves.

A comparison of aerial feeding in the White-rumped and Australian Swiftlet to the similarly sized Pacific Swallow *Hirundo tahitica* and Welcome Swallow *H. neoxena* is shown in Table 2. In both Fiji and Queensland each pair of swiftlet parents made only one to five nest visits per day (n = 49) to feed nestling(s) (Tarburton 1986b, 1987, 1988a). By contrast, nestlings of the Welcome Swallow in New Zealand received 430 trips from their parents in one day and it would appear that they deliver only one or two invertebrates at a time (Tarburton 1993).

TABLE 2

Number of feeding visits to nestlings (per adult pair/per day) for cave breeding and non-cave breeding avian aerial feeders.

Species	Location	Feeding visits per day (Mean ± se)	Sample Size
White-rumped Swiftlet	Fiji	2.8 ± 0.26	20 nests
Australian Swiftlet	Queensland (wet year)	5.2 ± 0.28	20 nests
Australian Swiftlet	Queensland (dry year)	2.9 ± 0.5	9 nests
Atiu Swiftlet	Cook Islands	6.1 ± 0.6	9 nests
Welcome Swallow	New Zealand	430	2 nests
Pacific Swallow	Papua New Guinea	161	3 nests

Fewer visits to nest sites reduce the risk of parents falling prey to predators at such sites.

Nest Sites and Predation

Swiftlet nesting sites in Queensland and in particular Fiji are often crowded with nests and sleeping birds. Nests are constructed on or above smooth overhanging rock faces. This had the effect of severely restricting access to pythons, tree snakes and mammals. I have seen Spotted Pythons *Antaresia maculosa* and a Brown Tree Snake *Boiga irregularis* fall off an overhanging cave wall as they tried to reach nests at Chillagoe. Other members of the Chillagoe Caving Club have also seen pythons fall from a wall as they tried to reach a cluster of nests. The one instance of a snake reaching a nest on an overhanging smooth surface was where a Brown Tree Snake was observed at a nest devouring a swiftlet at the colony on Bedarra Island in November 1955 (Busst 1956). The observer stated, "It is difficult to understand how it could ascend the lower surface of a sloping wall inclined at 45 degrees" (Busst 1956, p. 3). The slopes on which they nest on the mainland are usually much steeper than 45 degrees and perhaps explain the snakes' inability to reach those nests.

Such naturally protected sites were not available in the two caves used on Atiu so nests can be reached by Coconut *Birgus latro* and Land *Cardisoma longipes* crabs that ventured over most (if not all) of the cave walls and ceilings. These crabs made tinkling sounds with their claws as they climbed across cave walls and stalactites. Swiftlets flew off their nests when this sound was simulated by tapping fallen stalactites together. On Atiu I watched crabs climbing over the most difficult parts of the cave ceilings. I also found two nestlings with deep and fatal incisions and found one nestling that had suffered a leg amputation, presumably inflicted by crabs. Two nests were found cut in two and several nestlings disappeared from nests. Crabs are the only known predator observed in these caves, and the damage done is commensurate with their having done it. Cats are the only other predator on the island that could possibly inflict similar damage, but they are unable to reach the nests involved because of darkness and nests being three or more metres above the cave floor. Also a cat could tear a nest in two; not cut it.

In Samoa, nests are placed on ledges or other protrusions from the walls of the lava tube caves and can sometimes be reached by rats. I saw rats *Rattus* sp. beyond the twilight zone of two caves and recorded losses of nestlings in these areas.

In Fiji I found Barn Owls *Tyto alba lulu* taking swiftlets in the twilight zone of cave entrances. The Dooloomai Falls colonies are twilight situations but do not have such large chambers and I have not observed owl activity at them. Some of the Chillagoe caves have large entrances that owls could use but owls are scarce in the area and I have no evidence of their taking swiftlets.

TABLE 3

Distances (cm) to the nearest neighbour's nest in swiftlet populations studied.

Swiftlet Population	Mean distance to nearest neighbour (cm)	*sd*	Min	Max	*n*	*P (t test,* 2 tailed, ≠ *v)*
A. s. spodiopygius	482	1017.9	0	8500	252	
A. s. chillagoensis	7.3	8.03	0	60	261	<0.05
A. s. terraereginae	1.1	1.93	0	10	143	<0.001
A. s. assimilis	3.7	6.19	0	40	495	<0.001
A. s. sawtelli	≈ 162	183.3	30	1300	78	<4.33

Spacing of Nests

Coconut Crabs were common on Espirito Santo, Vanuatu where the nests of the Uniform Swiftlet *Aerodramus vanikorensis* were placed 1–3 metres apart (Lou Pecotich, pers. com.).

On Atiu, Coconut and Land crabs were mostly seen in the twilight sections of the caves, but they did prey on nestlings in the dark. As crabs were able to reach nests in both nesting caves on Atiu, it would appear that the birds have responded by separating their nests as much as possible to make them more difficult to locate. In comparison, the crab-free caves in Queensland and Fiji have nests that often touch one another, and in some cases these are not attached to the wall but only to other nests (see Table 3).

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REFERENCES

Brooke, R. K. (1972). Generic limits in old world Apodidae and Hirundinidae. *Bull. Brit. Ornithol. Club* **92**: 53–57.

Busst, J. (1956). Nesting of Grey Swiftlet on Bedarra Island. *North Queensland Naturalist* **116**: 1–3.

Chillagoe Caving Club (1982). 'Chillagoe Karst: A speleological field guide of the towers and caves of the Chillagoe - Mungana - Rookwood areas in far north Queensland, Australia'. (Queensland Government Printer: Brisbane.)

Christidis, L. and Boles, W. E. (2008). 'Systematics and Taxonomy of Australian Birds'. (CSIRO: Melbourne.)

Collins, C. T. (1973). Development of temperature regulation in the House Swift. *Pavo* **11**: 1–11.

Collins, C. T. and Murphy, R. (1994). Echolocation acuity of the Palawan Swiftlet (*Aerodramus palawanensis*) *Avocetta* **17**: 157–162.

Cooke, P. (1965). Breeding of Mottled Swifts *Apus aequatorialis* (von Muller) in the Matapos Hills, S. Rhodesia. *Ostrich* **36**: 38–39.

Cody, M. L. (1966). A general theory of clutch size. *Evolution* **20**: 174–184.

Francis, C. M. (1987). 'The management of edible bird's nest caves in Sabah'. (Sandakan. Wildlife Section, Sabah Forest Department: Sandakan, Sabah, Malaysia.)

Lack. D. (1968). Ecological Adaptations for Breeding in Birds. (Methuen: London.)

Medway, L. and Pye, J. D. (1977). Echolocation and the systematics of swiftlets. In B. Stonehouse and C. Perrins (Eds). 'Evolutionary Ecology'. (Macmillan: London.)

Pecotich, L. (1982). Speciation of the Grey Swiftlet *Aerodramus spodiopygius* in Australia. *Tower Karst* **4**: 53–57

Ricklefs, R. F. (1980). Geographic variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk* **97**: 38–49.

Smyth, D. M., Pecotich, L. and Roberts, J. R. (1980). Notes on the distribution and breeding of the Grey Swiftlet, *Aerodramus spodiopygius*. *The Sunbird* **11**: 1–19.

Tarburton, M. K. (1986a). The food of the White-rumped Swiftlet (*Aerodramus spodiopygius*) in Fiji. *Notornis* **33**: 1–16.

Tarburton, M. K. (1986b). Breeding of the White-rumped Swiftlet in Fiji. *Emu* **86**: 214–227.

Tarburton, M. K. (1986c). A comparison of the flight behaviour of the White-rumped Swiftlet and the Welcome Swallow. *Bird Behaviour* **6**: 72–84.

Tarburton, M. K. (1987). An experimental manipulation of clutch and brood size of White-rumped Swiftlets in Fiji. *Ibis* **129**: 107–114.

Tarburton, M. K. (1988a). Breeding biology of the White-rumped Swiftlet at Chillagoe. *Emu* **88**: 202–209.

Tarburton, M. K. (1988b). What swiftlets do in the caves at Chillagoe and some ideas on how cavers can share those caves without interference. Preprints of papers for the 17th Biennial Conference of the Australian Speleological Federation. Pp. 98–107.

Tarburton, M. K. 1990. Breeding biology of the Atiu Swiftlet in the Cook Islands. *Emu* **90**: 175–179.

Tarburton, M. K. (1993). A comparison of the breeding biology of the Welcome Swallow in Australia and recently colonized New Zealand. *Emu* **93**: 34–43.