Swiftlet Isles Revisited: Population trends and sibling incubation in colonies of the Australian Swiftlet, *Aerodramus terraereginae terraereginae*, on North Queensland Islands

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Abstract

This article presents breeding data for colonies of the Coastal Australian Swiftlet, *Aerodramus terraereginae terraereginae*, on the Family Islands, off the coast midway between Townsville and Cairns, Queensland, Australia, obtained on visits to the islands between 2015 and 2022. This information is supplemented by published data going back to 1908 to provide an indication of population trends over a time span of 114 years. While colony sizes appear to have fluctuated significantly from year to year, possibly in response to cyclone impacts, the island populations of this swiftlet have remained fairly stable over the longer term – despite well-documented population declines in their main food source, insects. The breeding season of the island colonies was found to extend from July to April, with some variability between colonies. Peak egg-laying occurred between November and February. We also provide a population estimate for a previously unrecorded Australian Swiftlet colony on nearby Hinchinbrook Island. This colony, which shares its sea cave with a large colony of insectivorous bats, is by far the largest known island colony of the species. Daily time-lapse photography on a swiftlet colony on Dunk Island in 2016 and 2017 revealed that up to three sequential clutches, each comprising a single egg, were laid per nest during the breeding season. Incubation of the second and/or third egg by a nearly-fledged older sibling confirmed that sibling incubation, which had previously been observed in the Chillagoe Australian Swiftlet, *A. terraereginae chillagoensis*, also occurs in the coastal subspecies.

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Introduction

The Australian Swiftlet, *Aerodramus terraereginae* (Ramsay 1874) Oberholser 1906 is a small (10–12 g) member of the swift family (Apodidae) that is endemic to North Queensland, Australia, nests in colonies in caves and rock shelters, and navigates in total darkness using low-frequency echolocation

(Roberts *et al.* 1976; Smyth 1979). Formerly ascribed to the White-rumped or Grey Swiftlet (*A. spodiopygius*) found in Papua New Guinea and islands of the western Pacific, the Australian Swiftlet was recognised as a separate species on the basis of DNA evidence (Price *et al.* 2004, 2005).

Two subspecies are currently recognised: the Chillagoe Australian Swiftlet, *A. terraereginae chillagoensis*, which is restricted to a region of extensive limestone caves near Chillagoe, 140 km west-southwest of Cairns; and the Coastal Australian Swiftlet, *A. terraereginae terraereginae*, found in coastal rainforests between Mackay and Cape York Peninsula, and on islands located a few kilometres offshore midway between Townsville and Cairns in North Queensland (Christidis & Boles 2008). The Chillagoe subspecies is paler, smaller and has a broader white rump than the coastal subspecies (Pecotich 1982).

The breeding season of the Australian Swiftlet has been variously described as October to March (Banfield 1911), September to February (Frith 1976), or July to February (Pizzey *et al.* 2012). Several sequential clutches are laid during the season, each comprising a single egg (Tarburton 1988).

Swiftlet nesting colonies have been recorded on Dunk Island, Timana Island, Bedarra Island and Wheeler Island of the Family Island group at irregular intervals since 1908 (Banfield 1911; Campbell 1916; Chisolm 1929, 1933; Busst 1956; Hayes 1965; Orrell 1967; Smyth 1979; Smyth *et al.* 1980; Schulz 1991). This article assesses the long-term trends in the Family Island swiftlet colonies by reporting observations made from 2015 to 2022, and makes the first observations of a previously unrecorded swiftlet colony on Hinchinbrook Island, 40 km south of Dunk Island.

Tarburton and Minot (1987) and Tarburton (2012) have noted that the Australian Swiftlet is the only bird species known to exhibit sibling incubation, which is the phenomenon of a well-developed nestling incubating the next egg laid in the nest. Examining 140 nests of the Chillagoe subspecies, Tarburton and Minot (1987) observed the presence of an egg in 86% of those that had a nestling near the age of fledging, and that the total incubation period of both adult-incubated eggs and nestling-incubated eggs was about 27 days (range: 25–29 days). The mean nestling age at the laying of the second egg was 32 days (range: 23–47 days) and the mean total nestling period was 47 days (range: 46–48 days), with the result that the incubating nestling always fledged and departed the nest prior to the hatching of the second egg.

With the exception of the White-rumped Swiftlet (*A. spodiopygius spodiopygius*) in Samoa, which lays one egg per clutch and breeds all year (Tarburton 2009a), other swiftlet species typically lay one or more clutches each breeding season. Each clutch comprises two eggs which are incubated together, and the nestlings are reared together. Tarburton (2012: 3) observed through experimentation that Australian Swiftlets could not capture enough prey to raise two nestlings at the same time, “making the sibling incubation strategy essential to their survival”.

The Chillagoe studies on swiftlet sibling incubation took place at a time when the Australian and Western Pacific Swiftlet populations were regarded as belonging to the same species. Tarburton and Minot (1987) therefore concluded that the presence of sibling incubation in the Chillagoe population and the absence of sibling incubation in the Fiji population (which lays two eggs and incubates them simultaneously) appeared to be “ecologically facultative”. This implied that ecological conditions at Chillagoe, particularly with respect to availability of food, were not conducive to successfully rearing two nestlings simultaneously. Prior to the present study, no attempts had been made to observe the phenomenon of sibling incubation in the coastal subspecies of the Australian Swiftlet.

Methods

The islands

With the exception of two privately owned islands (Bedarra and Timana), all the islands in the Family Group and Hinchinbrook Island (Fig. 1) are National Parks and lie within the Great Barrier Reef World Heritage Area. They also form part of the Girringun Indigenous Protected Area (Girringun Aboriginal Corporation 2023), which is managed by Girringun Aboriginal Corporation in collaboration with Queensland and Australian Government agencies.

The group name for the Family Islands, dubbed *The Swiftlet Isles* by novelist James Porter (Porter 1977), derives from having a father isle (Dunk), a mother isle (Bedarra), a set of twins (Wheeler and Coombe), a set of smaller triplets (Smith, Bowden and Hudson), and several singletons (Timana, Kumboola, Mung-Um Gnackum, Purtaboi and Woin Garin) around Dunk Island (Porter 2000) (Fig. 2).

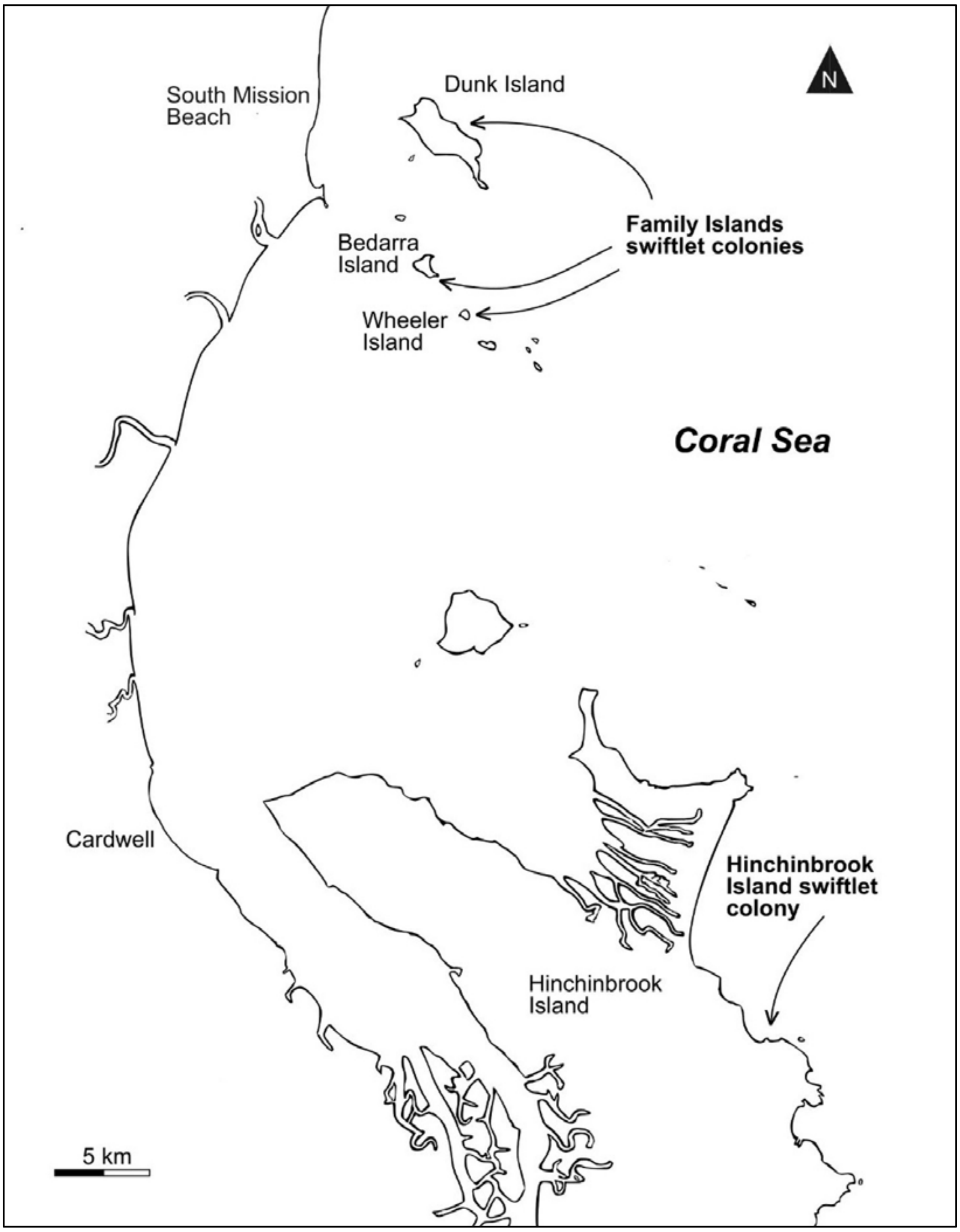

Figure 1. Study area including Family Islands and Hinchinbrook Island, showing approximate locations of swiftlet colonies. Image: David Blair.

All the islands share a family resemblance in that they are densely vegetated in rainforest, and elevated in the centre, with an eastern shore comprising granite boulders that create many cave-like rock shelters. It is in these shelters, located in the zone just above the highest astronomical tide level and just below the vegetation line, that most swiftlet colonies on the Family Islands have been recorded. Each island also possesses a distinctive sandspit protruding from the west or northwest corner, formed by sea currents driven by the south-easterly wind that prevails for most of the year along the north Queensland coast.

Dunk Island (1,000 ha), known as *Coonanglebah* in the local Djiru language, is situated 4 km off the coastal town of South Mission Beach, and is the largest and most northerly island of the Family Island group. It is almost 7 km long and 2 km wide, oriented along a southeast-northwest axis. At 271 m, Mt Kootaloo is the highest point on a ridge running along the length of the island.

Edmund (Ted) Banfield, who lived on Dunk Island from 1897 to 1923, recorded two swiftlet colonies on the island: a fragment of a nest adhering to the roof of a cave on one of the highest points of the island, and a colony comprising 53 nests close to the water's edge, on the eastern side of the island (Banfield 1911). Most subsequent information about the Dunk Island swiftlets has been restricted to the coastal colony that Banfield described, and which is referred to in this paper as the Dunk Island Main Colony. However, Martin Schulz reported finding five coastal colonies and one inland colony "above Palm Valley some distance from the sea" (Schulz 1991: 1). Palm Valley runs north-south in the centre of the island, reaching the southern coastline at Coconut Bay. During the present study, two coastal colonies on Dunk Island were visited on multiple occasions – the Main Colony, and the smaller Dunk Island Colony 2. From the description provided by Schulz (1991), it is highly likely that his Site A corresponds to the Main Colony. It is likely, but not certain, that our Dunk Island Colony 2 corresponds to Schulz's Site B, because this colony is located close to the Main Colony. Due to this uncertainty, Schulz's data are presented separately here for all his sites except the Main Colony, for which we combined the data from all published sources. The rocky shoreline in the vicinity of the Dunk Island Main Colony is shown in Fig. 3.

Figure 2. Map of Family Islands. Image: David Blair.

Timana Island (16 ha), also known as Thorpe Island, is small, oblong-shaped, about 70 m high at its centre, oriented east-west and situated between Dunk Island to the north and Bedarra Island to the south. Shallow reef flats close to the Timana shoreline make access to it more difficult than to the other nearby islands.

Figure 3. Shoreline in vicinity of Dunk Island Main Colony. Photo: Dermot Smyth.

Figure 4. Bedarra Island swiftlet colony location, looking south towards Wheeler Island. Photo: Dermot Smyth.

Busst (1956) reported that a former resident of Timana Island (Fred Boland) had observed a small colony of swiftlets nesting on a sheltered rock in 1944, but that the colony had not been seen since the subsequent collapse of the rock face. We are not aware of more recent reports of swiftlets nesting on Timana Island; the island was not visited during the present study.

Bedarra Island (100 ha), a misrepresentation of the Aboriginal name *Biagurra*, also known as Richards Island, lies about 3 km south of Dunk, is roughly triangular in shape, about 1.5 km each side, with a central elevation of 88 m. Bedarra Island comprises three separate land tenures, and includes several exclusive tourist resorts. The swiftlet colony on Bedarra was first recorded and photographed by CSIRO ecologists Len Webb and Harold Hayes in 1950 (Hayes 1965). Resident artist and naturalist, John Busst, recorded breeding data on the Bedarra Island Colony during the 1950/1951, 1955/1956 and 1961/1962 breeding seasons (Busst 1956; Hayes 1965). The colony is located on the south-east corner of the island, in a rock shelter accessible directly from the sea, as well as via a track leading from nearby Wedgerock Bay. The rocky coast in the vicinity of the Bedarra Island Colony is shown in Fig. 4.

Wheeler Island (31 ha), *Toolgbar* in the local Aboriginal language, is almost circular, with a freshwater spring inland from the National Park camping area, adjacent to the sandspit on the western side. Some of the granite boulders on the eastern shoreline are very large and it is beneath one of these that the swiftlet colony is located about 2 m above high tide (Fig. 5) (Orrell 1967). The Wheeler Island Colony is located in a shelter beneath the boulder that is approximately 9 m high by 9 m wide, with the nests occupying an area of 5 m high by 3.5 m wide on the westward-facing rock wall sloping at approximately 30°.

Hinchinbrook Island (39,300 ha), on the traditional country of Bandjin and Girramay peoples, is separated from the mainland by a narrow, mangrove-lined channel between Cardwell and Lucinda. A ridge of mountain peaks, the highest being Mt Bowen at 1,140 m, runs down the spine of the island, which is 15 km long and 6.5 km at its widest, oriented along a northwest-southeast axis, parallel to the mainland coast. In contrast to the granite boulders of the Family Islands, the eastern (seaward) coast of Hinchinbrook Island consists of a series of sandy bays, separated by rocky headlands.

Orrell (1967) reported that a Bedarra Island resident, Noel Wood, had observed a flock of swiftlets at Hinchinbrook Island, without giving an indication of the sighting location. On a visit to Cape Richards in 2020 during the present study, we encountered a professional sea kayaking guide who reported seeing swiftlets circling near the entrance to a sea cave at

Figure 5. Wheeler Island swiftlet colony location. Photo: Dermot Smyth.

Figure 6. Entrance to the Hinchinbrook Island swiftlet cave. Photo: Dermot Smyth.

the southern end of Ramsay Bay. We subsequently located and visited the sea cave, in which the large Hinchinbrook Island Colony is located, three times during the present study.

The sea cave is on a north-facing headland about 1 km west of Agnes Island on the eastern (seaward) side of Hinchinbrook Island (Fig. 6). The cave is only accessible by water, and the entrance at low tide is just wide enough for a kayak to fit through. The cave is about 30 m long, with two opposing walls sloping steeply upwards to meet at about 5 m above the high tide level.

The islands are located in the Wet Tropics Bioregion of north-east Queensland, where rainfall occurs throughout the year, mostly during the wet season from December to March, which are also the hottest months. Climate records from Dunk Island (Elders Weather 2024) show maximum wet-season temperatures typically 30–33° C, and average minimums 20–25° C, with an annual average rainfall of about 2 m on Dunk Island. The driest months are September to November, and the coolest month is July with an average maximum temperature about 25° C and an average minimum temperature about 15° C. The area is subjected to cyclonic activity, with an annual average of four cyclones occurring in the Coral Sea, one of which is likely to cross the north Queensland coast (Bureau of Meteorology 2024a). Named cyclones that severely impacted island and coastal environments during the period covered by this article include Agnes (1956), Keith (1977), Otto (1977), Winifred (1986), Larry (2006) and Yasi (2011).

Another climatic feature of the region is the prevailing moist south-east wind that blows from the Pacific Ocean, across the islands and onto the mainland throughout most of the year, often reaching speeds of 50 to 60 km/hr especially from March to July (Bureau of Meteorology 2024b). Island-dwelling swiftlets typically fly into these strong winds on their return from their mainland feeding grounds after as much as 14 h foraging on the wing.

Accessing the swiftlet colonies

The present study involved opportunistic visits to the previously documented swiftlet colonies on Dunk, Bedarra and Wheeler Islands between 2015 and 2022, as well as visits to the previously undocumented swiftlet cave on Hinchinbrook Island in 2018 and 2021. Most of the recorded Family Islands swiftlet colonies are located on the eastern side of the islands, making access by boat difficult because of the prevailing winds, poor anchorages and hazardous shore landings on oyster-encrusted rocks washed by ocean swells. Access to these colonies is therefore restricted to exceptionally calm sea conditions (all islands), arduous treks around the shoreline (Wheeler Island), or when permission is granted by the landowner (Bedarra Island).

When conditions were favourable, we travelled to the Family Islands on either a 6-m sailing trimaran (2015–2016) or a 10-m sailing catamaran (2017–2022), which we anchored as close as possible to the shore. On one occasion, a group of Girringun Rangers accompanied us to the Dunk Island colonies, travelling in the Girringun patrol vessel. Transfer to the shore was completed on a 3.5-m tandem polyethylene kayak or a 3-m aluminium punt, each of which was robust enough to cope with landing on the oyster-covered rocks.

Access to the Hinchinbrook Island Colony required anchoring a vessel nearby and entering the narrow sea cave on the tandem kayak in exceptionally calm conditions.

Documenting swiftlet populations

By agreement with Traditional Owners and Queensland National Parks and Wildlife Service, this project was conducted with minimal disturbance, no physical handling of the birds and no structural impact on the rock shelters. On each visit to a swiftlet colony, counts were made of nests, eggs and nestlings, and the nesting colonies were photographed for later analysis. The time spent at each swiftlet colony was limited to 5 to 10 min, to minimise disturbance to the birds. Challenges in comparing and combining information collected by different observers over time are discussed below.

At any point in time, swiftlet nests observed on the wall of a cave or rock shelter included nests currently being used for raising young, nests not currently in use, and nests under construction. Some observers have also counted the number of nests that have fallen off the wall onto the cave or shelter floor. Tarburton and Tarburton (2013), during censuses of swiftlet colonies around Chillagoe, identified nests in use by “the sparkle of fresh saliva on them”, whereas Schulz (1991) identified “used nests” and “nests not in use” on Dunk Island by the presence or absence of an egg. In the present study, all nests that appeared capable of being used (i.e., complete and not in disrepair) were counted, whether or not they exhibited fresh saliva and whether or not an egg or chick was present. Dunk Island swiftlet nests that are clearly in use often do not exhibit shiny white saliva patina (Fig. 7), perhaps suggesting another difference between the two subspecies.

The pearly-white swiftlet eggs lying in the shallow, cupped nests are easily seen, even in dim daylight inside the island rock shelters. However, in larger colonies it is not always possible to look directly into every nest, particularly those located high up on a rock face and those that are obscured by other nests to which they are attached. Likewise, while eggs stand out starkly in photographs, some eggs may not be in the camera’s field of view. Also, it is not

Figure 7. Nests, eggs and nestlings, Dunk Island Main Colony (December 2018). Photo: Dermot Smyth.

possible to count eggs that are obscured by roosting nestlings or adults. Egg counts are therefore likely to provide an underestimate of the total egg numbers at any one time.

For most of the swiftlet breeding season, nestlings from pink hatchlings to almost fledged, adult-sized birds could be seen scattered throughout the colonies. Tarburton (2012) has pointed out that some observers have mistaken large nestlings for adults that stubbornly refuse to leave their nests when approached by humans. He noted that "the pale edging of the primary feathers indicate that the sitting bird is clearly a nestling, and therefore not capable of flying off". While some adult birds do "stubbornly" remain on their nests on the arrival of humans, almost all birds seen on nests are likely to be nestlings, the adults having temporarily departed in response to the disturbance.

Some observers have recorded just the total number of nestlings, while others have distinguished between pink newly-hatched, partially feathered, or fully feathered nestlings. These distinctions (when available) are described in this article as follows: Pink (newly hatched); Part (partially feathered); Full (fully feathered). In reality, all the nestlings are on a continuum between newly hatched to fully feathered, so the three categories are artificial and somewhat subjective. As noted above, the total nestling count can also be problematic when large, fully feathered nestlings have been wrongly assumed to be adult birds.

During the current study, Dunk Island swiftlet colonies were visited 17 times from 2015 to 2022, providing opportunities for nests, eggs and nestlings to be counted over seven breeding seasons. All but one of these visits occurred between August and March, reflecting calmer weather conditions during this period and encompassing most of the breeding season.

The Bedarra Island Colony (Fig. 8) was accessed twice from the sea in 2015, and permission was granted in February 2022 to access the cave via the land route when the nearby tourist resort was closed for maintenance.

The Wheeler Island Colony (Fig. 9) was located in March 2022 with the aid of a site photograph provided in Orrell (1967), after unsuccessful attempts had been made to find the colony in August 2015, February 2019 and February 2022. The colony was revisited in August 2022.

We visited the Hinchinbrook Island Colony (Fig. 10) in

Figure 8. View into Bedarra Island swiftlet cave (February 2022). Photo: Dermot Smyth.

Figure 9. Inside Wheeler Island swiftlet cave (March 2022). Photo: Roger Fryer.

Figure 10. Inside Hinchinbrook Island swiftlet cave, showing flying and roosting swiftlets and bats, looking up to roosting bat colony on the ceiling (March 2022). Photo: Roger Fryer.

January and October 2018, and again in November 2021. During each visit, swiftlets were seen flying in and out of the cave, and many swiftlet nests on the eastern wall were visible from the cave entrance. However, it was only on the last visit that sea conditions were calm enough for us to enter the cave and to remain inside for about five minutes.

With the kayak moving in the swell, and many swiftlets and bats flying around inside the cave, it was not possible to carry out a reliable count of the large number of nests on the rock wall above us. Instead, a comprehensive series of photographs of the walls and ceiling of the cave were taken. Swiftlet nests and roosting swiftlets were subsequently counted from enlarged photographic images, which were then combined to create a photo-mosaic of the swiftlet nesting colony. Also counted were the numerous insectivorous bats (*Miniopterus* spp. and possibly *Hipposideros diadema*) roosting on the cave ceiling and among the swiftlet nests.

Sibling incubation

Evidence of sibling incubation in island populations of the Coastal Australian Swiftlet was obtained from analysis of photographs taken in the Dunk Island Main Colony from September 2016 to March 2017 using a Swift 3C High-Speed Motion Camera. The camera was fitted with a mobile SIM card and long aerial, which enabled images to be transmitted to a website operated by Outdoor Cameras Australia. The images could then be accessed remotely from any internet-connected computer. The camera was installed on a bespoke mount, and held in place with sandbags, without physical disturbance to the rock surfaces.

The camera was set on time-lapse mode to record two images every 24 hours – once during the day (approximately noon) and once at night (approximately midnight). The daytime images were captured using ambient light (Fig. 11); the night-time images were captured using an automatic infra-red light – a so-called "black flash" – that was not visible to the swiftlets (Fig. 12). The state of battery charge was recorded on each image, so battery status could be monitored remotely in order to schedule battery replacement.

Consistent with our agreement not to handle the birds, sibling incubation could only be directly

Figure 11. Daylight time-lapse photo of Dunk Island Main Colony (December 2016). Image: Dermot Smyth.

Figure 12. Black-flash time-lapse photo of Dunk Island Main Colony at night (April 2017). Image: Dermot Smyth.

observed by glimpsing an egg beneath a feathered-but-not-fledged nestling on a nest. The daily photographs provided the opportunity to track breeding sequences in individual nests directly and indirectly. For example, the appearance of an egg in a nest that had been empty the previous day provided direct evidence of the date the egg was laid; and the appearance of a newly hatched nestling provided indirect evidence of the date the egg was laid and when the nestling would fledge, assuming an incubation period of 27 days and fledging time of 47 days, based on knowledge of the Chillagoe subspecies (Tarburton & Minot 1987).

Daytime time-lapse images taken over 150 days were analysed to locate sequences of sufficient duration and quality to track the progression of egg-laying, hatching and fledging, which were inferred for 10 nests visible in the daily photographs during the 2016/2017 breeding season in Dunk Island Main Colony.

Constraints and limitations of this technique for acquiring sibling incubation data include: uncertainty about whether the first sighting of an egg or nestling coincided precisely with a laying or hatching event; periodic deterioration of image quality caused by moisture or sea spray on the camera lens; insufficient resolution to distinguish between an almost-fledged nestling and an adult incubating an egg; interference with the camera by a Carpet Python, *Morelia spilota*, which resulted in termination of daily photography in September 2018 (Fig. 13). Nevertheless, the combination of opportunistic photos, and the estimation of egg-laying, hatching and fledging events based on evidence from daily images, as well as knowledge of incubation and fledging durations in the Chillagoe subspecies, made it possible to infer breeding sequences to determine whether sibling incubation occurs in island populations of the Coastal Australian Swiftlet.

Results

Breeding data

Dunk Island

Population data for the Dunk Island Main Colony (Table 1) extends over a period of 114 years (1908 to 2022 – the longest time span for any swiftlet colony records in Australia. Maximum nest numbers varied from year to year, and from month to month, with the highest nest numbers recorded between November and February. Nest numbers recorded during the peak period provide a more reliable proxy for total population numbers than at other times, because nests may deteriorate and fall off the nesting wall towards the end of the season, and may not have yet been rebuilt by early in the following season. The two highest nest numbers were recorded in November 1921 (220 nests) and February 2018 (250 nests), suggesting long-term population stability, despite apparently substantial population declines in some years. However, because the data do not include nest counts for each month of each year, the precise extent of annual population fluctuations remains uncertain.

Figure 13. Carpet Python, *Morelia spilota*, on time-lapse camera, Dunk Island Main Colony (September 2018). Image: Dermot Smyth.

Figure 14. Python on the floor of Dunk Main Colony, 20 August 2020. Image: Dermot Smyth.

Table 1. Summary of nest counts and breeding data from Dunk Island Main Colony from 1908 to 2022.

Breeding season	Date	Nests on wall	Nests on floor or disrepair (if known)	Eggs	Nestlings Pink / Part / Full (if known)	Nestlings total	Source
1908/09	17 Nov 1908	53		20			Banfield 1911
1909/10	10 Jan 1910	No data		In 50% of nests			Banfield 1911
1914/15	No date	50–60		12		0	Campbell 1916
1921/22	Nov 1921	220		110		55	Chisolm 1929
1976/77	17 May 1977	48		0		0	Smyth *et al.* 1980
1977/78	28 Dec 1977	48		17		17	Smyth *et al.* 1980
1989/90	8/9 Sept 1989	167	30	91		0	Schulz 1991
2015/16	20 Aug 2015	1	60				Present study
	26 Nov 2015	126		21		36	Present study
	27 Jun 2016	135	4				Present study
2016/17	24 Aug 2016	58		1			Present study
	1 Sep 2016	60		5			Present study
	5 Mar 2017	76	8		-/-/11	11	Present study
	19 Mar 2017	95			-/-/8	8	Present study
2017/18	06 Aug 2017	61	40	0		0	Present study
	02 Feb 2018	250	12	12		18	Present study
2018/19	28 July 2018	74	0	1		0	Present study
	17 Sept 2018	125	0	24	1/-/-	1	Present study
	13 Dec 2018	237		20	12/14/76	102	Present study
	16 Feb 2019	65	40	0	1/-/28	29	Present study
2019/20	26 Nov 2019	164		44	10/-/60	70	Present study
2020/21	20 Aug 2020	20 +6 under construction	35	1			Present study
	8/9 Dec 2020	280		1 egg hatching	7/7/110		Present study
2021/22	10 Feb 2022	150		1	7/12/4	23	Present study

Counts of 48 nests in May and December 1977 suggest that there was a substantial population decline, or at least that breeding was severely reduced, during that year.

During the present study, a Carpet Python was observed in the Dunk Island Main Colony on three two occasions: coiled around the time-lapse camera on 17 September 2018 (Fig. 13), and on the floor of the rock shelter on 17 February 2019 and 20 August 2020 (Fig. 14). We did not witness interactions between a python and swiftlets on any of those occasions.

While breeding commenced in Dunk Island Main Colony as early as July, there was a higher proportion of nests with eggs during August in Dunk Island Colony 2 (Table 2) than in the Dunk Main Colony, suggesting that on average breeding starts earlier in Dunk Island Colony 2 than in the Dunk Island Main Colony. The absence of eggs and nestlings in Dunk Island Colony 2 in February 2018, 2019, and 2022 suggests that this colony also finishes breeding earlier than the Dunk Island Main Colony – raising the possibility of breeding asynchrony between colonies just 200 m apart.

Table 2. Summary of nest counts and breeding data from Dunk Island Colony 2 from 2016 to 2022 during the present study.

Breeding season	Date	Nests on wall	Nests on floor or disrepair (if known)	Eggs	Nestlings Pink / Part / Full (if known)	Nestlings total
2016/17	3 Sep 2016	23		12		
	19 Mar 2017	56			-/-/6	6
2017/18	06 Aug 2017	66	0	4	0	0
	01 Feb 2018	68		0		
2018/19	28 Jul 2018	16				
	13 Dec 2018	25	0	1	2/1/11	14
	16 Feb 2019	23	0	0	1/-/23	29
2019/20	26 Nov 2019	25		8	4/-/-	4
2020/21	20 Aug 2020	23	10	2		
	8 Dec 2020	37		13	5/-/17	22
2021/22	10 Feb 2022	36 (+ 10 in disrepair)	36			

Table 3. Nesting data from additional Dunk Island colonies recorded by Schulz (1991).

Breeding season	Date	Site	Nests on wall	Nests on floor	Total nests	Eggs
1989/90	8/9 Sept 1989	B (coastal)	34	5	39	22
	8/9 Sept 1989	C (coastal)	0	8	8	0
	8/9 Sept 1989	D (coastal)	32	10	42	24
	8/9 Sept 1989	E (coastal)	52	12	64	32
	8/9 Sept 1989	F (inland)	0	20	20	0

Schulz's swiftlet nest and egg counts from his five coastal sites (B, C, D and E in Table 3, and A in Table 2) indicate breeding is well underway by September, with egg-laying likely commencing in August. These data confirm that breeding commences earlier in these colonies than in the Dunk Island Main Colony.

Bedarra Island

The Bedarra Island Colony, as indicated by nest numbers over 67 years from 1955 to 2022, has also fluctuated (Table 4). For example, the nest counts from 1973 to 1977 were substantially higher than the counts before and since that period. The very low nest count (2) in August 2015 may indicate either a low swiftlet population or simply the loss of many nests in the non-breeding season. The relatively low nest counts (52) in November 2015 and (5) January 2007 suggests greatly reduced breeding during those seasons, with or without a reduction in the swiftlet population.

The presence of eggs in the Bedarra Island Colony on 27 July 1974 establishes that breeding can commence during July. If the single egg observed in the Bedarra Island Colony on 7 April 1974 had been recently laid, the resulting nestling would not fledge until mid-June, indicating the potential for a 12-month breeding season from July of one year to June of the next. It is also possible that the egg observed in April was a non-viable egg laid sometime earlier; to date no nestlings have been recorded in May or June in any of the island colonies.

Wheeler Island

Breeding observations of the Wheeler Island Colony indicate population stability over the 57 years from 1965 to 2022 (Table 5). This may reflect the highly protected nature of the cave, especially compared to the more exposed setting of the Bedarra Island Colony. However, no data are available from Wheeler Island for the 1915/16 or 2006/07 breeding seasons

Table 4. Summary of nest counts and breeding data from Bedarra Island Colony from 1950 to 2022.

Breeding season	Date	Nests (+ incomplete)	Nests on floor	Eggs	Nestlings Pink / Part / Full (if known)	Nestlings total	Source
1950/51	16 Dec 1950			64		17	Hayes 1965
	27 Dec 1950	110		57		12	Hayes 1965
	01 Jan 1951			57		10	Hayes 1965
	06 Feb 1951			6			Hayes 1965
	14 Mar 1951					1	Hayes 1965
1955/56	27 Oct 1955	72 (21)		17			Busst 1956
	04 Nov 1955	121 (22)		19			Busst 1956
	10 Nov 1955	129 (27)		27			Busst 1956
	24 Nov 1955	197 (6)		67	1/-/-	3	Busst 1956
	01 Dec 1955	204 (6)		59		9	Busst 1956
	09 Dec 1955	204	30	91		8	Busst 1956
	19 Jan 1956	224 (7)		3		7	Busst 1956
	16 Feb 1956	224 (7)		3		7	Busst 1956
	23 Mar 1956	224 (2)		1		2	Busst 1956
	07 Apr 1957	224		0		0	Busst 1956
1961/62	11 Jan 1962	128		40		30	Hayes 1965
1973/74	7 Apr 1974	400		1		0	Smyth *et al.* 1980
1974/75	27 Jul 1974	400		4		0	Smyth *et al.* 1980
	8 Sep 1974	400		100		2	Smyth *et al.* 1980
	1 Dec 1974	400		185		68	Smyth *et al.* 1980
	10 Apr 1975	400		0		0	Smyth *et al.* 1980
1975/76	3 Oct 1975	375		0		0	Smyth *et al.* 1980
1976/77	4 Sep 1976	350		1		0	Smyth *et al.* 1980
	5 Oct 1976	350		215		2	Smyth *et al.* 1980
	9 Oct 1976	370		130		11	Smyth *et al.* 1980
	12 Nov 1976	353		126		51	Smyth *et al.* 1980
	5 Dec 1976	365		122		21	Smyth *et al.* 1980
	28 Dec 1976	380		93		79	Smyth *et al.* 1980
2006/07	Late Jan 2007	5					Tarburton & Tarburton 2013
2015/16	18 Aug 2015	2	40	0		0	Present study
	28 Nov 2015	52	40	6	1/5/3	76	Present study
2021/22	10 Feb 2022	220 (+ 15 in disrepair)		13	6/15/24	45	Present study

which were associated with apparent population declines in the Bedarra Island Colony. In most years for which data are available, the Wheeler Island Colony was the largest known in the Family Islands.

Table 5. Nest counts and breeding data from Wheeler Island from 1965 to 2022.

Breeding season	Date	Nests	Eggs	Nestlings	Source
1965/66	Early June 1965	400-425			Orrell 1967
1974/75	28 July 1974	400	7		Smyth *et al.* 1980
1976/77	11 Nov 1976	289	161	70	Smyth *et al.* 1980
1977/78	14 Nov 1977	500	96	368	Smyth *et al.* 1980
	27 Dec 1977	500	112	44	Smyth *et al.* 1980
2021/22	11 Mar 2022	470 + 2 on ground	1 half eggshell	70 fully feathered	Present study
2021/22	08 Aug 2021	406	8		Present study

Table 6. Swiftlet and bat data from the Hinchinbrook Island Colony.

Date	Nests on wall	Swiftlets on nests	Bats roosting on ceiling	Bats roosting among swiftlet nests
13 Nov 2021	1,763	647	589	71

Hinchinbrook Island

Population data for the Hinchinbrook Island Colony was restricted to the analysis of photos taken on a single visit to its cave (Table 6). The location of the nests high up on the cave wall made it impossible to view or photograph inside the nests to count the number of eggs present. However, the data indicate that breeding was well underway in November, consistent with the other island swiftlet colonies. Over 1,700 nests were counted on the cave wall, which indicates that this is the largest island Coastal Australian Swiftlet colony so far recorded. The presence of a large number of roosting bats, and the floor of the cave permanently awash with seawater were distinctive features of this colony. If all the nests photographed were used for breeding in one season, with an average of two nestlings per nest, the swiftlet population (adults and nestlings) could be as high as 6,800 (1,700 × 4) by the end of the breeding season, assuming 100% nestling and adult survival.

Sibling incubation

Daily time-lapse photography revealed a range of breeding outcomes including: eggs laid that were subsequently lost before hatching; hatchlings that were lost before fledging; nests that fell from the wall before eggs hatched or nestlings fledged; successful hatching and fledging with or without sibling incubation; one, two or three sequential egg-laying, hatching and fledging events. In the nests studied, all sequences that resulted in two or three fledged nestlings involved sibling incubation (Table 7, Fig. 15).

Table 7. Summary of inferred sibling incubation period per egg and total for each nest based on data from the 2016/2017 breeding season in the Dunk Island Main Colony (see Appendix S1).

	Sibling incubation period (days)		
Nest	**Egg 2**	**Egg 3**	**Total**
1	25		25
2	11	19	30
3	25		25
4	16		16
5	17	14	31
6	26	5	31
7		16	16
8	17		17
9	22		22
10	14		14

Based on our photographic evidence of nesting stages, sibling incubation occurred in all 10 nests, ranging in duration from five to 26 days per egg. The maximum total sibling incubation for one nest was 31 days, with an average of 22.7 days per nest. A third egg was laid in three of the 10 nests in which the first two eggs hatched and the nestlings fledged. A third egg was laid in a further two nests in which either the first or second egg was lost. Occasionally, an egg was sighted beneath a nearly mature nestling (Fig. 16), providing direct evidence of sibling incubation.

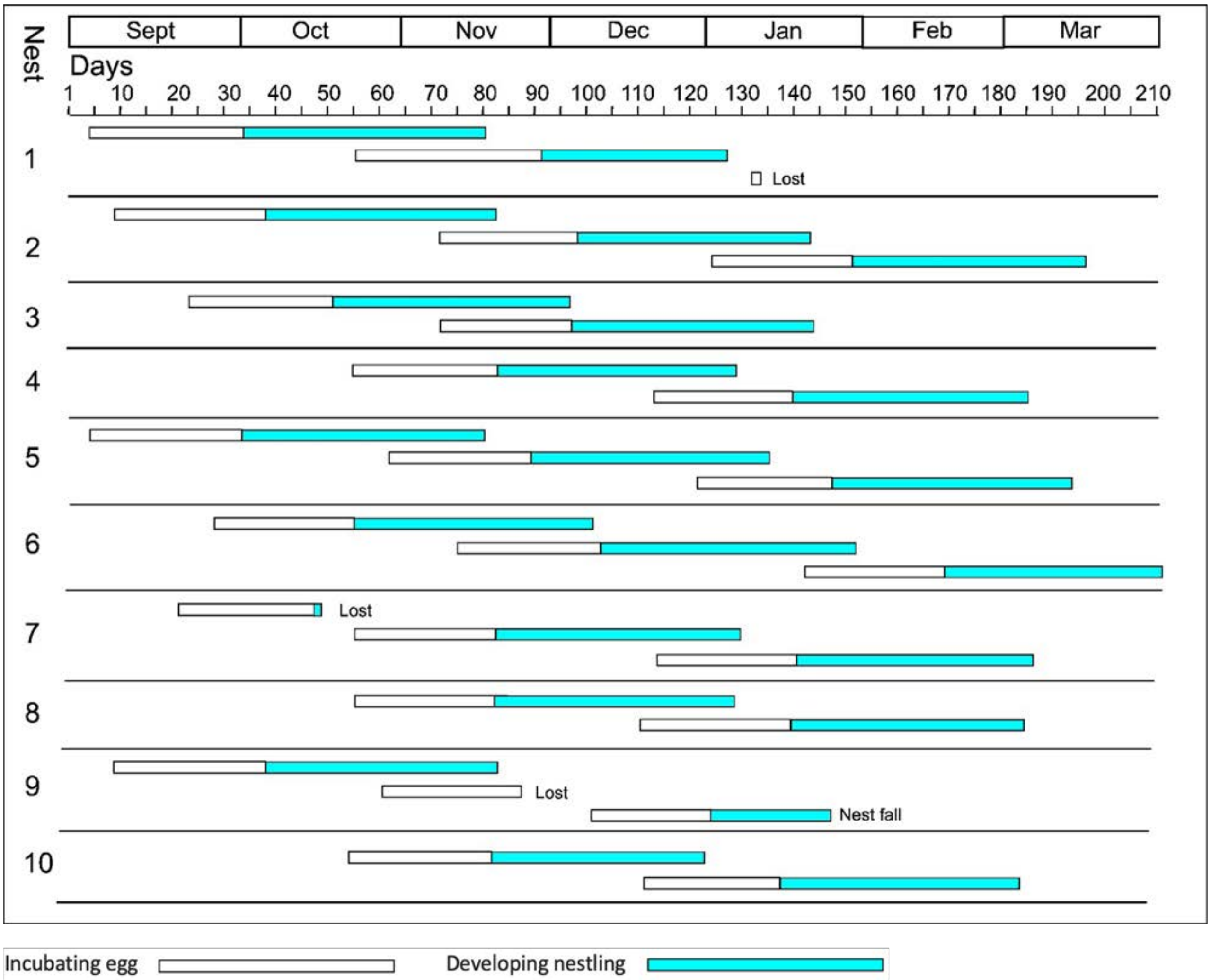

Figure 15. Incubation and fledging times for 10 nests in the Dunk Island Main Colony during the 2016/2017 breeding season. Sibling incubation is indicated when egg incubation overlaps with developing nestling. Image: David Blair.

Figure 16. Sibling incubation in Dunk Island Main Colony (December 2018). The pale edging of the primary feathers indicate that the sitting bird is a nestling (following Tarburton 2012). Image: Dermot Smyth.

Discussion

Population trends

Despite the intermittent nature of the observations, and the different time spans over which data were collected from each colony, the data summarised in this article indicate that – notwithstanding apparent population fluctuations in particular colonies – the swiftlet population of the Family Islands has remained relatively stable over the long term in a region often subjected to challenging weather conditions, including frequent cyclones. Long-term population stability is exemplified by the breeding data from the Dunk Island Main Colony collected over more than a century, from the Bedarra Island Colony over more than 70 years, and from the Wheeler Island Colony over almost 60 years.

Fluctuations in Dunk Island and Bedarra island swiftlet populations present a mixed picture of the impact of cyclones. Banfield (1911) reported that a cyclone that severely impacted Dunk Island left the Main Colony unaffected, while low nest numbers recorded in the same colony in December 1977 indicate that two cyclones (Keith and Otto) early in 1977 (Bureau of Meteorology 2024a) may have contributed to reduced breeding success that year. Tarburton and Tarburton (2013) estimated a 45% decline in the Dunk Island swiftlet population between 1989 and 2007, based on counts of swiftlets flying from South Mission Beach towards Dunk Island at dusk in those two years; they concluded that Cyclone Larry in March 2006 may have been responsible for this decline.

Busst (1956) reported that Cyclone Agnes on 6 March 1956 had no apparent impact on the Bedarra Island Colony, while Tarburton and Tarburton (2013) reported that the five nests observed in the Bedarra Island Colony in January 2007 were not in use during the peak breeding season, suggesting that Cyclone Larry caused the demise of this colony. Our low nest counts in the Bedarra Island Colony in August and November 2015 were possibly due to the lingering impact of Category 5 Cyclone Yasi, which crossed directly over the Family Islands in early February 2011 (Bureau of Meteorology 2024a).

Tarburton and Tarburton (2013), concluded that colonies of the Chillagoe and Coastal subspecies (the latter near Mackay) over 28 and 25 years, respectively, responded to severe weather events by changing their nesting location and breeding time, and that such events can result in the extinction of the most exposed colonies, and population reduction in others.

We found that the breeding season of the Coastal Australian Swiftlet extends from July to April, with some variation between colonies, though more frequent observations of all colonies at the beginning and end of the breeding season are required to ascertain the existence or extent of any breeding asynchrony between colonies.

Records of predation on swiftlets are limited, and do not suggest that it is a major cause of population fluctuation. However, Djiru Traditional Owners regard swiftlets as important food for pythons (Leonard Andy, personal communication 2020), as supported by the three sightings of a python in the Dunk Island Main Colony during the present study. Nests in the island swiftlet colonies are built on sloping walls that are hard for snakes to access, and sufficiently distant from vegetation to prevent pythons from using it to access nests and roosting birds. Tarburton (2009b) reported several occurrences of pythons and tree snakes falling off walls while apparently attempting to reach nesting swiftlets in the Chillagoe caves. Busst (1956), however, observed a tree snake partly coiled around a nest in the process of devouring a swiftlet, headfirst, on the lower surface of a sloping wall inclined at an angle of 45° in the Bedarra Island Colony.

Smyth *et al.* (1980) reported that ants were seen attacking newly hatched swiftlet nestlings in the Bedarra Island Colony, causing them to fall out of their nests and fall prey to skinks on the cave floor. This phenomenon was not observed in any of the colonies during the present study. One timelapse photo taken in the Dunk Island Main Colony shows a Ghost Bat (*Macroderma gigas*) roosting on the nesting wall. Ghost Bats are known to prey on birds (Boles 1999), with a preference for colonial roosting species less than 20 g in size. Boles (1999) included the Fork-tailed Swift (*Apus pacificus*) among the 58 bird species whose skeletal remains had been found at Ghost Bat feeding roosts; we have no information on the extent of Ghost Bat predation on island swiftlet populations. Tarburton (2009b) has noted that circling in groups before leaving and entering a cave or rock shelter, and high flying speeds when entering or leaving colonies are behavioural strategies that swiftlets deploy to avoid predation.

The long-term population stability of the Dunk, Bedarra and Wheeler Island swiftlet populations reported here coincides with a period of decline in abundance of insect populations in Australia and globally (Leather 2018; Lister & Garcia 2018;

Sánchez-Bayo & Wyckhuys 2019). While the cause of this decline is not well understood, it is thought to result from urbanisation, habitat loss and agricultural land use, and is implicated in the decline of woodland bird species in Australia and elsewhere (Braby *et al.* 2023).

Smyth (1980) reported that Diptera (flies) comprise about 50% of the swiftlet diet, based on analysis of regurgitated food boluses collected from 10 swiftlets captured on Dunk Island during November 1976 and November 1977. Other insect prey included Coleoptera (beetles, 12.4%), and Hemiptera (bugs, 26.9%). By comparison, a study of 45 boluses obtained from the Chillagoe subspecies (Tarburton 1993) found the main food items were Homoptera (planthoppers, 47%) and Diptera (24%). The conservation status of these insects, and invertebrates generally, is not well documented in the Queensland Wet Tropics (Wet Tropics Management Authority 2023), so the extent of insect population decline in swiftlet feeding areas is not known. If prey populations are declining in north-eastern Queensland, there is no evidence that the decline is affecting swiftlets. Protected rainforest areas within coastal national parks, in combination with lowland sugar cane farms, may provide plentiful aerial insect resources for island-dwelling swiftlets. It is also possible that if declining, insect populations have not reached a level that is limiting to swiftlets, and/or that swiftlet population sizes may be determined by other factors, such as the availability and viability of nesting sites. It is also not known whether the diversity of prey species changes throughout the year. However, Harrison (1974) concluded that there was little prey specificity within or between swiftlet species in the vicinity of the large swiftlet colonies at Niah Cave, Sarawak in Malaysia.

The island swiftlet colonies that we observed share the following characteristics: they are located on the eastern (seaward) side of the islands; they are close to the shoreline but above the reach of normal tides and sea spray; they are westward-facing (or in one case eastward-facing but protected by a nearby rock outcrop); they nest and roost on ‘snake-proof’ sloping walls and at a ‘python-safe’ distance from vegetation. These features combine to aid protection from predation and ameliorate the impact of severe storms and cyclones. Difficulty of access may also provide protection from human interference; there was no evidence of Aboriginal harvesting of swiftlets or their eggs in this study or in the literature.

Another feature of these island swiftlet colonies is that their location is identifiable some distance away by landscape features, such as exceptionally large boulders, striking rock formations or, in the case of the Hinchinbrook Colony, a very prominent headland. It is possible that these features, which are unique to each colony, aid navigation to returning swiftlets in low light conditions at or after dusk. If this is so, further surveys for island or coastal swiftlet colonies may benefit from a focus on the presence of similarly distinctive features. Tarburton and Tarburton (2013) noted that Australian Swiftlets in Chillagoe enter their nesting caves through only one or two entrances, but exit through up to five openings, suggesting that the Chillagoe subspecies may also use distinctive landscape markers to locate their colonies. Tarburton (2009b) has suggested that the use of multiple exits may be a strategy for avoiding predators at the cave opening.

Sibling incubation

Our daily time-lapse photos taken in the Dunk Island Main Colony during the 2016/2017 breeding season confirmed the occurrence of sibling incubation in an island population of the Coastal Australian Swiftlet – a phenomenon previously known to occur only in the Chillagoe subspecies (Tarburton & Minot 1987). In our sample of 10 nests, maturing nestlings incubated the eggs of their younger siblings for a total of 14 to 31 days per nest, thereby reducing the total duration of breeding by the same number of days had each egg been incubated sequentially by a parent bird. This compares with the total reduction in breeding time of 23 to 47 days documented in the Chillagoe subspecies. The Chillagoe study revealed a maximum of two eggs per nest in a breeding season, unless one of the eggs was lost in which case a third egg was laid; whereas the Dunk Island study revealed up to three eggs per nest, even when the first two eggs successfully hatched, and the nestlings subsequently fledged. Sibling incubation of at least one egg was inferred in all 10 nesting sequences we analysed.

The production of up to three nestlings per nest per year in the island swiftlet populations, compared to a maximum of two nestlings observed in the Chillagoe studies, may represent a difference in fecundity between the two subspecies, or it may reflect differences in resource availability and energy expenditure of island versus mainland populations. This could be clarified through further study of mainland breeding colonies of the coastal subspecies, such as that found at Tully Gorge (Pecotich 1974). The likely greater availability of aerial insects in coastal and island rainforest throughout the year, compared to the drier inland environment around Chillagoe, may extend the coastal and island breeding season and facilitate raising a third nestling. Alternatively, island swiftlet populations may require a higher fecundity to maintain population stability in response to the particular ecological pressures of these environments – including the daily commute between island roosting caves and mainland feeding grounds, often in adverse weather conditions.

Confirmation that both subspecies of the Australian Swiftlet exhibit sibling incubation begs the question: is this the only swiftlet species, or indeed the only bird species, that employs this breeding strategy? If so, what are the selective pressures and advantages that have driven the evolution of this phenomenon? Is it a response to the long incubation time of swiftlet eggs, necessitated by their relatively slow development rate, and the inability of Australian Swiftlet parents to feed more than one nestling at a time, as Tarburton (2012) has suggested? If so, are there other bird species operating under similar constraints which might be found to exhibit sibling incubation. Alternatively, is the efficiency of simultaneously incubating multiple eggs, which is the dominant breeding strategy amongst birds in general, so selectively advantageous that it is only in the unique circumstances faced by Australian Swiftlets that sibling incubation provides greater efficiency, and their evolutionary success?

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