THE BREEDING BIOLOGY OF TWO POPULATIONS OF THE WHITE-RUMPED SWIFTLET (*Aerodramus spodiopygius assimilis*) IN FIJI and (*Aerodramus spodiopygius chillagoensis*) IN QUEENSLAND, WITH SPECIAL REFERENCE TO FACTORS THAT REGULATE CLUTCH SIZE IN BIRDS.

A thesis presented in partial fulfilment
of the requirements for the degree
of Doctor of Philosophy
in Zoology at
Massey University

Michael Kenneth Tarburton

1987

MASSEY UNIVERSITY

Instructions:

(1) Please complete two of these forms, by providing title details and striking out one option from each of the sections 1-3.

(2) If you select option b of any section you must include a specific time period. The maximum permitted period is 24 months.

(3) Include the two forms with the copies of your thesis submitted to your supervisor.

(4) The Library must receive the original of your thesis.

(5) We strongly recommend that you provide the Library with two copies of your thesis if it has colour plates.

Massey University Library. Thesis Copyright Form

Title of thesis: The breeding biology of two Populations of the White-rumped Swiftlet Aerodramus spodiopygius assimilis in Fiji and Aerodramus spodiopygius chillagoensis in Qld.

(1) ~~(a) I give permission for my thesis to be made available to readers in the Massey University Library under conditions determined by the Librarian.~~

(b) I do not wish my thesis to be made available to readers without my written consent for 12 months.

(2) ~~(a) I agree that my thesis, or a copy, may be sent to another institution under conditions determined by the Librarian.~~

(b) I do not wish my thesis, or a copy, to be sent to another institution without my written consent for 12 months.

(3) ~~(a) I agree that my thesis may be copied for Library use.~~

(b) I do not wish my thesis to be copied for Library use for 12 months.

Tarburton

Signed M.K. Tarburton.

Date 22 May 1987

The copyright of this thesis belongs to the author. Readers must sign their name in the space below to show that they recognise this. They are asked to add their permanent address.

NAME AND ADDRESS DATE

Th
Tar

ABSTRACT

White-rumped Swiftlets Aerodramus spodiopygius (Apodidae) build nests of vegetable material and cement (from their saliva) in the dark sections of caves at Chillagoe in Queensland, Australia, and in Fiji. Fijian colonies average 1,762 nests while the colonies at Chillagoe contained an average of 77 nests. Breeding takes place between September and March in Fiji, and from October to March at Chillagoe. There is no sexual dimorphism and both sexes share in incubation and the feeding of nestlings.

At Chillagoe the clutch is one egg whereas in Fiji it is two eggs laid three to five days apart. At Chillagoe incubation took 27.8 days in the poor year and 26.6 days in the good year. In Fiji incubation averaged 23 days and 58% of eggs hatched compared to 64% of eggs at Chillagoe. The Fijian birds successfully fledged an average of 92%, a breeding success of 53% or 1.1 young fledged per breeding pair. From the two single-chick broods the birds at Chillagoe fledged 69%, a breeding success of 44% or 0.9 young fledged per pair in the good breeding season. In the poor year at Chillagoe hatching success was 60%, fledging success was 50%, reducing breeding success to 30%. At Chillagoe the fledging period was increased from 46.9 days in the good year to 49.8 days in the poor year.

At both locations most chick mortality resulted from chicks falling from their nests. Lost eggs or chicks were normally replaced by eight to fourteen days. Chicks in Fiji were fed an average of 2.2 times a day, whereas those at Chillagoe were fed an average of 5.2 times a day in the good season and 3.0 times a day in the poor season.

Placing the data for this species with those for other species of apodids shows a positive correlation between egg size and adult size and a negative correlation between feeding frequency and the nestling period.

Producing a third egg would not benefit the Fijian Swiftlet, which could not hatch significantly more eggs when given a third egg and could not fledge significantly more chicks when given three chicks instead of their normal brood of two.

Fijian birds fed the artificially enlarged broods more frequently than normal sized broods, but neither the number of feeds per chick nor the number of chicks fledged in the larger broods was increased. Parents are apparently maximising the number of fledglings that they can raise.

It is suggested that when there is a food shortage in the breeding season some passerines will lose more newly fledged chicks than normal whereas White-rumped Swiftlets in Fiji will lose more nestlings than normal.

Nest size is not restricting clutch size as swiftlets at Chillagoe did not raise more young when their nests were enlarged, and predators cannot be restricting clutch size because their nests are in total darkness. The swiftlets at Chillagoe are on the "mainland" yet produce a smaller clutch than those on the Fiji Islands. This is the reverse of predictions from the theory of "competitive release" on islands, therefore this theory cannot be used to explain the smaller clutch size of the birds at Chillagoe.

The remaining factor is the food supply which is controlled by the occurrence of rain. The abundance of aerial insects was greater during days when rain fell.

Adult swiftlets gathered less food in the dry season and in the dry periods between rain, and chicks put on more weight during rain periods, indicating that food was the critical factor restricting chick growth. Additionally, artificially enlarged broods grew more slowly and never fledged more chicks than single-chick broods. This demonstrates that the abundance of food during the breeding season is the factor that not only regulates chick growth but also restricts clutch size.

The food supply at Chillagoe does not last long enough for swiftlets to raise two single-chick broods, but it does last long enough for a unique strategy to have been developed which allows them to raise two chicks without producing a two-chick brood. This strategy involves the female laying the second egg after the first chick is fully feathered so that the first chick completes most of the incubation of the egg. The second egg hatches after the first chick fledges. The timing of laying the second egg leaves both parents free to forage for one chick only and allows them to raise two chicks in the shortened breeding (rainy) season that is characteristic of the savannah.

INTRODUCTION

Swifts and swiftlets form the avian family Apodidae. The 84 species in the family (Brooke 1971a), are easily identified by their long curved wings and characteristic flight. However identification at the level of the species has proved much more difficult. This means that one always has to be alert to the possibility (particularly in old publications), that particular data may not apply to the species under which the data were first published. Early methods of identification involved the use of relative wing and tail lengths, furcation of the tail (Stresemann 1931), and the amount of feathering on the tarsus (Oberholser 1906), or all of these (Mayr 1937). More recent studies have found these characters, along with colour variation, sufficiently diagnostic for the swifts (Brooke 1970, Collins & Brooke 1976), but inadequate for the swiftlets. The type of nest and the ability or not to echolocate, have been used to reduce the confusion in identifying swiftlets (Medway 1966, Medway & Pye 1977).

Swiftlets are also different to the larger Apodidae in that some aspects of their biology make them easier to study. This is because the swiftlets not only nest and roost in larger colonies than the swifts, but they also use the same locations for both activities and are therefore in the one cave, every evening throughout the year. This means data can be collected more quickly and easily. This advantage over the study of swifts has helped in the study of the breeding ecology of the Mossy-nest Swiftlet (Aerodramus vanikorensis), the Black-nest Swiftlet (Aerodramus maximus) and the Glossy Swiftlet (Collocalia esculenta) (Medway 1962 a,b); as well as the Edible-nest Swiftlet (Aerodramus fuciphagus) (Langham 1980). These two studies were made in Malaysia where a longstanding interest in the culinary use of swiftlet nests has developed.

It is probably the restricted distribution of swiftlets within the poorly studied tropics of the Indo-Pacific region that has delayed the study of breeding in other species.

The majority of swiftlets have been placed in the genus Aerodramus because of their ability to orient acoustically within the dark zones of caves, or into the cave entrances at night, by means of echolocation. This ability is found in only one other bird, (the Oil Bird, Steatornis) and so it is not surprising that a number of studies has been made on the acuity of this ability (Griffin 1958, Novick 1959, Vincent 1963, Medway 1967, Fenton 1975, Roberts et al. 1976, and Smyth & Roberts 1983). One study has been made on the Syringeal mechanism for producing the echolocatory "clicks" (Suthers & Hector 1982, 1985).

The remaining swiftlets have been placed in the genus Collocalia and the monospecific genus Hydrochous. None of these species echolocate and hence they cannot leave the roosting site before daylight. This means they cannot reach distant foraging locations in time to benefit from feeding there during the prey-rich, pre-dawn period. Nor can they remain in distant feeding areas through the similarly rewarding period of evening twilight. Hence it is likely the colonies of non-echolocating species will be smaller than those of Aerodramus and in any case will not be found in the relatively predator-free zone of total darkness. This is the case in Niah Cave, Borneo, where the single non-echolocating species, forms a minority of the 4.5 million birds using the cave. (Harrisson 1976, Medway 1962a,b).

The White-rumped Swiftlet (Aerodramus spodiopygius assimilis) is the only swiftlet feeding over the insect rich forests of Fiji. There are numerous caves in Fiji, providing more breeding sites than on Borneo and perhaps as a consequence the largest known colonies there number only tens of thousands.

However, these colonies are larger than the breeding colonies of all swifts except the White-naped Swift (Streptoprocne semicollaris) (C.T. Collins pers. comm.) or even those of this species in Australia, which is the only other location where a number of colonies belonging to this species have been censused.

Large colonies should provide a good sample size for determining the breeding, feeding, flight and longevity parameters studied in this thesis and as these parameters have not been previously determined for this species or for any other in the South Pacific, it was useful for this study to have such numerous subjects. However it was found that having such large numbers can itself create certain problems, for example in gathering an adequate sample of recaptures.

The main object of conducting observations and experiments on assimilis in Fiji was to determine which (if any) of the theories on the factors regulating clutch size in birds applies to this species in particular and possibly to swifts in general. By conducting similar observations and experiments on (A. s. chillagoensis) in the unpredictable savannah climate of the Chillagoe district, it was intended to examine the question of why this species was an exception to the rule of savannah birds producing larger clutches than their close relatives in tropical rainforest.

In presenting the results of my work on the White-rumped Swiftlet in Fiji and at Chillagoe in Queensland the general breeding data for both subspecies are dealt with together but the data from the experimental work on the clutch size for both subspecies are considered separately for clarity. The discussion and conclusions for both studies are placed together, as some aspects involve both studies.

ACKNOWLEDGEMENTS

The help of the following persons has been appreciated and is therefore acknowledged. Charles T. Collins has provided much comparative information, both published and unpublished. Mary Lecroy kindly provided data on swiftlets and nests in the collections of the American Museum and Kimball Garrett provided measurements of swifts in the Los Angeles County Museum. Swallows in the National Museum of New Zealand were measured by N.H.S. Hyde. H. Rahn kindly sent copies of material that is unavailable in New Zealand.

Valuable field assistance in Fiji was given by: M. & A. Ahkoy, E. Bolst, A. Curry, P. Hoffman, T. Kabu, R. Litster, T. Osborne and J. Wells. At Chillagoe the help of Queensland National Parks and Wildlife staff (particularly J. Barton, D. Flett and L. Little), members of the Chillagoe Caving Club (particularly A. Cummins, K. Offer, T. Porritt and K. Ridgway) and L. Pecotich is gratefully acknowledged.

The helpful advice and criticism given by supervisors Dr. Edward Minot and Prof. Brian Springett has been of inestimable value. This help was most forthcoming in Section 4, as Dr. Minot and I published a part of that work after my first season at Chillagoe.

Financial assistance towards the last visit to Chillagoe from the Frank Chapmam Memorial Fund is acknowledged in appreciation.

TABLE OF CONTENTS

Section 1

BREEDING BIOLOGY OF THE WHITE-RUMPED SWIFTLET IN FIJI AND CHILLAGOE

Results & Discussion

TABLE OF CONTENTS Cont.

Section 2

AN EXPERIMENTAL MANIPULATION OF CLUTCH AND BROOD SIZE TO DETERMINE WHETHER LONG-LIVED TROPICAL SPECIES ARE MAXIMISING THEIR FOOD SUPPLY.

Results

Section 3

CLIMATE & INTRA-TROPICAL VARIATION IN CLUTCH SIZE

Results

TABLE OF CONTENTS Cont.

Section 4

A NOVEL STRATEGY IN INCUBATION - CHICK INCUBATION

Section 5

APPENDICES

TABLE OF CONTENTS Cont.

LIST OF FIGURES

LIST OF TABLES

Section 1

BREEDING BIOLOGY OF THE WHITE-RUMPED SWIFTLET IN FIJI AND CHILLAGOE

ABSTRACT

The White-rumped Swiftlet (*Aerodramus spodiopygius* Peale) was studied in Fiji (*A. s. assimilis*) and Chillagoe, Queensland, Australia (*A. s. chillagoensis*). At the majority of both *assimilis* and *chillagoensis* colonies, nests were in totally dark sections of caves. Local habitat determined which vegetable materials were cemented into the nests. Colonies in Fiji contained from 49 to 7,370 nests and in Chillagoe from 1 to 264 nests. The colonies in Fiji are the largest yet recorded for the species. Eggs were found in Fijian nests only between September and March. The clutch, which is one in *chillagoensis* and almost invariably two eggs laid three to five days apart in *assimilis*, was incubated for an average of 26.6 days during the better season in the former subspecies and an average of 23 days in the latter. Fifty-eight percent of Fijian eggs hatched successfully compared to 64% of eggs at Chillagoe. If the total clutch or young brood was lost, it was usually replaced within 14 days. The fledging success of 92% gave a breeding success of 53% or 1.1 young fledged per breeding pair of *assimilis*. In *chillagoensis* the fledging success for the better season was 69% giving a breeding success of 44% or, 0.9 young fledged from the two broods of a breeding pair. In the poor year at Chillagoe incubation took 27.8 days, hatching success was 60%, fledging success was 50% and the nestling period had increased from 46.9 days in the better year to 49.8 days in the poor year.

Most chick mortality resulted from the chicks (in both subspecies) falling from their nests. There is no sexual dimorphism and both sexes share in incubation and feeding nestlings.

New data are compared with those for other Apodidae and Hirundinidae. They show a positive correlation between egg size and adult size and a negative correlation between feeding frequency and the nestling period. Each Fijian chick was fed on average only 2.2 times each day, making them one of the least frequently fed of the Apodidae. Chillagoe chicks were fed an average of 5.2 times a day. The major ectoparasites observed on the birds or their nests were Louse-flies (Hippoboscidae). *Myophthiria fijiarum* was being hosted by *assimilis* and *Myophthiria spp* was found parasitising *chillagoensis*.

INTRODUCTION

Chillagoensis inhabits inland peninsular Queensland, and has only recently been separated from *terraereginae* which inhabits coastal Queensland (Pecotich 1982). No details on the breeding of either subspecies have been previously published. *A.s.assimilis* inhabits many of the islands of Fiji, and although it has been known since 1912 has never been studied previously. In this section I describe the basic breeding biology of the two subspecies. Egg size, incubation period, hatching success, nestling development, nestling development period, frequency of chick feeding and fledging success for both sub-species are discussed and compared. The relationships between egg weight and adult weight in the Hirundinidae and Apodidae are defined as is the relationship between incubation period and nestling period in the apodids. Because many of the data in this section are new, it serves as a basis for the experimental work on clutch size in the following section.

DESCRIPTION OF STUDY AREAS

FIJI ISLANDS

Fiji is an archipelago of islands situated at latitude 18°S and 178°E in the South Pacific. Much of Fiji is composed of sedimentary rocks. The commonest are limestone and soapstone and so caves have formed in many areas including some small islands as well as the larger islands. Piercing through this layer of sediments are numerous volcanic outcrops which give a rugged appearance to some regions. Viti Levu is the largest and tallest island, having 32 peaks that exceed 1,000 metres. Viti Levu and the other large islands are covered with rainforest and where that has been recently cleared, tall grasses, creepers and shrubs still give the countryside a tangled green look. The green look of the dense forest surrounds the caves on Viti Levu and is quite different to the sparse savannah vegetation of Chillagoe even though both areas are about 17 degrees south of the equator.

Many of the smaller islands are coral atolls or volcanic peaks. Cikobia-i-Lau in Eastern Fiji is small, but having both coral and volcanic origins is provided with a mountain and surrounding reefs. Enough sediment had been deposited before its uplift to provide sufficient limestone for the island's only cave. This cave contains a swiftlet colony and is one of those studied in this thesis. There is little forest on such islands, as the village gardens and coconut trees occupy most of the areas with soil.

Village gardens also comprise a reasonable portion of the area on Viti Levu, where the other swiftlet colonies studied in this thesis are located. The commonest plants in these gardens are cassava, dalo and bananas, while the less common plants include pineapples, pawpaws, bele, daruka, corn, pumpkin, egg plant, yams and sweet potatoes. Swiftlets were seen feeding over these gardens and over regrowth areas of grass, sedge and guavas but they collected most of their food over the forests.

Mosses, lichens and filmy ferns from forest trees are commonly used for nest construction but in the drier parts fibres from the crown of the coconut trees and grasses are used in conjunction with the birds' saliva for nesting materials.

CHILLAGOE REGION

The town of Chillagoe is adjacent to a series of National Parks that stretch through two cattle stations at 17°S and 144°E 130 km due west of Cairns, Queensland, Australia. The Chillagoe region consists of a parallel array of chert ridges interspersed with granite outcrops. Both of these elevated areas as well as the intervening low country are covered with ironbark savannah woodland. More impressive, though more confined is the three to five km wide belt of abrupt grey towers of sculptured limestone extending from south of Chillagoe, 45 km north through Chillagoe and Mungana to the Walsh River, where the limestone belt subsides beneath the plain. These towers project up to 70 m from the surrounding plain and are often partly covered by vine thicket.

Both the savannah woodland and vine thicket communities contain species that sustain high insect populations which in turn support a number of species of insectivorous birds. Because many of the insects are aerial or have alate stages in their life cycle, the insectivorous birds include several aerial feeders. Two of these, the Rainbow Bee-eater (merops ornatus) and the Fork-tailed Swift are migratory and time their arrival into this district to coincide with that of the rainy season. The White-rumped Swiftlet and the Black-faced Woodswallow (Artamus cinereus) are the major resident aerial insect eating birds. There is no swallow or martin that is common in the district.

Amongst the commonest of the trees in the woodland over which the swiftlets do most of their feeding are the Cullens Ironbark (*Eucalyptus cullenii*), Ghost Gum (*E. papuana*), the Variable-barked Bloodwood (*E. dichromophloia*), Cocky Apple (*Planchonia careya*) and the Cooktown Ironwood (*Erythrophloeum chlorostachys*). Two of the eight plants from the poaceae that grow beneath and between these trees are the Black Spear Grass (*Heteropogon contortus*) and Kangaroo Grass (*Themeda australis*). These two grasses are the major vegetable component in the swiftlets' nests. By regularly burning these grasses the stockmen of Chillagoe and Rookwood stations damage other flora as well. However, the limestone towers offer protection from most fires. In these towers the Broad-leafed Kurajong (*Brachychiton australe*), the Red Bauhinia (*Lysiphyllum cunninghamii*), the White Bauhinia (*L. hookerii*) and the Helicopter Tree (*Gyrocarpus americanus*) find protection from fire. Six figs, including the Sandpaper Fig (*Ficus coronata*) and the Cluster Fig (*F. racemosa*) send their roots down the grikes and weak joints in the limestone to aquifers that otherwise would be out of reach. These trees support several plants such as the Jasmine Vine (*Jasminium recemosum*), the Pisonia Vine (*Pisonia aculeata*) and the mistletoes (*Lyperanthus spp*). Both these supportive and climbing plants support, directly and indirectly, a wide variety of birds and insects. Some of the more abundant of the latter include the jumping plant lice, termites, flower wasps and ants.

Many of the grikes and collapses in the limestone towers open into caves that fracture large areas of the limestone. About 27 of the 400 caves explored and tagged by the Chillagoe Caving Club, contain swiftlet colonies. Swiftlets use these caves for roosting each night and for breeding each wet season (October - March).

Many of the caves have phreatic passages (formed by flowing water) suggesting that the past may have been wetter than the present.

The remnant presence of plants such as the Stinging Tree (Dendrocnide moroides), the False Stinger (Pipturus argenteus), Maiden Hair Fern (Adiantum spp), Fishbone Fern (Blechnum spp), and the Black Orchid (Cymbidium calycalatum) as well as rainforest birds such as the Australian Brush Turkey (Alectura lathami), the Cassowary (Casuarius casuarius) and the Figbird (Sphecotheres vieilloti) also suggest recent desiccation. The Chillagoe form of the White-rumped Swiftlet is the only one of eight subspecies to inhabit such a dry area and so it too may be viewed as part of Chillagoe's relict tropical rainforest community.

METHODS

The nesting (and roosting) colonies of assimilis most frequently visited were those of Dry and Waterfall Caves at Nasinu 9 Mile, located nine miles north of Suva, Fiji. Visits lasted two to four hours and were made in most months during 1974 to 1976 inclusive. In addition, frequent visits were made during the early part of the 1976 breeding season to determine the incubation periods for individually marked nests. From 1977 until 1986 these colonies were visited in most years to collect longevity data from banded birds. Day-long visits involving clutch and brood manipulation experiments (Tarburton 1987a, Appendix 4 p.164.) were made throughout December 1981 and again in December 1983.

In October-November 1976 the insertion of triangular pieces of galvanized iron with individual numbers punched into them proved quite satisfactory for identification of nests, and incubation periods were determined. Because the galvanized labels might weaken nests, paint was used to mark a number beside the nests used in the manipulation experiments of December 1981 and December 1983. This method of nest identification proved successful and so has also been used at Chillagoe.

Ten visits were made during 1974 and 1975 to Ono Cave near Wailotua Village in the Wainibuka Valley, 45 miles NNW of Suva.

Waiyala Cave in the Sigatoka Valley 80 miles west of Suva was visited throughout 13 January 1975. The only cave on Cikobia-i-Lau in the east of Fiji was visited on 7 January 1976.

The 1981 and 1983 experiments were conducted in the Waterfall Cave, which is less accessible and rarely visited by other people. However, because many of the 150 marked nests were difficult to reach and some Common Swifts desert easily (Lack 1956a), I visited nests at two or three day intervals.

Data for chillagoensis were obtained in the main from colonies in Gordale Scar Pot (CH 187) and Guano Pot (CH 146). These were visited six days a week 28 November 1985 - 27 January 1986 and 2 December 1986 - 23 January 1987. Other sites were visited on one or more occasions. Two all-day chick watches were made in Gordale Scar Pot, to determine the number of times a day each chick was fed. The first one was made from 0600 - 1300 hrs on 18 December and from 1300 - 1800 hrs on 19 December 1985 and the second was from 0615 - 1715 hrs on 22 December 1986.

The first season at Chillagoe was a normal wet season in which chicks grew more quickly and fledged in higher numbers than in the following season. The second breeding season was markedly dry and for the first time I found nestlings that had starved to death. Because of this the 1985/86 season is referred to as the good season and the 1986/87 season is refered to as the poor season.

The positions of the Fijian sites are shown in Figure 1 and those of Chillagoe sites in Figures 2 and 3.

Permission from the Fiji Department of Forestry and Fisheries was gained to trap and band wild birds. Formal permission was obtained from Queensland National Parks and Wildlife Service before entering any of the Chillagoe sites as they are within Chillagoe National Park.

Figure 1. Location of White-rumped Swiftlet colonies studied in Fiji

Figure 2 Distribution of *chillagoensis* & *terraereginae*

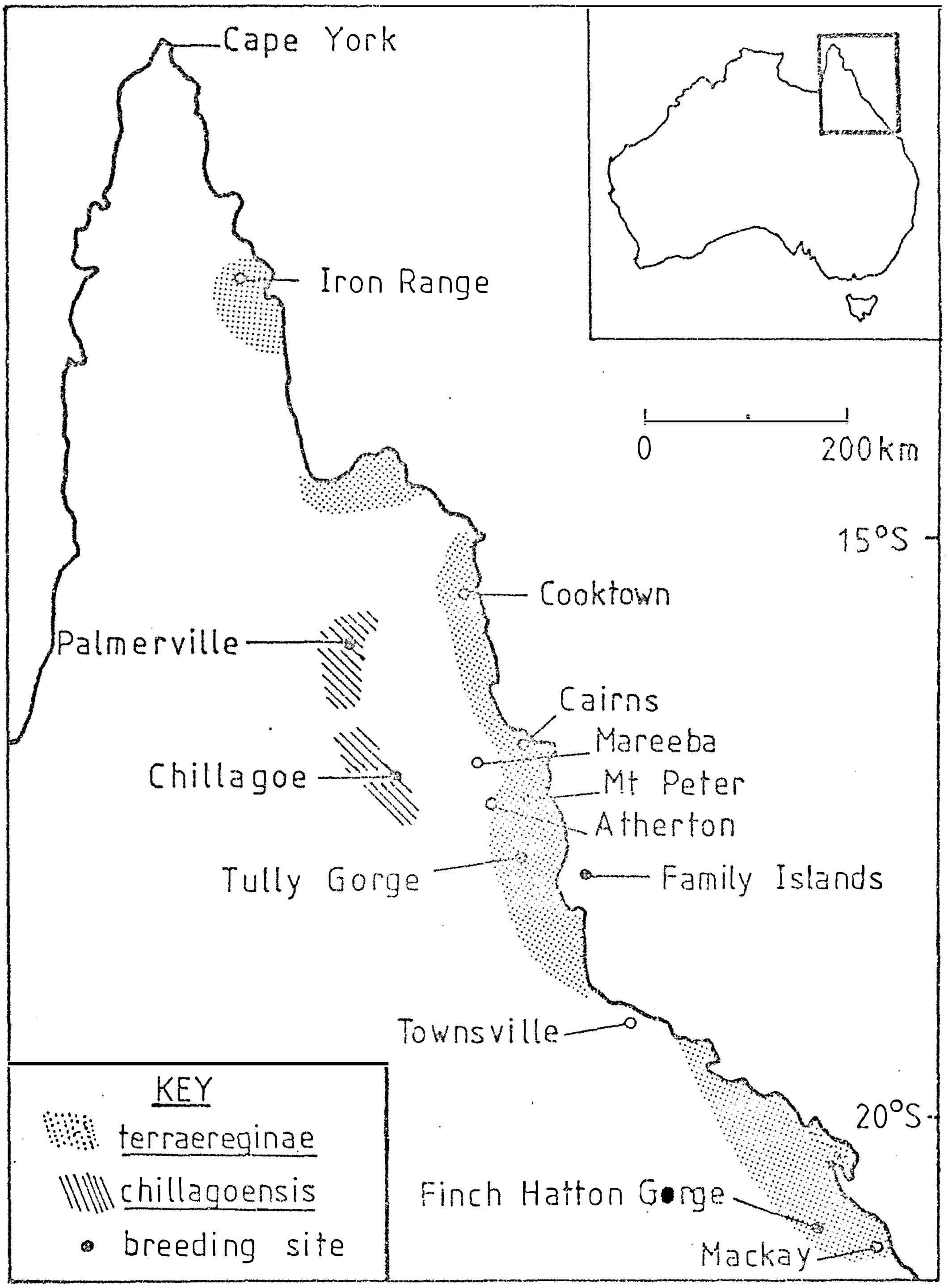
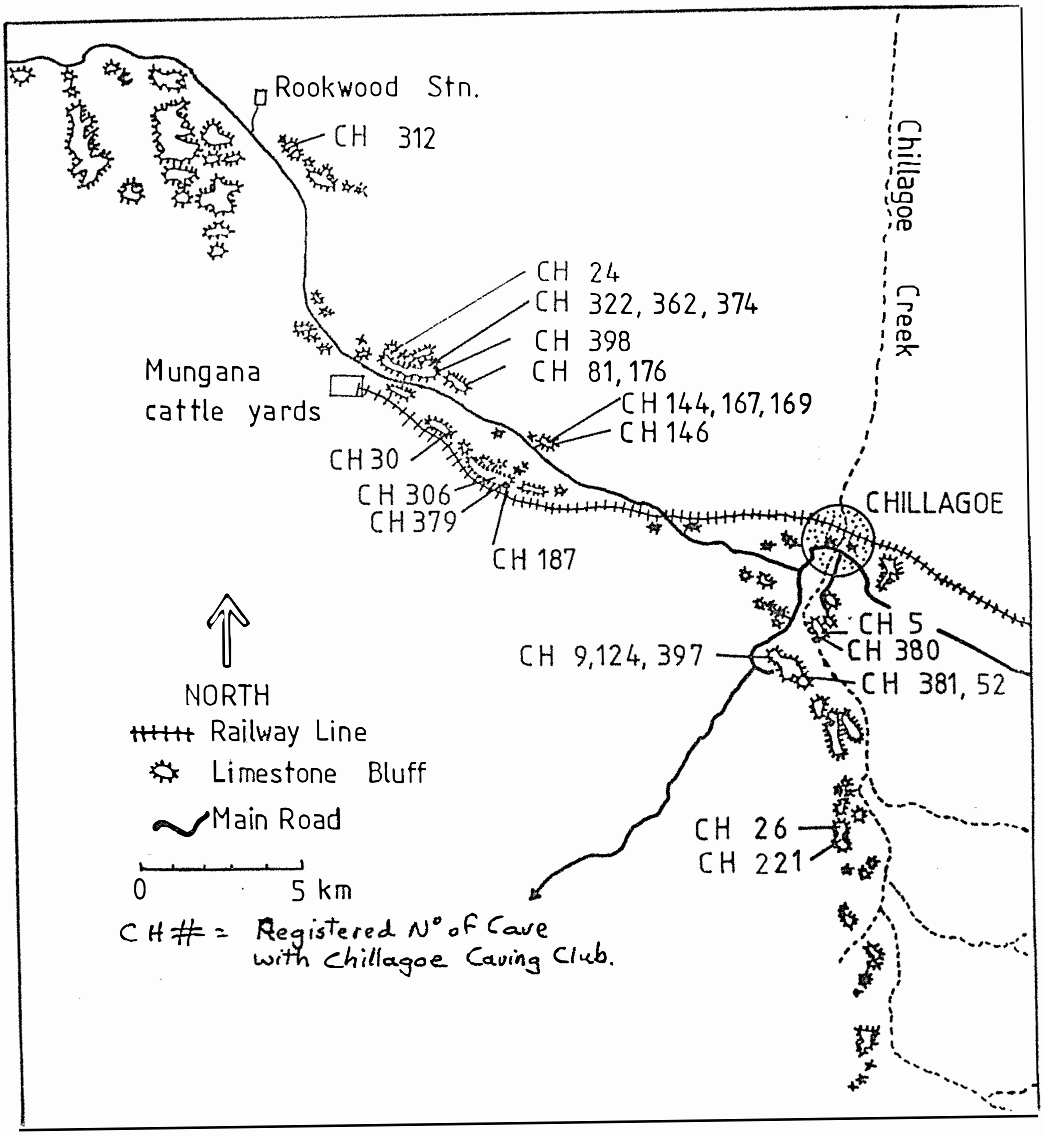


Figure 3 Location of chillagoensis colonies visited in this study



Individual chicks were identified with daubs of fast drying model paint placed on their head, shoulder or rump. Once the chicks were old enough both those in Fiji and Queensland had an individually numbered aluminium band from the Australian Bird and Bat Banding Scheme, Canberra, Australia, placed on one leg. Wing growth, which Lack & Lack (1951) demonstrated to vary with the quantity of food supplied, was determined by measuring from the carpal joint to the tip of the longest primary when the wing was held flat on a ruler. Weights were measured on 5, 10 and 50 g Pesola spring balances. The differential growth in the wing, and weight, for experimental broods of one, two and three are dealt with in section 3. In this section only the normal sized broods of one from Chillagoe and one and two from Fiji are considered.

Nest volume was not determined exactly because that was not possible using the published average measurements of nests with which I wanted to make comparisons, so I used an approximation. This approximation, the volume index, is derived by multiplying the average length, breadth and depth measurements together.

RESULTS & DISCUSSION

Breeding Distribution

Swiftlets nest in caves more frequently than the larger swifts and the White-rumped Swiftlet is no exception. All colonies of chillagoensis and assimilis visited in this study were located in caves, where the majority of nests were in total darkness. In addition to the islands of Viti Levu and Cikobia-i-Lau where I describe nesting (Figure 1), I have seen assimilis on the following islands in the numbers indicated: Vanua Levu 20, Qamea 5, Taveuni 7, Raranitiga 3, (all August 1976); Vanua Balavu 40, (there is a nesting cave near Moalevu), Naitauba 8, Laucala 3, (all January 1976); Ono 2, (May 1975).

I did not see them on Vatu-i-Ra, Sovu, Nanuku Levu, Matagi or Mabulau. Although these last five islands are lower than any of the others they are larger than Raranitiga on which swiftlets were found. Beck and Correia found them nesting on Ovalau and Katavanga (American Museum). Layard (1876) recorded the birds from Waikaia, Mokani, Taveuni, Mango and Kandavu.

While it is clear that assimilis is widespread in Fiji it is also clear that Mayr's (1945) statement that this swiftlet is found on all Fijian islands needs qualification. In addition to the islands on which I did not find it, Clunie (1984) records their absence from most of the Lomaiviti group, though Watling (1982) refers only to their being generally distributed.

That I found it on hilly islands which were smaller than flat islands on which it was not found may demonstrate that the birds require rocky chasms or caves for nesting. However, this swiftlet is capable of flying daily the distance to some of these islands (Appendix 6 p. 193) that it is not found on. So, assuming that assimilis is not inhibited by the ocean, it is likely that these islands do not have a broad enough range of habitat to provide an attractive food supply.

Another area of Fiji that is unattractive to swiftlets is the rainshadow (NW) side of the larger Fijian islands such as Viti Levu, where assimilis is much less common than in the areas of rainforest. It may be that such a climate is less suitable. This interpretation is consistent with chillagoensis producing only single egg clutches and being unable to raise a manipulated two-chick brood at Chillagoe which has a climate similar to that of the rainshadow area of Fiji.

Although terraereginae is not studied in this thesis, its distribution is close to that of chillagoensis and so its distribution is covered here.

It has a patchy distribution along coastal Queensland from Iron Range in the north to near Mackay in the south, though it has only been found breeding between Mount Peter and Finch Hatton Gorge (Pecotich 1982). The breeding of chillagoensis is more restricted, being found inland around the Chillagoe and Mitchell-Palmer districts. The two subspecies are probably geographically separated, for, at intervening savannah districts such as Mareeba, swiftlets are never seen (Bill Long, pers. comm.). Swiftlets are present on the edge of the rainforest where, for example, near Atherton I have seen feeding flocks of up to 48 birds. As Figure 2 shows, the distribution of both subspecies is still unclear in the northern portions of their ranges.

The positions of those breeding colonies of chillagoensis that have been visited in the course of this study are shown in Figure 3.

The nests

Except at Veidrala, the nests on Viti Levu were composed of foliose and crustiose lichens, liverworts, filmy fern and club moss, held together and to the wall with copious amounts of nest-cement (the birds' saliva). Each of two nests in the Waterfall Cave had an 80 mm long angiosperm leaf built into their structure. Pecotich (pers. comm.) described those at Veidrala as being made of local grass material. Those in the cave on Cikobia-i-Lau were composed mainly of crown-sheath fibre, mid-rib and leaf lamina from coconut trees.

Internal nest size of 36 nests from Nasinu averaged 50.0 ± 4.4 mm ($\bar{x}$ ± SD) left to right; 49.7 ± 4.4 mm front to rear; 21.1 ± 6.0 mm, depth from lowest part of front rim. The average volume index of these nests is 52 cm^3. The weight of four nests ranged between 9.2 g and 22.3 g, averaging 15.3 g.

Twenty-one nests from Veidrala, measured by L. Pecotich (pers. comm.) averaged 46 mm x 56 mm x 29 mm, giving an average volume index of 75 cm^3, which is larger than the Nasinu nests.

The nests of chillagoensis have similar construction to those in Fiji except that they are composed of dried grasses. The most common grass species used are Kangaroo Grass (Themeda australis) and Black Spear Grass (Heteropogon contortus).

The internal dimensions of 100 nests averaged 49.9 ± 0.5 mm across, 42.7 ± 0.5 mm front to back, and 11.9 ± 0.4 mm in depth. The depth of the Chillagoe nests is significantly ($t = 20.3$. $P < 0.001$, df = 134) shallower than the Fijian nests ($\bar{x} = 21.1$ mm). The front to back measure of Chillagoe nests (42.7 ± 0.5 mm) was also significantly smaller ($t = 14.4$, $P < 0.001$, df = 134). The volume index of the Chillagoe nests (25 cm^3) is consequently smaller than that of the Fijian nests (52 cm^3). This is to be expected as the Fijian nests hold two young at a time, whereas Chillagoe nests have to hold only one young.

The nest site and colony size

All assimilis and chillagoensis colonies visited in this study were in totally dark sites, though some assimilis nests at the edge of colonies were found in the twilight zone of the cave. The majority of Fijian nests were located high on the walls and ceilings of the caves. In Ono Cave, Wailotua, some nests were 30 m from the floor. A few nests were supported on ledges or protuberances from the wall but the majority were fully self supporting. Few nests fell and most nests were used in successive years. None was within 2 m of the cave floor, except for one or two in Dry Cave, Nasinu.

The typical colony site at Chillagoe is on a smooth concave wall 2 - 20 m above the cave floor. However small protrusions such as solution furrows or fault cracks in the limestone are often favoured within the colony. Thus rows of nests appear in the general random scatter, with those alongside closer than those above and below.

Some assimilis nests sat a metre or two or in one case 70 m away from other nests.

Most nests, however, were much closer together and many adjoined neighbouring nests; sometimes many did so, forming clusters so that some nests were not attached to the wall at all but only to other nests. The average distance between nests at Chillagoe was greater than that between Fijian nests. This may result from *chillagoensis* having more caves in which to nest, though the situation is not clear for even in colonies of *assimilis* where many nests were joined, there appeared to be large areas of suitable cave wall and ceiling unused. The average distances between Chillagoe nests were 7.9 cm (n = 20) at Gordale Scar Pot, 17.4 cm (n = 36) at Guano Pot, 29 cm (n = 41) at Crack Pot, 29.4 cm (n = 11) at Keef's Cavern, an estimated 10 - 40 cm at Squeeze Pot and an estimated 3 - 4 cm at Mudlark Cave (n = 31). The greatest distances between nests were found in Flow Cavern, where nests were 10 cm to 5 m apart (n = 8). A new site with just one nest was established in Swiss Cottage Chamber of Royal Arch Cave (CH 9) during October 1986. This site is about 90 m from the other site in this cave.

Unlike most other swifts, most swiftlets, whether in the echolocating genus *Aerodramus* or the non-echolocating genus *Collocalia*, usually build their nests on the walls and ceilings of caves. Recorded exceptions are not numerous and because they can help us derive common generic nesting requirements, are related here. The Glossy Swiftlet (*C. esculenta*) has been found nesting in overhanging cliffs and the roots or cavities of large Banyan and *Erythrina* trees in the south-west Pacific (Layard & Layard 1882; Mayr 1945; Parker 1967), old buildings in Java (Medway 1962d) and man-made tunnels in Sumatra (Wells 1975). The Himalayan Swiftlet (*A. brevirostris*) nests in fissures in the walls of volcanic craters on Java (Medway 1962d) and the Edible-nest Swiftlet (*A. fuciphagus*) frequently breeds colonially in old buildings in Malaysia (Langham 1980).

In Java the mono-generic Giant Swiftlet (Hydrochous gigas) nests behind or adjacent to waterfalls, where it and its nest are wet by continual spray (Stresemann 1928, Somadikarta 1968, Becking 1971); and the Mossy-nest Swiftlet (A. vanikorensis) has also been recorded nesting in the man-made tunnels on Sumatra (Wells 1975).

However there are three nest sites used by larger swifts for which there is no record of use by swiftlets. The first is the nest of another species; for example the feather-lined mud nests of two swallow species that are taken over in East Africa by White-rumped Swifts (Apus caffer), (Moreau 1942b, Brooke 1957). There is one record of White-rumped Swifts using the nest of a House Swift (Apus affinis) (Brooke 1963). The second site is amongst the foliage of a tree. The Fork-tailed Palm Swift (Reinarda squamata) of Brazil (Sick 1948) and the African Palm Swift (Cypselus parvus) of tropical Africa (Moreau 1941) both build their nests on the frond of a palm. The eggs of both palm swifts are glued to the nest and palm frond to prevent their falling to the ground. The last site is amongst the sand on the floor, or on ledges, in caves, where the White-naped Swifts (Streptoprocne semicollaris) of Mexico, lay their eggs in depressions, without nesting material. This may be the only swift that does not use saliva in constructing a nest (Rowley & Orr 1962). In summary Aerodramus requires a solid vertical object with some overhang, preferably in a dark location, for the location of its nests.

While there are no records of assimilis nesting in man-made environments in Fiji, there are records of them nesting in other than caves. They have been reported nesting against overhanging rocks in deep gullies (Mercer 1966; Sibson, in Belcher 1972; Clunie 1984). There are similarly situated colonies of terraereginae in coastal Queensland, such as at Finch Hatton Gorge (Crouther 1983).

This last subspecies also exists in a colony of three nests located along with colonies of several species of bats in the Twins Mine Shaft, Mount Peter (Smyth *et al*. 1980). Another non-cave site used by this species is the underside of a fallen tree, used by *reichenowi* in the Solomon Islands (Haddon 1981). In New Caledonia *leucopygia* nests in caves, leaving the Glossy Swiftlet to use more open situations (Vuilleumier & Gochfeld 1976). An earlier record from New Caledonia (Leach 1928), of White-rumped Swiftlets nesting in the basement of a hotel and in a fowl house, as well as in a cave entrance, must be suspect, even though one nest had two eggs (the Glossy Swiftlet rarely has a clutch of two); as the author grouped the Glossy Swiftlet with the White-rumped Swiftlet. Whether Hannecart & Letocart (1980) repeat Leach's record or have personal knowledge of the White-rumped Swiftlet nesting in abandoned houses and cellars is unclear. Last century most *leucopygia* nested in caves, though some used the underside of sloping rocks (Layard & Layard 1878, 1882). In Samoa, where there are no congeners, *spodiopygius*, prefers cave locations for nesting (Armstrong 1932).

Swiftlets nest in larger colonies than most swifts and it is not unusual for several species to share the same cave. The largest recorded colony contains 4.5 million birds of three species that share Niah Cave in Borneo, with half a million bats (Harrisson 1976). However colonies as small as one to three nests do occur and the White-rumped Swiftlet itself shows a considerable range in size of breeding colonies. In Fiji it also shares its caves with bats.

The number of nests in the Fijian colonies visited were: Veidrala One, 34 nests; Veidrala Two, 78 nests, (both Feb. 1976); Cikobia-i-Lau, 70 nests, (3 Jan. 1976); West-end colony Ono Cave, Wailotua, 115 nests (1975); Dry Cave, Nasinu, 163 nests (Jan. 1975); Waiyala Cave, 2,810 nests (Feb. 1975); East-end colony, Ono Cave, 3,455 nests (June 1975); Waterfall Cave, Nasinu 7,370 nests (Dec. 1976).

The population size of chillagoensis colonies visited, as determined by the number of active or fresh nests, is given in Table I.
With the average colony size of chillagoensis being 77 nests, it is clear that this subspecies breeds in much smaller colonies than the Fijian subspecies which has an average colony size of 1,762 nests. However it must also be noted that colonies of chillagoensis are much closer to one another than those of assimilis. This means the population density per hectare for the two subspecies might not be as different as the difference in colony size might at first indicate.

The breeding season

In Fiji the annual feather moult is complete by August and nest building or repair begins soon after. The first eggs are usually laid in September or October. In 1976 the first eggs were seen on 7 September, the same day that gonads of two other birds were found to be enlarged and an egg was felt inside another. Working from the oldest chick found on 1 December 1981 (which had a 48 mm wing), the first egg was laid about 21 October. The oldest chick found on 11 December 1983 (wing 81 mm) gives a laying date for that year of approximately 5 October. Most chicks at the time of the two latter visits were much younger than the largest chicks and as eggs soon appeared in the few empty nests and no juveniles were seen sleeeping in the cave at night, it was clear that the larger chicks were amongst the earliest, if not the earliest, for the season.

Table I

The Size of Breeding Swiftlet Colonies at Chillagoe

CCC No	Cave	Number of currently used nests previous	'85/86	'86/87
CH5	Tower of London Cave: site A	-	0	1
	site B	80*	0	0
	site C	-	-	23
CH9	Royal Arch Cave: Swiftlet Cavern	122#	15	26
	Swiss Cottage	0	0	1
CH24	Keef's Cavern	P~	109	-
CH26	Clam Cavern	23#	11	11
CH30	Stop Press Cave	P~	-	4
CH46	Snakey Cavern	46*	-	0
CH52	Swiftlet Cave	P~	-	129
CH81	New Southlander Cave	P~	22	14
CH124	Flow Cavern	13#	-	8
CH133	But Good Cave	P~	-	0
CH138	Chinese Cavern	P~	-	0
CH144	Christmas Pot (a)	P~	29	-
	(b)	P~	44	-
CH146	Guano Pot	P~	81	88
CH167	Crack Pot	P~	194	188
CH169	Squeeze Pot	P~	135+	-
CH176	Capricorn Cave	47#	0	-
CH187	Gordale Scar Pot	500?#	169	162
CH221	September Cave	P~	-	118
CH227	Pope John Paul I	P~	-	0
CH306	Mudlark Cave	P~	31	28
CH312	Project 31	60+~	-	253
CH322	Swiftlet Scallops Cave	-	-	8
	Entrance CH 374	P~	-	49
	Hercules Cave CH 362	P~	-	23
CH379	Tarby's Swiftlet Pot	-	180	179
CH380	Golgotha Cave (a)	-	48	-
	(b)	-	69	-
CH381	Swiftrimlet Cave	-	25	29
CH382	Otobeaswiftlet Cave	-	P	P
CH397	Shirl's Triple Twirl	-	-	21
CH398	Swiftlet Swallet	-	-	264

Note An * indicates that only the marks left on the walls by previous nests were counted and so that this number existed at the one time cannot be guaranteed. + indicates that there were possibly a few more nests on a small shelf that was not fully visible. ? indicates that I have some doubt that this number of nests were recently found in this cave. # refers to data from Smyth et al. ~ indicates a figure taken from the records of the Chillagoe Caving Club. P indicates swiftlets present.

An examination of 104 nests on 22 October 1976 revealed that 60% of nests were empty, 16% had one egg and 24% had two eggs. One week later 45% of 149 nests were empty, 16% had one egg, 38% had two eggs and 1% contained a chick. By November only 10% of nests remained empty.

On 14 November 1974, 50% of Nasinu nests had eggs and 50% had young. These nests had similar percentages the following year and were closely synchronized with the Wailotua population, which had chicks in 52% of their nests on 25 November 1974.

In years such as 1974 and 1976, when laying started in September, the first chicks were found flying in the last week of December. However, in each year studied, the majority of chicks fledged during January. Because lost clutches and sometimes lost broods are replaced, the breeding season is extended into February or even March. On 2 February 1975 about 80% of Nasinu nests were empty, with large chicks occupying the remainder. However, there is some geographic variation because a few days later Pecotich (pers. comm.) found a few eggs at Veidrala. Veidrala is in a drier region and such a climate may delay the breeding season. It is also possible that human or other disturbance may have caused more than normal losses and thus more than normal re-lays.

Turning to the Chillagoe situation and working from the oldest chick (which had a 51 mm wing), found in Gordale Scar Pot and Guano Pot at Chillagoe on 29 November 1985, the first egg was laid about 6 October. The oldest chick found on 3 December 1986 (wing 57 mm) gives an estimated laying date of 4 October for the first egg that season. In both seasons the first few eggs were followed two weeks later by a heavy bout of laying.

The importance of discovering the proximate physical cause for triggering laying is that it may link into a major ultimate factor for regulating clutch size in the life history of the species.

To discover this for the White-rumped Swiftlet is the function of Section Two and so is worth pursuing.

Various external stimuli may initiate or inhibit the culmination phase of the reproductive cycle (Marshall 1961). In many birds, the presence of a mate, nesting site, nesting material and finally the nest itself would be necessary stimuli for egg laying. All of these may be operative on the White-rumped Swiftlet, but they do not affect the timing of egg laying.

Adult White-rumped Swiftlets roost with their mate each night of the year at their nest, and will add nesting material to it over an extended breeding season if it is needed.

We are left then with food supply and climatic factors as possible stimuli for egg laying. While I do not have food samples for the non-breeding period, it is likely that if food is a proximate factor that climate will still be the ultimate factor, as the abundance of aerial insects is closely linked to climatic factors (Lack & Owen 1955, Hespenheide 1975). It is clear that egg laying in assimilis corresponds with the increase in rainfall that occurs in September and October (Appendix 1a. p.130). However egg laying in chillagoensis precedes the increase in rainfall during November (Appendix 1b. p.131). In 1985 there had been no rain for 28 days (Appendix 1c. p.132) prior to the laying of the first egg for the season and there had been only small showers prior to the peak laying period. So rain does not stimulate laying in chillagoensis even though rain (as is shown later) is essential to raising chicks.

The average date of first layings in the Great Tit (Lack 1966) has a high correlation with temperatures for March and April and thus temperature might have a direct effect on the tit. This is the more likely because food levels do not increase until after egg laying (Lack, Gibb & Owen 1957).

Because chick mortality rate is lowest in those years that the Alpine Swift (*Apus melba*) produces larger clutches than normal it was postulated that the swifts were responding to some unknown factor during the laying time that is correlated with the food level three weeks later (Lack & Arn 1947). Further evidence that the unknown factor in the Apodidae might be temperature is that the years when the Common Swift (*Apus apus*) produces larger than average clutches are characterized by the period immediately prior to laying being warm and sunny (Lack 1956a). If the weather turns cold in central Europe after the Common Swift has laid, it will throw one, two or three eggs ("the worse the weather the more eggs") out of the nest (Koskimies 1950).

In considering temperature as a possible trigger for laying it is clear that maximum temperatures are more likely to affect feeding White-rumped Swiftlets or their food, than minimum temperatures which occur when the bird is in the insulated environment of the nest and the cave. Such a relationship has been found between air temperature and egg laying in the House Swift (Naik & Razack 1967). While it was found that the minimum air temperature had little effect, eggs were laid following a week where the average maximum temperature was between 34°C and 36°C.

The maximum temperatures for 1985 indicate that the first White-rumped Swiftlet egg was laid after a week of temperatures above about 32°C. However in 1986 a week of similar temperatures occurred in early September, a month before the first recorded egg appeared. Hence maximum temperatures probably do not stimulate laying in this swiftlet even though they do in the House Swift.

The eggs

As in all swifts but one, the eggs are white and without gloss. The exception, the Cape Verde Swift (*Apus alexandri*), has small reddish-brown spots on its eggs (Alexander 1898, Brooke 1971a,b).

The average dimensions of 118 *chillagoensis* eggs (from Gordale Scar Pot and Guano Pot) were 19.81 ± 0.06 x 13.04 ± 0.04 mm ($\bar{x}$ ± S.E.). Both the length (t = 12.3, P< 0.001) and the width (t = 10.1, P< 0.001) of these eggs are significantly larger than 50 *assimilis* eggs from Nasinu Caves in Fiji (18.37 ± 0.1 x 12.14 ± 0.08 mm ($\bar{x}$ ± SE)). However both the length (t = 0.2, ns) and the width (t = 1.0, ns) are not significantly smaller than eight *assimilis* eggs from Waiyala, which measured 19.87 ± 0.32 x 13.3 ± 0.27 mm. As might be expected, both the length (t = 4.47, P <0.001) and the width (t = 4.12; P <0.001) of *assimilis* eggs from Nasinu are significantly smaller than the *assimilis* eggs from Waiyala. The eggs from Dry Cave were not significantly different from 52 slightly smaller eggs that came from replacement clutches in the same cave. These averaged 18.11 ± 0.12 x 11.99 ± 0.05 mm. However these replacement eggs (1.53 ± 0.02 g) were heavier than the larger original eggs (1.42 ± 0.02 g), probably because they were newly laid when weighed, whereas some of the original eggs were not.

The fresh egg of the Chillagoe Swiftlet (1.83 ± 0.01 g n=102) is significantly heavier (t = 13.4, P< 0.001) than 52 freshly laid eggs from Nasinu Caves Fiji (1.53 ± 0.02 g). The average weight of the Chillagoe eggs had declined to 1.66 ± 0.03 g a day or two before hatching. The average fresh weight of the Chillagoe eggs represents 19.7% of the average adult weight. This is slightly more than the 18.7% for eggs and birds at Nasinu, Fiji.

The proportion of the weight of the eggs to the weight of the five swiftlets (19.5% ± 2.15; x ± S.E.) shown in Table II is significantly greater than the proportion of the eggs of the 25 swifts (10.3% ± 0.77) and that of the six swallows and one martin (10.8% ± 0.65). The comparison with hirundines is included because they are similar sized birds that have had to cope with similar ecological problems as the swiftlets.

TABLE II

Various Apodid and Hirundine egg and clutch weights

Species	Egg mean wt(g)	Female mean wt(g)	Egg (% ad wt)	Clutch size	Clutch (% ad wt)	Source
Edible-nest Swiftlet *Aerodramus fuciphagus*	2.16	8.1	26.7	1.96	52.3	Becking 1971; Langham 1980
Grey-rumped Swift *Chaetura cinereiventris*	3.06	13.8	22.2	5.00	110.9	Schonwetter 1970; Snow 1962; Sick 1948
Mossy-nest Swiftlet *Aerodramus vanikorensis*	2.42	11.3	21.4	2.00	42.8	Becking 1971
White-rumped Swiftlet *Aerodramus spodiopygius*	1.53	8.2	18.7	2.00	37.4	This paper
White-collared Swift *Streptoprocne zonaris*	12.00	65.8	18.2	1.00	18.2	Schonwetter 1970; Snow 1962 Sick 1948
Glossy Swiftlet *Collocalia esculenta*	1.21	7.1	17.0	1.95	33.2	This paper; Medway 1962a
Giant Swiftlet *Hydrochous gigas*	5.06	37.0	13.7	1.00	13.7	Becking 1971; Somadikarta 1968
Band-rumped Swift *Chaetura spinicauda*	1.88	14.2	13.2	-	-	Schonwetter 1970; Snow 1962
Wire-tailed Swallow *Hirundo smithi*	1.65	12.7	13.0	4.00	52.0	Schonwetter 1970; Donnelly 1974
Chestnut-collared Swift *Cypseloides rutilus*	2.67	21.0	12.7	2.00	25.4	Schonwetter 1970; Snow 1962 Lack 1956b

Table II cont..

Species	Egg mean wt(g)	Female mean wt(g)	Egg (% ad wt)	Clutch size	Clutch (% ad wt)	Source
Welcome Swallow *Hirundo neoxena*	1.75	13.9	12.6	3.90	49.0	This paper; Schonwetter 1970
	1.52	13.9	10.9	3.50	48.8	This paper
White-rumped Swift *Apus caffer*	2.75	22.1	12.4	2.50	31.1	Schonwetter 1970; Brooke 1971d
Black Swift *Cypseloides niger*	5.57	45.6	12.2	1.00	12.2	Schonwetter 1970; Collins unpub.
Lesser Striped Swallow *Cecropis abysinica*	2.02	17.0	11.9	3.00	35.6	McLachlan & Liversidge 1978;Schonwetter 1970 Walters 1980; Donnelly 1974
White-tipped Swift *Aeronautes montivagus*	2.19	19.7	11.0	2.00	22.0	Schonwetter 1970; Collins 1972 Collins pers. comm.
Bat-like Spinetail *Neafrapus boehmi*	1.61	15.3	10.5	3.00	31.6	Schonwetter 1970; Lack 1956b Donnelly 1974
African Black Swift *Apus barbatus*	4.40	42.3	10.4	2.00	20.8	Brooke 1971a; Schonwetter 1970 Brooke 1970
Horus Swift *Apus horus*	2.77	27.4	10.1	2.00	20.2	Schonwetter 1970; Walters 1980
House Swift *Apus affinis*	2.75	27.2	10.1	3.70 (a)	37.4	Chih-Tung 1973
				2.50 (b)	25.3	Chih-Tung 1973
Pacific Swallow *Hirundo tahitica*	1.45	14.7	9.8	2.98	29.2	Hails 1984
Mosque Swallow *Hirundo senegalensis*	4.00	40.7	9.8	*c*.3.50	34.4	Schonwetter 1970; Donnelly 1974
Barn Swallow *Hirundo rustica*	1.90	19.5	9.7	4.40	42.9	McLachlan & Liversidge 1978; Adams 1957
Fork-tailed Palm Swift *Reinarda squamata*	1.01	10.3	9.7	3.00	29.3	Schonwetter 1970; Lack 1956b

Table II cont..

Species	Egg mean wt(g)	Female mean wt(g)	Egg (% ad wt)	Clutch size	Clutch (% ad wt)	Source
House Martin						Collins unpub.
Delichon urbica	1.90	19.8	9.6	*c*.4.00	38.4	McLachlan & Liversidge 1978; Walters 1980
Vaux's Swift						Schonwetter 1970
Chaetura vauxi	1.73	18.1	9.6	*c*.4.40	42.0	Schonwetter 1970; Lack 1956b
Pallid Swift						Baldwin & Zaczkowski 1963
Apus pallidus	3.50	36.7	9.5	*c*.2.00	19.1	Schonwetter 1970; Walters 1980
Fork-tailed Swift						Palomeque *et al* 1980
Apus pacificus	2.75	29.0(d)	9.3	2.50	23.2	Lack 1956b; Gibson 1981
	2.75	43.5(e)	6.3	2.50	15.8	Dementiev *et al* 1951
	4.40(g)	35.5(f)	12.4	2.50	30.1	Shaw 1936; Bent 1940
Sabines Spinetail						Dementiev *et al* 1951
Chaetura sabini	1.42	16.6	8.6	*c*.2.50	*c*.1.4	Lack 1956b; Brooke 1971c
Common Swift						
Apus apus	3.62	42.7	8.5	2.27	19.2	Lack & Lack 1951
Chimney Swift						
Chaetura pelagica	1.88	24.1	7.8	4.20	32.8	Fischer 1958
White-throated Needletail						
Hirundapus caudacutus	8.45	113.7	7.4	5.25	38.9	Neufeldt & Ivanov 1960;
White-naped Swift						Lobko-Lobanovski 1956
Streptoprocne semicollaris	12.50	*c*.175.0	7.1	2.00	14.3	Schonwetter 1970; Collins 1968b
African Palm Swift						Rowley & Orr 1962
Cypsiurus parvus	1.00	14.6	7.0	2.00	14.0	Brooke 1971a

Table II cont..

Species	Egg mean wt(g)	Female mean wt(g)	Egg (% ad wt)	Clutch size	Clutch (% ad wt)	Source
Chapmans Swift						
Chaetura chapmani	1.76	25.5	6.9	*c*.2.50	17.3	Schonwetter 1970; Snow 1962
White-throated Swift						Collins 1968b
Aeronautes saxatalis	2.10	32.3	6.5	*c*.4.30	28.0	Schonwetter 1970; Walters 1980
Alpine Swift						Behle 1973; Bent 1940
Apus melba	6.05	98.0	6.2	3.50	21.6	Lack & Lack 1951; Schonwetter 1970
Brown Needletail						Lack & Arn 1947
Chaetura gigantea	8.35	137.0	6.1	*c*.3.50	21.3	Schonwetter 1970; Lack 1956b
						Collins & Brooke 1976

NOTES: The species are arranged in descending order of the ratio between egg weight and female weight. (a) size of first brood, (b) size of second brood. (*c*.) *circa*, indicates an approximate figure taken from another source & used because original studies did not specify this parameter. (d) weight of an emaciated bird from the Aleutian Islands. (e) weight of two birds from Russia. (f) median weight of birds from China. (g) egg weight for Japanese birds.

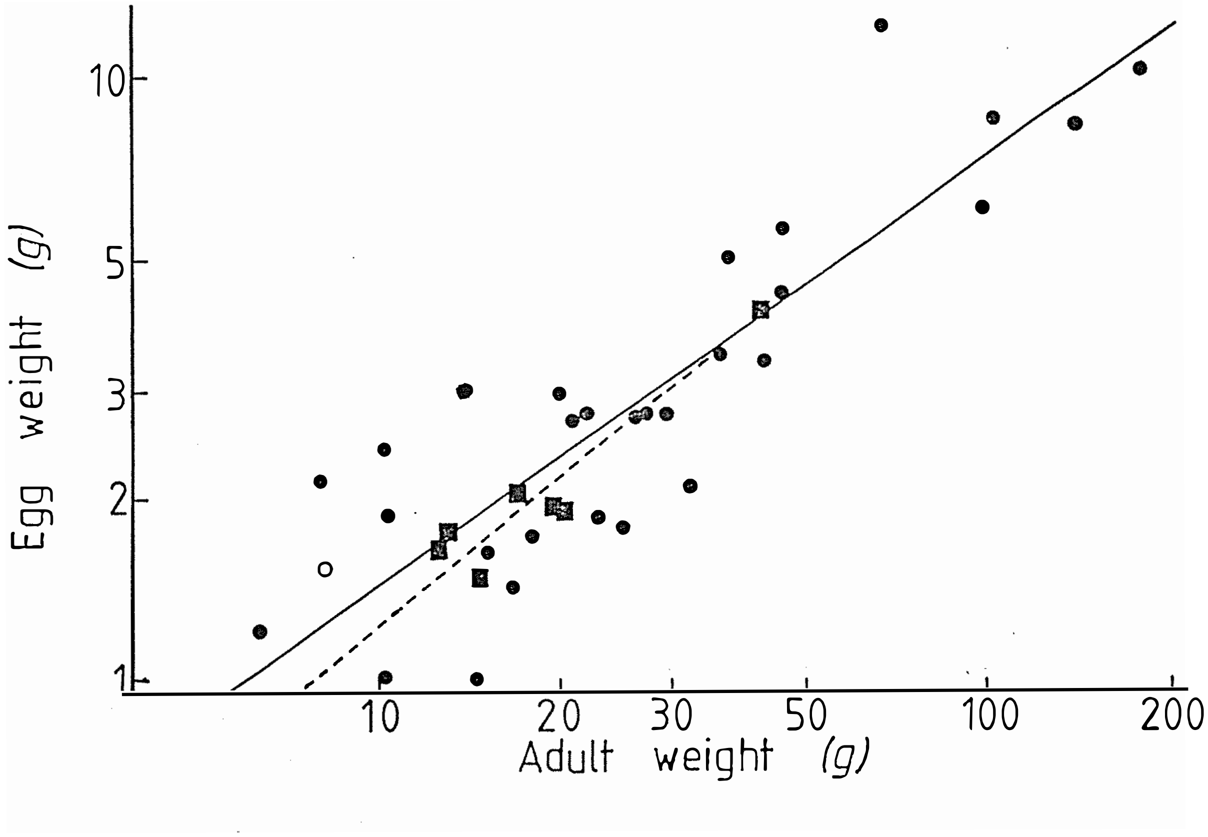


Figure 4. Relationship between adult weight and egg weight in the swifts (circles) and swallows (squares).

The solid line is the line of best fit for the Apodidae ($Y = 0.28 X^{0.71}$, $R^2 = 76\%$, $P < 0.001$). The dotted line is the line of best fit for the Hirundinidae ($Y = 0.20 X^{0.79}$, $R^2 = 89\%$, $P < 0.001$). In both equations Y = egg weight, X = adult weight, R^2 = coefficient of determination. The White-rumped Swiftlet is designated by the hollow circle.

The relationship between adult weight and egg weight for those species shown in Table II is shown in Figure 4. The lines of best fit for the Apodidae and the Hirundinidae both agree with the general trend of large birds laying smaller eggs in relation to the parents' size than do small birds (Heinroth 1922). While the White-rumped Swiftlet, represented by the hollow circle in Figure 4, lays a proportionately large egg, the egg is not extreme for swiftlets.

It is unfortunate that there is some discrepancy over the weight of the egg of the Edible-nest Swiftlet. Langham (1980) gives the average weight of 15 eggs as about 1.2 g or 10% of adult weight. This contrasts with the figure (26.7%) used above (Becking 1971). The greater weight has been accepted because the eggs of the Edible-nest Swiftlet have larger dimensions (Morgan 1875, Gibson-Hill 1948), than those of assimilis and so could be expected to weigh more than assimilis eggs do (1.53 g).

One of 57 assimilis clutches had one egg - the rest had two eggs. This gives a mean clutch size of 1.98, which is greater than that of the four other swiftlets whose clutches have been recorded. As assimilis persists in laying a second egg even when provided with a second one, and as it will lay no more than two if its second egg is removed the day after laying, this species is a determinate layer (Cole 1917). Other swifts vary their clutch size. Chimney Swifts (Chaetura pelagica) increase average clutch size from 3.5 in their first year to 4.1 in successive years (Dexter 1981) and House Swifts, which are double brooded, produce a mean of only 2.5 eggs in their second brood compared to 3.7 in their first (Chih-Tung 1973). These changes in clutch size are, however, proportionately much smaller than that which the White-rumped Swiftlet would have to make in altering its clutch size by just one.

The laying interval for assimilis in ten instances was found to average four days, with a range of three to five days. This interval and that of the Edible-nest Swiftlet (three days, Langham 1980) is larger than that of the Mossy-nest Swiftlet (two days), the Glossy Swiftlet (two days, both Medway 1962a) and most Common Swifts (two or three days, Lack & Lack 1951). Similar sized Passerines usually lay on successive days (Welty 1975, Marchant 1984) as does the Welcome Swallow (Hirundo neoxena)(Marchant & Fullagar 1983). The reason for a longer laying interval in the swiftlets is very likely the greater proportion of the weight of their egg to that of the adult producing it.

Moult in the Breeding Season

The synchrony of breeding and moulting in this species is discussed more fully in Appendix 5 (pp.181,182.) where possible benefits of this uncommon combination are suggested. Data in Table III show that moult of the primaries begins for most Chillagoe birds in late November or early December.

Table III
Progress of Moult in the Primary Flight Feathers

	29 Nov -8 Dec	9-18 Dec	19-28 Dec	29 Dec -7 Jan	8-17 Jan	18-27 Jan
No. examined	108	97	87	106	50	55
No. not in moult	23	9	1	0	0	0
No. in moult						
P1	58	17	2	3	-	-
P2	20	29	30	10	2	-
P3	6	14	27	36	10	2
P4	1	18	14	33	20	10
P5	-	7	13	13	16	31
P6	-	2	3	1	2	10
P7	-	-	-	-	-	2
P8	-	-	-	-	-	-
P9	-	-	-	-	-	-
P10	-	-	-	-	-	-

NOTE: Pn = the number of the most recently moulted (smallest or missing) flight feather.

Moult follows immediately upon egg laying and because of the difficulty of sexing individuals it is not certain whether one sex starts before the other. Male and female House Swifts moult their primary feathers together and also begin immediately after egg laying (Naik & Shivanarayan 1969).

If the rate of moult in the primaries continues for another two months as it does during December and January (Table III), then moult of the primaries takes four months to complete.
This length of time equals that taken by assimilis in Fiji (Appendix 5 p.181.) and that taken by the Chimney Swift (Johnston 1958), but is shorter than the seven months taken by both the Black-nest Swiftlet (Aerodramus maximus) (Medway 1962c) and the Alpine Swift (Stresemann pers comm in Naik & Naik 1965). The time required for primary moult is apparently less in passerines than in swifts. Some passerine examples and the time taken for them to achieve a complete moult are: Redpolls, (Acanthis flammea), 48 - 56 days (Salomonsen 1972); House Sparrows (Passer domesticus), 64 - 83 days (Haukioja & Reponen 1969); Eurasian Yellow-breasted Buntings, (Emberiza aureola), 42 - 63 days (Stresemann & Stresemann 1966); Steller Jays (Cyanocitta stelleri), 60 - 70 days (Pitelka 1958); Andean Sparrows (Zonotrichia capensis), about 60 days (Miller 1961).

Incubation

The incubation period in chillagoensis was found to average 26.6 ± 0.23 days (n = 27) and to range between 25 and 29 days. This is three and a half days longer than incubation (from the laying to the hatching of the second egg) in assimilis (Range = 22 - 25 days, n = 7). From the relationship between adult weight and incubation period shown below, I would have predicted that chillagoensis had a shorter incubation period than assimilis.

However, as apodid chicks are poikilothermic (Collins 1968a, 1973b), the cooler temperature in the Chillagoe caves may be at least a contributing cause. During incubation the temperature in Gordale Scar Pot never varied more than half a degree from $23^{o}C$ whereas Fijian cave temperatures ranged between 24.8 and 26.4 ^{o}C. Temperatures outside the Fijian cave ranged between 21.7 and 31.8 ^{o}C.

Table IV shows the incubation period to be similar to that of the Edible-nest Swiftlet, the Mossy-nest Swiftlet, the Chestnut-collared Swift, the White-rumped Swift and the House Swift; less than that of the Black-nest Swiftlet; and longer than that of the other apodids shown in the table.

Using the length of the incubation period of the 12 apodids for which egg length and adult weight was also known, no significant correlation was shown between egg size and the length of the incubation period (Spearman Rank Correlation, $r_s = 0.14$). However, there was a significant inverse correlation between adult weight and incubation period ($r_s = -0.55$; $P < 0.01$); and a significant correlation between adult weight and egg size ($r_s = 0.71$; $P < 0.001$). These results suggest that, although larger swifts tend to lay larger eggs, it is larger adult size rather than larger egg size that accompanies a reduction in the incubation period.

The observation of marked birds in Fiji during four full days of nest watching revealed that, as in all swifts so far studied, incubation was shared by both parents and that they changed duties at about 24 h intervals. Once an incubating bird at Chillagoe was caught it would tend to fly from the nest on successive approaches and it subsequently became easier to catch its mate when it was incubating. Catching and banding such birds did show that, like the Fijian subspecies, both sexes share in incubation.

PLATE 1 Adult White-rumped Swiftlet (*Aerodramus spodiopygius assimilis*) incubating.

Brooding adults of both subspecies may be identified by the dark tipped primaries which extend well beyond the tail. Note also that in *assimilis* nests are often joined to others. This means that as additional saliva (visible in the photo) is applied to strengthen the nest's attachment to the wall during incubation, the wings of sleeping birds in adjoining nests are sometimes glued to the nest resulting in their death.

TABLE IV

Length and Success of Incubation and Fledging Period in Various Swifts and Swallows

Species	Incubation Period (days)	Mean Clutch Size	Hatching Success (%)	Fledging Period (days)	Fledging Success (%)	Breeding Success (%)	Young Fledged /Breeding Effort	Source
White-rumped Swiftlet								
A. s. assimilis	23.0	1.98	58.0	46.0	92.0	53.0	1.1	Tarburton 1986b
A. s. chillagoensis	26.6	1.00	64.0	46.9	69.0	44.0	0.9	This thesis
Glossy Swiftlet								
Collocalia esculenta	21.5	1.95	76.1	38.5	75.0	57.0	1.1	Medway 1962a, Medway & Pye 1977
Black-nest Swiftlet								
Aerodramus maximus	28.0	1.00	29.3	60.0	57.3	17.0	0.2	Medway 1962a, Medway & Pye 1977
Mossy-nest Swiftlet								
Aerodramus vanikorensis	23.0	1.70	51.5	48.0	74.1	38.0	0.8	Medway 1962a, Medway & Pye 1977
Edible-nest Swiftlet								
Aerodramus fuciphagus	23.0	1.96	79.4	43.0	61.9	49.0	0.9	Langham 1980
Chimney Swift								
Chaetura pelagica	19.0	4.20	89.5	30.0	96.1	86.0	3.6	Fischer 1958
Short-tailed Swift								
Chaetura brachyura	17.5	3.80	57.7	*c.*33.0	53.5	27.0	1.1	Collins 1968a
	17.5	3.60	-	35.0	-	-	-	Snow 1962
Chapman's Swift								
Chaetura chapmani	17.5	2/3	-	-	-	-	-	Collins 1968b
Vaux's Swift								
Chaetura vauxi	18.5	6.30	100.0	28.0	67.0	67.0	4.0	Baldwin & Zaczkowski 1963
Chestnut-collared Swift								
Cypseloides rutilus	22.8	1.98	63.0	39.6	63.0	40.0	1.3	Snow 1962
	22.5	1.90	65.8	40.0	68.4	36.0	0.9	Collins 1968a
Common Swift								
Apus apus (Britain)	19.6	2.27	78.0	42.0	74.5	58.0	1.3	Lack & Lack 1951
(Switzerland)	20.0	2.70	76.0	42.0	74.5	65.0	1.7	Weitnauer 1947
(Moravia)	20.1	2.71	70.7	42.3	88.6	63.0	1.7	Pellantova 1975

TABLE IV cont..

Species	Incubation Period (days)	Mean Clutch Size	Hatching Success (%)	Fledging Period (days)	Fledging Success (%)	Breeding Success (%)	Young Fledged /Breeding Effort	Source
Alpine Swift								
Apus melba	21.0	3.00		*c*.59.0	81.0	70.0	1.8	Lack & Arn 1947
	-	4.00	86.0	-	60.0	-	*c*.2.4	Lack & Arn 1947
White-rumped Swift								
Apus caffer (Kenya)	23.0	2.00	88.7	42.0	86.0	75.0	1.5	Moreau 1942b
(South Africa)	-	-	81.0	46.0	70.3	57.0	-	Schmidt 1965
(Rhodesia)	24.5	2.00	91.0	42.0	60.0	55.0	1.0	Brooke 1957
House Swift								
Apus affinis (India)	22.0	*c*.3.00	-	40.0	-	-	-	Ali & Dillon 1970
(Tanzania)	23.0	2.50	89.2	38.5	-	-	-	Moreau 1942a
(Malaysia)	21.1	3.70	89.4	43.6	-	-	-	Chih-Tung 1973
Fork-tailed Swift								
Apus pacificus (nat.cliffs)	16.9	2.10	58.8	40.4	63.6	37.4	0.8	Yuren & Benxiang 1985
(walls)	16.9	2.30	75.7	40.4	63.6	48.1	1.1	
African Palm Swift								
Cypsiurus parvus	20.0	1.90	66.0	32.9	26.0	17.0	0.3	Moreau 1941
	-	2.00	-	-	-	-	1.9	Brooke 1963
Barn Swallow								
Hirundo rustica	15.0	4.40	78.2	18.5	91.7	71.9	3.1	Adams 1957, Bent 1942
Pacific Swallow								
Hirundo tahitica	16.2	2.98	54.0	19.8	69.0	37.6	1.1	Hails 1984
Welcome Swallow								
Hirundo neoxena	15.8	3.90	71.4	*c*.21.0	73.8	52.7	2.0	Marchant & Fullagar 1983
Mangrove Swallow								
Tachycineta albilinea	17.0	4.00	62.5	25.0	-	-	1.0	Dyrcz 1984
Grey-breasted Martin								
Progne chalybea	16.7	3.30	94.0	26.5	-	-	2.4	Dyrcz 1984

Both birds usually brooded, or at least sat on the nest, at night. By contrast, in some hirundines, for example, the Pacific Swallow (Hirundo tahitica), males do not help incubate (Hails 1984).

Sex determination

Being able to identify the sex of individual breeders can help in understanding breeding behaviour but sexing swifts externally is difficult (Brooke 1971b). The following characters were measured and analysed to detect any sexual dimorphism in unsexed birds: exposed culmen, wing length, body length, tail length, outer rectrix length, emargination of the outer rectrix, weight and intensity of plumage colour. None of these demonstrated any dimorphism that might be sexually based. As the following examples show this situation is normal in apodids. An examination of the Chimney Swift for 12 physical and four behavioural characters that may vary diagnostically between the sexes found that none was reliable. (Fischer 1958, Zammuto & Franks 1979). Brooke (1971b) found in a number of swifts that both sexes had similar ranges for the standard measurements, though the females averaged heavier. Collins (1968a, 1972), however, found males to average heavier in the Chestnut-collared Swift and the White-tipped Swift. It has been claimed that the emarginate tail of the male Black Swift (Cypseloides niger) sometimes allows sexual identification even in the field (Rathbun 1925). However, Brooke (1969) and Bent (1940) use the elongated and emarginate fifth rectrix of this species to separate non-juveniles from juveniles. The point is that there is no external character that can be used to differentiate the sex of all individuals in any species of swift.

This lack of variation in colour and size has even been considered fortunate by taxonomists (Oberholser 1906) who appreciated that a lack of sexual variation reduced the complications of what was already a very difficult group to identify.

When I graphed the wing-span of 54 assimilis known to be older than 18 months, a slightly bimodal distribution appeared, but when I found a dead male and female (sex determined by examination of gonads) each with wing-spans in the upper quartile it became clear that this method could not be used to sex this species. The wing-span measurement has been useful in sexing Kestrels (Cam & Cam 1975) and Lewin Honeyeaters (Smedley 1977). In graphing 176 wing-span measures from free-flying birds of unknown age no bimodal form was evident. Three more birds with wing-spans above the average (261.4 mm) proved by gonad inspection to be two females and one male.

Egg loss and replacement

In assimilis, the first egg to replace lost clutches or even lost broods of up to 22 days of age was laid within 10 to 17 days of the loss. The average time taken was 12.6 days (n = 22). It was assumed that replacements were made by the original pair using the nest. One pair was not seen to re-lay in the 27 days after the loss of their clutch - the time when observations ceased. But as two birds were found on the nest 10 days after the loss, it is possible that a replacement egg was lost before I could see it.

In chillagoensis twelve out of fourteen (89%) first clutches were replaced an average of 9.4 days (range = 6 - 14 days) after they had been lost or removed. The other two clutches were not known to have been replaced. As this average time of replacement was not significantly different (t = 1.8, df = 15, ns) to the average elapsed time for replacement of lost replacement clutches nor to the average time for replacement of lost broods (t = 0.63, df = 12, ns), all three averages have been pooled. The average time for the replacement of all lost clutches (that were known to have been replaced), and broods less than ten days old, was 10.4 ± 0.4 days (Range = 8 - 18 days, n = 41).

This range is similar to that of Fijian birds (10 - 17 days) although the lower minimum time may indicate that <u>chillagoensis</u> has larger body reserves, is able to gain the required food more quickly, or has a more active ovary than <u>assimilis</u>.

When <u>chillagoensis</u> lost chicks older than 20 days, the nest either already contained the second egg, or the replacement egg appeared in less than six days, probably as a result of previous development of a follicle in the ovary in preparation for the first chick to incubate it.

Of 58 eggs produced by <u>chillagoensis</u> in 1985/86, 69% (40) were successfully hatched. In the dry season of 1986/87, 60% (40) of 67 eggs were hatched. The average hatching success for both years was 64% (n = 125). This compares with 58% (n = 159) of eggs successfully hatched by Fijian swiftlets. Of those that failed to hatch, 78% disappeared, compared with 88% in Fiji. Both these figures are a little higher than the 64% similarly lost by the Edible-nest Swiftlet (Langham 1980). However if we take account of the 17% of Edible-nest Swiftlets lost through nest harvesting and nest fall, the results are very close. Another 11% were infertile (10% in Fiji), and 11% broke (2% in Fiji). By comparison 14% of Edible-nest Swiftlet eggs failed to hatch (Langham 1980).

That some of the eggs that disappeared were infertile, cracked or addled is possible, for Lack & Lack (1952) found that Common Swifts usually ejected cracked eggs and sometimes ejected infertile eggs.

None of the manipulated clutches of two or three was included in the above egg losses, but it is interesting to note that one manipulated egg hatched five to ten days after the first, while others remained six, ten, eleven and fifteen days after the hatching of the first chick before disappearing.

Extra parental 'co-operation' or 'egg dumping'?

In Fiji several events have suggested that occasionally more than one female may lay in one nest. Eleven days after one of two eggs were taken from nest 108, a replacement was laid. The first egg hatched six days later and the second egg disappeared, suggesting that the first female had been incubating for some time prior to the laying of the third egg. In the second event, three eggs were laid in nest 86, one on the 20th ± 1, one on the 23rd ± 1, and the last on the 27th ± 1, December 1981. In that one egg disappeared four days later, another two days after that and the third within another three days, it is probable that a second female was involved and squabbling at the nest meant all the eggs were lost.

Such incidents are not without precedent in the Apodidae. Nine eggs laid in 14 days by a Short-tailed Swift (Chaetura brachyura) were assumed to be the product of two females, as one female normally lays every second day. All nine eggs were successfully hatched even though they were two or three deep in the nest (Snow 1962). Collins (1968a) once found two eggs had been added to a nest of this species somewhere between 4 and 16 days after the first female had commenced incubation of four eggs. This meant four chicks had considerable advantage over the other two, which died within a day of hatching. That evening three adults were found roosting near the nest, one of which was a yearling raised in that same nest cavity. Three eggs laid in the short period of three days by the Ashy-tailed Swift (Chaetura andrei) and found broken later on the third day, were also attributed to two females (Sick 1959).

Clutches of eight and nine produced by the Chimney Swift and attributed to two females were found by Fischer (1958). However, extra parental co-operation is known to be well established in the Chimney Swift (Dexter 1952).

Snow (1962) proposed that the reason for multiple female use of the one nest by Short-tailed Swifts was a shortage of holes suitable for nesting. This is not applicable to the White-rumped Swiftlet in Fiji (or Chillagoe), as there is still considerable room left in each cave. Three other causes are possible. As nests take one or two months to construct, a fallen nest or the failure of a pair to construct one may pressure a bird to lay in the nest of another. Secondly, as these nests are in total darkness, the normal ability to recognise nests may fail. Thirdly, birds may purposely 'dump' their egg in another bird's nest.

There is only one other record of a swiftlet nest having an extra 'egg'. One of the eight nests in a Glossy Swiftlet colony in New Guinea had two eggs and a newly hatched young (Mackay 1968). Whatever the origin, a third egg in the nest of any swiftlet so far studied is uncommon and, when it does occur, there is no clear evidence to suggest that one female was responsible for laying all three eggs.

The situation of extra eggs in the nest at Chillagoe is unique and so is developed as a separate topic in Section 3.

Nestling development

In Fiji the second chick usually hatched within a day and a half of the first, even though the laying interval averaged four days. This is because the first egg is left unattended during the day until the second is laid. One exception to this occurred where I had introduced a second egg into a nest. It hatched five to ten days after the first and grew normally until a much larger chick moved into the nest and the first two starved to death.

The average weight of newly hatched assimilis chicks was 1.14 ± 0.03 g (range = 0.9 to 1.4 g, n = 23), while that of chillagoensis was 1.31 ± 0.01 g, (range = 1.09 to 1.60 g, n = 52). This difference is significant (t = 5.1, $P<0.001$, df = 73). One remaining egg shell from assimilis weighed 0.2 g.

Usually egg shells rapidly fragmented with the pieces remaining in the nest for one to three days. Whether it was the adults, American Cockroaches (Blattaria americana) or chicks that removed the pieces is uncertain.

All swifts are naked upon hatching and most remain naked until their flight and contour feathers emerge. However, the three tree swifts (Hemiprocnidae) and the African Palm Swift (Cypsiurus parvus) develop nestling down, presumably for warmth and camouflage as they nest in exposed sites (Lack 1956a). Down also develops in the Black Swift (Bent 1940) and the Chestnut-collared Swift (Snow 1962; Collins 1963, 1968a). Snow (1962) and Collins (1968a) suggest that the down is needed in these two swifts because the nest-sites selected by them are cooler (18.8 to 26.2 °C) than the surrounding habitat. That the parents consistently brood the young until the down grows, supports their suggestion. The young of the House Swift (Moreau 1942a), the White-rumped Swift (Moreau 1942b) and the Pallid Swift (Apus pallidus) (Kainady 1976), are also brooded for at least the first week, by which time downy semi-plumes appear on restricted parts of the chick's body. The temperatures near the nests of the African swifts range between 15 °C and 41 °C (Moreau 1942a; Taylor 1942). This is more extreme than the range of 24.8 °C to 26.4 °C in the caves at Nasinu, Fiji. Hence downy plumage grows on those species nesting in locations that experience cooler temperatures than do the swiftlets.

In assimilis the developing feathers appear as dark dots along the feather tracts a few days after hatching. The first to break through the skin are the remiges, which do so on the eleventh day (range = 8th - 15th day); though in one manipulated brood they never broke through in the third chick until the 17th day.

The average wing length at the time of emergence was 15.6 ± 0.42 mm ($\bar{x}$ ± SE, range = 12 - 20mm) and even the manipulated late sprouter in the exceptional brood mentioned above had a wing of 14 mm when the pins broke through. The eruption of the remiges was only one day later than the single-brooded Black-nest Swiftlet (Medway 1962a), but seven or eight days later than in the Short-tailed and Chestnut-collared Swifts (Collins 1968a).

In assimilis the average time taken for the first flight feathers to break out of their sheaths was 18.6 ± 0.31 days, (range = 15 - 27 days, n=61), when the wing measurement was between 25 and 39 mm (32.1 ± 0.46 mm, n=61). In chillagoensis the average time for this event was 18.7 ± 0.4 days (range = 16 - 24 days, n = 24), when the wing measurement was between 25 and 36 mm (29.3 ± 0.6,). It is interesting that although the newly hatched chicks at Chillagoe were significantly heavier than newly hatched Fijian chicks, the time taken for the first flight feathers to erupt was not significantly different (t = 0.2, df = 52). The eruption of flight feathers in both subspecies was six days later than in Short-tailed and Chestnut-collared Swifts (Collins 1968a).

Swiftlets use their feet to hang on to the small nest during the nestling period and most chick deaths occur because the chick had fallen from its nest. This probably explains why a grasping reflex was developed in day-old chicks and why in assimilis the tarsus reached full adult size by the 14th day. By contrast, adult weight was not reached until the 23rd day (21st day in chillagoensis); and adult wing size in both subspecies was only reached after fledging.

Chick begging calls are described in Tarburton (Appendix 7 p.218, in prep.).

The nestling period

Twenty one assimilis chicks fledged at an average of 46 days (range = 41 - 51 days).

Eighteen chillagoensis chicks fledged at an average age of 47.9 ± 0.7 days (range = 43 - 51 days), which is similar to the age at which Fijian birds fledge. The 21 Fijian chicks had at last measurement a wing length of from 99 to 107 mm. The average wing length of Chillagoe chicks at the time of fledging was 101.6 mm which is 95% of adult wing length. The minimum wing length at fledging (range = 91.3 - 108 mm), was 85% of adult wing length. This is just 3% below the minimum I found in Fijian birds and that which Lack & Lack (1951) found in the Common Swift. As the wing was growing from 2-3.5 mm a day in the nestling's last week, it would take only two to five days for the fledgling's wing to approximate the average adult length.

The nestling periods of 46 days for assimilis and 46.9 days for chillagoensis are similar to those of other Apodidae having similar incubation periods. Most other apodids and all the hirundines shown in Table IV have shorter nestling periods. The nestling period varies with brood size as it does in the African Palm Swift (Moreau 1941), and so this is discussed more fully in Section Two.

The increased safety from nesting in inaccessible places has relaxed the selection pressure for raising young as quickly as possible (Snow 1962). The White-rumped Swiftlet and other cave-nesting species have relatively long incubation and fledging periods compared to those species, such as the Common and House Swift, that do not nest in caves (Table IV). This slow egg and nestling development has possibly been reinforced by the swiftlets' practice of breeding in large colonies, forcing birds to forage further afield and to feed the chicks less frequently than do the swifts.

Fledging success

Despite the low rate of hatching in assimilis compared to other Apodidae, their fledging success of 92% was surpassed only by the fledging success of the Chimney Swift (96.1%).

The success of other Apodidae (Table IV) ranged between 26% and 89%. The fledging success of 69% (n = 29) for chillagoensis in the 1985/86 season was well below that for Fijian birds. However, because of the high hatching rate the breeding success was 44%, which is only 9% below that of the Fijian birds. Chillagoe birds raise a second brood whereas the Fijian birds do not. This means the Chillagoe birds raise an average of 0.9 chicks per season which is very close to the average of 1.1 chicks that Fijian birds raise per season. However, in poor seasons such as the 1986/87 season, fledging success in chillagoensis was only 50% (n = 18) and with hatching success reduced from 69% to 60%, the breeding success achieved was only 30% a brood and therefore only 0.6 chicks per season.

In producing 1.1 fledglings per clutch (breeding effort), the production by assimilis equals that of the Short-tailed Swift, the Glossy Swiftlet and the Pacific Swallow (Table IV). Although the Glossy Swiftlet has three breeding peaks per year there is no evidence that the same birds produced any more than one clutch (Medway 1962a). Of the three swiftlets producing fewer fledged young per brood than the White-rumped Swiftlet, the Black-nest and Mossy-nest Swiftlets are known to produce second clutches as well as replacement clutches (Medway 1962a) and the Edible-nest Swiftlet is presumed to lay second and third clutches (Langham 1980).

Chick mortality

While the majority of chicks were in their nests at each visit and stayed there during four separate days of nest watching in Fiji, some occasionally fell from the cup and spent considerable time clinging to the underside of the nest. When small, such chicks were unable to return to the nest cup and fell to the floor. Chicks presumably fell out of the nest during or shortly after feeding visits or other periods of activity.

My chick measuring visits certainly increased the numbers 'falling' out of the nest during the first few minutes after my visit. This necessitated my keeping an eye on each nest for two or three minutes after I had returned the chicks.

In Fiji only three chicks were found dead in the nest. Two of these had been starved and trampled by a larger chick that intruded into their nest. The disappearance of most chicks must have resulted from falling out of the nest, as there was no evidence of predation in the colonies which were in totally dark sectors of the caves. Chicks were seen dangling below nests and numerous dead or dying chicks found on the cave floor. Some chicks seemed prone to falling or being knocked out of their nest. For example one chick was replaced three times in one day and on three other days. One chick, rescued from the ground three metres below its nest, grew to fledging, but normally most fallen birds disappeared within a day.

An analysis of the age of 69 chicks that disappeared from the nest revealed that younger chicks were most susceptible. Thirty-three percent were less than 10 days old, 40% were between 10 and 20 days old. The question arises, were those that fell from nests with broods of two or three more likely to be the younger chick in the brood? The answer is no. Twenty-eight percent of the 69 chicks that disappeared were sole occupants, so siblings could not have caused their fall. Thirty-four percent were the smaller of the two chicks (including 1% that were older). Twenty-six percent were the larger of the siblings (including 1% that were younger). The remaining 12% were equal to their sibling at the time they were last measured before their disappearance. So, while the first chick to hatch usually remains the larger, being older gives it no clear protection against falling from the nest.

During nest inspection, most sitting and brooding birds flew from the nest at my approach.

A few birds sat tight, even while I felt under them for eggs, but even these flew if I took the eggs or chicks out of their nest. At one nest a parent was often found in attendance, even brooding the chicks on five occasions. On the last of such occasions the older chick was 24 days old.

Most chicks that died at Chillagoe, did so, as did the Fijian chicks, from falling out of the nest. Because of the chicks' resistance to starvation, many of the chicks picked up from the ground and placed in nests recovered. However, contrary to the Fijian situation, most of the chicks which fell to the ground had disappeared by my next visit. It is presumed that Childrens Pythons (Liasis childreni) and Brown Tree Snakes (Boiga irregularis) were responsible for their disappearance as these were seen near nest sites in some of the caves. Rats may also prey on fallen chicks for John Barton of Queensland National Parks and Wildlife Service has reported seeing rats in several caves. There was no evidence of predation upon chicks in the nests, almost all of which were in totally dark sectors of the caves. Confirmation that snakes cannot reach most nests, which are high up on smooth concave surfaces, comes from Vince Kinnear (pers comm), who has watched Childrens Pythons fall off the smooth wall as they have tried to reach nests. Subsequently, I have observed a Childrens Python on the wall adjacent to the nests in Mudlark Cave, but as all the nests still contained their egg or chick, it was evident that the python could not cross the smooth overhanging wall that surrounded the colony. I have also seen a 1.5 m Brown Tree Snake fall from the smooth wall above the nesting colony in the New Southlander Cave. Evidence that the tree snake could only cross the smooth wall where it did not overhang was that there were only two empty nests and these were both on vertical wall. In Fiji fallen chicks were still to be found on the cave floor far more fequently than at Chillagoe.

This is probably because Fijian Pythons Enygrus bibronii (presumably due to the activities of the Mongoose) and rats are uncommon in caves. I only ever saw one python and one rat in Fijian caves.

Adult mortality at the nesting caves

Although snakes cannot reach most swiftlet nests adult birds are not free from predation by snakes. I have watched Childrens Pythons position themselves on the wall adjacent to narrow sections of cave passage through which swiftlets must fly to reach their nests. Numerous elongated scats containing swiftlet flight feathers in the vicinity of such pythons in Golgotha Cave, Project 31 Cave, September Cave and in the tube connecting Christmas Pot and Squeeze Pot, indicated that the python's ambush method was successful.

There are also other predators at Chillagoe. The entrance to Swiftlet Cavern is a low crawl from a daylight chamber of Royal Arch Cave and the ground is littered with swiftlet feathers. John Barton and Lionel Leafe (cave guides with QNPAWS) had seen cats in the vicinity and were convinced they were preying on the swiftlets. A pile of feathers but no scats is indicative of cat predation. That the subsequent laying of baits for the cats was successful is indicated by the reduction of swiftlet feathers at the cave entrance and the increase in the size of the breeding colony in the second season (1986/87). Similarly fresh feather piles were observed at Clam Cavern, Swiftrimlet cave, Hercules Cave and Project 31 Cave. A decaying pile of feathers was seen in the entrance to September Cave indicating that cats had discontinued killing swiftlets at that site.

On 25 January 1986 I was watching about 50 swiftlets feeding very close to some rocky pinnacles, above Otobeaswiftlet Cave, which I had discovered just that day. There had been an exchange of birds through the cave entrance when a Brown Goshawk (Accipiter fasciatus) landed in a nearby tree.

The birds responded suddenly and in unison by rapidly dispersing in all directions just as noddies (pers. obs.) and terns (Cullen & Ashmole 1963) do in their "dread" or "panic" behaviour. The noise of their wings made a loud swish, which I have only heard when much closer to individual birds making their power dives into or from cave entrances. However in this event I could hear the noise from most birds, many of which were 20 to 40 m away. About five to ten minutes later the swiftlets began to reassemble overhead at an altitude of about 130 m from where they made a call (a high pitched 'shree') I had not heard before.

A Brown Goshawk had been seen outside the swiftlet entrance to Guano Pot on 20 January 1986, where after sitting in a tree it appeared to make a stoop at a swiftlet that was flying steeply and slowly out of the cave entrance. The next day another Brown Goshawk sat outside the entrance to Tarby's Swiftlet Pot. All three observations of Brown Goshawks near entrances to Swiftlet breeding caves were at the time when most first brood chicks were taking their first flights. The young swiftlets are much slower than adults when leaving cave entrances and it is likely that Goshawks are able to take young birds in this situation. On 4 January 1987 I saw a Brown Goshawk put the swiftlets over Gordale Scar Pot and Tarby's Swiftlet Pot into 'dread' behavour when it caught an individual out of the flock. Four days later an unidentified falcon circling approximately 80 m above the same two caves caused abnormal behaviour (mainly erratic flying) in the swiftlets and so it is possible that falcons as well as owls and goshawks take swiftlets.

Birds of prey have been seen taking two other species of swifts in similar situations and the same hesitancy shown by the swiftlets to enter small openings was displayed by the swifts.

The first instance involved a flock of 1,500 Chimney Swifts entering a chimney for roosting purposes, when a Sharp-shinned Hawk (*Accipiter striatus*) flew into the flock at the point where they slowed down to drop into the chimney and carried away a squealing swift (Musselman in Bent 1940). The second instance occured when a flock of Vaux's Swifts were entering a chimney and a Merlin (*Falco columbarius*) made a stoop which due to the swifts scattering was unsuccessful (Rathbun in Bent 1940). It appears that adult colonial swifts are most vulnerable while entering or leaving their nesting and roosting sites. It is only in this situation that the birds show hesitancy by flying circuits just inside or outside the entrance. That the entrance or exit is performed at high speed once initiated is further evidence of the swiftlets' vulnerability to predators at this point. By timing *chillagoensis* over a measured eight metres at the entrance to Tarby's Swiftlet Pot, the average speed was determined to be 37 km/hr. The maximum speed recorded was 111 km/hr which is similar to that (106 km/hr) recorded for *assimilis* entering Waterfall Cave (Tarburton 1986b, Appendix 5 p.180).

Nest sanitation and ectoparasites

From the first day, nestling White-rumped Swiftlets defaecate over the low front rim of their nest, thus leaving the nest free of faecal contamination. Similar behaviour has been described in the Common Swift (Lack 1956a), the Chimney Swift (Fischer 1958), the Chestnut-collared and Short-tailed Swifts (Collins 1968a). When newly hatched Chimney Swifts did not void their faeces over the front of the nest the parents either ate the faeces or threw them out of the nest (Fischer 1958). Common Swifts were not so clean, as the adults would not remove old faeces from their nests and towards the end of the nesting period the parents also became less regular in removing fresh faeces (Lack & Lack 1952).

The only fouling found in White-rumped Swiftlet nests was the broken remains of hatched egg-shells but even these were either eaten or removed in many nests. It is possible that the American Cockroaches were responsible for removing some eggshell. The eggshell was not removed from the nests of the three species of swiftlet that nest in Niah Cave, Borneo (Medway 1962a). Neither in Fiji nor Borneo were dead eggs left in the nest for very long and Weitnauer (1947), Lack & Lack (1952) and Lack (1956c) record the ejection of eggs by the Common Swift.

While the chick's practice of defaecating over the front of the nest provides nutrient for the guanophile community on the cave floor, or for the aquatic community downstream, it deprives those ectoparasites that thrive in fouled nests, of an important source of food.

Both *assimilis* and *chillagoensis* are parasitised by louse-flies (Hippoboscidae). When adults left their nests these flies were often left behind and they moved rapidly over the nests, cave wall and the chick. They also moved rapidly over and through the feathers of adults in the hand. In repeatedly examining chicks from more than 100 Fijian nests through December 1981, the few chicks in nests isolated by more than 0.5 m from other nests had no louse-flies. Birds in nests having contact with surrounding nests had the most flies.

The fly found in Fiji was separated as a new species (*Myophtheria fijiarum*) and placed in the new sub-genus *Myophthiria* (Maa 1980). This sub-genus was used to group 11 species of flies hosted by several species of swiftlets distributed on islands or archipelagoes between Sri-lanka and Fiji and at the same time separating them from two louse fly species hosted by three new world swifts (Black Swift, White-throated Swift (*Aeronautes montivagus*) and White-tipped Swift (*Aeronautes saxatalis*). Maa (1980) quotes Rondani 1878 as cause for listing *M. fijiarum* as being hosted by the "Mossy Swiftlet" as well as the White-rumped Swiftlet on Viti Levu.

However, the Mossy-nest Swiftlet does not occur in Fiji. Consequently this species of louse-fly is hosted only by the White-rumped Swiftlet in Fiji. Only one of the other 10 species of louse-flies named by Maa is hosted by another subspecies of the White-rumped Swiftlet. This fly is *M. neocaledonica*, hosted by *A. s. leucopygius* on New Caledonia. The louse-fly *M. queenslandae* which Maa suggests is hosted by either the White-rumped Swiftlet or the Glossy Swiftlet, is probably the species found on *terraereginae* (Pecotich 1974). This means three species of louse-fly have each been found on one of three separate subspecies of the White-rumped Swiftlet.

Fifty-six louse-flies collected from Nasinu Caves in 1974 and December 1981, were five to seven mm long and weighed 0.016 - 0.044 g. Their wings were only one mm long. Having such short wings probably explains why the flies were found in the nests as well as on the chicks and adult birds. When moving between nests and over the birds the flies moved very rapidly. When they stopped they were usually well hidden in a crevice or under some feathers. However those on birds that were being handled were easy to flush and so easy to catch.

Although a search for other ectoparasites was not made it is possible they exist as a number of others have been found on other apodids, some of which move through or inhabit the south-west Pacific. Russian workers have found ticks (Ixodidae) on the Fork-tailed Swift (*Apus pacificus*) which winters in the south-west Pacific (Bolotin & Kolonin 1979, Kolonin & Bolotin 1977). Ticks have also been found on the Glossy Swiftlet in Java (Hoogstraal *et al* 1974) and the Alpine Swift (*Apus melba*) in Eurasia (Tovornik & Cerny 1974; Filippova & Panova 1975). The ticks on the Glossy Swiftlet may be significant as the parasitic louse-fly from the swiftlets in Java are the most closely related to those on the Fijian swiftlets (Maa 1980).

Feather-mites (A carina) have been recorded from African swifts including the House Swift (Gaud & Atyeo 1976) and the African Palm Swift (Cort 1975). Mites have also been found on the Short-tailed Swift and the Chestnut-collared Swift in Trinidad (Collins 1968a). Such a wide distribution on apodids suggests they could be expected on swiftlets in the south Pacific. Feather-lice (Mallophaga) have been reported on the two swifts studied by Collins (1968a) in Trinidad as well as on the Chimney Swift, along with parasitic bugs (Cimicidae, Hemiptera) in North America (Fischer 1958). Lice are common ectoparasites on birds and being small could have been easily overlooked on the Fijian swiftlets.

A variety of insects inhabit the swiftlet nests at Chillagoe. Apart from the Louse-fly, none was abundant except towards the end of January when a tiny feather louse covered some chicks. The largest ectoparasite seen was the Louse-fly Myophthiria spp. Maa (1980) stated that flies in this genus are never found in high densities, hence are very difficult to collect. However this Louse-fly was common on adults and chicks at Chillagoe. By collecting and recording the number of Louse-flies found on the chicks or in their nests, the data in Table V were accumulated.

Table V

The numbers of Louse-flies found on Chicks at 10 day age intervals.

Period (days)	0-10	11-20	21-30	31-40	41-50
Total from 142 Fijian nests	0.0	1.0	12.0	6.0	1.0
$\bar{x}$/nest at Chillagoe	1.0	1.5	5.9	4.0	3.1
n	46.0	38.0	26.0	20.0	10.0
SE	0.21	0.23	0.78	0.74	0.78

These data indicate that this ectoparasite is least common on 1 - 10 day-old chicks and not significantly more common on 11 - 20 day-old chicks ($t = 1.5$,). The flies are significantly more common on 21 - 30 day-old chicks than on 11 - 20 day-old chicks ($t = 5.5$, $\underline{P} < 0.001$). The decline in numbers found on 31 - 40 day old-chicks, and the further decline on 41 - 50 day-old chicks, are not significant ($t = 1.8$ & 0.8 respectively). In spite of this decline, the average number of Louse-flies on 41 - 50 day-old chicks was still significantly greater ($t = 2.029$, $\underline{P} < 0.05$) than those found on 11 - 20 day-old chicks. This peak of density on 21 - 30 day-old chicks coincided with that for the Louse-fly cogener in Fiji. However, the fly was much less common in Fiji where the numbers shown in Table V constitute the total for 142 nests rather than the average per nest as shown for the Chillagoe birds.

The average distance between nests at Chillagoe was greater than that between Fijian nests and should have proved a greater deterent to the spread of ectoparasites such as the Louse-flies. Because many nests were joined together in Fijian colonies, the spread of Louse-flies should have been facilitated, so finding them to be less common on Fijian chicks is surprising, although they were not as uncommon on adult Fijian swiftlets (though unfortunately uncounted) as on Fijian chicks.

Feeding of young

From observations on 20 assimilis nests for one full day in December 1981 a daily feeding rate of 2.8 ± 0.26 ($\bar{x} \pm$ S.E.) was determined. Although six of these nests contained only single chicks the number of visits to these nests was not significantly different to the number of visits to those nests with two chicks. Each chick received an average of 1.7 feeds per day.

From observations on chillagoensis nestlings for one full day during both the good season (December 1985, n = 20) and the poor season (22 December 1986, n = 9) rates of 5.2 ± 0.28 ($\bar{x}$ ± S.E.) for the good season and 2.9 ± 0.5 for the poor season were determined. The rate for the good season is significantly (t = 6.3, $P < 0.001$, df = 38) above that for Fijian birds (2.8 ± 0.26). The rate for the poor season was not significantly different ($t = 0.4$, ns, df = 25). That Swiftlets at Chillagoe have an easier time providing for their single brood in good seasons, than Fijian birds in providing for their brood of two, is also suggested by the shorter daily period the Chillagoe birds spend foraging (Section 2). However there are two factors which prevent chillagoensis from raising two chicks. The first is that the density of available prey is much below the density of that available in Fiji (Appendix 3 p.158). The second is that the irregularity of extreme wet and dry periods throughout the breeding season at Chillagoe means that prey species such as termites are not flying each day for they only fly a day or two after each period of rain ends.

The number of feeding visits other Apodidae make to their chicks varies within and between species (Table VI). Some species such as the Alpine Swift (Arn-Willi 1960), the White-rumped Swift, the Palm Swift (both Moreau 1942b), and the House Swift (Moreau 1942a), increase their feeding rate for larger broods. Some Apodidae such as the Chimney Swift (Kendeigh 1952, Fischer 1958) and the Black Swift (Michael 1927), vary their feeding rate with the age of the chicks. Other Apodidae such as the White-rumped Swift (Moreau 1942b) and the Chimney Swift (Fischer 1958), increase their feeding rate prior to sunset, though the amount of food brought at each trip decreases (Fischer 1958). As has been shown in the Black Swift (Michael 1927, Collins & Landy 1968), more than one bolus of food may be brought to the chick in one visit. Changes in the weather may cause variations in the feeding rate as Zammuto et al. (1981) have shown in the Chimney Swift.

TABLE VI

Frequency of Chick Feeding

Species	Brood size	Mean number visits / day	Mean time between visits (min)	Range between visits (min)	Mean feeds / Chick / Day	Source
White-rumped Swiftlet						
Aerodramus						
spodiopygius (Fiji)	1.7	2.8	-	-	1.7	This study
(Chillagoe wet yr)	1.0	5.2	-	-	5.2	This study
(Chillagoe dry yr)	1.0	2.7	-	-	2.7	This study
Black-nest Swiftlet						
Aerodramus maximus	1.0	2.0+	-	-	-	Medway 1962a
Mossy-nest Swiftlet						
Aerodramus						
vanikorensis	2.0	*c*.3.0	-	30-?	-	Medway 1962a
Chimney Swift						
Chaetura pelagica	*c*.4.0	*c*.49.0	14.6	-	12.3	Zammuto *et al*. 1981
	4.0	-	-	1-28	*c*.11.8	Bent 1940
1st week	*c*.4.0	-	*c*.30.0	-	*c*.7.7	Fischer 1958
2nd week	*c*.4.0	-	*c*.45.0	-	*c*.7.0	Fischer 1958
day 1-4	-	-	20.0	-}	11.7	Kendeigh 1952
day 5-14	-	-	15.0	-}		
day 16-20	-	-	60.0	-}		
Short-tailed Swift						
Chaetura brachyura	3.8	*c*.36.0	20.5	3-45	*c*.9.5	Collins 1968a
Vaux Swift						
Chaetura vauxi	4.0	*c*.48.0	15.0	-	*c*.12.0	Bent 1940
	c.4.0	-	18.0	-	*c*.11.0	Baldwin & Zackowski 1963
	4.0	-	-	15-20	*c*.13.0	Finley & F. 1924
	4.0	*c*.69.0	10.0	1-21	17.3	Davis 1937
Chestnut-collared Swift						
Cypseloides rutilus	1.9	-	-	36-100++	-	Collins 1968a
Black Swift						
Cypseloides niger	1.0	1.0	-	-	1.0	Michael 1927
Common Swift						
Apus apus wet	2.0	7.0	-	-	3.5	Lack & Owen 1955
fine	2.0	14.0	-	-	7.0	
Pallid Swift						
Apus pallidus	2.0	*c*.17.8	-	-	*c*.8.9	Affre & Affre 1967
Alpine Swift						
Apus melba	*c*.3.0	24.0	-	-	8.0	Bartels 1931
	2.0	7.5	-	-	3.8	Arn-Willi 1960
	3.0	8.5	-	-	2.8	Arn-Willi 1960
White-rumped Swift						
Apus caffer	1.0	8.8	-	-	8.8	Moreau 1942b
	2.0	13.2	-	-	6.6	Moreau 1942b

TABLE VI cont....

Species	Brood size	Mean number visits / day	Mean time between visits (min)	Range between visits (min)	Mean feeds / Chick / Day	Source
House Swift						
Apus affinis	1.0	6.6	118.0	8-254	6.6	Moreau 1942a
	2.0	10.2	73.5	<8-120+	5.1	Moreau 1942a
	3.0	13.8	54.3	<8-120+	4.6	Moreau 1942a
	3.1	25.8	35.3	-	8.3	Chih Tung 1973
White-throated Swift						
Aeronautes am	4.0	-	21.5	3.36	*c.*9.0	Collins un-
saxatalis dusk	4.0	-	11.5	2.27	*c.*9.0	pub.
African Palm Swift						
Cypsiurus parvus	1.0	12.4	*c.*60.0	<15->90	12.4	Moreau 1941
	2.0	19.3	*c.*40.0	-	9.7	Moreau 1941

NOTE: *c.* indicates an approximation derived from data, that did not cover the full diurnal period, or that was not precise.

Interspecific comparisons are most valid when the size of the brood is taken into account. This is done in the final column of Table VI where the average number of feeding trips made per chick per day is shown. In spite of the perturbations caused by the above factors, a strong inverse correlation (r = -0.80; n = 18; P< 0.001) exists between the length of the nestling period and the number of feeds a chick receives in a day (Figure 5). This correlation should not be used to suggest that the number of feeds per chick, per day, determines the length of the nestling period. That would ignore the role of genetic constraints on the growth rates of chicks. Some species develop at a slow rate no matter how much they are fed. Ultimately, this may be related to selection of growth rates based on food supply. Genetic constraints are clearly shown by the ability of the Black Swift to raise its chick successfully on one feed (visit) per day, whereas the Black-nest Swiftlet is unable to do so on less than two feeds a day (Medway 1962a).

Adult Morphology

A sample of adults of both sub-species was measured in order to compare the wing length and weight of nestlings with that of their parents and with other subspecies. These data are summarized in Table VII. The average wing length of 300 adult chillagoensis was 107.1 ± 0.1 mm (range = 101 - 113 mm). This was significantly (t = 14.4, P< 0.001, df = 400), smaller than the wing of Fijian birds. That my average measurement is also significantly (t = 12.8, P< 0.001, df = 350) larger than that taken by Pecotich (1982) on the same population is less easily explained.* The average weight of 300 adult chillagoensis was 9.3 ± 0.04 g (range = 7.9 - 12.1 g). This is significantly (t = 15.4, P< 0.001, df = 400) heavier than Fijian birds and significantly (t = 10.0, P< 0.001, df = 350) lighter than the average weight given by Pecotich (1982) for the same population.

* He probably used a different method of measurement.

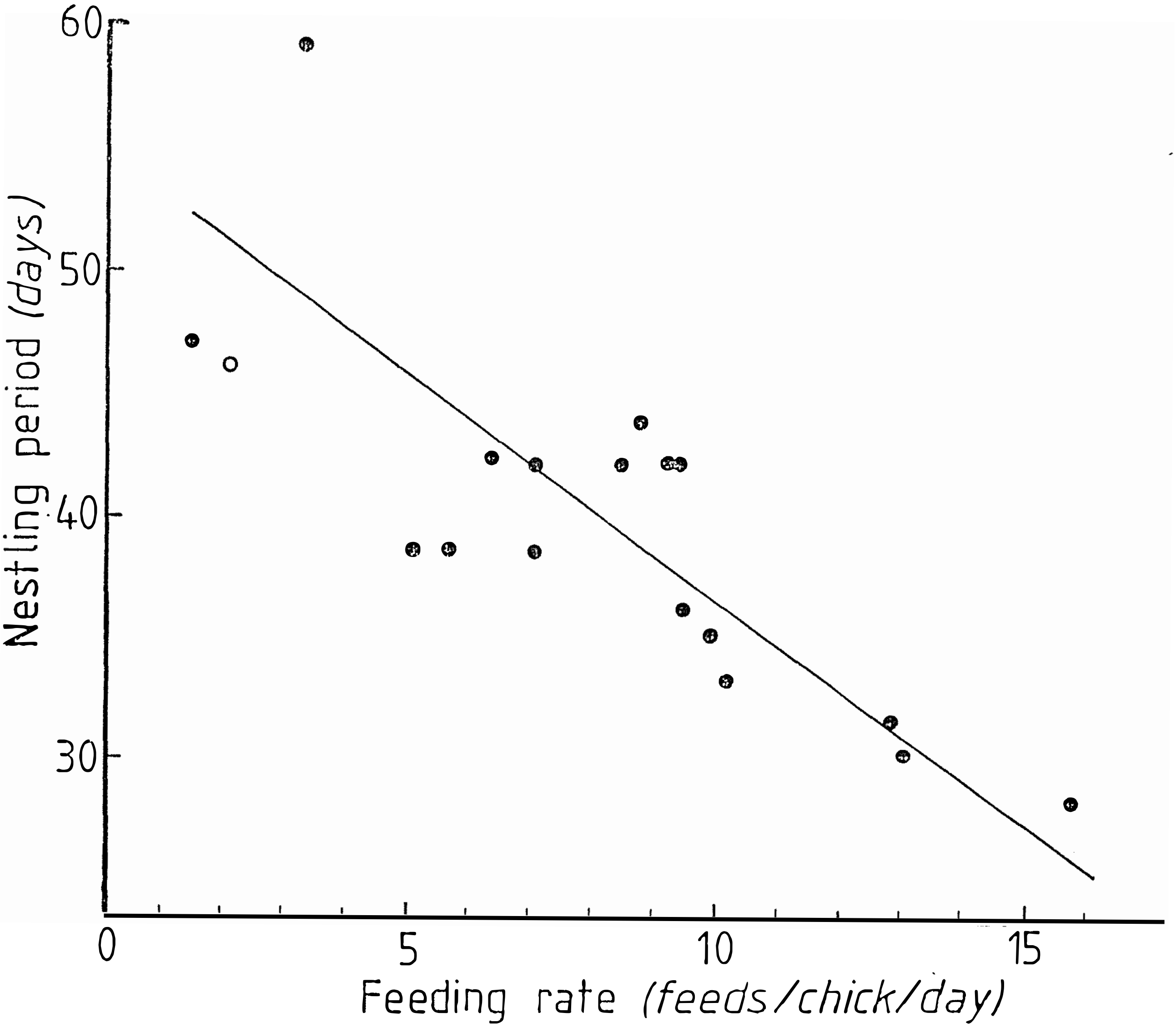


Figure 5. Relationship between feeding rate and nestling period in swifts.

The White-rumped Swiftlet is designated by the hollow circle. The line is the reduced major axis (Clymo 1983). The correlation is significant ($r = -0.80$, $n = 18$, $P<0.001$).

TABLE VII
Morphology of four subspecies of the White-rumped Swiftlet

	A.s.spodiopygius $\bar{x}$±S.E. (a)	A.s.assimilis $\bar{x}$±S.E. (b)	A.s.terraereginae $\bar{x}$±S.E. (c)	A.s.chillagoensis $\bar{x}$±S.E. (c)	A.s.chillagoensis $\bar{x}$±S.E. (b)
Length (mm)	102 (d)	103.1±0.4	109.3±0.3	97.2±0.4	105.8±0.2
Wing (mm)	111.7±0.8	112.0±0.3	110.6±0.2	102.5±0.3	107.1±0.1
Wing Span (mm)	-	261.0±0.6	-	-	249.9±0.5
Outer Rectrix(mm)	52.8±0.6	44.7±0.2	52.3±0.3	47.3±0.2	47.4±0.2
Tarsus (mm)	8.5 (e)	10.6±0.1	10.0±0.1	9.1±0.2	-
Exposed Cul.(mm)	4.5 (e)	3.8±0.03	4.5±0.01	4.5±0.01	-
Gape (mm)	-	11.2±0.08	-	-	-
Mid.Toe (mm)	-	4.7±0.05	-	-	-
Mid.Claw (mm)	-	3.8±0.03	-	-	-
Weight (g)	8.1±0.4	8.2±0.06	12.2±0.07	10.5±0.1	9.3±0.04
n	8	102	50	50	300

NOTE: (a) United States National Museum; (b) This paper; (c) Pecotich 1982; (d) Armstrong 1932; (e) Oberholser 1906.

That *chillagoensis* weighs more than *assimilis* and yet has a shorter wing suggests that selection pressures to decrease wing length have been operating on *chillagoensis*. Alternatively, selection pressures might have increased wing length in *assimilis* as it flies further and longer each day than *chillagoensis* (Appendix 3, p.159). It might also be that it is to the advantage of *chillagoensis* in its erratic climate with long dry winters to have a good body store of energy.

Even though a statistically significant difference was shown between the size of eggs in the Waiyala and Nasinu colonies, Student's *t* tests on the wing, weight and wing span of adult birds indicated no significant differences. Furthermore, there was no significant difference between either of these populations and the sample measured from the Ono Cave population. Most of the data from these colonies have therefore been pooled, to provide a sample of 102 birds from which the standard morphological measurements have been taken for this subspecies. Table VII compares these measurements with those of the two Queensland subspecies, and those of the Samoan subspecies.

The Fijian subspecies has the largest wing and tarsus, but the second lightest weight of the four subspecies shown. The wing range of 115-120 mm given for the species by Medway (1966), is too high for any of the above subspecies. It is also too high for *A.s.leucopygius* on New Caledonia, which has a wing range of 95 - 99.5 mm (Oberholser 1906). Two individual birds alone with wings of 116.5 mm reach the range given by Medway. One is a specimen of *A.s.townsendi* from Tonga and the other is *A.s.spodiopygius* from Samoa (Oberholser 1906). The range of wing length for the species should be 95 - 117 mm.

CONCLUSIONS

As swiftlets are smaller than swifts, the prediction that swiftlets will lay heavier eggs than swifts, in proportion to adult weight (Lack 1968) is supported by this study. While larger Apodidae lay larger eggs, it is larger adult size that accompanies a reduction in the incubation period. The cause for this is probably that larger birds are better able to maintain their proportionately smaller eggs at the optimum temperature for reducing the incubation period. This effect is probably reinforced by swiftlets gaining the increased safety of nesting in places that are inaccessible to predators and which Snow (1962) maintains relaxes selection pressures to hatch and raise a brood as quickly as possible. By nesting in larger colonies than swifts and on "cliff" sites that have greater safety because of their dark location, we would correctly conclude that swiftlets will have longer incubation periods than swifts.

Because incubation periods in swiftlets are inversely related to the size of the species, and chillagoensis (which is larger than assimilis) has a longer incubation period than assimilis, it may be that factors such as the cooler temperature in the caves at Chillagoe can affect this basic relationship between adult size and incubation period.

Because the length of fledging periods is related to the length of incubation periods and because chillagoensis (which has a longer incubation period than assimilis), has a similar fledging period to assimilis, it is concluded that factors such as the cooler temperature in the Chillagoe caves can also affect the basic relationship between incubation and fledging periods. If this is so then it is likely that the extra feeding visits to chillagoensis chicks (100% more than to assimilis), are being used to keep the chicks warm through extra feeding. Alternatively, the reason for adults spending more time with their chicks at Chillagoe than in Fiji is to keep them warm.

Section 2

AN EXPERIMENTAL MANIPULATION OF CLUTCH & BROOD SIZE TO DETERMINE WHETHER LONG-LIVED TROPICAL SPECIES ARE MAXIMISING THEIR FOOD SUPPLY

The fact that the number of eggs per clutch generally increases with latitude has been confirmed many times (Lack 1954,1968) since the discovery of the phenomenon early last century (Wagner 1957). However, the search for a general theory to explain these observations and the exceptions still continues. Hesse (1922) suggested that the longer day experienced in high latitudes increased the amount of food parents could make available to nestlings and therefore facilitated the production of a larger clutch than related species breeding in the tropics. Lack (1947:331) pursued this line of reasoning with a study of seasonal and regional variations in the number of eggs which birds lay and concluded that "in most species clutch-size is considered to be ultimately determined by the average maximum number of young for which the parents can find food".

Such reasoning presumes that tropical birds raise as many young as they can nourish. Skutch (1949) believed this was not the case as some tropical birds can feed their brood at a rate faster than normal. This occurs where parents are prevented from feeding their brood for some time or have laid more eggs than normal. Skutch also found that species in which both parents feed the nestlings usually raised no more chicks than species where only the female attends the nestlings. Further evidence came from birds such as the Senegal Fire Finch (*Lagonosticta senegala*) which can raise the large chick of a parasitic weaver in addition to and at the same time as raising its own brood (Morel 1967). These and other situations have led to several modifications to Lack's theory.

In one of these modifications, Winkler & Walters (1983) state "birds lay that number of eggs that result in the parents operating at the optimal working capacity". In stating this, they accept Ashmole's update (1961, 1963) of Lack's hypothesis (1947) that birds are maximising their clutch size in respect to the quantity of food that is immediately available during the breeding season. However they also allow for parents which may be maximising their reproductive output over their entire lifetime rather than within a single breeding attempt. A number of authors use the latter view to predict that some brood sizes will be below the maximum that parents can feed in a particular season (eg. Williams 1966; Murphy 1968; Gadgil & Bossert 1970; Charnov & Krebs 1974; Goodman 1974; Pianka & Parker 1975).

It would be expected that long-lived birds with small clutches would be amongst those most likely to be working below their capacity to gather food, in order to enhance their lifelong capacity to raise more young. Although it has been doubted that a bird presented with an extra chick could be expected to attempt to raise it, the more recent view is that the manipulative addition of eggs to broods can be useful in helping to determine whether a bird is maximising its food supply or not at the time of breeding (Klomp 1970). It has been shown by monitoring chick growth in artificially enlarged broods that some birds have been able to gather enough food to raise more chicks than normal at one time. However, all such results were obtained with temperate species and no such manipulations have been carried out on swiftlets which are long-lived and tropical.

By monitoring hatching success, chick growth and fledging success, in normal sized and experimentally enlarged clutches and broods of the White-rumped Swiftlet in Fiji, this section of the thesis demonstrates the inability of this species to raise more young than is normal.

METHODS

The subjects of this manipulation experiment were White-rumped Swiftlets nesting in 'Dry' and 'Waterfall' caves, Nasinu, north of Suva (Section 1, page 8, Tarburton 1986). Daily visits were made to these colonies throughout December 1981 and again in December 1983. On these visits eggs were checked for hatching, and measurements were made of each chick's wing, tarsus and weight. Six natural single-egg clutches and 37 natural two-egg clutches were monitored as controls along with the manipulated clutches. Single-egg clutches were created by removing one of the two eggs from 24 normal clutches. The eggs that were removed were added, as were another three, to normal clutches to make up 27 three-egg clutches. Six two-egg clutches were also made up by swapping eggs so that none of these birds was incubating its own eggs. The rates of growth for 13 one-chick and 39 two-chick natural broods were compared with those for 37 one-chick, seven two-chick and 23 three-chick manipulated broods.

Lack (1956) reported some parental desertion when the nests of Common Swifts were disturbed. To test the effect of disturbance on the swiftlets I visited one isolated group of nests less frequently than other nests in the study. The chicks at frequently-visited nests grew at the same rate as those in nests visited less frequently. Nests were approached slowly to allow incubating parents time to leave the nest without the haste that caused increased egg loss. After being handled most chicks were restless and likely to fall from the nest. This made it necessary to keep an eye on a brood for about a minute after replacing it.

Individual chicks within a brood were initially identified by placing a daub of dark green quick-drying model paint on the head, shoulders or rump.

Once the tibia was large enough to retain a band, individually numbered size one aluminium bands from CSIRO, Canberra, Australia were used. I banded all swiftlets on the tibia instead of the usual tarso-metatarsus. Bands applied to the tarsus often slip over the toes (Tarburton, unpublished). The swiftlets usually stay on the wing all day (except when breeding) and this prevents the band from damaging the thin skin and feathers of the tibia.

The day of hatching was known for only 22 chicks. Their wing, tarsus and weight measurements exhibited an even exponential growth form through day eight. In order to increase the sample of aged chicks, those up to eight days old when found, were aged with a formula derived using regression analysis of measurements of known-age chicks.

Four full-day watches were made at a sample of manipulated and untouched nests to determine the daily feeding rate of the different sized broods. The low beam on a miners lamp was used to make the observations. The median test was used to compare the feeding rates because it makes no assumptions on distribution and is more conservative than the t test used for other comparisons.

RESULTS

Hatching Success

The hatching successes of natural clutches and manipulated clutches were not significantly different. Those with a natural clutch size of one, hatched an average of 0.43 ± 0.18 ($\bar{x}$ ± SE, n = 9) eggs, while the manipulated ones hatched an average of 0.61 ± 0.12 (n = 20), (Median test, $X^2 = 0.28$, n.s.). Pairs with a natural clutch size of two hatched on average 1.18 ± 0.15 (n = 34) and the manipulated twos, 1.0 ± 0.26 (n = 6), (Median test, $X^2 = 0.6$, n.s.).

The combined hatching success of single-egg clutches was 0.52 ± 0.09 (n = 29) and that of the combined two-egg clutches 1.15 ± 0.14 (n = 40) eggs, showing a clear advantage to the two-egg clutch ($t_{65} = 3.81$, $P < 0.001$). The manipulated three-egg clutches had an average clutch hatching of 1.22 ± 0.17 (n = 27), which was not significantly larger than that of the two-egg clutches ($t_{55} = 0.33$, n.s.).

Chick Growth

Figures 1, 2 and 3, show the mean daily increase in length of wing and tarsus, and weight for individuals in broods of all three sizes. The overlapping standard errors on the wing growth curves indicate no significant difference between broods of one and two whereas that of three is significantly less than both one and two after the tenth day. Average adult wing length was not reached before birds fledged, though the minimum adult wing length was reached by most fledglings.

The weight of chicks in broods of three was also significantly lower. After day 12 a significant difference could be detected between those of single and two-chick broods, but it was not as great as between those of two and three-chick broods. One-chick broods reached adult weight on day 19, twos on day 22 and those of three-chick broods on about 30 to 50 days.

Tarsal growth exhibited the least variation with no consistent differences amongst chicks of differing clutch sizes. Of the three measures taken, the tarsus achieved adult size the most rapidly. This took an average of 13.5 days.

Fledging Success

In order to determine brood success an arbitrary point of success needed to be established due to the difficulty of knowing when the nestling period ended.

Figure 1. Mean daily increase in the wing length of chicks in different sized broods:

The means for broods of one are represented by hollow circles, broods of two by horizontal bars and broods of three by solid circles. Standard errors of the means (vertical lines) for chicks in broods of three rarely overlap those for chicks from single or double broods after the tenth day. Although n = 118, not all chicks were measured each day, hence the unevenness of the growth curves.

Figure 1. Mean daily increase in wing length of chicks in different sized broods

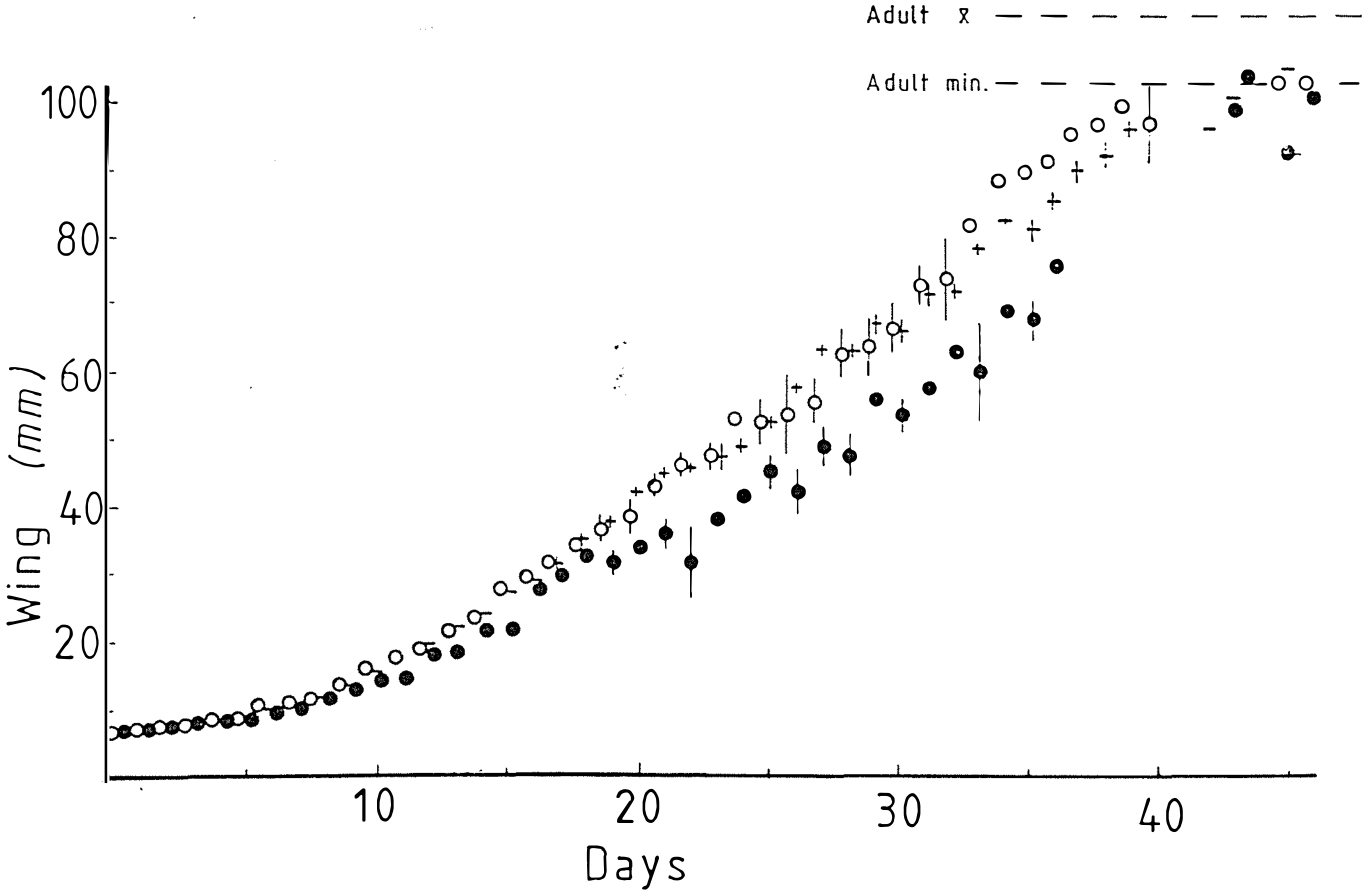


Figure 2. Mean daily increase in chick weight:

The means for broods of one are represented by hollow circles, broods of two by horizontal bars and broods of three by solid circles. Standard errors of the means (vertical lines) for chicks in broods of three rarely overlap those for chicks from single or double broods after the tenth day. Although n = 118, not all chicks were measured each day, hence the unevenness of the growth curves.

Figure 2. Mean daily increase in chick weight

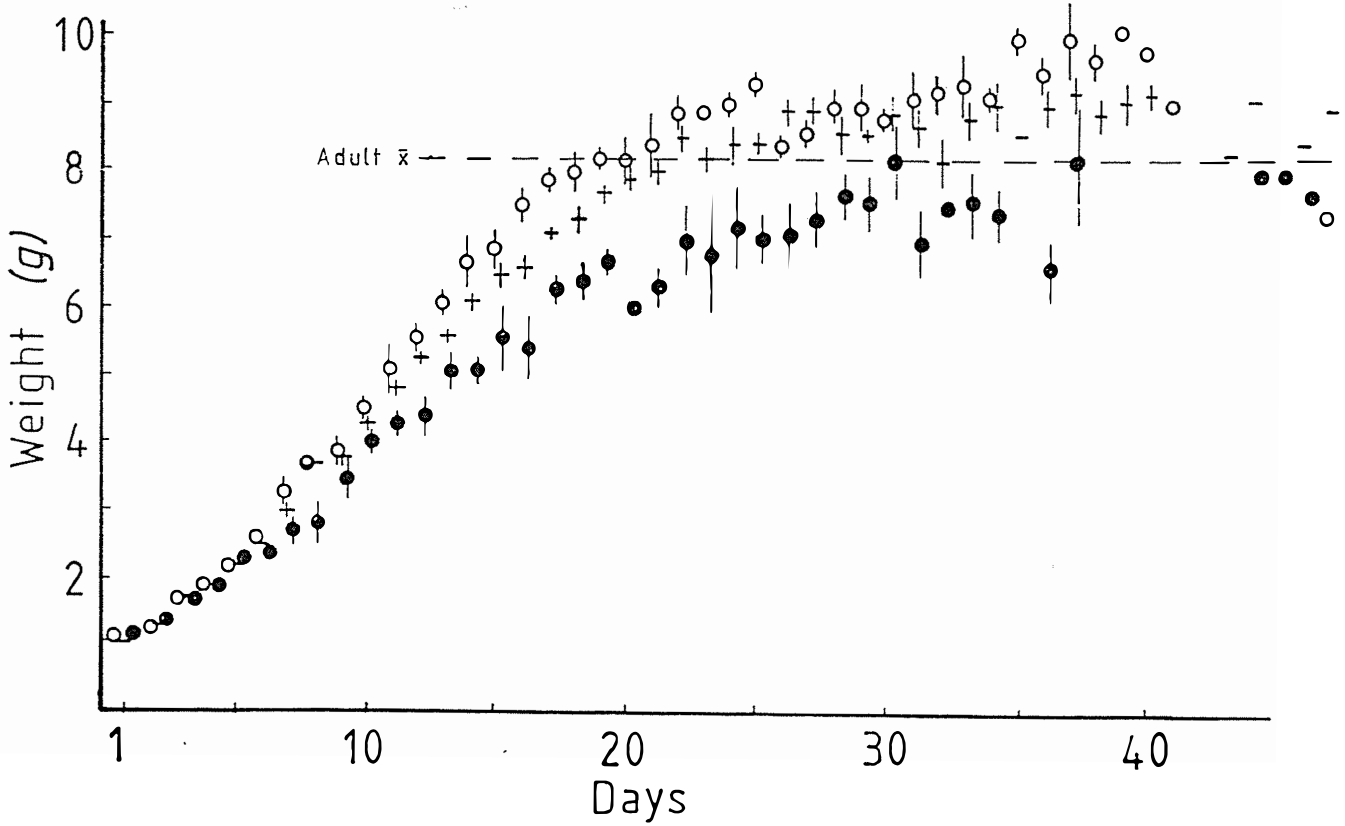
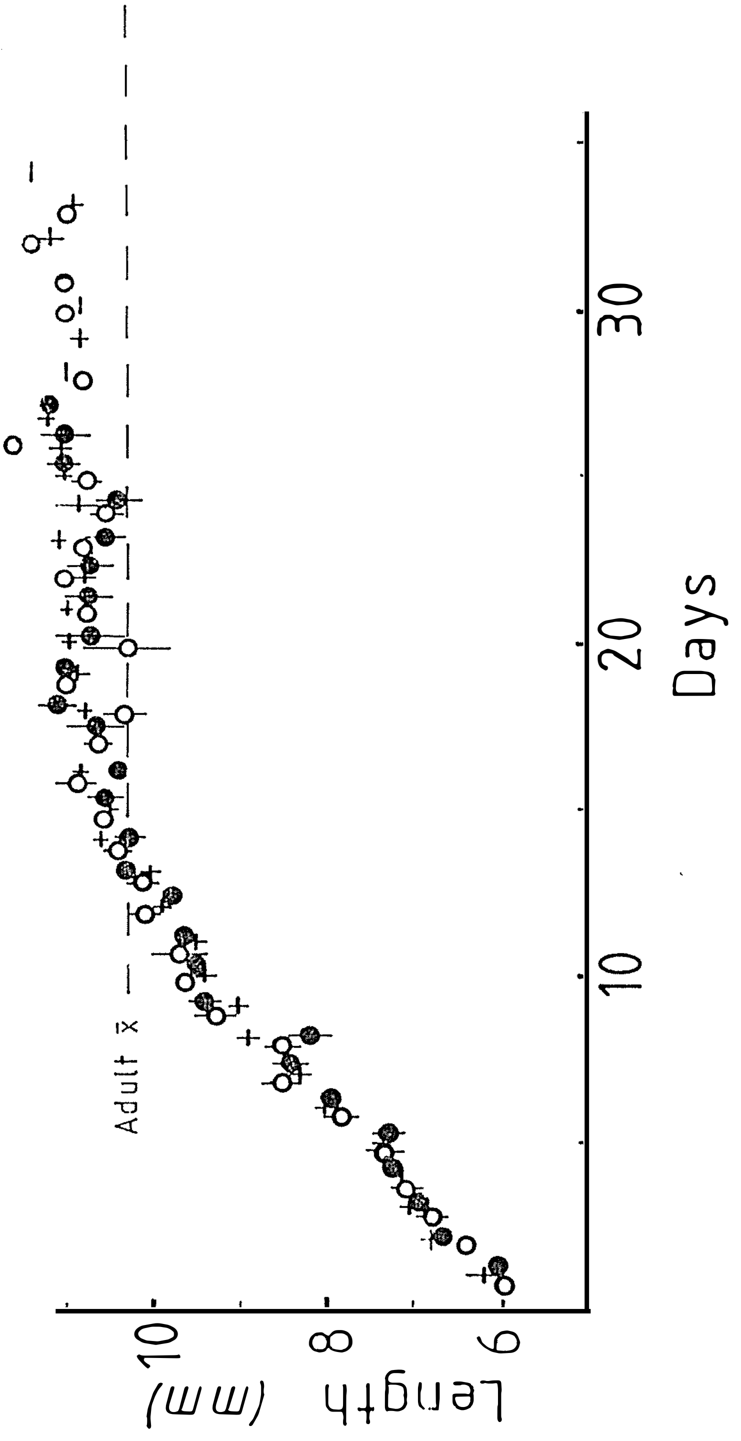


Figure 3. Mean daily increase in tarsal length:
The means for broods of one are represented by hollow circles, broods of two by horizontal bars and broods of three by solid circles. The consistent overlap between the standard errors (vertical lines) of chicks from all three clutch sizes indicates the small effect food supply has on tarsal growth.

Figure 3. Mean daily increase in tarsal length



The difficulty was caused by the wandering habits of older chicks, which although possibly beneficial in exercising their wings as they "walked" around on the cave walls, made location of marked birds more difficult. Taking a wing length of 90 millimeters as indicating that a nestling is likely to fledge, the following determinations were made. Parents with a brood of one raised 0.43 ± 0.11 chicks ($\bar{x} \pm$ SE, n = 24). Those with a brood of two raised 0.92 ± 0.15 (n = 25) and those with a brood of three raised 1.09 ± 0.3 (n = 11).

These data show that a pair with a brood of two, rear significantly more young than those with a brood of one (t_{44} = 2.57, $P < 0.01$), while those with a brood of three do not rear significantly more than those with broods of two (t_{15} = 0.59, n.s.).

Because average growth curves conceal certain characteristics of the individual growth curve and in particular the variation within a brood, the progress for a selection of individuals has been plotted in figures 4 and 5. It will be noticed that even in the brood of three (and this was true for all other broods of three), death was not preceded by a drop in weight as was found in the Common Swift in wet summers (Lack & Lack 1951) and sometimes in the smaller siblings of the Edible-nest Swiftlet (Langham 1980).

Feeding Rate

The four full-day observations on a sample of the manipulated nests demonstrated that the average of 2.9 ± 0.34 visits ($\bar{x} \pm$ SE, n = 11) to broods of three was significantly greater (Median test, X^2 = 4.97, $P <$ 0.05) than the 2.2 ± 0.1 visits (n = 18) to broods of two. The 2.1 ± 0.01 visits (n = 18) to broods of one was not significantly different (Median test, X^2 = 0.8, n.s.) from the number of trips to broods of two. While the increased number of feeding trips made to broods of three might be taken to indicate that the chicks in the enlarged broods would receive adequate food for normal growth, this is not the case.

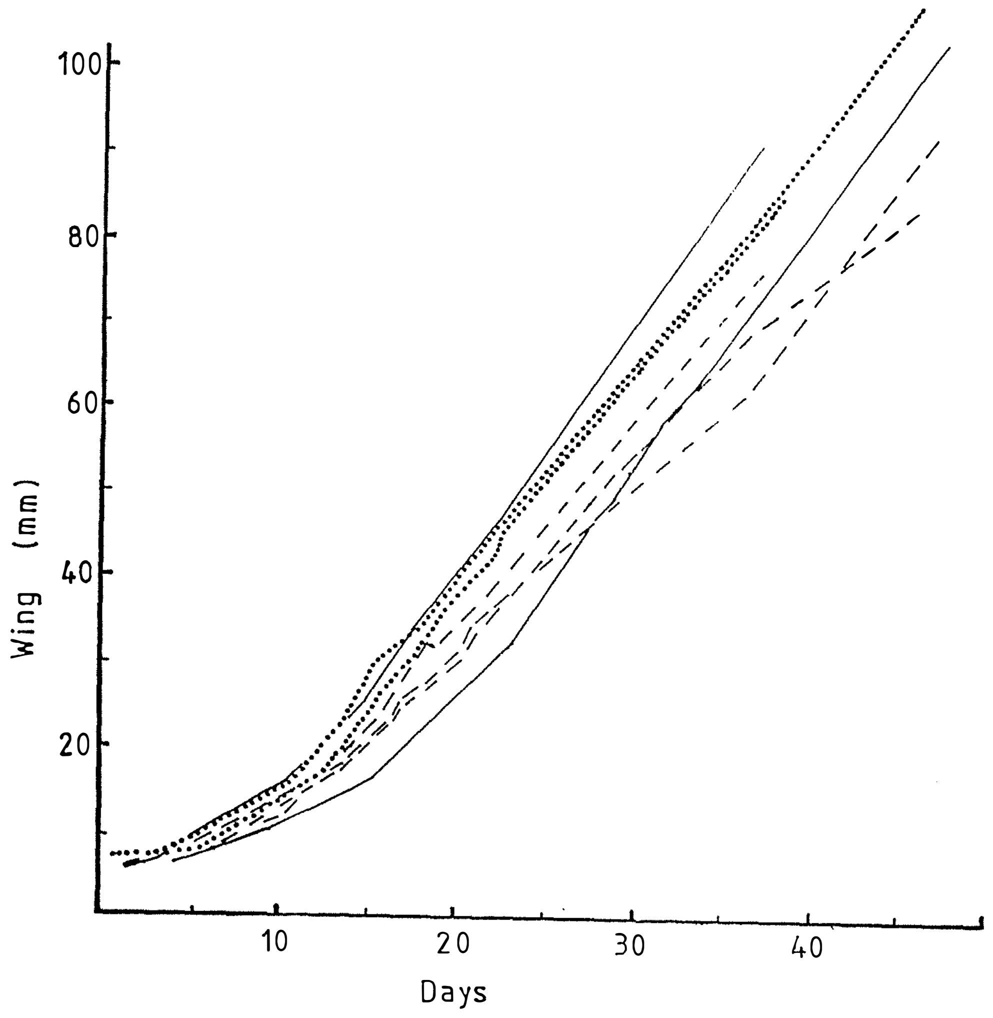


Figure 4. Wing growth in individuals from broods of all three sizes. Chicks from single broods are represented by continuous lines, those from broods of two, by dotted lines and those from broods of three by pecked lines.

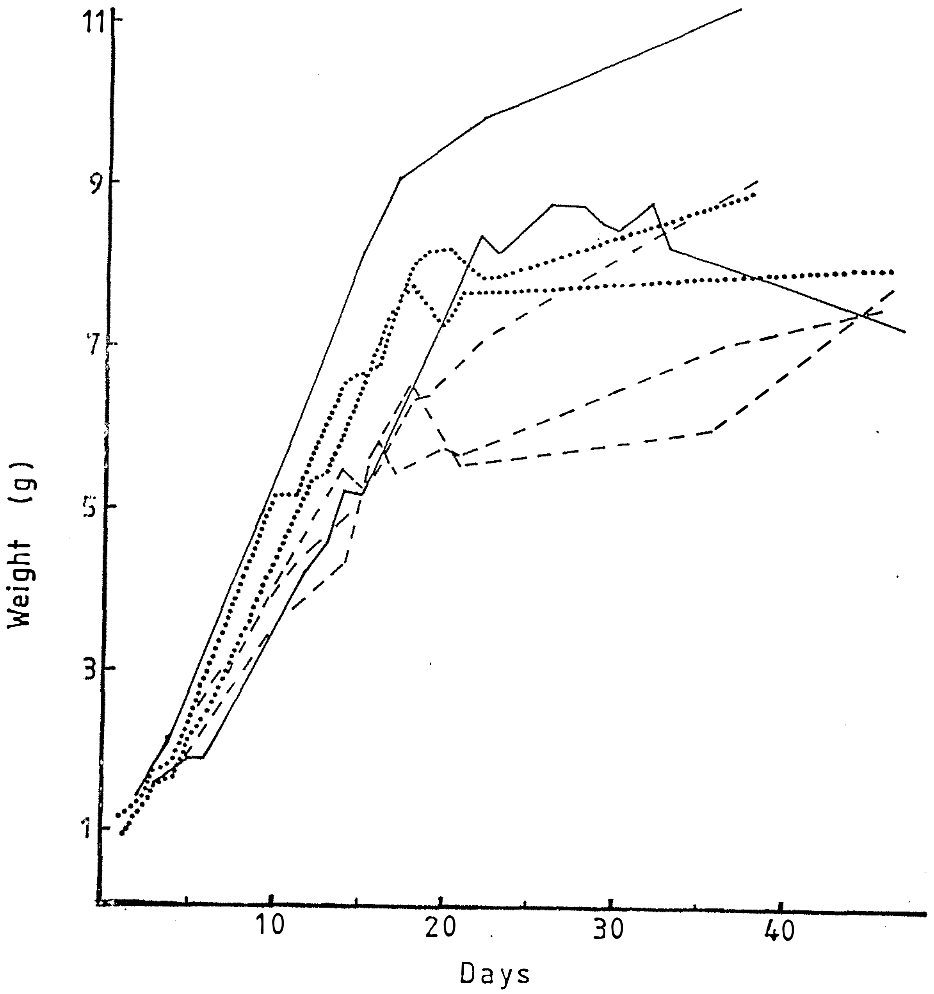


Figure 5. Weight increase in individuals from all three sized broods. Chicks from single broods are represented by continuous lines, those from broods of two, by dotted lines and those from broods of three by pecked lines.

The feeding rate per chick (1.0 feed each) in broods of three was not significantly different ($t_{27} = 1.1$) from the feeding rate (1.1 feeds each) per chick in broods of two.

During the full-day's observation on manipulated nests in 1981 a simultaneous collection of data was made on 20 undisturbed nests. These were not part of the manipulation experiment and were so high as to be out of reach. An average of 2.8 ± 0.26 feeding visits was made to these nests. This was significantly different ($t_6 = 2.15$, $P < 0.05$); to visits to the lower nests.

DISCUSSION

Despite the apparently favourable weather for gathering food, the chicks from artificially enlarged broods of three experienced significant delays in wing growth and weight increase. These results are inconclusive because survival studies following brood manipulation on the Puffin (*Fratercula artica*) (Harris 1982) and the Blue Tit (*Parus caeruleus*) (Nur 1984a,b) show that delayed fledging does not necessarily reduce the future survival of either chicks or parents, and this should be particularly true in the Apodidae where chicks are adapted to withstand long periods without food. Although post-fledging survival is higher for individuals from smaller broods than those from larger broods in species such as the Starling (*Sturnus vulgaris*) (Lack, Gibb & Owen 1957) and the Great Tit (*Parus major*) (Perrins 1965), this does not mean the same phenomenon applies to the Apodidae.

The only study on clutch-size and post-fledging survival in an apodid is that of Lack & Arn (1947), which showed post-fledging mortality in the Alpine Swift to be independent of brood size. In both the Common Swift (Weitnauer & Lack 1955, Perrins 1964) and the Alpine Swift (Lack & Arn 1947), nestling survival decreases with an increase in natural brood size.

It may be that the effect of insufficient food for breeding apodids is seen in the death of the nestlings rather than the newly fledged young. In the final analysis the extended nestling period that all apodids experience and which may be considered as a first line of defence against starvation in nestlings, appears insufficient to ensure that all chicks fledge when there is a food shortage. That assimilis chicks from artificially enlarged broods spent longer in the nest (than those from normal sized broods) in order to reach adult weight before departing the nest, may indicate why the underfed apodid nestling is more likely to die before fledging than soon after. By contrast, Starlings (Lack, Gibb & Owen 1957) and Great Tits (Perrins 1965, Moss 1972, Garnett 1981) fledged at the normal time but at lighter than normal weights, when there was a shortage of food at the time of breeding. The adaptive pressure for apodids to remain in the nest is that once they leave it they have to gather food for themselves. This is not the case in the Starling (Feare 1984), Great Tit (Gibb 1960), or even birds that are ecologically similar to swiftlets, such as swallows (Gooders 1975, Frith 1976), which after leaving the nest are still fed to some extent by their parents.

Because the 20 undisturbed high nests undoubtedly contained both one and two-chick broods their visitation rate can be compared to the combined average of 2.17 ± 0.06 visits to manipulated broods of one and two chicks. Because the difference is significant ($t_{34} = 2.36$, $P < 0.05$), the possibility arises that my presence was reducing the number of feeding visits made by parents whose chicks were being regularly handled. Such an effect would be equal on clutches of all sizes and so not affect the comparison between different sized clutches. However birds nesting at greater heights might be older, have closer feeding ranges and/or have some other benefit that will increase their capacity to provide for their brood.

CONCLUSIONS

Because parent assimilis could not hatch significantly more chicks when given a third egg, or fledge significantly more chicks when given a third chick, it is clear that the parents would not gain any advantage by producing a clutch of three themselves.

Because broods of three were fed significantly more than broods of two it appears that assimilis is not maximising its harvest of the available food supply during the breeding season. Even though the feeding rates per chick in broods of two and three were not significantly different, parents could not hatch significantly more chicks when given a third egg, or fledge significantly more chicks when given a third chick. It is clear that parents are maximising the number of fledglings they can raise. The inability to rear three chicks may mean that food boluses are smaller when the feeding rate increases thus preventing significantly more chicks fledging from the larger broods.

Although this swiftlet is not maximising its harvest of the available food supply, this does not mean that they are reducing annual production in order to optimise their life-long production. However, the effort saved by not working at its maximum food-gathering capacity may help explain why assimilis is a long lived species for its size (Tarburton 1987b).

It is concluded that whereas a shortage of food in the breeding season means some passerines will lose more recently fledged chicks than normal, the White-rumped Swiftlet (and probably other apodids in the same circumstance) will lose more nestlings than normal.

Section 3

INTRA-TROPICAL VARIATION IN CLUTCH SIZE

INTRODUCTION

It has long been held that bird species nesting in the tropical savannah will have larger clutches than the same or closely related species nesting in tropical rainforest (Moreau 1944; Ashmole 1961; Lack & Moreau 1965; Skutch 1967, 1976; Lack 1968; Ricklefs 1970, 1980,). However, it has taken some time to find an acceptable explanation for this phenomenon. While most are agreed that a large clutch is an adaptive compensation for a shortened average life expectancy, there is a variety of views as to what controls the increase in clutch size. In Lack's theory (particularly as modified by Ashmole, 1961, 1963) of maximum reproduction by maximum use of food available to breeding birds, it is suggested that high mortality during the non-breeding season in the savannah, would mean more food per pair for those that survive until the next breeding season. Having more food than those in a stable environment consequently allows for larger clutches. Alternatively, Skutch (1949, 1967) reasoned that the reproduction rate is determined by the average annual mortality rather than the other way round and that therefore, in places such as the savannah, the high mortality of the non-breeding season would increase the clutch size. Cody (1966) maintained that birds nesting in stable environments such as tropical rainforests would have little need for large clutches as part of high reproductive rates and would profit from placing more energy into *K*-selected activities that would prolong their own life. These would be activities such as predator avoidance and competition. Alternatively, birds living in savannah would do best to concentrate on *r*-selected activities such as increasing clutch size to help replace the large numbers lost each winter.

Ricklefs (1980) has also lent support to the general prediction that savannah birds will have larger clutches than close relatives in the rainforest.

He has shown that clutch size is determined by the ratio of the food supply to its demand by the population of breeding adults. As the supply depends largely upon the habitat during the breeding season and the demand is regulated by density-dependent factors acting upon the population during the non-breeding season, the population density is predicted to be regulated primarily by winter mortality and not by territorial behaviour during the breeding season as Wynne-Edwards (1962,1963) had maintained.

It has been suggested (Winkler & Walters 1983) that studies of exceptions to this widely supported trend should be especially instructive. Because *A. s. chillagoensis* from the savannah environment of Chillagoe produces a clutch of one, and *A. s. assimilis* from the rainforest environment of Fiji produces a clutch of two, it would appear that this species is an exception to the rule and therefore worthy of study.

In comparing the White-rumped Swiftlets of Fiji and Chillagoe (Queensland), several factors that have complicated other studies on clutch size are avoided. The variation in day length with a change in latitude and hence the unequal time to gather food for breeding purposes is avoided. Problems arising from the observation that some savannah birds are seed eaters, while their rainforest relatives are insect eaters (Lack & Moreau 1965), are also avoided. In fact, very few studies comparing clutch size in savannah and rainforest have used the same species.

To these advantages can be added the occurrence of a good season during the 1985/6 breeding period and a poor season during the 1986/7 breeding season at Chillagoe.

The rain that fell during December and January of the good season represented 152 per cent of the average rainfall and this correlated with a much higher density of available insects than was found in the poor season, when for the most part only 35 per cent of the average rainfall was recorded. Having a good and a poor season has allowed for a clearer assessment of the birds' ability to feed an extra chick under both abundant and scarce food supply situations.

METHODS

A sample of nests in Gordale Scar Pot (CH 187) and Guano Pot (CH 146) was used for controls and for manipulation experiments. Methods used are similar to those used in Fiji (section 1), except that because the only natural clutch is one, it was necessary to manipulate only clutches and broods of two. Both control and manipulated nests were visited six days a week between 28 November 1985 - 27 January 1986 and 2 December 1986 - 23 January 1987. Two additional experiments were run simultaneously. The first involved feeding meat based-dog food twice a day to seven manipulated twins. The amount given was as much as the chicks would take during two to three minutes. Once it was realized that the average growth rate of chicks on the supplemental food was still falling behind that of those from single-chick broods and these chicks were still falling from the nest, another strategy was tried. Insects such as winged termites collected from their mounds, and Emperor Gum Moths collected from the windows of lit rooms at night, were given to the chicks instead of the dog food. That on three occasions chicks were seen regurgitating the dog food also validated the need for a change in diet. The second additional experiment involved enlarging eight nests by gluing a length of 6 mm manila rope along the rim of the nest and to the wall with "supa glue". This made nests as deep, as long and as wide as Fijian nests which normally accommodate two chicks.

RESULTS

Hatching Success

The hatching success of 58 single-egg clutches (0.69 ± 0.06) in the good season of 1985/86 at Chillagoe was not significantly different (t_{125} = 1.05, n.s.) from the hatching success in the poor season (0.60 ± 0.06) of 1986/87 and so the results may be pooled. This average (0.64 ± 0.06) is not significantly different (t_{154} = 0.15, n.s.) from the hatching rate of single-egg clutches from Fiji (0.52 ± 0.09, n = 29). The hatching success of 10 two-egg clutches in the good season at Chillagoe was 1.8 ± 0.09. It is obvious that this is significantly better than the hatching rate for single egg clutches and is also significantly greater (t_{58} = 3.9, $P<0.001$) than the hatching rate for two-egg clutches in Fiji (1.15 ± 0.14, n = 40). However, in the poor season at Chillagoe the hatch rate of twin eggs was only 0.7 ± 0.3 (n = 6), which is significantly less (t_{26} = 3.5, $P< 0.02$) than the hatching rate in the good season and not significantly different (t_{46} = 1.36, $P> 0.1$) from the Fijian hatching rate.

Chick Growth

Figures 1 and 2 show the mean daily increase in length of wing and weight for individuals in broods of one and two during the favourable season of 1985/6. The standard errors on the wing growth curves indicate a significant difference between these broods after the eighth day. This divergence occurred earlier than in *assimilis* where it was the tenth day before it was evident that the broods with the extra (third) chick were dropping significantly behind those in normal sized broods. Average adult wing length was not reached before birds fledged though the minimum adult wing length was reached by most fledglings.

Figure 1. Mean daily increase in wing length of chicks at Chillagoe 1985/86.

The means for broods of one are represented by solid circles, broods of two by hollow circles and those of surviving chicks by addition signs. Standard errors of the means rarely extended beyond the symbols used and so are not shown.

Figure 1 Mean daily increase in wing length of chicks at Chillagoe 1985/86

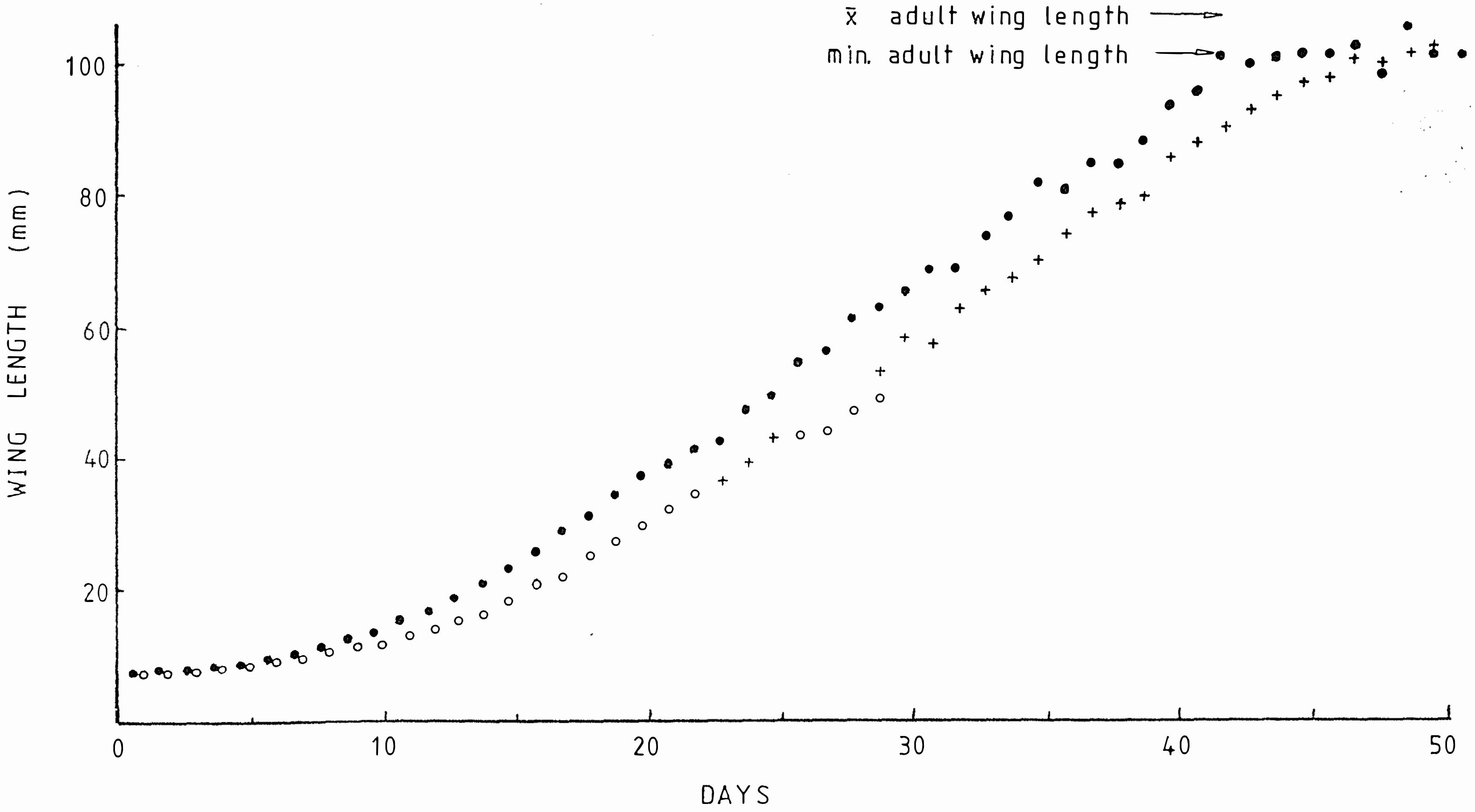
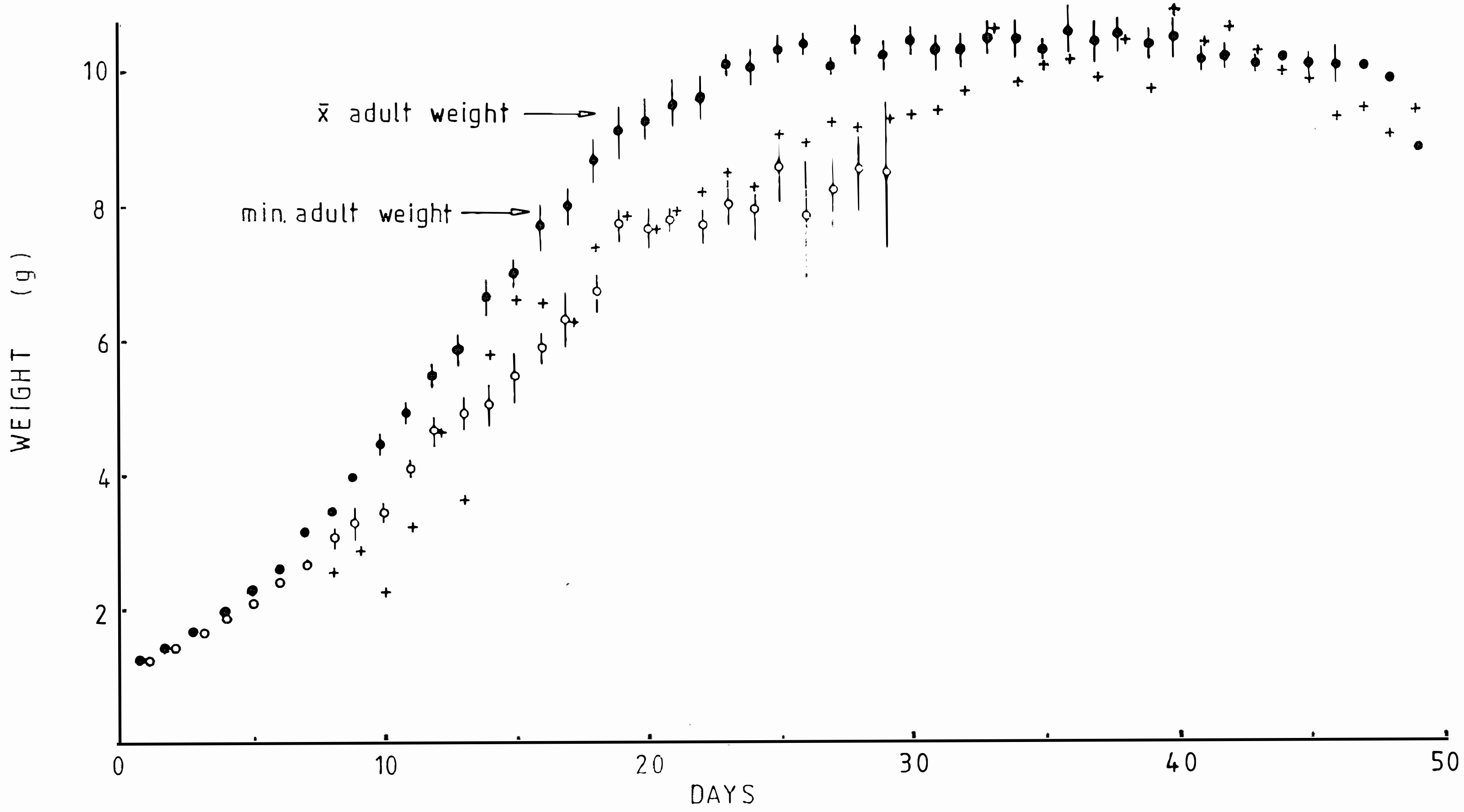


Figure 2. Mean daily increase in weight of chicks at Chillagoe 1985/86.

The means for broods of one are represented by solid circles, broods of two by hollow circles and survivors from broods of two by addition signs. Standard errors of the means (vertical lines) for chicks in broods of two do not overlap those for chicks from single broods after the fifth day.

Figure 2 Mean daily increase in weight of chicks at Chillagoe 1985/86



In the poor season of 1986/7 the significant difference between the average wing length of the two broods did not appear until the tenth day (Figure 3). Figure 3 also shows that the wings of chicks from single broods grew significantly more slowly in the poor year than in the good year. Not only did the chicks from manipulated two-chick broods grow significantly more slowly than those from single-chick broods but in all cases one died and the survivor's wings took an average of 10 days longer to reach minimum adult length.

The weight of chicks in broods of two was also significantly lower than the weight of those from single broods. On the fourth day a significant difference could be detected between the weight of those chicks in single-chick and two-chick broods during the good season. The performance in the poor season (Figure 4) was even worse for it was the sixth day before the weight of the single chicks increased significantly above that of the two-chick broods. Comparing these measurements with those for *assimilis* chicks from one and two-chick broods, which were not significantly different until the 12th day, it is clear that *chillagoensis* is much less able to cope with an extra chick. Chicks from single broods reached adult weight by the 17th day whereas surviving chicks from two-chick broods did not reach adult weight until the 23rd day. These times are respectively only two and one day earlier than those from the same sized broods in Fiji. In the good season chicks from single broods did not attain average adult weight until the 36th day. In the poor season it was the 42nd day before the average chick reached average adult weight.

The long-lasting effect of insufficient food for chicks in two-chick broods is shown by the longer time taken by them to reach maximum weight when compared with single-brood chicks. During the good season single-brood chicks took 23 days to reach an asymptote whereas the survivors of the two-chick broods took 35 days to reach the same level.

Figure 3. Mean daily increase in wing length of chicks at Chillagoe 1986/87.

The means for broods of one are represented by solid circles, broods of two by hollow circles and survivors from broods of two by addition sign. As this was the poor season and the previous season was a good one, the mean daily growth curve (using solid squares) for the preceding season has also been plotted.

Figure 3 Mean daily increase in wing length of chicks at Chillagoe 1986/87

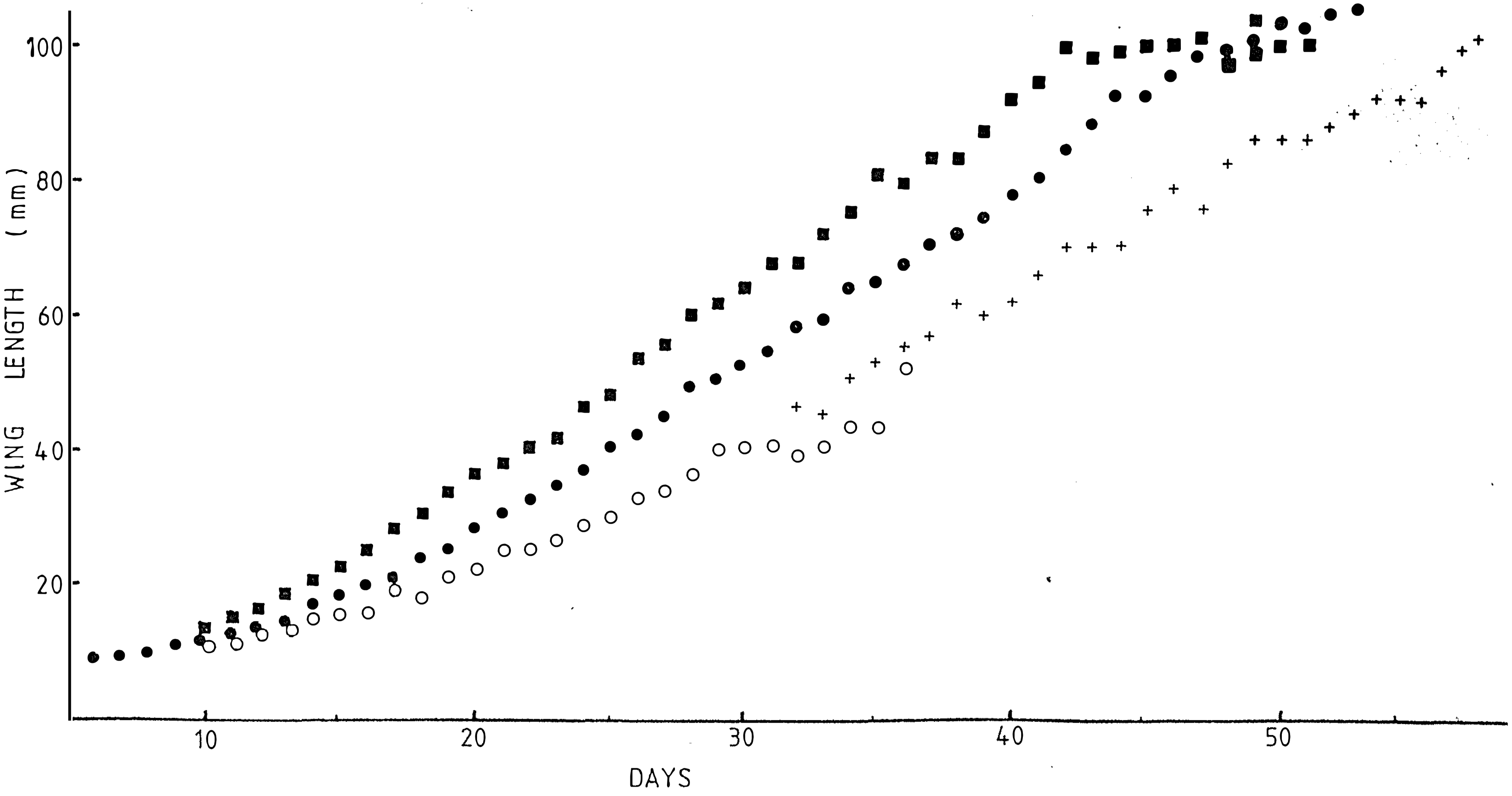
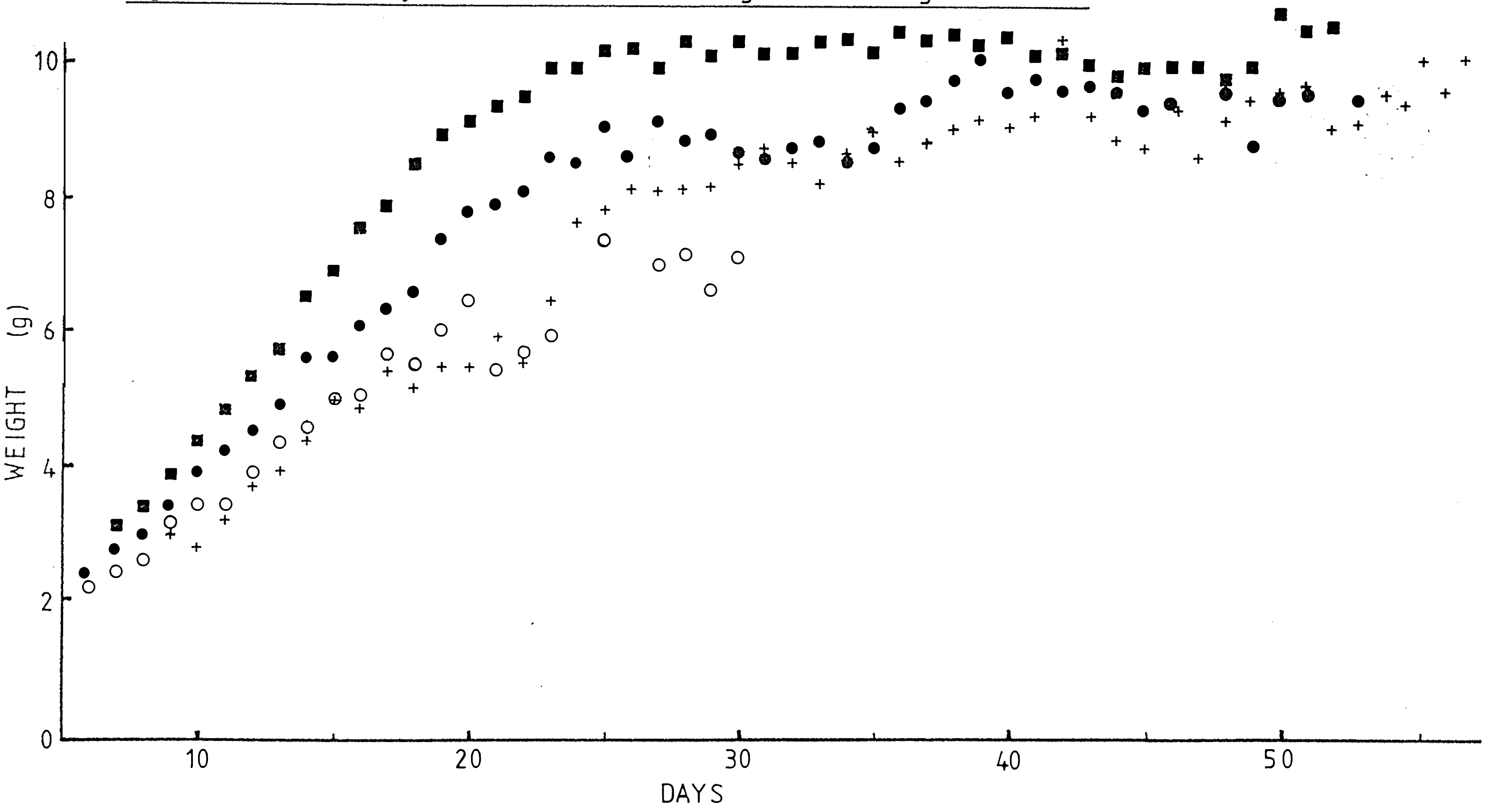


Figure 4. Mean daily increase in chick weight at Chillagoe 1986/87.

The means for broods of one are represented by solid circles, broods of two by hollow circles and survivors from broods of two by addition signs. The solid squares represent the growth curve for chicks from the same colony in the previous season which was a good season in terms of growth and survival rates.

Figure 4 Mean daily increase in chick weight at Chillagoe 1986/87



Wing growth in these two-chick brood survivors was also delayed, taking 47 days to reach 100 mm, whereas single-brood chicks took only 43 days to reach the same wing length.

By graphing the average daily weight changes in all chicks per calendar day it became apparent that at periodic intervals the average weight gain was noticeably higher than usual. These days are shown (Figure 5) to correspond with the first days on which rain fell.

Fledging Success

In the good season, chillagoensis parents with a brood of one raised 0.69 ± 0.09 chicks, which is not significantly different ($t_{38} = 0.65$, n.s.) from the 0.56 ± 0.18 chicks raised from broods of two. The fledging success with single broods was also not significantly different ($t_{54} = 1.83$, n.s.) from the 0.43 ± 0.11 chicks raised from single broods in Fiji. However, in not one case in either the poor or good year at Chillagoe were both chicks from a two-chick brood successfully fledged ($n = 34$). In the poor season chillagoensis with broods of one raised 0.31 ± 0.12 chicks, which is significantly less ($t_{45} = 2.5$, $P < 0.02$) than those raised from single-chick broods in the good season. In the poor season chillagoensis with two-chick broods raised 0.71 ± 0.11 chicks. This is significantly more ($t_{34} = 2.46$, $P < 0.02$) than those raised from single chick broods in the same season.

Only one chick fledged from each of the two-chick broods that were given supplementary food. Similarly only one chick fledged from each of the two-chick broods that were provided with enlarged nests.

Because average growth curves conceal certain characteristics of the individual growth curve and in particular the daily variation within a brood, the daily increase in weight of a selection of individuals has been plotted in Figure 6.

Figure 5. Average daily change in relative chick weights (1986/87).

The plotted indices are daily means derived from the log of the weight of a chick on one day divided by the chick's weight on the previous day. This method makes the index sensitive to the amount of food collected but less sensitive to the age of the chicks. The distinction is important as larger chicks are normally fed more food than smaller chicks and because there are more large chicks later in the season. Together these factors would distort the index if absolute weight changes were used rather than relative weight changes. The index clearly shows the above average weight increases that follow rain days (shown by arrows above the date line).

FIGURE 5 Average Daily Change in Relative Chick Weights (3 Dec. 1986 - 23 Jan. 1987)

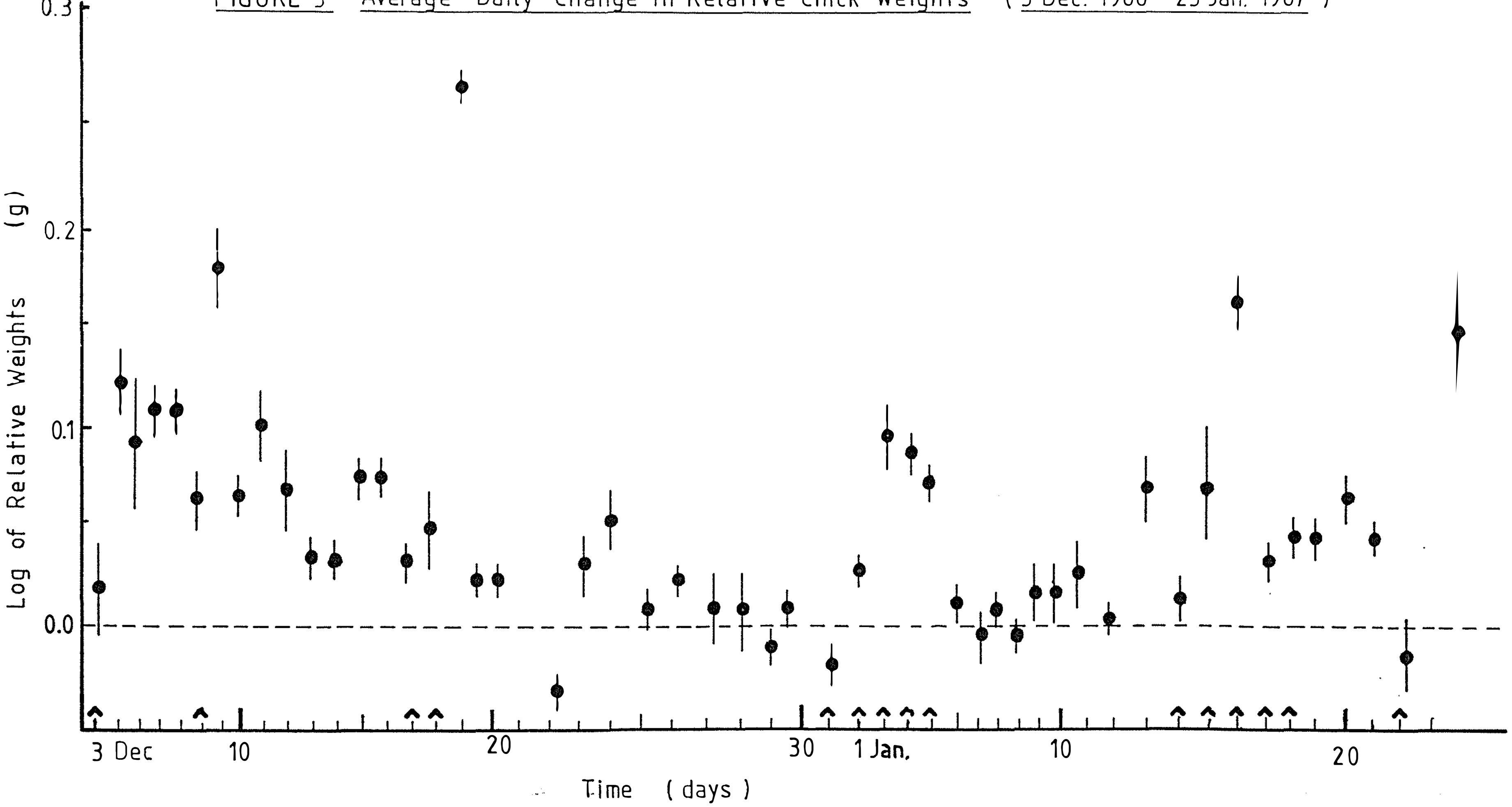


Figure 6a. Average weight increase 1986/1987.

This graph shows average weight increase for single-brood chicks of equal age during the good season of 1986/87. It is placed here for comparison with the growth curves of the individual chicks shown below.

Figure 6b. Daily weight change in two single-brood chicks.

Steps in the growth curve in response to rain (shown by arrows above the date line) are more marked in chicks when they are large.

Figure 6c. Daily weight change in a pair of manipulated chicks.
Rises in the growth curve in response to rain are not so evident as they are in chicks from single-chick broods. Growth responses to rain in the surviving chick are more pronounced.

FIGURE 6a Average Weight Increase (1986/87)

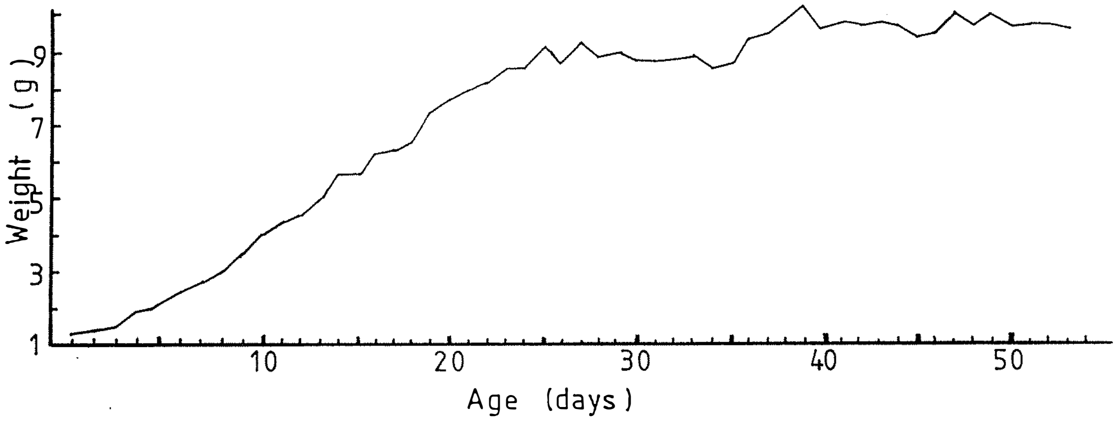


FIGURE 6b Daily Weight Change in Two Single Brood Chicks

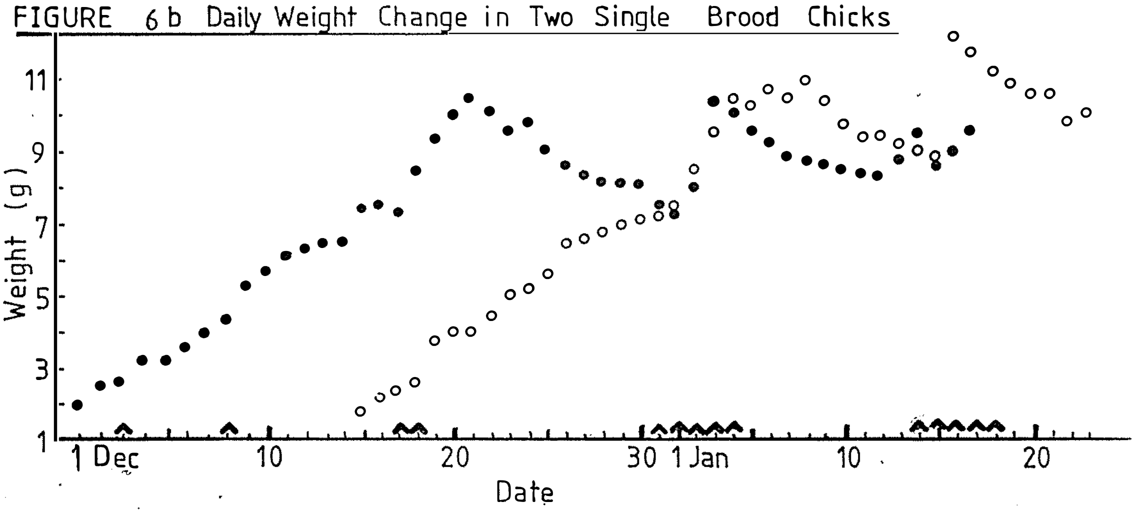
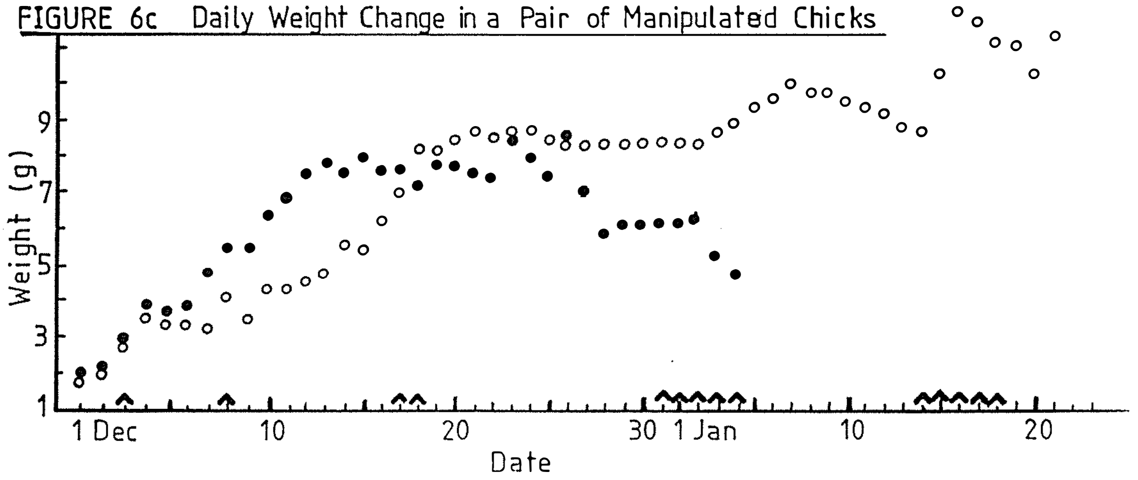


FIGURE 6c Daily Weight Change in a Pair of Manipulated Chicks



The individual growth curves of chicks from single-chick broods (Fig. 6b) show greater deviation in response to rain than the deviations for chicks from two-chick broods (Fig, 6c) when compared to the average growth curve (Fig. 6a). However, the decline in the weight of starving chicks is very clear in the individual growth curves for chicks from two-chick broods (Fig. 6c). Some chicks that died did not show weight declines because they fell from their nests.

Feeding Rate

The full day's observation on a sample of the manipulated nests of *chillagoensis* in the good season demonstrated that the average of 4.7 ± 0.67 feeding visits ($\bar{x} \pm$ SE, n = 3) per day to broods of two was not significantly greater ($t_{21} = 0.43$, n.s.) than the 5.2 ± 0.3 visits (n = 20) to broods of one. Another full day's watch on *chillagoensis* nests in the poor season similarly demonstrated that the average of 2.7 ± 0.3 visits (n = 3) to broods of two was not significantly greater ($t_9 = 0.39$, n.s.) than the 3.0 ± 0.7 visits to broods of one. However, the number of visits to broods of one in the poor season was significantly ($t_{26} = 2.9$, $P < 0.01$) less than during the good season. Similarly, the number of visits to two-chick broods in the poor season was significantly ($t_6 = 2.7$, $P < 0.05$) less than in the good season. The number of visits to single broods of *chillagoensis* in the good season was significantly greater ($t_{38} = 6.3$, $P < 0.001$) than that of feeding visits to single broods of *assimilis* (2.8 ± 0.3, n = 20). In the poor season, however, the number of visits to single broods of *chillagoensis* was not significantly greater ($t_{26} = 0.26$, n.s.) than the number of feeding visits to single broods of *assimilis*.

Available food supply

The average number of insects (95 ± 29) caught in the sweep net samples of available prey in Fiji was significantly more ($t_{32} = 3.0$, $P < 0.01$) than the average number caught in the sweep net during the good year at Chillagoe (9.7 ± 1.0). The average number of insects (5.0 ± 1.1) caught in the sweep net at Chillagoe in the poor year was significantly less ($t_{40} = 2.1$, $P < 0.05$) than that caught there in the good year.

It was significantly (Median test, $X^2_1 = 6.55$, $P < 0.05$) more likely than not, to catch more than the average number of insects caught in the sweep net when either rain fell or the irrigation sprinklers on the block adjacent to the main sample site had been running in the previous 24 hours. It was significantly (Median test, $X^2_1 = 6.55$, $P < 0.05$) more likely that swiftlets would be feeding in the vicinity of the sweep net site on those occasions when the net gathered more than the average number of insects. There was no significant correlation ($X^2_1 = 2.3$, n.s.) between whether swiftlets were feeding or not in the area adjacent to the sweep net sampling site, and whether either rain had fallen or the irrigation sprinklers had been operating in the previous 24 hours.

DISCUSSION

Despite the apparently favourable weather for gathering food in three of the four breeding seasons followed in this study, neither *chillagoensis* nor *assimilis* were able to raise significantly more chicks from artificially enlarged broods than from normal sized broods. These results mean that *chillagoensis* is not responding to the harsh extremes of the savannah climate in the way that a number of theories predict.

Rather than producing a larger clutch than *assimilis*, *chillagoensis* produces a smaller clutch.

Even the higher fledging rate of two-chick broods in the poor season at Chillagoe can be explained by the supplementary feeding given to most twins, but not to chicks in single-chick broods. This situation therefore needs to be evaluated from several theoretical standpoints.

Clutch size and 'competitive release' on islands

It is commonly stated that island species of birds have smaller clutches than their closest mainland relatives. Lack (1954) gives evidence of this for the limicoline birds from the Falkland islands compared with South America and for ducks (Lack 1968) on a number of remote islands. Cody (1966) cites evidence for smaller clutches in passerines on small oceanic islands off the coast of New Zealand. These examples are all from temperate regions, and when Klomp (1970) includes the Caribbean examples given by Cody (1966) as further examples of reduced clutches on islands, he has missed the point Cody was making. Cody (1966) was predicting, from his model relating clutch size to the birds' allocation of time and energy, that although temperate islands should have reduced clutch sizes, tropical island clutch sizes, if different at all, will be only slight and not necessarily smaller. Cody (1966, 1971) believes birds on temperate islands will have smaller clutches because they are likely to have fewer predators, a more equable climate and larger ecological niches than on the mainland. His reason for predicting little difference between island and mainland clutches in the tropics is that on tropical islands there is little difference in climatic stability and the main deciding factor will be the level of predation on the island.

On the other hand, Murphy (1968) asserts that predation has nothing to do with clutch size in the tropics and that smaller clutches have evolved on tropical islands in response to the uncertainty of survival from zygote to maturity resulting from populations at or near saturation.

The 100% increase in clutch size that assimilis has over chillagoensis is not insignificant and therefore is not supportive of Cody's prediction. This is not the only example in the Apodidae where island subspecies have larger clutches than their mainland counterparts. The African Palm Swift has a clutch of two throughout its range on the African continent but a clutch of three on Madagascar (Moreau 1941, Brooke 1971a). That this palm swift also has a more restricted breeding season on Madagascar (Rand 1936) than it does on the mainland, suggests that on islands there are more factors controlling breeding strategies such as clutch size, than have so far been accounted for. Other evidence that there are more factors is found in the variation in clutch size within a swiftlet species that is found only on the oceanic islands of Micronesia. The Caroline Swiftlet (Aerodramus inquieta) lays one egg on Kusaie and Ponape, yet two eggs on Truk Island (Brandt 1966). All three islands are in similar latitudes, have similar altitudes and area, and are similar distances from the Asian mainland.

Two of these other factors thought to contribute to the regulation of clutch size are nest size per se and predation. Both deserve a closer look as data for six subspecies of the White-rumped Swiftlet and three subspecies of the Caroline Swiftlet allow for an examination of these as possible causes in regulating clutch size.

The Theory that Nest Size Influences Clutch Size

Quite separate from the effect that food abundance may have on clutch size is the constraint of the nest itself. Snow (1978) has made the point that the structure and the size of the nest has never been properly considered as a factor that limits the maximum clutch-size of a species. He begins by taking the extreme example of the nest of the Tree Swifts (Hemiprocnidae), which can hold only one egg. He suggests that these nests point to a problematic situation rather common in tropical birds: the need for an inconspicuous and inaccessible nest.

However, it is difficult to see how the benefits of an inconspicuous nest, made so by its small size, could operate in the case of the White-rumped Swiftlet, where the darkness of the cavernicolous nest sites it chooses make the nests invisible to predators and competitors alike. Inaccessibility is achieved by the placement of the nests on the rock walls and ceilings of the caves, mostly in complete darkness. Such sites offer no restriction as there are considerable areas suitable for nesting in each of the six caves examined in Fiji and at 21 of the 22 caves examined at Chillagoe. These vacant nest sites are not confined to the entrance areas where predation (by Barn Owls (Tyto alba) in Fiji, and raptors and cats in Queensland) occasionally occurs, but between areas used for nesting.

That some of the swiftlet nests and their chicks in Guano Pot, Chillagoe, were washed off the wall by seepage from heavy rains in January 1986 suggests another reason why nests may not be built in what appear to be suitable areas of a cave. This also suggests that nest size may be affected by water. Nests becoming wet from water flowing over rock surfaces is apparently more common in the smaller coastal Queensland colonies, where Smyth et al (1980) suggest that this wetting has contributed to the failure of such vulnerable sites in wet years. While it is theoretically possible that building smaller nests would reduce the chance of the nest being on a wet portion of a cave wall, this suggestion has not been researched. The suggestion may benefit from further study as none of the five caves I visited in Fiji, where the birds raise two chicks, were seen to lose nests due to wetting and so such a pressure to reduce nest size may not exist there. That a number of Apodidae frequently nest behind waterfalls with at least one species regularly building in the spray of waterfalls without detriment to their breeding effort (Stresemann 1928, Somadikarta 1968 & Becking 1971) does not necessarily mean that this species can do likewise.

However, the second season at Chillagoe was very dry and a number of nests fell apart as a consequence, so both extremes of wet and dry can be detrimental to nest durability.

The common need for the total brood to be effectively warmed by one parent until their feathers grow may place an upper limit on brood size. However, this is not a serious restriction to the Apodidae as the young are resistant to long periods of cooling and as in all swiftlet species the White-rumped Swiftlet is confined to the tropics where cooling is less likely to cause death than in temperate regions.

Even in Blue Tits and House Sparrows the saving in metabolic energy made by individuals in larger broods than average when the environment was at 15°C was not made at 20°C (O'Connor 1975). As assimilis and chillagoensis chicks experience temperatures between 23°C - 26°C it appears that larger broods will not benefit significantly from losing less heat than smaller broods.

It may be suggested that the weight of an extra chick causes a significant increase in the number of nests that fall from the roof, but none of the nests in Fiji or Chillagoe that were given an extra chick fell.

Notwithstanding that there is no apparent environmental selection pressure that would favour swiftlets with smaller nests, there is evidence that such pressures exist for other birds. For example the hole-nesting tits lay larger clutches and raise larger broods when given larger nest cavities or larger nest boxes. Ludescher (1973) has shown this in the Marsh Tit (Parus palustris) and Willow Tit (P. montanus), while Lohrl (1973) demonstrated it in the Great Tit (P. major).

In a situation more applicable to the Swiftlets, the Barn Swallow (Hirundo rustica) has been shown to lay significantly larger clutches in larger nests (Moller 1982). So we may well ask does the size of the nest vary in the White-rumped Swiftlet?

Thirty *terraereginae* nests from the Tully Falls Cave in coastal Queensland (Pecotich 1974) averaged 56 x 45.5 mm in length and width and 3 mm in depth, giving a volume index of 7.6 cm^3. One hundred *chillagoensis* nests from Gordale Scar Pot and Guano Pot had an average size ($\bar{x} \pm$ SE) of 49.9 ± 0.49 x 42.7 ± 0.47 x 11.9 ± 0.42 mm and a volume index of 25.4 cm^3. Larger than both of these were thirty-six nests from Fiji which averaged 50.0 ± 0.7 x 49.7 ± 0.7 x 21.1 ± 1.0 with an average volume index of 52.4 cm^3. Thus the nests of *assimilis* attain a much larger volume through being much deeper than the nest of either *terraereginae* or *chillagoensis*. From this difference Moller (1982) would correctly predict that the Fijian birds would be the ones to produce the larger clutch. Why then should the Fijian birds produce the larger nests, which Moller suggests leads the laying female to respond by producing a larger clutch?

The answer may depend on the length and therefore the darkness of the caves. The three 'caves' with swiftlets at Tully Falls are very short (the longest is 21m), forcing the birds to nest close to the entrance (Pecotich 1974). It is therefore possible that predatory pressures would exceed those of the Fijian situation where the nests closest to a cave entrance are at least 30m from it. It is possible that greater predatory pressures on *terraereginae* have led to a reduction in nest size and therefore a reduction in clutch size. However, if predation (aided by twilight) was such a selective force how could it explain a clutch of one in *chillagoensis* where all but one of the 27 colonies I visited were in total darkness?

Apparent support for the predator effect on nest size comes from earlier measurements of *chillagoensis* nests which were more than 40m from the entrance and more than 5m from the floor. These nests averaged 55 x 45 x 35mm (Pecotich 1974) giving a volume index of 86.6 cm^3, which is even greater than that of Fijian nests.

In apparent contradiction to these measurements Smyth et al (1980) summarize the range of Queensland nests as 40 - 60mm left to right, 30 - 70mm front to back and 3 - 30mm deep. This clearly ignores the 35 mm deep nests at Chillagoe. The same authors however report considerable variation in nest dimensions between colonies in Queensland. In any case nest size in the White-rumped Swiftlet does not consistently correspond with clutch size.

The Theory that Relates Clutch Size to Predation

Following an experimental increase in brood size that showed predation to be a greater cause for death than starvation, Lill (1975) has suggested that nest predation (selecting for small and inconspicuous nests) rather than the ability of the female to feed the young, has been the main factor determining the natural clutch size of the White-bearded Manakin (Manacus manacus). Could it be that predation has directly reduced the clutch size of the two Queensland subspecies of the White-rumped Swiftlet? Predation may be a stronger force in Queensland, for the coastal 'caves' are shorter and therefore the nest sites are better lit, allowing predators to see the colony. There are more species of predators in Australia and so there is a greater chance that at least one is able to utilize swiftlet nest sites.

As the largest Queensland colonies only have 500 nests (Smyth et al 1980), compared to the average of 2,785 nests for my sample of five Fijian caves, it might be that predatory pressure is responsible for the small colony size in Queensland. However, there are many more species of prey in Queensland than in Fiji and the whole concept may not be transferable from manakins to swiftlets as the former are not colonial whereas swiftlets are. Colonial nesting is usually thought of as reducing the effects of predation.

My discovery of six new colonies at Chillagoe, including one (Tarby's Swiftlet Pot, CH 379) only 34 m from the previously largest Chillagoe colony (Gordale Scar Pot, CH 187) brings the number of known Chillagoe colonies to 27. This number of colonies (and there are surely more) is greater than would be found in a similar area of Fiji and so what is lost in colony size by chillagoensis is at least partly made up for in the greater number of colonies. So then the smaller colony size at Chillagoe does not necessarily indicate higher predation than in Fiji.

However, higher predatory pressure might exist in coastal Queensland, caused by a lack of long caves suitable for nesting in the dark. The consequent increase in predation when compared to that in Fiji might have reduced nest and brood size making the nest as inconspicuous as possible and the nestling period as short as possible.

Contrary to this proposal is the theoretical consideration given by Perrins (1977). He suggests that birds laying very small clutches and/or having very long incubation periods (White-rumped Swiftlets would be covered by both criteria) will be unlikely to have evolved a reduction in clutch size solely as a result of predatory pressure because the increased risk involved in laying an extra egg would be small (5% in examples used by Perrins, probably 15% in the White-rumped Swiftlet, which does not lay on consecutive days) compared with doubling the number of young raised.

The predation proposal looks less likely when one considers how little the reduction of the height of the nest cup would contribute to hiding a nest from a predator. Recent measurements in Queensland caves have shown that nest sizes vary even within a single cave (Pecotich pers. comm.).

This could mean that the published data may not give a true picture of nest size in Queensland - though the greater exposure of *terraereginae* nests to sunlight and so possibly to predation remains real. The Caroline Swiftlet (*A. inquieta*) has one subspecies (*A. i. rukensis*) that lays a clutch of two in deep, completely dark caves, and two subspecies (*A. i. inquieta*) and (*A. i. ponapensis*) that lay single-egg clutches in less dark situations (Brandt 1966). An interesting aspect is that the subspecies with the larger clutch is more often found nesting singly or in small groups as well as in large colonies. As solitary nesters are more prone to predation, the finding of the dark-nesting subspecies in solitary situations may indicate that nesting in the dark section of caves reduces predation to a very low level. One untested possibility is that the Queensland nests that are in total darkness may be larger (within the limits imposed by the materials available to build it) than those in the twilight, but if this is so why do they not have two eggs?

The theory that predation pressure can influence the size of the clutch (Snow 1978) would suggest that White-rumped Swiftlets nesting in the total darkness of a cave will suffer less predation than those nesting near the entrance or under overhanging rock. If predation had caused the White-rumped Swiftlet to alter its clutch size we would expect those subspecies that use dark caves to be consistent in producing a larger clutch than those nesting in lit locations. This, however, is not the case. *Terraereginae* generally nests in lit locations (Pecotich 1982; Smyth *et al*. 1980), while *chillagoensis* (pers. obs.) and the Samoan subspecies *spodiopygius* (Whitmee 1875), which nest in dark caves, each produce a single-egg clutch. The other subspecies known to produce two-egg clutches do so regardless of whether the nests are concealed by darkness or not. Known examples follow. On Bougainville Island *reichenowi* has been found nesting in abandoned mine shafts and under a dead leaning tree (Haddon 1981).

In Tonga, townsendi produces its two-egg clutches in sea caves where some nests are only 3m from the entrance (M. Potts pers. comm.). In New Caledonia leucopygia also appears to nest in twilight situations (Hannecart & Letocart 1980).

A non clutch-size strategy

One means that both Queensland subspecies may use to overcome a smaller clutch than that of the Fijian birds is to produce more than one clutch, apart from replacements. This suggestion is not new; Banfield (1912) suggested that the swiftlets on Dunk Island may rear four clutches in a breeding season and Smyth et al (1980) give some credence to the suggestion, adding that they have been found breeding from July to April. However, they found only four eggs in July and only one in April, compared with several hundred found in October, November and December, the three months that are clearly the peak laying and incubation period.

On average, a pair of chillagoensis take 27 days to incubate their eggs and 47 days to fledge their chicks. Thus it takes a pair of Queensland swiftlets two and a half months to raise a single brood (ignoring any time nest building may take). To raise the four broods suggested by Banfield would take 10 months without any time for building a nest. However, the summary (Smyth et al) of Queensland breeding data (which included the colony Banfield wrote about) in no way indicates that the colony is in peak breeding activity for that long. In fact the Queensland breeding season seems little longer than the Fiji season and the activity of early layers, the production of late replacement clutches and annual variation in the commencement and termination dates would better explain the extended, though light, tail-end portion of the breeding period seen in the Queensland data.

Three other factors rule against Queensland birds breeding for ten months.

Firstly, the large seasonal variation in rainfall would indicate a large variation in the abundance of aerial insect prey which would not therefore be likely to support breeding for so long if food is the limiting factor in determining clutch size. Secondly, if predation is the mechanism that holds the clutch size to one, surely breeding for ten months would make the parents more vulnerable than when raising as many in half the time. Thirdly, the smaller size of the Queensland colonies tends to indicate that they are not producing twice as many replacements as the Fiji birds.

Regulation of clutch size by stability of food supply

The generalized assumption that where a population and the environment are reasonably stable the clutch size will be at an optimum, has been extended by Hogstedt (1981). He found that the quality (largely determined by food quality and quantity) of the territory held by the Magpie (Pica pica) determined both clutch size and adult survival. He further suggested that territory quality probably explains the finding that in many passerines the most productive clutch size is larger than that which is most common (Klomp 1970).

In the Apodidae the quality of the territory is correlated with the abundance of flying arthropods, which is inversely correlated with rainfall (Lack 1956a, Hespenheide 1975 and Emlen 1982). This, in conjunction with Ricklefs' (1980) modification of Lacks hypothesis (that clutch-size is related directly to the resources available during the breeding season and inversely to the density of the population), suggests that there should be a correlation between the evenness of the year's rainfall and clutch-size. To test this I have expressed the average rainfall of the month with the lowest rainfall during the non-breeding season as a percentage of that for the month with the highest rainfall during the breeding season, for several localities where the clutch size for the White-rumped Swiftlet is known.

By following this procedure the resulting figure should be comparable between tropical localities. The data from Koronivia (near the Nasinu Caves) gives 39% while those from Tully and Chillagoe (which are near the main breeding caves of the two Australian subspecies) give 13% and 2% respectively. It may be argued that the total rainfall for the year will be more important than the variance between the wet and dry season. However, total rainfall seems less important than the seasonal variation, for, while the Tully district has a higher annual rainfall than Koronivia, Chillagoe's is much lower yet both Australian subspecies produce a clutch of one. Full climatological comparisons are given in Appendix 1A to 1D.

Rainfall data from both the dry and wet sides of New Caledonia indicate low variance (39% and 24% respectively), more like that of Fiji than Queensland. These data are consistent with my finding that low variance corresponds with the larger clutch of two.

Savannah is not the only example of a harsh climate (one having extremes) and there may be some carry-over from experimental work in other situations. For example, it has been suggested (Salomonsen 1972) that because Arctic birds sometimes do not breed at all in inclement years, laying a small clutch would be a compromise between breeding and not breeding. In short, it would be expected that Arctic birds would have smaller clutches than temperate birds. Evidence for this reversal of general predictions comes from a study on 15 passerine species (Jarvinen 1986) that breed in southern Finland as well as at a mountain site in Arctic Lapland. Only one of the species produced a larger clutch in the more extreme climate. This view had been predicted by Kendeigh's (1976) suggestion that a species devotes about the same amount of energy to reproduction regardless of where it breeds.

The idea of similar energy being put into reproduction regardless of environment contradicts the theory of r- and K-selection (MacArthur and Wilson 1967) when it is applied to the same species. The 'bet-hedging' theory (Murphy 1968, Schaffer 1974) attempts to solve the discrepancy between the r- and K-selection theory and such observations as given above. By pointing out that mortality in unstable environments is higher for juveniles than in stable environments, 'bet-hedgers' will produce smaller clutches and concentrate on raising a higher percentage than they would from a larger clutch.

Greenslade (1983) suggests that invertebrates respond to not only r- and K-selection pressures, but also to adversity or A-selection pressures, which might be found in predictably unfavourable conditions. One of the suggested responses to this third pressure is reduced fecundity.

Another response to A-selection pressures in birds of harsh environments might be to moult flight feathers while breeding during the short favourable period. Payne (1969) suggests that the general pattern of non-overlap between breeding and moulting means that similar demands on the energy requirements of breeding and moulting operate in both the tropic and temperate regions. Moulting while breeding would also tend to reduce clutch size as both activities take up large amounts of energy and nutrients. Such an effect has been suggested for Arctic birds (Haukioja 1971), and it may be that swiftlets have smaller clutches than most swifts because they moult while breeding, whereas swifts breed and moult at separate times. Data in Table 1 confirm these relationships. Swifts commence moult after laying or after the fledging of their chicks. However, because swifts are larger than swiftlets and their eggs are proportionately smaller than the adult, swifts could be expected to produce larger clutches even with partial overlap of moult and breeding.

TABLE 1 SYNCHRONIZATION OF MOULT & BREEDING

Species	Synch- ronous	Discreet	Moult after laying	Clutch size	Climate	Source/Moult
Apus apus		x		2.3	temp.	Lack & Lack 1951
Apus melba		x		3/4	temp.	Lack & Arn 1947
Apus berliozi				2.0	temp.	Brooke 1969
Apus acuticaudis			x		temp.	Brooke 1971a
Apus affinis			x	3.0	trop.	Naik *et al* 1969
Apus myoptilus			x		trop.	Prigogine 1966
Chaetura brachyura			x	3.8	trop.	Collins 1968a
Chaetura chapmani			x	2/3	trop.	Collins 1968b
Chaetura boehmi		x		3.0	trop.	Brooke 1966
Chaetura ussheri		x		4.0	trop.	Brooke 1971a
Chaetura sabini			x	2.5	trop.	Brooke 1971e
Chaetura cineriventris		x			trop.	Snow 1962
Chaetura pelagica		x		4.2	temp.	Zammuto *et al* 1979
Chaetura vauxi			x	4-6	temp.	Bent 1940
Cypseloides rutilus			x	1.9	trop.	Collins 1968a
Neafrapus cassini	some	some	some		trop.	Brooke 1971a
Aerodramus fuciphagus	x			2.0	trop.	Langham 1980
Aerodramus maximus	x			1.0	trop.	Medway 1962c
Aerodramus spodiopygius	x			1/2	trop.	Tarburton 1986b

Whether synchronous moult and breeding restricts brood size or not, that both assimilis and chillagoensis moult while breeding means that the only remaining variable between the subspecies that is likely to affect clutch size is the food supply. Because food supply varies with rainfall (Figure 5) and the rainfall total and pattern for the two regions differ so much, further consideration should be given to that aspect.

It was the generally low level and high variability in food supply rather than an inability of the parents to obtain food that restricts clutch size to one. When a pair of chillagoensis were provided with a second chick they increased the number of feeding trips to the nest on days when food was abundant. The number of extra feeds, however, was insufficient to raise a second chick, even in a good season. Food availability was too variable. The number of poor days were too frequent and even the maximum number of insects caught in the sweep net was below the average number caught in Fiji.

If the food was available parents were able to collect sufficient for two chicks. When rain ended a dry period even in the poor season, their chicks gained weight rapidly (up to one third of adult weight in one day). In the good season parents fledged their single broods in the same time as Fijian birds with single broods did. However, with the greater variability of food supply in the poor season, parents took significantly ($t_{11} = 3.2$, $P < 0.01$) longer to fledge single chicks in that season than in the good season.

The significant relationships between the abundance of flying insects and either rainfall or watering by irrigation, and between the greater likelihood of finding feeding swiftlets overhead on those occasions when the sweep net caught more than average numbers of insects, indicate the dependence of this bird's food supply upon the rainfall. Whether swiftlets were feeding overhead or not was not significantly correlated to whether rain had fallen (or the irrigation sprinklers had been used) in the previous 24 hours or not. This lack of correlation is probably due to the birds foraging in other untouched areas after several days of rain.

CONCLUSIONS

Most field data and most models concerned with the regulation of clutch size have shown or predicted that clutch size in birds inhabiting regions with climatic extremes will be larger than that of close relatives living in more uniform environments. However, the finding of this study, that chillagoensis is unable in its savannah environment to raise an artificially enlarged brood of two which assimilis normally does in the more uniform climate of Fijian rainforest, is an exception.

This section has shown a number of theories to be ineffective in explaining this phenomenon. Because enlarging nests did not increase the fledging rate I have shown that nest size is not effective in controlling clutch size in chillagoensis. Because predators cannot reach the nests of spodiopygius, the number of chicks in a nest cannot influence the rate of predation. Because chillagoensis is the mainland subspecies and yet has a smaller clutch than assimilis, which is the reverse of that predicted by the theory of "competitive release" on islands, that theory cannot explain the smaller clutch size of chillagoensis. Finally, chillagoensis does not have enough time to compensate for its smaller clutch by raising two consecutive broods in the normal manner. This is due to the shortness of the wet season, which is shown to coincide with an abundance in the food supply. In other words, food is the limiting factor that prevents chillagoensis from raising two chicks at one time. A newly discovered response to the shortness of the period when food is abundant has been evolved by chillagoensis to enable it to raise two chicks within a season. This is examined in the next section.

Further evidence that food is the limiting factor restricting the clutch size of chillagoensis to one is shown by the following.

Broods with an extra chick had significantly shorter wings than those in natural broods of one by the eighth day, while the average weight of the same chicks fell significantly behind that of the two-chick broods earlier than assimilis chicks from artificially enlarged broods. This is taken to indicate the greater difficulty chillagoensis has in collecting adequate food for two chicks.

That chillagoensis made significantly fewer feeding visits to chicks in the poor season than in the good season and that two-chick broods were not fed significantly more often than single-chick broods in either the poor or good season, indicates that this bird is struggling to adequately feed one chick in a poor season and cannot feed two chicks even in a good season. The correspondence of the days of largest weight gain to the first days of each bout of rain further demonstrates the need for frequent rains in the maintainance of high food levels. Together, these data demonstrate that a lack of available food was the major cause preventing chillagoensis from fledging significantly more chicks from manipulated two-chick broods than from natural single-chick broods.

Section 4

A Novel Strategy in Reproduction

CHICK INCUBATION

INTRODUCTION

The breeding biology of birds has been extensively studied and it would seem that every conceivable pattern for accomplishing the essential task of incubating the embryo in birds' eggs has been recorded. The basic categories are incubation by: 1) both parents, 2) one parent only, 3) other adult conspecifics, 4) other species (e.g., cuckoo), and 5) non-animal heat (e.g., megapodes)(Van Tyne & Berger 1976). All five strategies depend on nearly constant care by an adult. With the exception of minor variants within categories all five have been known for nearly 150 years (Maunder 1854, Serventy & Whittell 1962). However, there is a sixth category, incubation by nestlings. This incubation pattern was first reported only recently (Tarburton & Minot 1987) yet appears to be normal practice in chillagoensis. In this population a single egg is incubated by the adults and a second egg is incubated by the first nestling before it leaves the nest. This behaviour reduces the time between successive nestlings and the time spent incubating by adults. Alternative evolutionary strategies, such as shorter development period, are constrained by an unreliable food supply which necessitates a long nestling period.

Because assimilis produces two-egg clutches and chillagoensis was known to produce only single-egg clutches (Smyth et al 1980), it was assumed that the Queensland bird was disadvantaged.

However, when daily nest inspections designed to gather data for the manipulations of Section 2 revealed an egg in the nest of a well grown chick for the second time, I began to question my previous conclusion that in the first instance the egg was either mistakenly placed or was a case of "dumping". Within a few days a number of other cases appeared and so a search of nests in other caves was made to determine whether the phenomenon was just the result of my disturbance of the two colonies I was working each day, or whether it was a normal event in undisturbed caves. The practice was found to be common in all breeding colonies inspected.

METHODS

During the daily checks of numbered nests in Gordale Scar Pot and Guano Pot the appearance of eggs under chicks and their subsequent history was recorded. These data demonstrated that the average age of a chick at the time it was given an egg to incubate was 32 days. As the chicks' average wing length at this age was almost 70 mm, it was decided to inspect nests for eggs in other caves when the chicks had wings larger than about 70 mm. Although this method means that some chicks would have been inspected before the second egg was laid, the results still show that most birds provide their first chick with an egg to incubate.

It is possible that the second egg was not produced by the mother of the first chick. Another female may have produced the egg and "dumped" it under any chick of adequate age and not already incubating an egg. I therefore decided to take two eggs from under chicks to see if they were replaced before the minimum time taken for an egg to be replaced.

RESULTS

Although chillagoensis was unable to raise artificial broods of two, in the good season of 1985/86, 86% (n=140) of large chicks (wings greater than 70 mm) were found to be incubating an egg. The proportion of incubating chicks was reduced to 68% (n=25) in the poor season of 1986/87. Nestlings exhibited active, responsive incubation behaviour. When an egg was removed from under a nestling and placed beside it or the nestling was placed at the edge of the nest, the nestling moved to resume incubation. Thus the presence of an egg in the nest was sufficient external stimulus to release incubation behaviour in the nestling.

The timing of the laying of the second egg was such that it would not hatch before the incubating chick fledged. The mean incubation period was 26.9 ± 1.2 days (± S.D., n = 40) and the mean nestling period was 46.9 ± 2.2 days (n = 13). The mean age of a chick at the laying of a second egg was 33.4 ± 1.3 days (range 23-47 days, n = 24). When the incubating chick fledged, the adults completed any remaining incubation.

Neither of the chicks that had their eggs removed, and neither of two other chicks which lost their eggs through other means, received replacements before the minimum period (eight days) required for a brooding female to replace its own lost egg. In addition, one of the chicks to which a manipulated egg was given, was also given a second egg, presumably by its mother.

Despite the differences in incubation strategies the annual production of chillagoensis was similar to that of assimilis in good years. A breeding pair of assimilis averaged 1.1 ± 0.11 (x ± S.E., n = 39) fledged young and a breeding pair of chillagoensis averaged 0.9 ± 0.15 (n = 27) fledged young in good seasons.

PLATE 2 White-rumped Swiftlet (Aerodramus spodiopygius chillagoensis) chick incubating its parents' egg.

Chicks of both subspecies may be separated from adults by their light tipped primaries, which, until their last week in the nest, do not extend beyond the tail. However, only chillagoensis chicks will be found incubating an egg. The egg in the photo was pushed into view so that it could be photographed. The chick's eyes are shut, as is most often the case until a few days before flying.

Although the fledging rate of 0.6 chicks per poor season for chillagoensis shows that this adaptive behaviour is unable to maintain the productivity of good seasons during poor seasons, the rate would be only half this without the delayed laying of the second egg.

CONCLUSIONS

Without incubation by nestlings at least 148 days would be required to rear two nestlings - one at a time - from egg to fledging at a single nest. This assumes 27 days incubation, 47 days as a nestling and laying on the day the first chick fledges. Incubation of the second egg by the first nestling makes it possible to save more than three weeks in the time needed to rear two young. (This assumes the second egg is laid when the first chick is 23 days old and the two chicks will be fledged in 121 days).

The incubation of a second egg by the chick from the first egg reduces both the time spent incubating by adults and the interval between successive nestlings. As nestlings do not incubate in other populations of this species, where a single clutch of two is incubated by the parents, the behaviour appears to be ecologically facultative.

Section 5

DISCUSSION

The 21 species of swiftlets generally inhabit the stable environment characterized by the tropical rainforests of the Indo-Pacific region. The majority of theories concerned with factors controlling clutch size predict low annual mortality in such a uniform environment because of a reliable year-round food supply. This low mortality results in high competition for food during breeding. Thus, although high survival requires only low replacement to maintain population levels, it is thought to be mainly the high competition for food at the time of breeding (rather than the low demand for replacement) that transmits a downward pressure on clutch size. An alternative view is that long-lived (K-selected) species such as swiftlets may be maximizing their output over a lifetime, which may mean producing a smaller clutch than the maximum for which parents can find adequate food.

While in general terms swiftlets conform to the trend of tropical species laying smaller clutches (no species lays more than two eggs) than temperate relatives (which lay up to six eggs), they could be raising less than they are capable of, so in Section A of this thesis I set out to test which theoretical construct applies to the White-rumped Swiftlet nesting in tropical rainforest. I have shown that the Fijian subspecies (assimilis) could not raise one chick more than the two they normally raise, and this finding supports the general theory that clutch size in small land birds is restricted to the number of chicks that the parents can adequately feed.

The habit most swiftlets have of nesting in relatively predator free cave sites has been considered analagous to the habit of nesting in hollows.

As the latter site is seen to provide protection from predators and allows the bird to produce and raise larger broods than those nesting in open nests, this reasoning may be inappropriately applied to swiftlets. As this thesis shows, swiftlets cannot raise an extra chick, thus any advantage deriving from safe nesting sites will only operate to improve the fledging rate and reduce adult mortality during breeding rather than to increase clutch size. However, as these two advantages contribute to higher survival and thus further increase the competition for food, they themselves will restrict clutch size.

As the general theories on the regulation of clutch size predict that clutches will be larger in environments that have more extreme or unpredictable climate, it would be expected that chillagoensis has a larger clutch than assimilis. It seemed that this exception to the prediction of the theories on clutch size would be worth examining. By artificially increasing normal broods of chillagoensis to broods of two and comparing their growth with that of single-chick broods, it was learnt that in the first season not one double brood was raised to fledging. Because growth was significantly slower in the double broods it appeared that chillagoensis could not collect enough food to raise two chicks at a time. That the birds were away from the cave feeding for a shorter time each day when compared with assimilis, is taken as a consequence of smaller colony size at Chillagoe (reducing the required time to travel to feeding areas), rather than that chillagoensis is having an easier time collecting as much food as assimilis. This does not deny that chillagoensis may work less to raise its brood of one than assimilis does to raise a brood of two, for that situation could exist and chillagoensis still not be able to adequately feed two chicks, even in a good year.

In the hope of learning more about the ability of chillagoensis to raise two chicks under differing climatic conditions, the experiments were repeated in 1986/7. Fortunately this season proved to have a delayed wet season.

The effects of the late rains in the 1986/7 season at Chillagoe provided several pieces of evidence that support the theory that the birds were unable to gather enough food to raise two chicks under such conditions. Aerial insect netting indicated very low densities of available insects - with noticeable increase after the rains. Not only did the density of the available insects increase when the rains eventually arrived, but so also did the average size of the available insects. More noteworthy was the death of several chicks from the manipulated broods. This did not happen the previous year or in Fiji. When the surviving chicks experienced a weight increase of up to 36% in the 24 hours following the arrival of the first good rains it became clear that the parents had been hard pressed to adequately feed one chick and so were unable to gather sufficient food to raise two chicks.

Because one of the chicks in the artificially enlarged broods of both assimilis and chillagoensis generally died by falling from the nest, it could be reasoned that insufficient nest space was the factor restricting clutch size. Support for this view comes from the observation that the larger chick was just as likely as the smaller chick to be the one that fell from the nest. Evidence from the ecologically similar hirundines infers such a relationship. However, by watching chicks compete for food and noting how often they fell from a nest while settling down after being handled, it is likely that disturbance created by increased competition for less food (per chick) is the real cause for chick loss where additional chicks are given to either assimilis or chillagoensis.

Enlarging nine chillagoensis nests to the size of those of assimilis only to find that one of the twin chicks still died or fell out, clearly shows that nest size might at best make only a small contribution to preventing extra chicks from fledging. That five of the two-chick broods which were provided with enlarged nests were also given supplemented food without showing improved fledging success, does not refute the finding that food supply limits clutch size in assimilis and chillagoensis. It might be that the dog food used to supplement the chicks' intake was inappropriate to digestive systems adapted to an insect diet, that two feeds an hour or two apart per day were insufficient, or that the parents' saliva used to bind the bolus together may be an essential part of the chicks' diet. The latter is suggested because saliva normally helps digest food but also because swiftlet saliva has been shown to have nutrient value in its own right (Wang 1921).

A trend found in both the aerially feeding families of Apodidae and Hirundinidae is that larger species lay smaller eggs (in relation to adult size) than do smaller species. This means swiftlets lay large eggs relative to the parents size. However, variation in egg size itself does not show a significant correlation with the period of incubation. This lack of correlation seems unreasonable if one reasons that large eggs should hold warmth better than small eggs. However, that there is a significant inverse correlation between adult weight and incubation period suggests that it is larger adult size rather than larger egg size that accompanies a reduction in the incubation period. Obviously other factors may affect this general trend because assimilis, which is lighter than chillagoensis, has a shorter incubation period. This variation is best explained by the warmer temperatures in Fijian caves.

Although *assimilis* and *chillagoensis* nest at similar sites and similar distances from cave entrances, the type of limestone foundation and nest materials used are different. That either of these factors affects the incubation period is unlikely, as the egg is mostly in contact with the air or brooding bird. In addition, *assimilis* uses a wide range of nesting materials in caves away from Nasinu, and in at least one nesting site these include grasses.

It is at the nesting site where predators concentrate their efforts to catch swiftlets. All known predators (with the exception of the cat in Fiji) rely upon the concentration of breeding swiftlets to be able to defeat this fast and manoeuvrable bird. Whereas snakes and cats generally cannot reach swiftlet nests, they can reach flying individuals if there are small constrictions in the passages between the nest site and the cave entrance. Snakes have the advantage of being able to use sections of passage that are narrow or low, whether dark or light. Owls and Goshawks take swiftlets from concentrations of birds at cave entrances. Despite these losses, adult White-rumped swiftlets have a further life expectancy greater than that of many similar sized passerines. This enhanced survival probably results from predator avoidance strategies such as nesting in the dark, feeding young at infrequent intervals, leaving and entering (where possible) through different cave entrances and doing so at high speed.

While gathering food without being taken as food occupies almost the whole of a swiftlet's active day, some aspects of its diet tend to indicate that it takes whatever it can find within the range it can handle. While the birds vary their feeding areas and time of feeding in a given area, this behaviour is best interpreted as that of groups proceeding to an area known to be productive and working it if the present density is rewarding, taking all available prey until the catch rate is low and then moving to other less preferred areas.

Because flocks feed more frequently over well watered areas than over open savannah shows they do select feeding areas. Finding that food boluses of some individuals consisted almost entirely of one species indicates that their feeding group had located an area with mono-specific high density prey. That food boluses of other individuals contained up to six or seven hundred individuals of up to 83 species indicates that the group these birds fed with took whatever was available as they did not encounter any swarms or other high density concentrations of one or two species.

While this thesis shows that neither assimilis nor chillagoensis are raising less than their capacity for gathering food will allow within a given season, it also shows that increasing clutch size is not the only way to improve production within a breeding season. While chillagoensis is shown to be unable to feed two chicks this thesis has uncovered a novel strategy that allows it to match the annual production of assimilis. By laying a second egg when the first chick is 32 days old, at which stage it is probably no longer poikilothermic, both parents are able to concentrate on gathering food for the chick doing the incubating. As the second egg does not hatch before the first chick fledges the parents are able to raise two chicks per season without having to attempt that which they cannot do: that is, find enough food to raise two chicks at the one time.

There are several potential advantages to nestling incubation: 1) More chicks can be fed at the time of greatest food abundance. 2) Adults can forage continuously rather than spending half their time incubating. 3) Predation risk to adults is reduced by making fewer trips into the cave.

These potential advantages suggest broader questions about the ecological and developmental constraints that may account for incubation by nestlings.

Why do the Chillagoe birds rear two young in succession? Among birds that feed their young in the nest, clutch size is largely limited by the number of young that can be fed (Lack 1968). The feeding rate of adult swiftlets depends on the abundance of flying insects. In the rain forest near Suva (annual rainfall 3200 mm) the swiftlets have a fairly stable food supply except when it is raining. However, on the Chillagoe savannah (annual rainfall 855 mm) insects are only abundant for several days following infrequent and unpredictable rains. This climatic difference seems to account for the swiftlets' ability to rear two young simultaneously in Fiji but only one at a time at Chillagoe.

For many species of birds, clutch size has been related to annual climatic variance with larger clutches found in areas of greater variance (Ricklefs 1980). There are two possible reasons for this. Firstly, a bird population in which numbers are severely limited in the non-breeding season will experience a competitive release in the breeding season. Secondly, adults with a low probability of surviving to breed in the next year may increase their breeding effort in the current year (Williams 1966). The rainforest near Suva has a low climatic variance. The ratio of mean rainfall in the driest month to mean rainfall in the wettest month is 1:2.6. In the savannah at Chillagoe it is 1:54. However, it is in the rainforest rather than the savannah, that the swiftlets have the larger clutch. If <u>chillagoensis</u> experiences any competitive release it is insufficient to rear more than one nestling at a time. However, they do prolong their breeding effort by rearing a second offspring in succession to the first. The success of this effort rests in part on incubation by the first nestling. It is worth noting that the time taken for eggs to hatch when incubated or largely incubated by chicks, was not significantly different ($T_{38} = 0.2$, ns) to that taken when hatched by adults.

When parents incubated, incubation took 26.9 ± 0.2 days ($\bar{x}$ ± SE, n = 32) and when chicks incubated, incubation took 26.8 ± 0.5 days (n = 8).

Why don't the young swiftlets develop faster? Lack (1968) argued that evolutionary selection for the rate of nestling development is driven by the average food supply during the nestling period. There should also be an effect from the temporal variation of the food supply for nestlings. Slowly developing nestlings do not require food at a fast rate and can better withstand several days without food as compared with quickly developing young. The generality of Lack's hypothesis of average food supply has been challenged recently (Shea & Ricklefs 1985), but it seems to apply to chillagoensis especially if modified to include the effect of a variable food supply. As a group, swifts have long nestling periods for their size and during the nestling phase must cope with adverse weather which severely restricts feeding by adults. A long incubation period is linked to the overall slow rate of development for a species (Lack 1968). Thus slow growth as a nestling is a developmental constraint on the rate of growth during the incubation phase. Amongst swifts the incubation period is dependent on both the nestling period and the size of the species: incubation period (days) = 0.28 ± 0.02 nestling period (days) - 0.073 ± 0.012 female weight (grams) + 11.7 (multiple linear regression of data from 16 species of swifts - Section 1, p.28). So altering the rate of egg development independent of the rate of nestling growth, is not a feasible evolutionary strategy for swifts. Incubation by nestlings is one way around this constraint.

How do nestlings perform what is typically a breeder's behaviour and actively incubate the second egg? Work on the endocrinological basis of incubation behaviour has often stressed the importance of increased levels of progesterone and prolactin at the end of the pre-incubation stage for both male and female adult breeders (Follett 1984).

However, those hormones seem to be as much a result of incubation behaviour as they are a cause of it (Brown 1985). Apparently little is known about the levels of these hormones in nestling birds but it can be assumed that the nestling swiftlets will not have been through the same hormonal cycle as the adults. Nevertheless, young birds are known to have high levels of growth hormone during the first half of the nestling period (Bates et al 1962) and growth hormone is functionally similar to prolactin (Scanes et al 1983). It should be interesting to look at the hormone levels in incubating and non-incubating nestlings to see if there is feedback from behaviour to hormones such as might, for example, lead to increased vascularization of the skin in the ventral region (swiftlets do not develop brood patches).

Alternatively it might be that the chicks are passive in their settling over the eggs as in most nests there is little room to sit beside an egg, without moving the egg to one side. (Although I have found one adult sitting beside its egg).

Incubation by nestlings is presumably linked to the cost of incubating relative to the gain in inclusive fitness. The cost of incubation in energy terms would seem to be fairly low. Using estimates of energetic cost (Drent 1975), it should be less than 5% of the basal metabolic rate of a bird incubating a single egg at an ambient temperature of $23^{\circ}C$. Unlike an adult, a nestling has no conflicting behavioural activities. The gain is a higher probability that a sibling will be reared. However, whatever the proximate or ultimate explanation for the behaviour, the nestling is exhibiting behaviour that in a similar adult context would be totally appropriate. In this sense there is a parallel to other 'helping' behaviour such as the provisioning behaviour of communal breeders where the response to a feeding stimulus is identical for both juveniles and adults (Jamieson & Craig 1987).

Why don't more species use this incubation method? I am confident that similar behaviour will be found in other species in similar circumstances. These circumstances would probably include:

1) no post-fledging parental care,
2) a savannah habitat where limitation of food supply is indicated by one-egg clutches and where survival during the non-breeding season is low, and
3) conditions suitable to breeding which last long enough to feed two nestlings in succession.

REFERENCES

ADAMS, L.E.G. 1957. Nest Records of the Swallow. Bird Study 4:28-33.

AFFRE, G. & L. Affre. 1967. Observations automnales sur une colonie de martinets pales, (Apus pallidus), a Toulouse. Alauda 35: 108-117.

ALEXANDER, B. 1898. Further notes on the Cape Verde islands. Ibis 7: 277-285.

ALI, S. & S.D. Ripley. 1970. Handbook of the birds of India & Pakistan:4. frogmouths to pitta's. Bombay.

ARMSTRONG, J.S. 1932. Handlist to the Birds of Samoa. London. Bale sons & Danielson.

ARN-WILLI, H. 1960. Biologische studien um alpensegler. Verlag Vogt-Schild, Solothurn.

ASHMOLE, N.P. 1961. The biology of certain terns. D.Phil. thesis (Oxford): cited by Lack & Moreau 1965.

-----. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103b: 458-473.

BALDWIN, P.H. & N.K. ZACZKOWSKI. 1963. Breeding Biology of the Vaux Swift. Condor 65: 400-406.

BANFIELD, E.J. 1912. My tropical isle. London. Fisher.

BARTELS, M. 1931. Beobachtungen un brutplazen des alpenseglers. (Micropus melba melba)(L.) J. fur Ornithol. 79: 1-28.

BATES, R.W., R.A. MILLER, & M.M. GARRISON. 1962. Evidence in the hypophysectomized pigeon of a synergism among prolactin, growth hormone, thyroxine, and prednisone upon weight of the body, digestive tract, kidney and fat stores. Endocrinology 71: 345-360.

BECKING, J.H. 1971. The breeding of (Collocalia gigas). Ibis 113: 330-334.

BEHLE, W.H. 1973. Clinal variation in White-throated Swifts from Utah & the Rocky Mountain region. Auk 90: 299-306.

BELCHER, W.J. 1972. Birds of Fiji in Colour. Auckland. Collins.

BENT, A.C. 1940. Life histories of American Cuckoos, Goatsuckers, Hummingbirds & their alies. U.S. Nat. Mus. Bull. 176: 254-271.

------. 1942. Life histories of North American flycatchers, swallows, larks and their allies. U.S. Nat. Mus. Bull. 179.

BOLOTIN, E.I. & G.V. KOLONIN. 1979. New data on the fauna of ixodid ticks in the Primorsky Krai (Soviet far east). Zool. ZH. 58: 435-436.

BRANDT, J.H. 1966. Nesting notes on the Collocalia of Micronesia & Peninsular Thailand. Oologists Rec. 40: 61-68.

BROOKE, R.K. 1957. On the breeding of the White-rumped Swift (Apus caffer caffer) in Gatooma. Ostrich 28: 164-169.

———. 1963. Little & Palm Swifts breeding on man-made structures in Rhodesia. Ostrich 34: 27-35.

———. 1966. The bat-like spinetail Chaetura boehmi Schalow (Aves). Arnoldia 2: 1-18.

———. 1969. Age characters in swifts. Bull. Brit. Ornith. Club 89: 78-81.

———. 1970. Geographical variation & distribution in Apus barbatus, A.bradfieldi and A.niansae (Aves: Apodidae). Durban Mus. Novit. 8: 363-374.

———. 1971a. Breeding of Swifts in Ethiopian Africa & adjacent islands. Ostrich 42: 5-36.

———. 1971b. Taxonomic notes on some lesser known Apus swifts. Bull. Brit. Ornith. Club 91: 33-36.

———. 1971c. Geographic variation in the Alpine Swift Apus (Tachymarptis) melba (Aves: Apodidae). Durban Mus. Novit. 9: 131-143.

———. 1971d. Geographic variation in the swifts Apus horus & Apus caffer (Aves: Apodidae). Durban Mus. Novit. 9: 29-38.

———. 1971e. Taxonomic & distributional notes on the African Chaeturini. Bull. Brit. Ornith. Club 91: 76-79.

BROWN, R.E. 1985. Hormones and paternal behaviour in vertebrates. Amer. Zool. 25: 895-910.

CAM, C.R. & A.E. CAM. 1975. A report on Nankeen Kestrel banding in New South Wales. Aust. Bird Bander 13: 27-30.

CHARNOV, E.L. & J.R. KREBS. 1974. On clutch-size and fitness. Ibis 116: 217-219.

CHIH-TUNG, K. 1973. Preliminary studies on the breeding behaviour of the House Swift. Acta Zoologica Sinica 19: 293-304. Eng sum. p303-304.

CLUNIE, F. 1984. Birds of the Fiji bush. Suva. Fiji Museum.

CLYMO, R.S. 1983. A trio of troubles. Brit. Ecol. Soc. Bull. 14: 150-155.

CODY, M.L. 1966. A general theory of clutch size. Evolution 20: 174-184.

———. 1971. Ecological aspects of reproduction. Avian Biology (Ed. by D.S. Farner & J.R. King) pp 461-512. New York. Academic Press.

COLE, L.J. 1917. Determinate & indeterminate laying cycles in birds. Anat. Record 11: 504-505.

COLLINS, C.T. 1963. The "downy" nestling plumage of swifts of the genus Cypseloides. Condor 65: 324-328.

——. 1968a. The comparative biology of two species of swifts in Trinidad, West Indies. Bull. Florida State Mus. 11: 257-320.

——. 1968b. Notes on the biology of Chapman's Swift Chaetura chapmani (Aves:Apodidae). Am. Mus. Novit. 2320: 1-15.

——. 1972. Weights of some birds of north-central Venezuela. Bull. Brit. Ornith. Club. 92: 151-153.

——. 1973a. Notes on survival and band wear in White-throated Swifts. W. Bird Bander 48: 20-21.

——. 1973b. Development of temperature regulation in the House Swift. Pavo 11: 1-11.

——. & M.J. LANDY. 1968. Breeding of the Black Swift in Veracruz Mexico. Bull. Sthn. Calif. Acad. Sc. 67: 266-268.

——. & R.K. BROOKE. 1976. A review of the swifts of the genus Hirundapus (Aves:Apodidae). Contributions in science; Los Angeles County Museum 282: 1-22.

CORT, M.P. 1975. A New species of Pellonyssus, Clark & Yunker, from the Ethiopian zoogeographical region (Acarina:Dermanyssidae) Acarologia (Paris) 16: 208-213.

Crouther, M.M. 1983. Observations on White-rumped Swiftlets breeding at Finch Hatton Gorge 1981-82. Aust. Bird Watcher. 10: 1-11.

CULLEN, J.M. & ASHMOLE, N.P. 1963. Black Noddy, Anous tenuirostris on Ascension Island. Part 2. Behaviour. Ibis 103: 423-446.

DAVIS, W.B. 1937. A Vaux Swift and its young. Condor 39: 222-223.

DEMENTIEV, G.P., N.A. GLADCOV, E.S. PTUSHENKO, E.P. SPANGENBURG, & A.M. SUDILOVSKAYA. 1951. Birds of the Soviet Union, Vol. 1. (English translation 1966). Israeli program for scientific translations, Jerusalem.

DEXTER, R. 1952. Extraparental cooperation in the nesting of Chimney Swifts. Wilson Bull. 64: 133-139.

——. 1981. Nesting success of Chimney Swifts related to age & the number of adults at the nest, & subsequent fate of the visitors. J. Field Ornith. 52: 228-232.

DONNELLY, B.G. 1974. Vertical zonation of feeding swallows and swifts at Kariba, Rhodesia. Ostrich 45: 256-258.

DRENT, R. 1975. Incubation. Pages 333-420 In Avian Biology Vol. 5 (eds. Farner, D.S. & J.R. King). London. Academic Press.

DYRCZ, A. 1984. Breeding biology of the Mangrove Swallow (Tachycineta albilinea) & the Grey-breasted Martin (Progne chalybea) at Barro Colorado Island, Panama. Ibis 126: 59-66.

EMLEN, S.T. 1982. The evolution of helping 1. An ecological constraints model. Am. Nat. 119: 29-39.

FEARE, C. 1984. The starling. Oxford. Oxford Univ. Press.

FENTON, M.B. 1975. Acuity of echolocation in *Collocalia hirundinaceae* (Aves: Apodidae), with comments on the distributions of echolocating swiftlets & molossid bats. Biotropica 7: 1-7.

FILIPPOVA, N.A. & I.V. PANOVA. 1975. *Ixodes caledonicus* Nuttall 1910 (Ixodoidea: Ixodidae), a little known parasite of wild birds, from the fauna of the U.S.S.R. Parazitologiya (Leningrad) 9: 339-347.

FINLEY, W.L. & I. FINLEY. 1924. Changing habits of Vaux Swift & Western Martin. Condor 26: 6-9.

FISCHER, R.B. 1958. The breeding biology of the Chimney Swift *Chaetura pelagica* (Linnaeus). N.Y. State Mus. & Sc. Serv. Bull. 368: 1-141.

FOLLETT, B.K. 1984. Birds. Pages 283-350 *In* Marshall's physiology of reproduction, 4th Edition (ed. Lamming, G.E.). Edinburgh. Churchill Livingston.

FRITH, H.J.(Editor). 1976. Readers Digest complete book of Australian Birds. Sydney.

GADGIL, M. & W.H. BOSSERT, 1970. Life historical consequences of natural selection. Am. Nat. 104: 1-24.

GARNETT, M.C. 1981. Body size, it's heritability and influence on juvenile survival among Great Tits, (*Parus Major*). Ibis 123: 31-41.

GAUD, J. & W.T. ATYEO. 1976. Ascouracarinae, a new subfamily of Syringobiidae, feather mites. Ascarologia (Paris) 18: 143-162.

GIBB, J.A. 1960. Populations of tits and goldcrests and their food supply in pine plantations. Ibis 102: 163-208.

GIBSON, D.D. 1981. Migrant birds at Shemya Island Aleutian Islands Alaska. Condor 83: 65-77.

GIBSON-HILL, C.A. 1948. The Malayan Swiftlets. Malayan Nat. J. 3: 190-200.

GOODERS, J. 1975. The great book of birds. New York. Dial Press.

GOODMAN, D. 1974. Natural selection and a cost ceiling on reproductive effort. Am. Nat. 108: 23-31.

GREENSLADE, P.J.M. 1983. Adversity selection and the habitat templet. Am. Nat. 122: 352-365.

GRIFFIN, D.R. 1958. Listening in the dark. New York. Yale Uni. Press.

HADDON, D. 1981. Birds of the North Solomons. Wau Ecol. Inst. Wau.

HAILS, C.J. 1984. The breeding ecology of the Pacific Swallow (*Hirundo tahitica*) in Malaysia. Ibis 126: 198-211.

HANNECART, F. & Y. LETOCART. 1980. Oiseaux de Nouvelle Caledonie et des Loyautes, vol.1. Auckland. Clark & Matheson.

HARRIS, M.P. 1982. Seasonal variation in fledging weight of the Puffin *Fratercula arctica*. Ibis 124: 100-103.

HARRISSON, T. 1976. The food of *Collocalia* swiftlets (Aves:Apodidae) at Niah Great Cave in Borneo. J. Bombay Nat. Hist. Soc. 71: 376-393.

HAUKIOJA, E. 1971. Summer schedule of some subarctic passerine birds with reference to postnuptial moult. Rep. Kevo Subarctic Res. Stat. 7: 60-69.

——. & J. REPONEN. 1969. On the molt of the House Sparrow, *Passer domesticus*. Ann. Rep. Ornithol. Soc. Pori. 1968: 49-51.

HEINROTH, O. 1922. Die beziehungen zwischen vogelgewicht, eigewicht, gelegegewicht und brutdauer. J. fur Ornithologie 70: 172-285.

HESPENHEIDE, H.A. 1975. Selective predation by two swifts & a swallow in Central America. Ibis 117: 82-99.

HESSE, R. 1922. Die bedertung der tagesdauer fur die vogel. Sitzber. Nathist. Ver. Bonn for 1922-1923, pp. A 13-17.

HOGSTEDT, G. 1981. Should there be a positive or negative correlation between survival of adults in a bird population & their clutch size? Am. Nat. 118: 568-571.

HOOGSTRAAL, H., S. KADARSAN, M.N. KAISER & P.F.D. VAN DEENEN. 1974. Ornithodoros (Alectorobius) Collocaliae, new species (Ixodoidea: Argasidae), parasitizing cave swiftlets (Aves: Apodidae) in Java. Ann. Entom. Soc. Am. 67: 224-230.

JAMIESON, I.G. & J. L. CRAIG. 1987. Critique of helping behaviour in birds: departure from functional explanations. *In* Perspectives in Ethology 7: (ed. Bateson, P. & P. Klopfer) New York. Plenum.

JARVINEN, A. 1986. Clutch size of passerines in harsh environments. Oikos 46: 365-371.

JOHNSTON, D.W. 1958. Sex & age characters & salivary glands of the Chimney Swift. Condor 60: 73-83.

KAINADY, P.V.G. 1976. Presence of down-like nestling plumage in Pallid Swift (*Apus pallidus*). Bull. Basrah Nat. Hist. Mus. 3: 139-142.

KENDEIGH, S.C. 1952. Parental care and its evolution in birds. Illinois Bio. Monog. 22: 1-356.

——. 1976. Latitudinal trends in the metabolic adjustments of the house sparrow. Ecology 57: 509-519.

KLOMP, H. 1970. The determination of clutch-size in birds, A review. Ardea 58: 1-124.

KOLONIN, G.V. & E.I. BOLOTIN. 1977. Rare species of ixodid ticks in the Primorski krai. Zool. zh 56: 475-476.

KOSKIMIES, J. 1950. The life of the Swift, *Micropus apus* (L). in relation to the weather. Ann. Acad. Sci. Fenn. Ser. A. 15: 1-151.

LACK, D. 1947. The significance of clutch size. Ibis 89: 302-352, 90: 25-45.

———. 1954. The natural regulation of animal numbers. Oxford Uni. Press. London.

———. 1956a. Swifts in a tower. London. Methuen.

———. 1956b. A review of the genera & the nesting habits of swifts. Auk 73: 1-32.

———. 1956c. Further notes on the breeding biology of the swift (Apus apus) Ibis 98: 606-619.

———. 1966. Population studies of birds. Oxford. Clarendon Press.

———. 1968. Ecological adaptations for breeding in birds. London. Methuen.

———. & H. ARN 1947. Die bedeutung der gelegrobe beim alpensegler. Orn. Beob. 44: 188-210.

———. J. GIBB & D.F. OWEN. 1957. Survival in relation to brood-size in tits.
Proc. Zool. Soc. Lond. 128: 313-326.

———. & E. Lack. 1951. The breeding biology of the Swift Apus apus. Ibis 93: 501-546.

——— & ———. 1952. The breeding behaviour of the Swift. Br. Birds 45: 186-215.

———. & R.E. MOREAU, 1965. Clutch-size in tropical passerine birds of forest & savanna. L'Oiseau 35: 76-89.

———. & D.F. Owen. 1955. The food of the swift. J. Anim. Ecol. 24: 120-136.

LANGHAM, N. 1980. Breeding biology of the Edible-nest Swiftlet (Aerodramus fuciphagus). Ibis 122: 447-460.

LAYARD, E.L. 1876. Description of a new species of a flycatcher (Myiagra) from the Fijis, & some remarks on the distribution of the birds found in those islands. 3,Ibis 6: 389-394.

———. & E.L.C. Layard, 1878. Notes on the avifauna of New Caledonia. 4,Ibis, 2: 250-267.

——————, 1882. Avifauna of New Caledonia. 4,Ibis 6: 493-546.

LEACH, J.A. 1928. Notes made during a holiday trip to New Caledonia. Emu 28: 20-42.

LILL, A. 1975. The evolution of clutch size & male "chauvinism" in the White-bearded Manakin. Living Bird 13: 211-231.

LOBKO-LOBANOVSKI, M.I. 1956. On the biology of the Needle-tailed Swift in the Sakhalin. Zool. Zhurnal 35: 1586-1587.

LOHRL, H. 1973. Einflusser brutraumflache auf die gelegegrosse der kohlmeise (Parus major). J. fur Ornithologie 114: 339-347.

LUDESCHER, F.B. 1973. Sumpfmeise (*Parus palustris palustris* L.) und weidenmeise (*Parus montanus salicarius* Br.) als symatrische zwillingsarten. J. fur Ornithologie 114: 3-56.

MAA, T.C. 1980. A preliminary revision of the genus (*Myophthiria*) Rondani, (Diptera:Hippoboscidae). Revue Suisse Zool. 87: 835-861.

McARTHUR, R.H. & E.O. WILSON, 1967. The theory of island biogeography. Princeton. Princeton. Uni.Press.

MACKAY, R.D. 1968. Unusual nesting site of Glossy Swiftlets. Emu 68: 219.

McLACHLAN, G.R. & R. LIVERSIDGE. 1978. Roberts birds of South Africa. Capetown. John Voelcker.

MARCHANT, S. 1984. Nest-records of the Eastern Yellow Robin *Eopsaltria australis*. Emu 84: 167-174.

-----. & P.J. Fullagar, 1983. Nest records of the Welcome Swallow. Emu 83: 66-74.

MARSHALL, A.J. 1961. Breeding seasons and migration. *In* Biology and comparative physiology of birds Vol.2. Ed. Marshall, A.J. New York. Academic Press.

MAUNDER, S. 1854. The treasury of natural history. London. Longman, Brown & Green.

MAYR, E. 1937. Notes on New Guinea birds. I (*Collocalia*). Am. Mus. Novit. 915: 1-19.

-----. E. 1945. Birds of the south-west Pacific. Hertsfordshire. Wheldon & Wesley.

MEDWAY, L. 1962a. The swiftlets (*Collocalia*) of Niah Cave, Sarawak part 1. Breeding Biology. Ibis 104: 45-66.

-----. 1962b. The Swiftlets (*Collocalia*) of Niah Cave, Sarawak part 2. Ecology & the regulation of breeding. Ibis 104: 228-245.

-----. 1962c. The relation between the reproductive cycle, moult & changes in the sublingual salivary glands of the swiftlet (*Collocalia maxima*) Hume. Proc. Zool. Soc. Lon. 138: 305-315.

-----. 1962d. The swiftlets (*Collocalia*) of Java & their relationships. J. Bombay Nat. Hist. Soc. 59: 146-153.

-----. 1966. Field characters as a guide to the specific relations of swiftlets. Proc. Linn. Soc. Lon. 177: 151-177.

-----. 1967. The function of echonavigation among swiftlets. Anim. Behav. 15: 416-420.

-----. & J.D. Pye. 1977. Echolocation & the systematics of swiftlets. *in* Stonehouse, B. & C. Perrins, Evolutionary Ecology. London. Macmillan.

MERCER, R. 1966. A field guide to Fiji birds. Suva. Fiji Museum.

MICHAEL, C.M. 1927. Black Swift nesting in Yosemite National Park. Condor 29: 89-97.

MILLER, A.H. 1961. Molt cycles in equatorial Andean sparrows. Condor 63: 143-161.

MOLLER, A.P. 1982. Clutch size in relation to nest size in the swallow (*Hirundo rustica*). Ibis 124: 339-343.

MOREAU, R.E. 1941. A contribution to the breeding biology of the Palm-swift *Cypselus parvus*. J. E. Afr. & Uganda Nat. Hist. Soc. 15: 154-170.

——. 1942a. (*Colletoptera affinis*) at the nest. Ostrich 13: 137-147.

——. 1942b. The breeding biology of (*Micropus caffer streubelii*), the White-rumped Swift. Ibis 84: 27-49.

——. 1944. Clutch size: a comparative study with special reference to African birds. Ibis 86: 286-347.

MOREL, M. 1967. Les Oiseaux Tropicaux Elevent-ils Autant de Jeunes Qu'ils Peuvent en Nourrir? Le cas de *Lagoostica senegala*. La Terre et la Vie 21: 77-82.

MORGAN, R.W. 1897. On the nidification of certain South-Indian birds. Ibis 5: 313-323.

MOSS, D. 1972. A statistical analysis of clutch size in the Great Tit *Parus major* L. Unpublished M.Sc. thesis, Univ. of Oxford.

MURPHY, G.I. 1968. Pattern in life history & the environment. Am. Nat. 102: 390-404.

NAIK, R.M. & S. NAIK. 1965. Studies on the House Swift, *Apus affinis* (G.E. Gray) 5. Moult cycle in the adults. Pavo 3: 96-120.

——, & A. RAZACK. 1967. Studies on the House Swift, *Apus affinis* (G.E.Gray) 8. Breeding seasons and their regulation. Pavo 5: 75-96.

——, & N. SHIVANARAYAN. 1969. Moult of the primary feathers in the House Swift, *Apus affinis*. Pavo 7: 19-42.

NEUFELDT, I. & A.I. IVANOV. 1960. Some notes on the biology of the Needle-tailed Swift in Siberia. Brit. Birds 53: 431-433.

NOVICK, A. 1959. Acoustic orientation in the cave swiftlet. Bio. Bull. 117: 497-503.

NUR, N. 1984a. The consequences of brood size for breeding Blue Tits I. Adult survival, weight change & the cost of reproduction. J. Anim. Ecol. 53: 479-496.

——. 1984b. The consequences of brood size for breeding Blue Tits II. Nestling weight, offspring survival & optimal brood size. J. Anim. Ecol. 53: 497-517.

OBERHOLSER, H.C. 1906. A monograph of the genus *Collocalia*. Proc. Acad. Nat. Sc. Phil. 53: 177-212.

O'CONNOR, R.J. 1975. The influence of brood size upon metabolic rate and body temperature in nestling Blue tits Parus caeruleus and House Sparrows Passer domesticus. J. Zool. Lond. 175: 391-403.

PARKER, S. 1967. Some eggs from the New Hebrides, south-west Pacific. Bull. Brit. Ornith. Club 87: 90-92.

PELLANTOVA, J. 1975. The course of breeding of the swift (Apus apus). Zool. Listy. 24: 249-262.

PALOMEQUE, J., J.D. RODRIGUEZ, J.D. PALACIOS & J.LANAS. 1980. Blood respiratory properties of swifts. Comp. Biochem. & Physiol. 67a: 91-95.

PAYNE, R.B. 1969. Overlap of breeding & moulting schedules in a collection of African birds. Condor 71: 140-145.

PECOTICH, L. 1974. Grey Swiftlets in the Tully River Gorge & Chillagoe Caves. Sunbird 5: 16-21.

——. 1982. Speciation of the Grey Swiftlet Aerodramus spodiopygius. Tower Karst 4: 53-57.

PERRINS, C.M. 1964. Survival of young swifts in relation to brood size. Nature 201: 1147-1148.

——. 1965. Population fluctuations & clutch-size in the Great Tit (Parus major) L. J. Anim. Ecol. 34: 601-647.

——. 1977. The role of predation in the evolution of clutch size. Chapter 16 In Stonehouse,B. & C.M.Perrins, Evolutionary Ecology. London. Macmillan.

PIANKA, E.A. & W.S. PARKER, 1975. Age specific reproductive tactics. Am. Nat. 109: 453-464.

PITELKA, F.A. 1958. Timing of molt in Steller Jays of the Queen Charlotte Islands, British Colombia. Condor 60: 38-49.

PRIGOGINE, A. 1966. Note on Chapin's Swift. Bull. Brit. Ornith. Club. 86:1-5.

RAND, A.L. 1936. The distribution and habits of Madagascar birds. Bull. Amer. Mus. Nat. Hist. 72: 143-499.

RATHBUN, S.F. 1925. The Black Swift & it's habits. Auk 42: 497-516.

RICKLEFS, R.F. 1970. Clutch size in birds: outcome of opposing predator & prey adaptations. Science 168: 599-600.

——. 1980. Geographic variation in clutch size among passerine birds: Ashmoles hypothesis. Auk 97: 38-49.

ROBERTS, J.R., D.M. SMYTH & A.V. SPAIN. 1976. Preliminary studies on acoustic orientation in Collocalia spodiopygia. Search 7: 97-98.

ROWLEY, J.S. & R.T. ORR, 1962. The nesting of the White-naped Swift. Condor 64: 361-367.

SALOMONSEN, F. 1972. Zoogeographical and ecological problems in Arctic birds. Proc. XV Int. Orn. Congr.: 25-77.

SCANES, C.G., T.J. LAUTERIO, & F.C. BUONOMO. 1983. Annual, developmental and diurnal cycles of pituitary hormone secretion. Pages 307-326 In Avian endocrinology (ed. Mikami, S., K. Homma & M. Wada). Tokyo. Japan Scientific Societies Press / Berlin. Springer-verlag.

SCHAFFER, W.M. 1974. Optimal reproductive effort in fluctuating environments. Am. Nat. 108: 783-790.

SCHMIDT, R.K. 1965. Brutbiologie des weissburzelseglers (Apus caffer caffer)(Lichtenstein) auf der kaphalbinsel. J. fur Ornith. 106: 295-306.

SCHONWETTER, M. 1970. Handbuch der Oologie. Akademie-Verlag. Berlin.

SERVENTY, D.L. & H.M. Whittell. 1962. Birds of Western Australia. Perth. Paterson Brokensha.

SHAW, T.H. 1936. Birds of Hopei Province (2 vols.) Peking. Fan Memorial Institute of Biology.

SHEA, R.E. & R.E. RICKLEFS, 1985. An experimental test of the idea that food supply limits growth rate in a tropical pelagic seabird. American Naturalist 126: 116-122.

SICK, H. 1948. The nesting of Reinarda squamata (Cassin). Auk 65: 168-174.

——. 1959. Notes on the biology of two Brazilian Swifts, Chaetura andrei & Chaetura cinereiventris. Auk 76: 471-477.

SKUTCH, A.F. 1949. Do tropical birds rear as many young as they can nourish. Ibis 91: 430-455.

——. 1967. Adaptive limitation of the reproductive rate of birds. Ibis 109: 579-599.

——. 1976. Parent birds and their young. Texas. Univ. of Texas.

SMEDLEY, D.I. 1977. Sexing of Lewin's Honeyeaters. Corella 1: 34.

SMYTH, D.M., L. PECOTICH, & J.R. ROBERTS. 1980. Notes on the distribution & breeding of the Grey Swiftlet, (Aerodramus spodiopygius). Sunbird 11: 1-19.

SNOW, D.W. 1962. Notes on the biology of some Trinidad Swifts. Zoologica 47: 129-139.

——. 1978. The nest as a factor determining clutch-size in tropical birds. J. fur Ornith. 119: 227-230.

SOMADIKARTA, S. 1968. The Giant Swiftlet, (Collocalia gigas), Hartert & Burler. Auk 85: 549-559.

STRESEMANN, E. 1928. Sauropsida:Aves. in W. KUKENTHAL (Ed.), Handbuch der Zoologie, 7. Halfte, Lieferung 4. Berlin: Walter de Gruyter.

——, & V. STRESEMANN. 1966. Die mauser der vogel. J. fur Ornithologie. 107: 1-445.

SUTHERS, R.A. & D.H. HECTOR. 1982. Mechanisms for the production of echolocating clicks by the Grey Swiftlet, (Collocalia spodiopygia). J. Comp. Physiol.; a sens Neural Behav. Physiol. 148: 457-470.

——— & ——— 1985. Production of sonar clicks by Grey Swiftlets. Tower Karst 5: 49-53.

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

-----, 1986b. A comparison of the flight behaviour of the White-rumped Swiftlet and the Welcome Swallow. Bird Behaviour 6: 72-84.

-----, 1986c. Breeding of the White-rumped Swiftlet in Fiji. Emu 86: 214-227.

-----, 1987a. An experimental manipulation of clutch and brood size of White-rumped Swiftlets Aerodramus spodiopygius of Fiji. Ibis 129: 107-114.

-----, 1987b. The population status, longevity & mortality of the White-rumped Swiftlet in Fiji. Corella 11:

-----, & E.O. Minot 1987. A novel strategy of reproduction in birds. Animal Behaviour in press.

TAYLOR, J.S. 1942. Notes on the martins, swallows & swifts: Graaff-Reinet. Ostrich 13: 148-156.

TOVORNIK, D. & V. CERNY, 1974. Finding of Haemaphysalis erinacei erinacei Pavesi 1884 on birds in Yugoslavia. Folia Parasitol (Prague) 21: 282.

VAN TYNE, J. & A.J. BERGER. 1976. Fundamentals of Ornithology. New york. John Wiley.

VUILLEUMIER, F. & M. GOCHFELD. 1976. Notes sur L'avifauna de Novelle-Caledonie. Alauda 44: 237-273.

VINCENT, E. 1963. Acoustic signals for auto-information or echolocation. In BUSNEL, 1963. Acoustic behaviour of animals.

WAGNER, H.O. 1957. Variation in clutch size at different latitudes. Auk 74 243-250.

WALTERS, M. 1980. The complete birds of the world. Sydney. Reed.

WANG, C.C. 1921. The composition of Chinese edible birds nests and the nature of their proteins. J. Bio. Chem. 49: 429-439.

WATLING, D. 1982 Birds of Fiji, Tonga & Samoa. Wellington. Millwood.

WEITNAUER, E. 1947. Am neste des mauerseglers, (Apus apus apus)(L.). Ornith. Beobachter 44: 133-182.

-----, & D. Lack. 1955. Daten zur fortpflanzungsbiolog des mauerseglers (Apus apus) in Oltingen und Oxford. Ornith. Beobachter 52: 137-141.

WELLS, D.R. 1975. The Moss Swiftlet (Collocalia vanikorensis) Quoy & Gaimard in Sumatra. Ardea 63: 148-151.

WELTY, J.C. 1975. The life of birds. Philadelphia. Saunders.

WHITMEE, S.J. 1875. List of Samoan birds, with notes on their habits & c. Ibis 5: 436-447.

WILLIAMS, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Nat. 100: 687-692.

WINKLER, D.W. & J.R. WALTERS. 1983. The determination of clutch size in precocial birds. Current Ornithology 1: 33-68.

WYNNE-EDWARDS, V.C. 1962. Animal dispersion in relation to social behaviour. London. Oliver & Boyd.

——. 1963. Intergroup selection in the evolution of social systems. Nature 200: 623-626.

YUREN, G. & BENXIANG, Z. 1985. The breeding behaviour and population dynamics of the large White-rumped Swift *Apus pacificus pacificus* (Latham) at Cheniushan Island in the Yellow Sea. Acta Zool. Sinica 31: 84-92.

ZAMMUTO, R.M. & E.C. FRANKS. 1979. Trapping flocks of Chimney Swifts in Illinois. Bird Banding 50: 201-209.

-----, & -----, & R.P. PRESTON. 1981. Factors associated with the interval between feeding visits in brood-rearing Chimney Swifts (*Chaetura pelagica*). J. Field Ornith. 52: 134-139.

Appendix 1A.

CLIMATOLOGICAL SUMMARY TABLE FOR KORONIVIA, FIJI AND OTHER BREEDING LOCATIONS

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
RAINFALL (mm)													
1950-1979	367	300	399	359	239	183	171	154	204	221	305	296	3198
1981	508	381	163	464	228	78	25	212	125	169	555	135	3043
1983	267	321	305	135	121	85	101	289	86	187	212	330	2440
HOURS / SUN													
1971-1979	171	161	149	143	135	127	124	145	128	157	149	167	1756
1981												197	
1983												142	
AV.TEMP.(°C)													
1965-1979	26.5	26.5	26.3	25.4	24.3	23.8	22.6	22.8	23.1	24.0	24.8	25.7	24.7
RAINFALL at TULLY (mm)													
Average	671	790	827	515	345	217	157	133	125	106	159	276	4321
RAINFALL at CHILLAGOE (mm)													
Average	217	216	147	30	14	10	4	4	6	14	55	138	855
RAINFALL at NOUMEA (mm)													
Average	114	108	119	115	94	114	83	70	47	47	47	64	1020
RAINFALL at POINDIMIE (mm)													
Average	378	307	398	245	157	238	171	96	102	99	180	172	2542

Appendix 1B

DAILY RAINFALL DATA FOR THE PERIOD OF THE MANIPULATION EXPERIMENTS

KORONIVIA, FIJI.

		1981 Rainfall (mm)	1983 Rainfall (mm)
November	25	74.2	
	26	24.4	
	27	1.8	
	28	86.5	
	29	2.8	
	30	-	
December	1	0.4	90.8
	2	-	-
	3	1.8	12.7
	4	3.7	16.0
	5	4.0	-
	6	6.8	0.5
	7	13.2	14.5
	8	-	23.8
	9	-	-
	10	-	-
	11	1.2	-
	12	-	0.7
	13	12.5	0.3
	14	-	-
	15	-	1.3
	16	4.1	15.6
	17	4.9	3.8
	18	24.4	-
	19	5.4	68.2
	20	7.5	15.7
	21	7.9	3.8
	22	9.9	9.5
	23	-	0.3
	24	3.5	0.5
	25	5.4	2.3
	26	2.0	0.5
	27	-	0.5
	28	11.3	-
	29	0.4	-
	30	-	20.4
	31	3.4	17.0
Dec. Total		135.0	330.0

Appendix 1C.
CLIMATOLOGICAL SUMMARY TABLE FOR CHILLAGOE, QLD.

RAINFALL (mm)

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
1902-1986	217	216	147	30	14	10	4	4	6	14	55	138	855
S.D.	116	117	106	43	27	19	10	11	15	18	48	100	276
1902	179	133	6	4	0	0	0	0	0	0	6	76	404
1903	319	117	352	118	10	31	0	3	0	14	80	410	1453
1904	206	276	180	84	0	0	0	0	14	62	134	160	1116
1905	463	82	15	13	50	0	0	0	0	0	41	0	663
1906	168	222	80	13	21	0	0	0	6	10	174	269	961
1907	113	196	71	0	24	45	0	0	0	34	35	154	672
1908	174	169	294	41	11	1	0	0	3	48	2	10	753
1909	82	79	284	0	0	43	3	0	14	23	67	122	715
1910	302	370	122	0	0	6	1	0	37	28	20	366	1252
1911	117	253	129	279	0	0	0	0	0	20	35	112	945
1912	124	51	154	1	3	24	0	0	1	25	9	90	482
1913	402	253	252	105	31	7	0	0	0	3	1	229	1281
1914	136	201	268	40	21	30	0	0	0	0	24	78	799
1915	72	154	41	0	3	0	0	0	5	0	35	122	432
1916	189	260	207	54	7	3	8	0	0	14	75	173	989
1917	278	329	154	17	48	0	0	1	4	25	86	150	1091
1918	244	181	90	26	0	0	0	0	0	0	50	122	713
1919	127	124	188	12	9	0	0	0	0	0	4	55	519
1920	427	103	69	3	71	10	5	3	0	0	7	107	806
1921	115	170	233	18	7	5	17	0	5	25	8	326	930
1922	181	414	84	4	1	2	8	0	0	10	37	162	904
1923	129	3	72	15	0	7	0	5	0	0	0	86	316
1924	138	258	151	52	0	3	0	18	5	25	93	123	868
1925	273	214	257	5	2	0	2	0	0	1	19	85	857
1926	171	19	41	7	14	2	0	0	12	0	3	201	470
1927	184	345	145	16	0	64	35	0	0	0	8	110	906
1928	97	106	54	6	0	0	0	0	0	12	38	196	508
1929	287	352	153	63	0	0	0	0	0	0	84	31	969
1930	465	149	48	29	136	0	0	0	0	41	70	46	983
1931	242	110	9	15	0	0	0	0	1	1	38	223	639
1932	312	94	52	0	9	0	0	0	0	0	0	394	861
1933	163	188	61	0	0	14	19	42	14	0	139	149	789
1934	239	241	45	32	18	52	14	14	4	6	157	18	839
1935	195	59	55	29	63	5	3	0	0	12	5	23	448
1936	207	245	270	55	0	28	1	0	3	49	27	241	1125
1937	140	121	293	0	12	0	6	0	0	1	54	52	681
1938	248	215	20	0	0	1	61	0	0	17	29	27	618
1939	240	239	161	39	2	60	0	1	0	19	115	110	985
1940	176	392	114	17	4	3	0	0	0	0	98	20	824
1941	263	161	279	14	19	6	1	0	0	0	51	51	844
1942	25	353	22	14	2	9	27	3	8	0	47	360	868
1943	136	439	38	0	0	12	0	0	19	79	11	90	822
1944	163	394	173	0	0	10	32	8	0	16	33	417	1245
1945	100	241	299	73	0	0	0	0	0	9	56	78	857
1946	407	196	81	14	0	0	2	0	0	0	48	145	894
1947	138	239	124	0	0	5	0	16	50	0	55	163	789
1948	122	101	101	5	2	3	4	0	0	1	44	58	440
1949	182	334	278	24	0	0	0	0	2	48	80	76	1023
1950	104	210	155	117	0	95	29	0	0	10	155	358	1234

CLIMATOLOGICAL SUMMARY TABLE FOR CHILLAGOE, QLD. cont.

RAINFALL (mm)

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
1951	415	251	188	0	0	0	1	0	0	15	50	41	960
1952	85	82	17	56	0	23	0	0	0	51	66	112	492
1953	153	261	27	0	0	0	0	26	1	0	12	105	587
1954	291	456	74	164	3	4	0	0	0	33	25	26	1078
1955	240	322	311	15	17	2	4	0	4	2	16	45	976
1956	262	568	257	36	112	50	3	12	43	3	74	376	1796
1957	290	176	162	44	0	1	0	0	0	32	63	86	853
1958	334	306	116	45	2	0	0	0	0	3	12	68	886
1959	299	115	154	20	18	15	1	0	0	0	41	291	953
1960	144	169	33	1	60	1	0	0	0	9	75	90	581
1961	110	109	117	6	3	0	0	1	1	3	52	92	492
1962	251	264	27	27	25	1	1	0	9	3	141	127	875
1963	214	374	79	17	0	1	0	0	0	0	16	87	787
1964	200	127	156	3	11	0	3	0	0	57	178	197	932
1965	137	49	160	24	0	25	0	0	2	0	4	90	491
1966	233	123	18	5	0	0	0	0	0	4	71	1	455
1967	81	251	371	14	2	93	0	0	0	3	28	158	1000
1968	276	261	130	3	14	0	10	0	9	9	37	146	894
1969	148	78	105	4	3	14	3	0	0	9	10	171	544
1970	134	90	66	8	0	0	0	82	0	14	102	219	715
1971	206	416	165	41	0	24	0	22	4	15	53	30	974
1972	232	322	389	15	11	8	0	0	1	0	28	44	1050
1973	91	409	158	34	7	2	0	20	37	12	238	177	1185
1974	667	380	425	1	5	0	0	18	1	0	29	153	1678
1975	262	114	214	17	0	6	0	5	102	1	148	180	1110
1976	207	238	426	26	2	1	0	0	0	31	106	188	1126
1977	66	353	270	12	100	0	0	0	0	0	74	163	1037
1978	77	126	19	80	1	0	30	1	0	0	47	153	534
1979	472	261	327	36	0	8	5	0	0	15	7	45	1176
1980	294	185	124	8	6	4	0	0	0	30	54	101	808
1981	459	355	46	27	79	3	0	0	3	7	52	179	1212
1982	240	40	130	34	3	3	0	1	2	0	39	131	617
1983	77	65	143	94	87	15	0	8	27	37	89	73	716
1984	385	217	72	8	3	0	0	0	5	19	20	100	828
1985	134	114	173	117	12	0	0	0	2	29	124	219	923
1986	320	179	58	40	2	0	0	12	35	48	11	48	753

Appendix 1D

DAILY RAINFALL 1985
CHILLAGOE (mm)

DATE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1			8.0									
2	1.8		36.8									
3				7.4								
4		3.8	3.0									
5	4.0			14.2								28.0
6			2.0	19.0						*		2.0
7				16.6								
8		6.0	2.6									
9		1.0							2.0			
10												129.0
11			1.6									11.2
12			3.8									
13			10.0									
14		18.4									2.4	
15											23.6	
16	5.6											
17			64.0							1.6		
18												10.0
19	2.4		8.8								4.6	
20												
21	4.0			3.0						4.0	2.6	
22	108.4	5.4		30.8								
23	7.6			26.0	3.8							
24					1.6						33.0	2.8
25		4.6	30.0		0.8						9.0	
26		74.8	0.1							21.0		4.0
27					5.6						43.0	1.6
28												6.0
29			1.6									24.0
30										2.0		
31												0.6
TOTAL	134	114	173	117	12	NIL	NIL	NIL	2	29	124	219

NOTE: * represents estimated date for the laying of the first egg.

Appendix 1D cont.

DAILY RAINFALL 1986/7
CHILLAGOE (mm)

DATE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN
1													
2	6.0	30.0											
3	33.6												4.8
4		6.0						4.0		*			1.6
5					1.0							6.2	2.8
6													
7		99.0		7.0									
8													
9				2.0									
10		4.4			1.2					3.0			
11			25.0										
12			2.0										
13													
14		17.0		2.4									
15				1.6									58.0
16	1.0							8.0					36.0
17													1.8
18											9.4	2.2	14.0
19											1.8	35.0	
20	26.6									1.0		4.0	
21	19.0												
22	51.0												
23	27.0	10.6	2.0										
24	25.0	2.8								43.6		0.8	
25	33.4												19.0
26		3.2	8.2										10.0
27		5.6	19.8	1.2									8.6
28	1.8		1.2	6.4									32.8
29	7.2			18.8									1.6
30	6.0								34·6				35.0
31	7.6												24.2
TOTAL	320	179	58	40	2	NIL	NIL	12	35	48	11	48	250

NOTE: * Represents the estimated date for the laying of the first egg.

Appendix 1E.

MAXIMUM TEMPERATURES AT CHILLAGOE 1985/86 (^{o}C)

	1985							1986						
DATE	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1	30	27	32	36	32	–	35	29	31	30	34	37	37	–
2	31	28	29	35	30	35	–	31	32	32	30	37	37	40
3	–	27	27	33	32	36	29	29	31	33	30	36	36	37
4	30	27	28	33	32	35	31	32	33	30	33	35	36	36
5	30	28	28	29	32	35	34	30	34	29	34	38	36	36
6	29	29	30	30	(32)	33	33	30	32	29	34	39	35	38
7	28	29	30	30	32	34	33	30	34	29	35	(39)	37	38
8	26	29	30	27	32	36	33	31	33	29	–	39	35	39
9	27	25	31	30	37	38	38	32	34	30	34	38	38	37
10	30	26	31	24	35	37	38	30	32	33	33	37	37	39
11	30	28	32	33	35	–	3	29	32	32	33	34	37	39
12	29	27	33	33	31	40	37	27	30	33	34	37	36	39
13	30	27	–	34	32	37	38	30	31	32	36	36	37	40
14	28	26	32	35	37	34	38	34	33	31	36	38	41	41
15	30	22	30	35	38	35	39	34	33	32	40	40	40	45
16	29	29	30	35	37	37	39	35	36	33	39	40	36	41
17	30	28	30	34	38	36	37	34	34	30	37	40	40	39
18	29	28	33	35	38	38	39	33	35	29	36	39	36	39
19	29	27	33	36	39	40	38	33	31	34	37	37	37	39
20	29	26	32	30	39	40	39	32	32	34	38	33	36	38
21	29	26	32	35	39	39	39	31	32	33	39	37	36	40
22	28	27	29	34	38	38	39	30	32	33	39	39	37	37
23	26	32	33	35	37	39	37	29	30	34	40	36	38	40
24	27	30	28	35	36	36	39	30	33	34	37	31	38	–
25	28	29	35	34	36	36	–	30	32	33	39	37	37	39
26	28	27	34	35	36	34	39	30	33	34	39	39	38	39
27	28	27	35	38	34	33	37	33	34	34	37	37	39	40
28	26	28	33	38	35	–	37	32	29	35	36	37	40	40
29	26	28	34	35	35	35	38	36	26	36	35	37	33	42
30	26	28	35	34	35	36	37	33	31	34	37	37	40	41
31		29	35		36		36		29	30		37		–

NOTE: Dates in parentheses are the estimated days on which the first eggs were laid in the two caves that were visited daily.

APPENDIX 2

NOTORNIS

is the journal of the Ornithological Society of New Zealand (Inc.)

Editor: B. D. Heather,
10 Jocelyn Crescent
SILVERSTREAM

Volume 33 **Part 1** **March, 1986**

THE FOOD OF THE WHITE-RUMPED SWIFTLET (Aerodramus spodiopygius) IN FIJI

By M. K. TARBURTON

ABSTRACT

Diptera (flies), Homoptera (planthoppers), Hymenoptera (social insects), Isoptera (termites), and Coleoptera (beetles) were the most numerous prey in 32 food boluses being delivered by parent White-rumped Swiftlets (*Aerodramus spodiopygius*) to their chicks inside two Fijian caves. Numerically the main food items were flies (37%) and planthoppers (33%). Both the season and the habitat over which the birds had been feeding seemed to determine whether flies or planthoppers predominated in a particular bolus sample. Flies predominated in the prey of swiftlets foraging over open country, whereas planthoppers predominated in the prey of swiftlets foraging over both forest and open country.

The number of insects in each food bolus ranged from 47 to 750 ($\bar{x}$ = 236). The average weight of a bolus was 0.225 g (range 0.1-0.43 g). The average length of all prey was 2.48 mm, which is larger than the average length of available prey (1.63 mm). The number of prey species ranged from 2 to 83 ($\bar{x}$ = 30 per bolus). Altogether, 167 species were recorded in food boluses. The White-rumped Swiftlet bred during the wet season, when insects were more abundant.

This study, along with others (largely unpublished), shows for the first time that flies are often the most common insect in the prey of swifts, swiftlets and swallows.

INTRODUCTION

Swifts have been shown to collect more food on fine days than on wet days, although the reasons differ with latitude. Lack (1956) found that, in temperate latitudes, nestling Common Swifts grew more in wing length and weight on sunny warm days than on dull, cold, wet days. He also found that the food boluses fed to chicks contained larger insects on warm days than on wet days. Aerial tow netting showed that flying insects were in greater densities on warmer days and so the swifts could select larger prey (Lack & Owen 1955).

NOTORNIS 33: 1-16 (1986)

In the tropics, however, Hespenheide (1975) found from tow net sampling that flying insects were at higher densities in wet weather. Despite this, he found that swifts and swallows

1. Took the same average size of insects on both wet and dry days;
2. Caught a greater size range on wet days, probably because the rain reduced their foraging time, forcing them to be less selective;
3. Showed a preference for swarms, when present; and
4. Did not favour flies, presumably because flies manoeuvre better than other insects.

The preference for swarms applied particulary to the larger swifts.

From these findings, Hespenheide suggested that flies are scarce in the diet of all aerially feeding insectivores because they are harder to catch, being more manoeuvrable than other insects. He also proposed that certain behaviour, characteristic of each insect order, caused the average size of prey taken from each insect order to be significantly different.

This paper has two purposes. The first is to show the number, size and identity of the White-rumped Swiftlet's prey in Fiji. The second is to determine whether Hespenheide's findings apply to this swiftlet, which is widely distributed in the tropical south-west Pacific, or to other aerial feeders such as the swifts and swallows, as reported in other studies.

METHODS

In December 1981 and 1983, I studied the food of swiftlets nesting at Nasinu Nine-mile, 9 miles north of Suva. Of the two nesting colonies in separate caves at Nasinu Nine-mile, I chose that in the larger Waterfall Cave, where my longevity studies that had run since 1974 had shown that the birds are disturbed less by the public than those breeding in the smaller colony in Dry Cave.

Birds were captured as they carried their prey to their chicks, mostly in nests built in totally dark sections of the cave. I caught the birds in a butterfly net before they reached their nests because Lack (1956) and Fischer (1958) had found with the Common Swift (*Apus apus*) and the Chimney Swift (*Chaetura pelagica*) that disturbing birds at their nests made some desert.

Whenever a bird had its throat distended with a food bolus, I gently prised open its mandibles using my thumbnail and pencil and, holding the bird upside down, rolled the food bolus out with the pencil.

I collected the food boluses in the wetter of Fiji's two seasons, the season shown by other studies to have more abundant insects. I weighed each food bolus and then preserved it in formaldehyde. In the laboratory, I sorted the prey into orders and into unnamed but distinctive groups, presumably species, and then counted and measured them.

I sampled potential prey by the methods of Hespenheide (1975). The two areas sampled were the 4.3 km along Wainibuku Road from the Suva-Nausori road to near the entrances of Dry and Waterfall Caves, and in Tamavua, 10 km from the cave. The first area consisted of small horticultural farms, together with some young scrub regrowth and occasional trees. Farm crops were mainly pineapples, taro and cassava among scattered coconut trees. The

Tamavua area was a well-vegetated well-spaced residential area with food crops, flowering shrubs, trees and lawns. Swiftlets were feeding down to 0.5 m in both areas and at times were feeding while I was collecting samples in the tow net.

RESULTS

Identity of prey

Flies were found in all food boluses but one and were the most numerous prey in 16 of the 32 boluses taken in December (Table 1). Flies made up 43% of the total sample of 7433 invertebrates. Planthoppers were in all 32 food boluses and were the most numerous in seven of them. Planthoppers made up 24% of the total sample.

TABLE 1 — Composition of White-rumped Swiftlet prey in 32 food boluses. 1981 & 1983 combined

Order	No. Where Dominant	% Where Dominant	% Range In All Boluses	$\bar{x}$ % of Samples Where Present ± SE	No. of Boluses Present in	No. in Total Sample	% Individuals In Total Sample
Diptera	14	37 - 88	0 - 88	37 ± 4.8	31	3176	43
Homoptera	7	37 - 100	1 - 100	33 ± 6.2	32	1748	24
Hymenoptera	2	62 - 83	0 - 83	18 ± 5.5	30	1615	22
Coleoptera	1	53	0 - 53	9 ± 2.1	28	484	7
Isoptera	1	45	0 - 45	15 ± 4.1	12	168	2
Heteroptera	0	0	0 - 2	<1.0	7	9	
Trichoptera	0	0	0 - 3	2 ± 1.0	3	7	
Thysanoptera	0	0	0 - 3	1 ± 1.0	8	23	
Megaloptera	0	0	0 - 1	1.0	1	3	
Lepidoptera	0	0	0 - <1	<1.0	2	4	1
Psocoptera	0	0	0 - 2	<1.0	4	6	
Ephemeroptera	0	0	0 - 1	1.0	1	1	
Neuroptera	0	0	0 - <1	<1.0	1	1	
Unidentified	0	0	0 - 1	<1.0	7	12	
Aranae	0	0	0 - 8	2 ± 0.5	17	52	1

Social insects were in 30 of the boluses but were the most numerous in only two boluses. They made up 22% of the total sample. Termites and beetles were the most numerous in one bolus each, but beetles were present more often than termites. Although termites occurred in only 12 of the 32 boluses, they sometimes did so in reasonable numbers (17-43 or 9%-45% of total insects in the bolus). They are available to swiftlets only while swarming, when they are the preferred food. Spiders, although very small, were found in 17 of the 32 boluses.

The 1983 samples, which were collected on two days, had a very different composition. The averages for the six boluses taken on 11 December were 84% planthoppers and only 3% flies (one bolus containing 100% planthoppers). However, in only two of the six boluses collected on 5 December were planthoppers predominant (an average of 59%). Thus the diet of swiftlets cannot be adequately assessed by means of brief and intermittent sampling.

Size of prey

The largest prey found in this study were two adult moths 11 mm long. Two moth larvae 4.5 and 9 mm long were also well above average prey size. Termites were the largest of the common prey, averaging 4.5 mm, then planthoppers (2.5 mm), social insects (2.3 mm), flies (2.2 mm) and beetles

(1.9 mm). The average size of the prey was 2.48 ± 0.11 mm ($\bar{x}$ ± SE), which is significantly greater ($t=6.4$, $p<0.01$, df=39) than that of the prey available (1.63 ± 0.12). The data for total prey was based on the means of all 32 boluses rather than that of each type so that the extreme means of the uncommon types did not swamp those of the majority. The average size of the flies, social insects and beetles was each significantly larger than that available ($t=3.2$-3.5, $p<0.01$, df=27-38).

The average size of the smallest group of insects (beetles) commonly found in the prey was not significantly smaller than that of the flies ($t=1.63$, $p>0.1$, df=54). The flies were not significantly smaller than the Hymenoptera ($t=0.12$, $p>0.1$, df=57), which however were significantly smaller than the termites ($t=9.5$, $p<0.001$, df=40).

The average size of each major insect order found in the boluses, whenever it was predominant in a bolus, was compared with the size of the same order from boluses when it was in the minority. The size of insects from a swarm (arbitrarily decided by Hespenheide to be when more than 20 of a species occur in a bolus) was compared with the size of the same insect order when found in fewer numbers. None of the comparisons were shown to be significant, except that of beetles. In the one bolus where beetles were dominant (54%), their average size of 5.7 mm ± 0.2 was significantly greater than the average of all others (1.7 mm ± 0.09).

A significant difference in size ($p<0.001$) was found between three of the four major insect orders when the two samples, each of six boluses and each taken in December 1983, were compared. These are shown in Table 2. These two groups of samples had three important differences. Those taken on the 5th were collected earlier (1300-1555 hours) than those taken on the 11th 1900-1918 hours). The 5th was largely an overcast day, but the 11th was the fourth consecutive sunny day. Both these differences may be expected to cause those collected on the 11th to be larger (Lack 1956, Hespenheide 1975). In addition, the boluses on the 11th were taken one hour after sunset, when the swiftlets were probably catching dusk-flying insects, which have been shown to be larger than those flying during the day (Lewis & Taylor 1967, Hespenheide 1975). So then, both prey size and prey type show daily changes.

The range of 21 White-rumped Swiftlet boluses was 0.1-0.43 g, averaging 0.23 g ± 0.02. A significant correlation was found between the number of insects in a bolus and the weight of a bolus (Spearman rank correlation $r_S = 0.66$, $p<0.002$, $n=21$). This, together with a negative correlation ($r_S = -0.84$, $p<0.001$, $n=21$) between the number and size of the insects in a bolus, indicates that a bird returns to feed its chicks when it has all it can hold.

TABLE 2 — Average size of common prey
(1983 sample in mm)

	5 December	11 December	Difference
Coleoptera	1.45 ± 0.084	2.35 ± 0.236	p<0.001
Hymenoptera	1.70 ± 0.110	3.06 ± 0.425	p<0.001
Homoptera	2.15 ± 0.180	2.86 ± 0.081	p<0.001
Diptera	2.16 ± 0.303	2.81 ± 0.482	N. S.

The almost spherical food boluses were about 6-7 mm in diameter. Some boluses were firm but others fell apart easily, making them hard to measure.

The number of insects in a bolus varied from 47 to 750. The average number for all 32 boluses was 236 ± 32. The 1981 sample averaged 269 ± 44 (n=20) and the 1983 sample averaged 178 ± 36 (n=12).

Combining the data for December 1981 and December 1983, as shown above, hides certain information. Whereas flies were dominant in most of the combined sample of food boluses, they were exceeded by planthoppers in seven of the 11 boluses from the 1983 sample. Further analysis of the numbers of individuals and species in the major orders is shown in Table 3.

TABLE 3 — Frequency of major prey in food boluses ($\bar{x}$ ± SE)

	Individuals 1981[1]	Species[4] 1981[3]	Individuals 1983[2]	Species 1983[2]
Diptera	123.9 ± 31.0	12.4 ± 1.7	58.4 ± 25.4	11.4 ± 3.1
Hymenoptera	71.2 ± 15.9	7.3 ± 1.8	16.3 ± 5.6	7.2 ± 1.0
Homoptera	40.2 ± 12.4	3.9 ± 0.4	84.9 ± 19.4	4.9 ± 1.0
Coleoptera	21.8 ± 4.2	5.6 ± 1.2	5.8 ± 3.0	2.8 ± 1.0
Isoptera	7.9 ± 1.8	0.3 ± 0.1	1.2 ± 0.6	0.3 ± 0.1
Total	269.2 ± 44	32.6 ± 5.2	170.0 ± 33.7	29.25 ± 7.4

NOTE:
1 Numbers in 20 boluses taken 2-24 December
2 Numbers in 12 boluses taken 5,11 December
3 Numbers in 12 boluses taken 2-24 December
4 'Species' is not a named species but is ascribed to individuals that are morphologically similar

The decrease in total insects per bolus between the years was not significant (t=1.79, p>0.1, df=30, two-tailed). Neither was there a significant change in the number of species within each major order or the total number of species per bolus between the years. This uniformity suggests that further comparative analysis would be valid. Such analysis shows that the decrease in the number of individuals per order in a bolus between 1981 and 1983 was significant (t=3.09-3.53, p<0.01, df=30) in the social insects, beetles and termites. This decrease was offset by a significant increase in planthoppers (t=2.23, p<0.05, df=30). The number of flies did not decrease significantly (t=1.63, p>0.1, df=30).

The number of species found in a bolus varied from 2 to 83 and averaged 29 in 1983 and 33 in 1981.

DISCUSSION

Prey size compared with that of other swiftlets

Prey size has been positively related to the body size of insectivorous birds (Hespenheide 1971, 1975; Dyrcz 1979). The White-rumped Swiftlet, with its light weight and small prey, fits into the general trend. It takes the smallest prey of any apodid so far studied (Table 4).

Table 5 shows that the White-rumped Swiftlet is typical of all aerial feeding birds studied to date (Hespenheide 1975, Waugh 1979) in that it takes larger prey than the average of that available.

TABLE 4 — Prey size of various Apodidae and Hirundinidae

Predator	$\bar{x}$ Size (mm)	S E	Range	Mode	Source
White-rumped Swiftlet					
Aerodramus spodiopygius	2.48	0.11	0.3-11	-	This paper
Glossy Swiftlet					
Collocalia esculenta	2.6	-	-	-	Waugh & Hails 1983
Mossy-nest Swiftlet					
Aerodramus vanikorensis	3.05	-	c.1.5-12.5	-	Harrisson 1976
Black-nest Swiftlet					
Aerodramus maximus	3.05	-	c.1.5-12.5	-	Harrisson 1976
Barn Swallow					
Hirundo rustica	3.3	-	-	-	Waugh & Hails 1983
Horus Swift					
Apus horus	3.71	0.08	0.8-9.0	2.6-3.0	Collins 1980
Short-tailed Swift					
Chaetura brachyura	4.0	0.07	1-9	3	Collins 1968a
Chimney Swift					
Chaetura pelagica	c.4.0	-	-	<5	Fischer 1958
Common Swift					
Apus apus	Fine 3.5	-	<2-	-	Lack & Owen 1955
	Wet 6.5	-	->10	-	Lack & Owen 1955
Pacific Swallow					
Hirundo tahitica	4.8	-	-	-	Waugh & Hails 1983
House Swift					
Apus affinis	5.09	-	-	-	Waugh & Hails 1983
Chestnut-collared Swift					
Cypseloides rutilus	6.9	0.2	5-10	7-8	Collins 1968a
Black Swift					
Cypseloides niger	8.68	-	2-12	9-10	Collins & Landy 1968
Grey-breasted Martin					
Progne chalybea	10.5	-	-	-	Dyrcz 1984
Mangrove Swallow					
Tachycineta albilinea	15.7	-	-	-	Dyrcz 1984

TABLE 5 — Size of prey of White-rumped Swiftlet (total sample)

	Actual prey			Potential prey		
	$\bar{x}$	SE	n	$\bar{x}$	SE	n
Diptera	2.21	0.11	31	1.64	0.14	9
Homoptera	2.47	0.10	32	-	-	-
Hymenopera	2.38	0.15	29	1.80	0.10	9
Isoptera	4.50	0.19	11	-	-	-
Coleoptera	1.88	0.17	26	1.26	0.05	7
Trichoptera	3.06	0.65	5	3.3	-	1
Thysanoptera	1.49	0.14	11	1.38	0.03	4
Megaloptera	2.67	-	1	-	-	-
Lepidoptera	9.00	-	2	3.4	-	2
Psocoptera	3.45	0.61	4	3.3	-	1
Neuroptera	1.50	-	1	-	-	-
Ephemeroptera	3.00	-	1	-	-	-
Heteroptera	2.47	0.29	6	2.0	0.26	4
Unidentified	2.28	0.34	5	-	-	-
Aranidae	1.67	0.12	17	4.5	-	1
Total	2.67	0.11	32	1.63	0.12	9

Hespenheide (1975) expected that the average size of each insect order in a swift's prey would be significantly different from that of the other orders. He derived this by assuming that the different orders of insects have different average flight abilities and that the birds spend about the same amount of energy in capturing any given prey item. Hespenheide (1975) found some evidence for these expectations in the prey of other swifts. However, this study shows evidence to the contrary in that swarming insects can negate both of Hespenheide's assumptions. An insect is seldom using or likely to use its full flight capabilities (in terms of high speed and manoeuvrability) while swarming, and an aerial predator will expend less energy in procuring a bolus of any high-density collection of insects.

The food bolus

Since Bartels (1931) demonstrated that the Alpine Swift fed its chicks infrequently with large boluses of food, such feeding behaviour has been shown for other Apodidae. The wet weight of the White-rumped Swiftlets' food boluses varied about as much (0.1-0.43 g) as those of the Common Swift (<0.7-2.5 g, Lack & Owen 1955), although less than those of the Edible-nest Swiftlet (*Aerodramus fuciphaga*) (0.13-1.08 g, Langham 1980) and the Chimney Swift (*Chaetura pelagica*) (0.2-0.9 g, Fischer 1958).

The average number of insects in a bolus (236) is much larger than the 94 average of 10 boluses from the same species in Queensland (Smyth 1980). From this one could predict (assuming that the above correlations between size and number of insects in a bolus hold) that the Queensland subspecies takes larger prey than the Fijian subspecies does. This is expected (Bergmann's rule) as the Queensland subspecies *A. s. terraereginae* is much larger (12.2 g) than Fijian birds (8.1 g). In the Edible-nest Swiftlet, which is similar in size, the prey numbered 100 to over 1200, with an average of more than 500 per bolus (Langham 1980). The much larger Common Swift usually has 300-1000 prey in a bolus, but the recorded range is 58-1500 (Lack & Owen 1955).

The number of species in a bolus varied from 2 to 83 and averaged 29 in 1983 and 33 in 1981. This is about half the number of species found in similarly sized samples from the stomachs of Short-tailed Swifts (Hespenheide 1975), perhaps because fewer species are available in Fiji than in Panama and Costa Rica, as one would expect by Fiji's small area and isolation. However, the average number of species taken by the White-rumped Swiftlets is lower than might be because 21 of the 24 birds apparently fed at swarms (as defined by Hespenheide 1975). The highest number of species in a bolus is only nine less than the highest in the Short-tailed Swift. One swiftlet had fed at six swarms and another at only two swarms, neither taking any other species. Five of the birds fed on fewer than 10 species to produce a bolus — a characteristic proposed for the larger swifts (Hespenheide 1975). The 24 boluses contained 167 species, of which 67 were flies, 44 social insects, 23 beetles, 18 planthoppers, 11 spiders, 5 each of sap-suckers (Heteroptera) and thrips (Thysanoptera), 2 book lice (Psocoptera) and 1 termite. An additional 29 species were taken in the tow net.

The above results show that only in one bolus, dominated by beetles, was the average size significantly different from the average for insects of the same order in all other boluses. In this case the beetles in the beetledominated bolus were larger than in all other boluses. This is the reverse of that expected if a bird feeding on a swarm is less selective, as Hespenheide (1975) proposed. As only two of the 50 beetles in the bolus were below the mean size of beetles in all other boluses, this bolus seems to have resulted from nothing more than the chance location of a swarm of larger than average beetles.

Taxonomic comparison between available prey and captured prey

For the most valid comparison between potential prey as sampled by the tow net and actual prey from the food boluses, both samples should be collected in the same season. Although this means ignoring the mass of data from 1981, I have chosen to do so because several of the 1983 net samples were taken at the same time as the swiftlets were capturing the insects in the food boluses. On several occasions swiftlets were foraging in the same air space and at the same time as the net samples were being taken. The resulting data are shown in Table 6.

TABLE 6 — Taxonomic proportions of prey compared with aerial invertebrates

Order	$\bar{x}$ % in Tow Net (Dec 83)	$\bar{x}$ % in Food Boluses (Dec 83)	$\bar{x}$ % in Homoptera Dominated Boluses	$\bar{x}$ % in Diptera Dominated Boluses
Diptera	66.9 ± 4.5	25.7 ± 8.3*	8.0 ± 3.6*	61.0 ± 8.5
Homoptera	3.8 ± 0.6	58.0 ± 9.8*	77.8 ± 7.0*	18.5 ± 6.4+
Hymenoptera	11.1 ± 3.5	9.9 ± 2.9	8.9 ± 4.3	11.7 ± 2.1
Coleoptera	15.9 ± 4.7	2.5 ± 1.0+	0.7 ± 0.3*	6.2 ± 1.7+
Isoptera	0	1.6	2.5	0
Trichoptera	0.1	0.2		
Thysanoptera	1.2	0.2		
Lepidoptera	0.7	0		
Psocoptera	0.1	0.3		
Heteroptera	1.1	0.2		
Ephemeroptera	0.2	0		
Unidentified	1.3	0.2		
Araneae	0.1	1.3		

NOTE: * Shows significant difference to tow net samples (p_t <0.001).
+ Shows significant difference to tow net samples (p_t <0.05).

Because two planthopper species (both Delphacidae) formed a clear majority in 8 ot the 12 boluses and only one of these species was rarely taken in the net, the birds with an abundance of planthoppers had apparently spent much of their foraging time in some other habitat than that sampled. Further confirmation of this is given by the significant difference between the percentage of flies in the boluses having mostly planthoppers and the percentage of flies in the tow net samples (t=4.4, p=<0.01, df=10) and no significant difference between the percentage of flies, social insects or beetles in boluses dominated by flies and the percentage of them in the tow net samples. Taken together, these data suggest that the birds with predominantly flies in their food boluses had been feeding in the open habitats that I had sampled with the net, whereas those with predominantly planthoppers had been feeding over the forests (which I did not sample with the net) to the west of the caves.

Of the fly species in the net samples, a similar proportion was found in the fly-dominant boluses (44%) and the planthopper-dominant boluses (47%). This similarity may mean that the swiftlets feeding on planthoppers foraged over the fly-rich open habitats as well as over the planthopper-rich forests. This is confirmed in that the planthopper-dominant boluses contained a larger percentage (43%) of fly species not found in the fly-dominant boluses than the small percentage (24%) of fly species found only in the fly-dominant boluses. This conclusion is consistent with my observation that the swiftlets periodically feed in the open habitat on their way to the forest. It is also consistent with the finding that a greater number of insect species fly over forest, which has a greater diversity of plants than open habitat (Hespenheide 1975, Waugh & Hails 1983).

It is interesting that the average percentages of the three most common insect orders taken in the net are each very close to those taken in Costa Rica and Panama with a similar net by Hespenheide (1975). The largest deviations from any of his results (which varied by season and location) are flies 8.2%, social insects 8.5% and beetles 9.4%. The main interest in this comparison arises from two phenomena. The first is that it would seem unusual for oceanic islands such as Fiji to have a similar proportion of flying insect groups to a region that is attached to two large land masses. The second is that, whereas the two swifts and the swallow studied in Central America did not make proportionate use of flies, the most common insect order, the White-rumped Swiftlet, did in Fiji.

The most common group of flying insects available to Fijian swiftlets was the flies. Hespenheide suggested that flies are more manoeuvrable than most insects and that this helps explain their infrequent occurrence in the prey of large swifts in particular and in aerial predators in general.

He cited studies of six species of large swifts that took a small range of prey species with flies not a major component. He reasoned that, because the larger swifts have greater foraging ranges than smaller swifts, they may specialise on insects in mating or dispersal swarms. However, there are two problems with this argument. The first is that some studies (seven of which have not been previously published) have shown that flies can be the predominant prey of large swifts. Table 7 shows that flies have dominated in the studied diets of eight species, three of which were large swifts. By comparison, the social insects were found to be dominant in the prey of 11 species, planthoppers dominant in the prey of three species and beetles dominant in the prey of two species.

The second problem is that, if flies were more difficult to capture and the difficulty increased with the size of the swift, as proposed by Hespenheide, there should be a good negative correlation between the weight of the swift and the percentage of flies in its diet. There is however only a low negative correlation between the predator's weight and the proportion of flies in the prey for the 37 studies in Tables 7 and 8 that provide numerical data as percentages (r_s= 0.28, $0.10 > p < 0.05$). It would appear that, regardless of the size of the predator, swifts, treeswifts or swallows do not show any preference for or against flies. The birds presumably take what is available, giving preference to swarms or other high-density concentrations, which are just as likely to

TABLE 7 — Percentage composition (numerically) of major prey of swifts

	Hymenoptera	Homoptera	Coleoptera	Isoptera	Diptera	Bird's Weight	Sample Size	Source
Philippine Spinetail								
Chaetura celebensis	99	-	-	-	-	180	14	Morse & Laigo 1968
Alpine Swift								
Apus melba	4th	-	3rd	-	1st	100	-	Arn 1945
	14	-	54	-	23	100	6	Arn 1945
White-collared Swift								
Cypseloides zonaris	94	<1	2	0	1	98	2	Rowley & Orr 1965
San Geronimo Swift								
Panyptila sanctiheronymi	-	-	-	1st?	-	57	2	Carr & Dickinson 1951
Black Swift								
Cypseloides niger	c.14	c.37	7	1	c.31	46	6	Rathbun 1925
	100	-	-	-	0	46	-	Collins & Landy 1968
Common Swift								
Apus apus	6	66	8	-	17	43	24	Lack & Owen 1955
	3rd	1st	4th	-	2nd	43	-	Koskimies 1950:25
	-	31	-	-	57	43	13	Collins pers. comm.
Zimmers Swift								
Cypseloides cryptus	-	-	-	-	0	39	1	Collins pers. comm.
White-throated Swift								
Aeronautes saxatalis	1st	-	2nd	-	-	33	2	Hespenheide 1975
	3rd	-	2nd	-	1st	33	21	Bent 1940
Fork-tailed Swift								
Apus pacificus	1st	5th	2nd	-	3rd	30	40	Litvinenko 1972
	97	-	-	-	<3	30	-	Chiba 1968
	1st	-	-	-	-	30	-	Lea & Gray 1935

TABLE 7 — continued

	Hymenoptera	Homoptera	Coleoptera	Isoptera	Diptera	Bird's Weight	Sample Size	Source
Horus Swift *Apus horus*	17	41	6	19	8	27	-	Collins 1980
House Swift *Apus affinis*	78	-	10	-	4	27	1	Waugh & Hails 1983
Cayene Swift *Panyptila cayennensis*	-	-	-	-	64	24	1	Collins pers. comm.
Chimney Swift *Chaetura pelagica*	-	-	1st	-	2nd	24	12	Warren 1890: 183
	3rd	2nd	-	-	1st	24	-	Fischer 1958
White-rumped Swift *Apus caffer*	1st	4th	2nd	5th	-	22	-	Moreau 1942
Chestnut-collared Swift *Cypseloides rutilus*	51	0	0	49	0	20	4	Collins 1968a
White-tipped Swift *Areonautes montivagus*	-	-	-	-	35	20	11	Collins pers. comm.
Vaux Swift *Chaetura vauxi*	-	1st	-	-	-	18	-	Davis 1937
	-	-	-	-	31	18	10	Collins pers. comm.
Short-tailed Swift *Chaetura brachyura*	29	2	8	5	42	18	17	Collins 1968a
	82	-	11	-	4	18	6	Hespenheide 1975
Grey-rumped Swift *Chaetura cineriventris*	-	-	-	-	27	16	7	Collins pers. comm.
Band-rumped Swift *Chaetura spinicauda*	55	-	25	-	4	14	-	Hespenheide 1975
Neotropical Palm Swift *Reinarda squamata*	-	-	-	-	53	10	6	Collins pers. comm.

Note: 1st = most common, 2nd = second most common, etc.

TABLE 8 — Percentage composition (numerically) of major prey of swiftlets and swallows

	Hymenoptera	Homoptera	Coleoptera	Isoptera	Diptera	Weight	Sample Size	Source
Purple Martin								
Progne subis	2	0	68	0	20	51	c.10	Johnston 1967
Grey-breasted Martin								
Progne chalybea	75	0.3	-	-	5	33.5	65	Dyrcz 1985
	32	1	41	0	3	51	c. 9	Johnston 1967
House Martin								
Delichon urbica	-	50	-	-	-	19.8	-	Bryant 1975
Barn Swallow								
Hirundo rustica	82	-	6	2	8	19.5	-	Waugh & Hails 1983
Pacific Swallow								
Hirundo tahitica	59	-	7	2	31	17.8	-	Waugh & Hails 1983
Black-nest Swiftlet								
Aerodramus maximus	60	-	-	27	<1	15.9	-	Harrisson 1976
Rough-winged Swallow								
Stelgidopteryx	69	-	23	-	4	13.7	4	Hespenheide 1975
ruficollis	31	-	-	-	33	15.75	-	Beal 1918
Bank Swallow								
Riparia riparia	33	8	14	-	27	14.6	-	Beal 1918
	6	24	3	-	32	14.6	-	Stoner 1936
	5	13	11	-	69	14.6	-	Waugh 1979
White-rumped Swiftlet								
Aerodramus spodiopygius	7	27	12	-	51	12.2	10	Smyth 1980
	26	15	8	3	46	8.2	20	This study
	10	48	3.5	0.5	36	8.2	12	This study
Mossy-nest Swiftlet								
Aerodramus vanikorensis	60	-	-	27	<1	11.3	-	Harrison 1976
Indian Edible-nest Swiftlet								
Aerodramus unicolor	-	c.80	c.10	-	-	c.11.0	-	Ali & Dillon 1980
Edible-nest Swiftlet								
Aerodramus fuciphaga	41	15	-	-	8	10.8	-	Langham 1980
Grey-rumped Swiftlet								
Aerodramus francica	-	-	-	-	49	c.10	2	Collins pers. comm.
Glossy Swiftlet								
Collocalia esculenta	48	15	-	-	26	8.3	-	Hails & Amirrudin 1981
	55	12	34	2	2	8.3	-	Waugh & Hails 1983
Mangrove Swallow								
Tachycineta albilinea	94	3	3	0	<1	14.5	2	Ricklefs 1971
	20	-	-	-	26	-	-	Dyrcz 1984

be flies as any other group. This is not surprising because many flies congregate at feeding or mating sites and so attract feeding swifts, swiftlets and swallows.

To explain the greater dominance of social insects over beetles in prey taken than in prey available, Hespenheide pointed out that the social insects tended to congregate more and so the birds could presumably find such concentrations. There is a similar disproportion in the prey of the White-rumped Swiftlet and the same reasoning could apply. My observations of feeding swiftlets flying in 10-30 m diameter circuits confirms that they do feed on insects that are swarming or in other high-density concentrations.

Hespenheide (1975) found that swifts and swallows preferred the larger catchable prey of the range they could manage. If the same holds for swiftlets, flies, the most abundant but second smallest prey taken of White-rumped Swiftlets in Fiji, could not be taken because of their size alone. Flies must be chosen because they are easier to catch and/or more abundant.

Tow net samples taken in Costa Rica and Panama consistently demonstrated that, although flies were 70-75% of airborne insects, they were only 4% of swift prey in the comparable wet season (Hespenheide 1975). Hespenheide presumed that the flies were harder to catch than other prey. If this is true of flies in Fiji, either the White-rumped Swiftlet is better able to catch flies than the swifts, swallows and other swiftlets whose prey contains few flies or the other kinds of flying insects are far less abundant in Fiji than in Central America and Malaysia. The latter cannot be so because the taxonomic proportions of the Fijian tow net samples (Table 9) are very like those of Central America. So perhaps the White-rumped Swiftlet has greater ability in securing more manoeuvrable prey, although, as Tables 3 & 4 show, it is not alone in this ability.

A likely alternative for flies being chosen, other than their being easier to catch or more abundant, is that in Fiji they occur in high density in small areas. In Central America, flies may not have been in swarms or swarms of larger prey may have been more attractive to the swifts and swallows.

Published comments suggest that mosquitoes are fewer in Fiji than elsewhere because the swiftlets hunt them tirelessly (Wood & Wetmore 1926, Sibson *in* Belcher 1972, Allison 1978/79). I doubt these statements because mosquitoes were 2.5% (21/852) of free-flying insects but only 0.58% (43/7433) of the swiftlet's prey. In addition, four of the six places I have lived at or visited within the range of the swiftlet had large numbers of mosquitoes.

Food abundance and the timing of breeding

Some evidence suggests that the dry season is a better breeding time than the wet season for birds that feed on the wing. Hespenheide (1975) noted that the swallows and most other insectivorous birds nest in the dry season. He also suggested that, although in the wet season the density of flying insects is higher in cloudy but dry periods and ants and termites seem to swarm most, the more frequent rains must reduce the bird's foraging time. In Asia, the Edible-nest Swiftlet (Langham 1980), the Black-nest Swiftlet and the Mossy-nest Swiftlet (Medway 1962) hatch most eggs during the dry period November to March.

However, such is not always the case. The Indian Edible-nest Swiftlet *Aerodramus unicolor* (Abdulali 1942), the Pacific Swallow and the Glossy Swiftlet *Collocalia esculenta* (Waugh & Hails 1983) produce most of their first broods with the onset of the monsoon rains in May.

In Fiji, the White-rumped Swiftlet also breeds during the season of heavy rainfall. Nests are built in September and October, corresponding with an increase in rainfall (Table 9). I suspect that increase to be the trigger because the increase in both rain and nest building occur so soon after August, the driest month of the year. Laying in November and early December corresponds with a further increase in rainfall. The high level of rainfall continues to April and so covers the period that young are being fed in the nest and the critical period during which the young are learning to feed themselves on the wing.

TABLE 9 — Monthly rainfall averages in millimetres — Koronivia Research Station (1950-1979)

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
367	300	399	359	239	183	171	154	204	221	305	296	3198

Further evidence that there is an increase in the number of flying insects during the wet season in Fiji is the high correlation ($r_s = 0.8$) between date and the number of insects caught in the aerial tow net during December. The raw data were 5 December 10 insects, 6 December 97 insects, 9 December 68 insects, 11 December 265 insects, 15 December 162 insects. Confirmation of this trend is needed from net samples taken in every month.

Although flies were dominant in most of the combined 1981 and 1983 boluses, that does not prove that this swiftlet specialises in flies. If I had taken more boluses in 1983, the overall result would probably show planthoppers as predominant because, as Table 10 shows, planthoppers made up 48% and flies only 36% of the total 1983 sample.

TABLE 10 — Composition of White-rumped Swiftlet prey

Order	% boluses dominant in		% boluses present in		% of total sample	
	'81	'83	'81	'83	'81	'83
Diptera	60	36	100	91	46	36
Homoptera	20	64	100	100	15	48
Hymenoptera	10	0	95	91	26	10
Coleoptera	5	0	95	73	8	3.5
Isoptera	5	0	40	27	3	0.5
					98%	98%

Inadequate sampling or a real change in prey composition over time has led several workers to make generalisations which later study has shown to be incorrect. The large range of foods in boluses collected at the one time from this and other studies demonstrates how sampling could give biased results. The abundance of various insects can fluctuate greatly for various reasons such as current and past insect density, disease, predation, climate, and responses in prey or plant food species (Bos & Rabbinge 1976, Dixon & Barlow 1979, Anderson & May 1980, Barlow & Dixon 1980, Randall 1982). Such fluctuations are likely in many insects and will restrict the choice of prey for aerial feeders.

ACKNOWLEDGEMENTS

For published and unpublished data on the food of several swifts, I thank Charles T. Collins of California State University. I also thank, at Massey University, Edward Minot for comments on two drafts of this paper and Ian Stringer for identifying the more difficult prey. For editing and criticism of the final drafts I thank Nigel Langham and Barrie Heather.

LITERATURE CITED

ABDULALI, H. 1942. The terns and edible-nest swiftlets at Vengurla, west coast India. J. Bombay Nat. Hist. Soc. 43: 446-451.

ALI, S.; DILLON, R.S. 1970. Handbook of the birds of India & Pakistan:4. frogmouths to pittas. Bombay.

ALLISON, N.A. 1978/79. Notes on birds of Viti Levu & Vanua Levu islands, Fiji. Sea Swallow 29: 10-11.

ANDERSON, R.M.; MAY, R.M. 1980. Infectious diseases & population cycles of forest insects. Science 210: 658-661.

ARN, H. 1945. Zur biologie des Alpenseglers *Micropus melba melba* (L.). Schweiz. Arch. Ornith. 2: 137-181.

BARLOW, N.D.; DIXON, A.F.G. 1980. Simulation of lime aphid population dynamics. PUDOC. Wageningen Netherlands.

BEAL, F.E.L. 1918. Food habits of the swallows, a family of valuable native birds. Bull. U.S. Dept. AG. 619.

BELCHER, W.J. 1972. Birds of Fiji in Colour. Auckland: Collins.

BENT, A.C. 1940. Life histories of American Cuckoos, Goatsuckers, Hummingbirds & their allies. U.S. Nat. Mus. Bull. 176: 254-271.

BOS, VAN DEN, J.; RABBINGE, R. 1976. The Grey Larch Bud Moth & its population dynamics. PUDOC Wageningen, Netherlands.

BRYANT, D.M. 1975. Breeding biology of House Martins *Delichon urbica* in relation to aerial insect abundance. Ibis 117: 180-216.

CARR, M.H.; DICKINSON, J.C. 1951. The San Geronimo Swift in Honduras. Wilson Bull. 63: 271-273.

CHIBA, S. 1968. Analysis of stomach contents of *Nucifraga caryocatactes* and *Apus pacificus* of Japan. Misc. Rep. Yamashina Inst. Ornith. 5: 287-297.

COLLINS, C.T. 1968a. The comparative biology of two species of swifts in Trinidad, West Indies. Bull. Florida State Mus. 11: 257-320.

COLLINS, C.T. 1968b. Notes on the biology of Chapman's Swift *Chaetura chapmani* (Aves:Apodidae). Am. Mus. Novit. 2320.

COLLINS, C.T. 1980. Notes on the food of the Horus Swift (*Apus horus*) in Kenya. Scopus 4: 10-13.

COLLINS, C.T.; LANDY, M.J. 1968. Breeding of the Black Swift in Veracrus, Mexico. Bull. Sthn. Calif. Acad. Sc. 67: 266-268.

DAVIS, W.B. 1937. A Vaux Swift and its young. Condor 39: 222-223.

DIXON, A.F.G.; BARLOW, N.D. 1979. Population in the lime aphid. Zool. J. Linn. Soc. 67: 225-237.

DYRCZ, A. 1979. Die Nestlingsnahrung bei Drosselrohrsanger (*Acrocephalus arundinaceus*) und Reichrohrsanger (*Acrocephalus scirpaceus*) an den teichen bei milicz in Polen und zwei seen in der Westschweiz. Orn. Beobachter 76: 305-316.

DYRCZ, A. 1984. Breeding biology of the Mangrove Swallow (*Tachycineta albilinea*) and the Grey-breasted Martin (*Progne chalybea*) at Barro Colorado Island, Panama. Ibis 126: 59-66.

FISCHER, R.B. 1958. The breeding biology of the Chimney Swift *Chaetura pelagica* (Linnaeus). N.Y. State Mus. & Sc. Sev. Bull. 368: 1-141.

HAILS, C.J.; AMIRRUDIN, A. 1981. Food samples and food selectivity of White-bellied Swiftlets (*Collocalia esculenta*). Ibis 123: 328-333.

HARRISSON, T. 1976. The food of *Collocalia* swiftlets (Aves:Apodidae) at Niah Great Cave in Borneo. J. Bombay Nat. Hist. Soc. 71: 376-393.

HESPENHEIDE, H.A. 1971. Food preferences and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. Ibis 113: 59-72.

HESPENHEIDE, H.A. 1975. Selective predation by two swifts and a swallow in Central America. Ibis 117: 82-99.

JOHNSTON, R.F. 1967. Seasonal variation in the food of the Purple Martin (*Progne subis*) in Kansas. Ibis 109: 8-13.

KOSKOMIES, J. 1950. The life of the Swift, *Micropus apus* (L), in relation to the weather. Ann. Acad. Sci. Fenn. Ser. A. 15: 1-151.

LACK, D. 1956. Swifts in a tower. London. Methuen.

LACK, D.; OWEN, D.F. 1955. The food of the swift. J. Anim. Ecol. 24: 120-136.

LANGHAM, N. 1980. Breeding biology of the Edible-nest Swiftlet (*Aerodramus fuciphagus*). Ibis 122: 447-460.

LEA, A.M.; GRAY, J.T. 1935. The food of Australian birds. Emu 35: 63-98.

LEWIS, T.; TAYLOR, L.R. 1964. Diurnal periodicity of flight by insects. Trans. Royal Ent. Soc. Lon. 116: 393-476.

LITVINENKO, N.M. 1972. On the food of the White-rumped Swift in the southern Primorye. Ornithologiya 10: 361-362. Trans. from Russian by A.N. HILKEVITCH, Calif.State Uni.

MEDWAY, L. 1962. The swiftlets (*Collocalia*) of Niah Cave, Sarawak. Part 1: Breeding Biology. Ibis 104: 45-66.

MOREAU, R.E. 1942. The breeding biology of *Micropus caffer streubelii*, the White-rumped Swift. Ibis 84: 27-49.

MORSE, R.A.; LAIGO, F.M. 1968. The Philippine Spine-tailed Swift, *Chaetura dubia* McGregor, as a honey bee predator. Phil. Entom. 1: 138-143.

RANDALL, M.G.M. 1982. The dynamics of an insect population throughout its altitudinal distribution: *Coleophora altecolella* (Lepidoptera) in northern England. J. Anim. Ecol. 51: 993-1016.

RATHBUN, S.F. 1925. The Black Swift and its habits. Auk. 42: 497-516.

ROWLEY, J.S.; ORR, R.T. 1962. The nesting of the White-naped Swift. Condor 64: 361-367.

SMYTH, D.M. 1980. Notes on the diet of the Grey Swiftlet, *Aerodramus spodiopygius*. Sunbird 11: 20-21.

STONER, D. 1936. Studies on the Bank Swallow, *Riparia riparia riparia* (Linnaeus), in the Oneida Lake region. Roosevelt Wldl. Ann. 4: 127-233.
WARREN, B.H. 1890. Report on the birds of Pennsylvania. Cwlth. Penn. Harrisburg.
WAUGH, D.R. 1979. The diet of Sand Martins *Riparia riparia* during the breeding seasons. Bird Study 26: 123-128.
WAUGH, D.R.; HAILS, C.J. 1983. Foraging ecology of a tropical aerial-feeding bird guild. Ibis 125: 2[illegible]0-217.
WOOD, C.A.; WETMORE, A. 1926. A collection of birds from the Fiji islands. (12) Ibis 2: 91-136.

MICHAEL K. TARBURTON, *Department of Botany and Zoology, Massey University, Palmerston North*

★

THE FOOD OF THE WHITE-RUMPED SWIFTLET (Aerodramus spodiopygius) IN QUEENSLAND

ABSTRACT

Homoptera (planthoppers), Diptera (flies), Hymenoptera (social insects) and Isoptera (termites), were the most numerous prey in 44 food boluses being delivered by parent White-rumped Swiftlets (Aerodramus spodiopygius chillagoensis) to their chicks inside six Chillagoe caves. Numerically the main food items were planthoppers (47%) and flies (24%).

The number of insects in each food bolus ranged from 7 to 587 ($\bar{x}$ = 149). The average weight of a bolus was 0.33 g (range 0.11 - 0.62 g). The average length of all prey was 3.6 mm, which is larger than the average length of available prey (2.2 mm). The number of prey "species" ranged from 2 to 83 ($\bar{x}$ = 40) per bolus. Altogether, 303 invertebrate "species" were recorded in food boluses.

The White-rumped Swiftlet breeds during the wet season, when insects are generally accepted as being more abundant. However the density of potential prey is shown to be significantly lower than that taken during the breeding season in Fiji.

INTRODUCTION

The White-rumped Swiftlet (A. s. assimilis) has been shown (Tarburton 1986, Appendix 2, pp 137 - 152) to take flies as its most common prey in some seasons and over certain habitats in Fiji. Because published studies (Hespenheide 1975, Lack 1956) had not shown flies to be the dominant taxon in the prey of other swifts, it appeared worthwhile to make an analysis of the prey of the same species where it feeds in different habitats and climates. There are a number of factors which might alter the type and size of the prey taken over the savannah at Chillagoe.

Chillagoensis being larger than *assimilis*, should enable it to take larger prey (Hespenheide 1971, 1975, Dyrcz 1979). Larger prey will only be available in similar taxonomic proportions as it was in Fiji if the different climate, food source for the prey and competition from what is likely to be a greater number of species of aerially feeding competitors, make them available. Having these variables as they apply to the same bird should help discern some of the causes for aerially feeding birds not taking prey in the taxonomic proportions that are found to be available.

METHODS

During December 1985, January and December 1986 and January 1987 I studied the food of *A. s. chillagoensis* nesting at Chillagoe. Food boluses were taken from adults caught in narrow sections of caves as they delivered the food to their nestlings. Such boluses were taken from Guano Pot, Gordale Scar Pot, New Southlander, Crack Pot, Keef's Cavern and Golgotha Cave. The approximate locations of these caves are shown in Section 1 (p. 10).

Swiftlet food samples were collected and measured in the same way as described in the previous Appendix (p 138).

In Fiji I sampled potential prey of *assimilis* by the methods of Hespenheide (1975), but *chillagoensis* rarely fed below 8 m in the first season, so I could not sample the air they were feeding in with the net mounted on a vehicle. Instead, I sampled the flying invertebrates (potential prey) by placing the same net as used in Fiji on a five m pole and then swung it through the air in circular and figure of eight motions. In order to reach the air space that the swiftlets were using I stood on the top of limestone outcrops (Suicide & Spring towers as well as tower 5126 in Chillagoe township) or on the tank stand at the rear of two Queensland National Parks & Wildlife homes.

Swiftlets often fed at these locations and were doing so while some of the samples were being collected. Nine samples were collected in a similar manner in Fiji.

Much of the statistical reporting is based on mean measurements and their standard errors and is shown in text and tables as $\bar{x} \pm$ SE. The data for determining the size of all prey were based on the means of all 44 boluses rather than that of each type so that the extreme means of the uncommon types did not swamp those of the majority. Whereas Table 2 shows the actual minimum and maximum sizes of all potential prey netted, those few measurements that were above or below the size that the birds were found to have taken were not used in calculating the average of available prey. It is assumed that insects smaller than those commonly caught are 'selected against' for perceptual or energetic considerations, and that the one insect that was larger than the maximum caught by the birds sampled, would be too large for the bird to handle.

RESULTS

Identity of prey

Planthoppers were found in all 44 food boluses and were the most numerous in 18 of them (Table 1) making 47% (3102 individuals) of the total sample of 6549 invertebrates. Flies were found in 41 of the food boluses, and were the most numerous prey in 11 of them making 24% of the total sample. Social insects were in 43 boluses and were the most numerous in three boluses. They made up 17% of the total sample. Termites were the most numerous in three boluses, but beetles, plant bugs (Hemiptera) and spiders were present in more boluses than were termites.

Thirty-one percent (1,669) of the 5,334 insects taken from boluses in the 1985/86 season were just three "species" of jumping plant-lice of the family Psyllidae.

Table 1 Composition of White-rumped Swiftlet prey in 32 food boluses: Chillagoe, 1985/6

Order	No. Where Dominant	% Where Dominant	% Range In All Boluses	$\bar{x}$ % of Samples Where Present ± SE	No. of Boluses Present in	No. in Total Sample	% Individuals In Total Sample
Homoptera	14	36 - 98	0 - 98	38 ± 3.9	30	2352	44
Diptera	11	38 - 56	0 - 56	27 ± 3.2	30	1440	27
Hymenoptera	5	42 - 68	<1 - 68	23 ± 3.0	32	880	16
Isoptera	2	48 - 98	0 - 98	28 ±11.0	8	81	2
Aranae	0	0	0 - 12	5 ± 0.7	24	265	5
Heteroptera	0	0	0 - 33	4 ± 1.6	20	182	3
Coleoptera	0	0	0 - 9	3 ± 0.6	21	109	2
Thysanoptera	0	0	0 - 1	<1	7	13	1
Lepidoptera	0	0	0 - 7	2 ± 1.1	6	11	
Phasmatodea	0	0	0 - <1	<1	1	1	
Unidentified	0	0	0 - <1	<1	1	1	

The total of 298 species for that season was made up of 90 Hymenoptera, 75 Diptera, 54 Araneida, 36 Homoptera, 25 Coleoptera, 11 Heteroptera, 3 Lepidoptera, 3 Isoptera, and 1 Thysanoptera.

Size of prey

The largest prey found in this study were three termites and a social insect, each 10 mm long. The next largest prey were 9 mm long and included four social insects, a moth, a fly and the only mantid in the sampled prey. Termites were the largest of the common prey, averaging 6.4 mm, then social insects (4.2 mm), plant bugs (3.0 mm), flies (2.5 mm), spiders (2.4 mm) and planthoppers (2.4 mm). The average size of all prey from the 44 boluses was 3.64 ± 0.24 mm ($\bar{x} \pm$ SE), which is significantly greater ($t_{77} = 3.89$, $p < 0.001$,) than that of available prey (2.4 ± 0.2).

While the average size of prey in each major taxon was not significantly greater than the average size of potential prey (except for the Hymenopterans where $t_{87} = 15.2$, $\underline{P} < 0.001$), the data as shown in Figure 1 clearly shows the captured prey to be consistently larger than the available prey. A comparison of the maximum and minimum lengths of potential and actual prey (Table 2) shows that although prey smaller than 1 mm is available, the birds do not take it. Termites and moths smaller than 3.5 mm are not common in either available or captured prey.

Table 2 Maximum and minimum sizes of potential and actual prey

taxon	bolus prey min.	bolus prey max.	potential prey min.	potential prey max.
Homoptera	1.0	10.0	1.0	2.6
Diptera	1.0	9.0	0.8	8.5
Hymenoptera	1.0	10.0	0.4	7.0
Isoptera	3.8	10.0	3.2	9.0
araneida	1.0	5.5	2.0	-
Coleoptera	1.0	3.3	1.0	6.0
Heteroptera	1.5	8.0	1.7	2.2
Thysanoptera	1.0	2.0	0.8	1.5
Lepidoptera	4.0	9.0	-	9.0
Phasmotodea	-	9.0	-	-
Blattodea	-	-	-	7.0

Abundance of potential prey

The sweep-net samples of potential prey at Chillagoe caught an average of 6 (SE = 1, n =39) insects of the size range found to be taken by the birds (1-10 mm). This estimate of density of available prey is far below the average of 95 (SE = 29, n = 16) insects caught in the same net in Fiji.

The Food Bolus

The weight of 32 White-rumped Swiftlet boluses ranged between 0.11 - 0.62 g, averaging 0.33 g ± 0.02.

The number of insects in a bolus varied from 7 to 587. The average number for all 44 boluses was 149 ± 21. Further analysis of the numbers of individuals and species in the major orders is shown in Table 3.

Table 3 Frequency of major prey in food boluses ($\bar{x}$ ± SE)

	Individuals	Species
Homoptera	71.0 ±16.0	5.0 ± 1.0
Diptera	35.0 ± 7.0	11.0 ± 1.0
Hymenoptera	26.0 ± 3.0	11.0 ± 1.0
araneida	6.0 ± 2.0	4.0 ± 1.0
Heteroptera	4.0 ± 2.0	1.0 ± 0.2
Coleoptera	3.0 ± 1.0	2.0 ± 0.4
Isoptera	4.0 ± 1.0	0.4 ± 0.1
Total	149.0 ± 21	32.0 ± 4.0

'Species' is not a named species but is ascribed to individuals that are morphologically similar.

DISCUSSION

Identity of prey compared with that of Fiji

While flies made up 43% of the 32 boluses collected from Fijian swiftlets they fell to being the second most common prey (21%) in the 44 boluses collected from swiftlets at Chillagoe.

Planthoppers, which made up 24% and were the second most common prey in Fiji, were the most common prey (37%) in the samples from Chillagoe. Most other taxa were found in similar proportions except for spiders which composed only 1% of prey in Fiji and made up 3% of prey at Chillagoe, and beetles which were 7% of prey in Fiji and were only 2% of prey at Chillagoe.

The most common flying insects available to swiftlets in Fiji and the second most common available at Chillagoe were flies. Whereas in Fiji the major portion of the prey was flies, they were not the most common prey in Chillagoe. This could be explained if the planthoppers which the Chillagoe birds concentrated on were to be found in swarms which I never sampled with my sweep-net.
Alternatively, one can accept Hespenheide's (1975) suggestion that flies are more manoeuvrable than most insects and that this helps explain their infrequent occurrence in the prey of aerial predators in general.
If this is the case then the White-rumped Swiftlet in Fiji has greater ability than most apodids, including chillagoensis, to capture more manoeuvrable prey. This is possible as assimilis weighs less and has longer wings than chillagoensis. That flies are not as large a majority in the available prey at Chillagoe as they are in Fiji also helps explain their under-representation in the diet of Chillagoensis.

It might be that non-fly prey is easier to obtain at Chillagoe. Evidence for this is that while Fijian birds forage for 15.5 hours a day swiftlets at Chillagoe forage for only 13 hours. Fijian swiftlets leave their caves just after 0400 hrs and return for the night mostly after dark between 1930 and 2000 hrs, while the majority of swiftlets at Chillagoe do not leave the cave until around 0530 hrs and most return before dark around 1830 hrs. However, there is also evidence against the view that the birds at Chillagoe have less difficulty finding enough food for their chicks.

Swiftlets at Chillagoe are only gathering food for one chick whereas Fijian swiftlets are collecting food for two chicks. Fijian birds also breed in larger colonies than those at Chillagoe, which means that on average they have to fly further to their feeding areas.

However, we need not appeal to either of these explanations for as was shown in the previous appendix (p 150), such variation could result from the time of sampling. Examples given there show that the most abundant taxon in the prey of apodids varies with time even though flies are consistently the commonest prey available. In one season in Fiji this swiftlet did not capture a majority of flies even though they were the most abundant taxon.

Table 4 Taxonomic Proportions of Prey Compared with Aerial Invertebrates

Order	$\bar{x}$ % in Sweep Net	$\bar{x}$ % in Food Boluses
Hymenoptera	41	27 ± 3
Diptera	39	21 ± 3
Thysanoptera	6	<1
Homoptera	5	37 ± 4
Coleoptera	5	2 ± 1
Isoptera	2	8 ± 3
Heteroptera	2	2 ± 1
Aranea	<1	3 ± 1
Lepidoptera	<1	<1
Blattaria	<1	<1

NOTE Taxa are arranged in descending order of the proportion available.

Chillagoensis does not take its prey in similar taxonomic proportions to those available within the size range that it handles (Table 4). If it did, flies would predominate, followed by social insects, thrips and planthoppers. The proportion of each taxon in available prey is very close to that available in Fiji and in Costa Rica and Panama (Hespenheide 1975), except that thrips replace beetles at Chillagoe. As Hespenheide (1975) predicted, the proportion of flies caught was below that available. The reason he gave was that the manoeuvrability of flies is said to be better than that of social insects and beetles.

However, as pointed out in the previous Appendix (p 150) the proportion of flies in a sample varies largely with the time of sampling and these data may not contradict those from Fiji where flies predominated in one of the two large samples. The under-representation of social insects in the diet of swiftlets from both Chillagoe and Fiji does not support Hespenheides' suggestion that the poor manoeuvrability and tendency to swarm make this prey taxon preferred above flies and beetles.

Size of prey

Because the Chillagoe birds ($\bar{x} = 9.3 \pm 0.04$ g) are significantly larger ($t_{400} = 15.4$, $\underline{P} < 0.001$) than Fijian birds ($\bar{x} = 8.19 \pm 0.06$ g), and because prey size has been positively related to the body size of insectivorous birds (Hespenheide 1971, 1975; Dyrcz 1979), it would be expected that the Chillagoe swiftlets would take larger prey than the Fijian swiftlets. The average size of prey taken by the swiftlets at Chillagoe (3.64 ± 0.24 mm) was significantly larger ($t_{74} = 4.32$, $\underline{P} < 0.001$) than the average size of prey taken by Fijian swiftlets (2.48 ± 0.11 mm). The available prey sampled by the sweep-net was significantly larger ($t_{32} = 4.37$, $\underline{P} < 0.001$) at Chillagoe (2.58 ± 0.17 mm) than at Fiji (1.74 ± 0.09 mm).

It has been suggested (Hespenheide 1975) that prey smaller than the minimum size taken is not taken due to either perceptual reasons or because the relative ease of capture for the different taxa converges at small sizes to very similar values.

Food abundance and the timing of breeding

The discussion in the previous Appendix (p 149) about breeding in the wet season versus breeding in the dry season hardly applies to birds in a savannah regimen as it is normal practice for birds to breed in the wet season.

However, in both Fiji (p 21) and Chillagoe (Table 5) it is the onset of the wet season that coincides with breeding in the White-rumped Swiftlets. Laying in November and early December corresponds with an increase in rainfall at both Chillagoe and Fiji. The high level of rainfall continues to April in Fiji but only until March at Chillagoe.

Table 5 Monthly rainfall averages in millimetres- Chillagoe P.O. (1902-1986)

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
217	216	147	30	14	10	4	4	6	14	55	138	855

CONCLUSIONS

Although flies were the commonest of the insects available they were second most common to planthoppers in the prey of chillagoensis. However, as only one of the 260 insects caught in the sweep-net was a jumping plant louse, which composed 31% of the prey in the good season, it is clear that the sampling technique was not adequate in all respects. Despite this deficiency it was shown that the swiftlets were taking larger prey than that which was available.

Chillagoensis took larger prey in larger boluses which contained fewer individuals than was the case for assimilis. Each bolus taken by chillagoensis had an average of 10 species more than those taken by assimilis. Thirty-two boluses of invertebrates taken by chillagoensis contained 303 species, whereas the same number of boluses taken by assimilis contained 167 species. The fact that there are no other swifts or swallows resident in the area accounts, as much as the difference in size between Australia and Fiji, for chillagoensis having larger prey of more species available to it than does assimilis.

ACKNOWLEDGEMENTS

I wish to acknowledge the helpful criticism of the drafts of this paper by Prof Brian Springett and the identification of the plant lice by Dr Ian Stringer. The Chillagoe National Parks staff were very helpful in allowing entry to their parks and homes for this study.

REFERENCES

DYRCZ, A. 1979. Die nestlingsnahrung bei drosselrohrsanger (*Acrocephalus arundinaceus*) und teichrohrsanger (*Acrocephalus scirpaceus*) an den teichen bei milicz in Polen und zwei seen in der Westschweiz. Ornithologie Beobachter 76: 305-316.

HESPENHEIDE, H.A. 1971. Food preferences & the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. Ibis 113: 59-72.

HESPENHEIDE, H.A. 1975. Selective predation by two swifts & a swallow in Central America. Ibis 117: 82-99.

LACK, D. 1956. Swifts in a tower. London. Methuen.

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

APPENDIX 4

An experimental manipulation of clutch and brood size of White-rumped Swiftlets *Aerodramus spodiopygius* of Fiji

M. K. TARBURTON

129: 107–114 Accepted 19 March 1986

By monitoring hatching success, chick growth and fledging success in normal sized and experimentally enlarged clutches and broods of the White-rumped Swiftlet *Aerodramus spodiopygius* in Fiji, this paper demonstrates the inability of this species to raise more young than is normal.

Winkler & Walters (1983) have stated that 'birds lay that number of eggs that resul in the parents operating at the optimal working capacity'. In stating this, they accep Ashmole's update (1961, 1963) of Lack's hypothesis (1947) that birds are maximizing their clutch size in respect to the quantity of food that is immediately availabl during the breeding season. However, they also recognize that parents may b maximizing their reproductive output over their entire lifetime rather than within single breeding attempt. A number of authors use the latter view to predict that som brood sizes will be below the maximum that parents can feed in a particular seaso (e.g., Williams 1966, Murphy 1968, Gadgil & Bossert 1970, Charnov & Krebs 1974 Goodman 1974, Pianka & Parker 1975).

It would be expected that long-lived birds with small clutches would be amongst those most likely to be working below their capacity to gather food in order to enhance their lifelong capacity to raise more young. It has been shown by monitoring chick growth in artificially enlarged broods that some birds have been able to gather enough food to raise more chicks than normal at one time. However, all such results were obtained with temperate species and no such manipulations have been carried out on swiftlets which are long-lived and tropical.

Methods

The subjects of this manipulation experiment were White-rumped Swiftlets nesting in 'Dry' and 'Waterfall' caves north of Suva (Tarburton 1986). Daily visits were made to these colonies throughout December 1981 and again in 1983. On these visits eggs were checked for hatching and measurements were made of each chick's wing, tarsus and weight. Six natural single-egg clutches and 37 natural two-egg clutches were monitored as controls along with the manipulated clutches. Single-egg clutches were manipulated by removing one of the two eggs from 24 normal clutches. The eggs that were removed were added, as were another three, to normal clutches to make up 27 three-egg clutches. Six two-egg clutches were also made up by swapping eggs so that none of these birds were incubating their own eggs. The rates of growth for 13 one-chick and 39 two-chick natural broods were compared with those for 37 one-chick, seven two-chick and 23 three-chick, manipulated broods.

Lack (1956) reported some parental desertion when the nests of Common Swifts *Apus apus* were disturbed. To test the effect of disturbance on the swiftlets, I visited one isolated group of nests less frequently than other nests in the study. The chicks at frequently-visited nests grew at the same rate as those in nests visited less frequently. Nests were approached slowly to allow incubating parents time to leave the nest without the haste that caused increased egg loss. After being handled most chicks were restless and likely to fall from the nest. This made it necessary to keep an eye on a brood for about a minute after replacing it.

Individual chicks within a brood were identified initially by placing a daub of dark green quick-drying model paint on the head, shoulders or rump. Once the tibia was large enough to retain a band, individually numbered size one aluminium bands from CSIRO Canberra, Australia were used. I banded all swiftlets on the tibia instead of the usual tarso-metatarsus. Bands applied to the tarsus often slip over the toes (Tarburton unpublished). The swiftlets usually stay on the wing all day (except when breeding) and this prevents the band from damaging the thin skin and feathers of the tibia.

The day of hatching was known for only 22 chicks. Their wing, tarsus and weight measurements exhibited an even exponential growth form through Day *8*. In order to increase the sample of aged chicks, those up to eight days old when found were aged with a formula derived using regression analysis of measurements of known age chicks.

Four full-day watches were made at a sample of manipulated and untouched nests to determine the daily feeding rate of the different sized broods. The low beam on a miner's lamp was used to make the observations.

Results

Hatching success

The hatching success of natural clutches and of manipulated clutches were not significantly different. Those with natural clutch size one hatched an average of 0·43 ± 0·18 ($\bar{x} \pm$ s.e., $n = 9$), while the manipulated ones hatched an average of 0·61 ± 0·12, ($n = 20$); (Median test; $\chi^2_1 = 0·28$, n.s.). Pairs with a natural clutch size of two hatched, on average, 1·18 ± 0·15, ($n = 34$) and the manipulated twos, 1·0 ± 0·26, ($n = 6$) ($\chi^1_2 = 0·6$, n.s.).

The combined hatching success of single-egg clutches was 0·52 ± 0·09 ($n = 29$) and that of the combined two-egg clutches 1·15 ± 0·14 ($n = 40$), showing a clear advantage to the two-egg clutch ($t_{65} = 3·81$, $P < 0·001$). The manipulated three-egg clutches had an average clutch hatching of 1·22 ± 0·17 ($n = 27$), which was not significantly larger than that of the two-egg clutches ($t_{55} = 0·33$, n.s.).

Chick growth

Figures 1, 2 and 3 show the mean daily increase in length of wing and tarsus and weight for individuals in broods of all three sizes. The overlapping standard errors on the wing growth curves indicate no significant difference between broods of one and two whereas that of three is significantly less than both one and two after Day *10*. Average adult wing length was not reached before birds fledged, though the minimum adult wing length was reached by most fledglings.

The weight of chicks in broods of three was also significantly lower. After Day *12* a significant difference could be detected between those of single and two-chick broods, but it was not as great as between those of two and three-chick broods. One-chick broods reached adult weight on Day *19*, two on Day *22* and those of three-chick broods on about Days *30* to *50*.

Tarsal growth exhibited the least variation, with no consistent differences amongst chicks of different clutch sizes. The tarsus was also the most rapid in achieving adult size, which on average took 13·5 days.

Fledging success

In order to determine brood success, an arbitrary point of success needed to be established, due to the difficulty of knowing when the nestling period ended. The difficulty was caused by the wandering habits of older chicks which, although possibly beneficial in exercising their wings as they 'walked' around on the cave walls, made location of marked birds more difficult. Taking a wing length of 90 mm as indicating that a nestling is likely to fledge, the following determinations were made. Parents with a brood of one raised 0·43 ± 0·11 chicks ($\bar{x} \pm$ s.e., $n = 24$). Those with a brood of two raised 0·92 ± 0·15 ($n = 25$) and those with a brood of three raised 1·09 ± 0·3 ($n = 11$).

These data show that a pair with a brood of two rear significantly more young than those with a brood of one, ($t_{44} = 2·57$, $P < 0·01$), while those with a brood of three do not rear significantly more than those with broods of two ($t_{15} = 0·59$, n.s.).

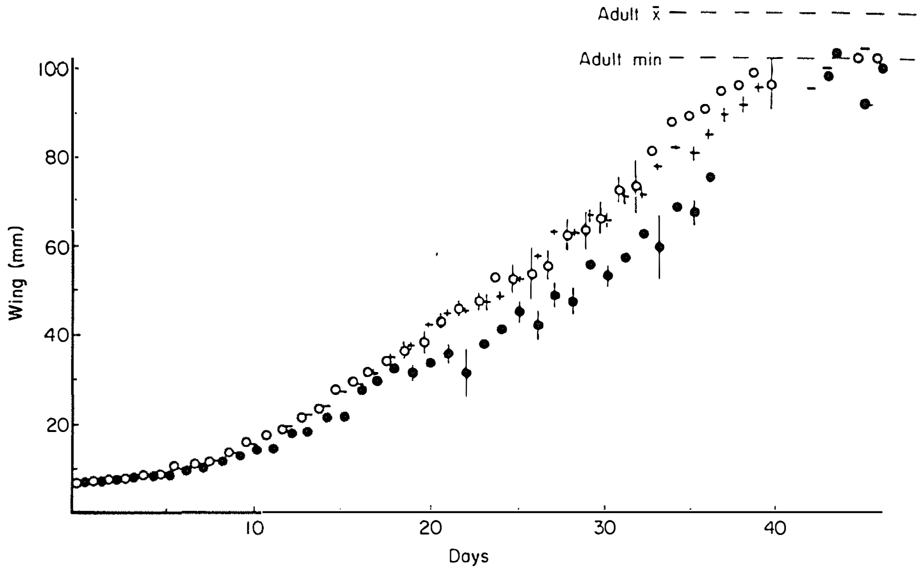


Figure 1. Mean daily increase in the wing length of White-rumped Swiftlet chicks in different sized broods: the means for broods of one are represented by hollow circles, broods of two by horizontal bars and broods of three by solid circles. Standard errors of the means (vertical lines) for chicks in broods of three rarely overlap those for chicks from single or double broods after the tenth day. Although $n = 118$, not all chicks were measured each day, hence the unevenness of the growth curves.

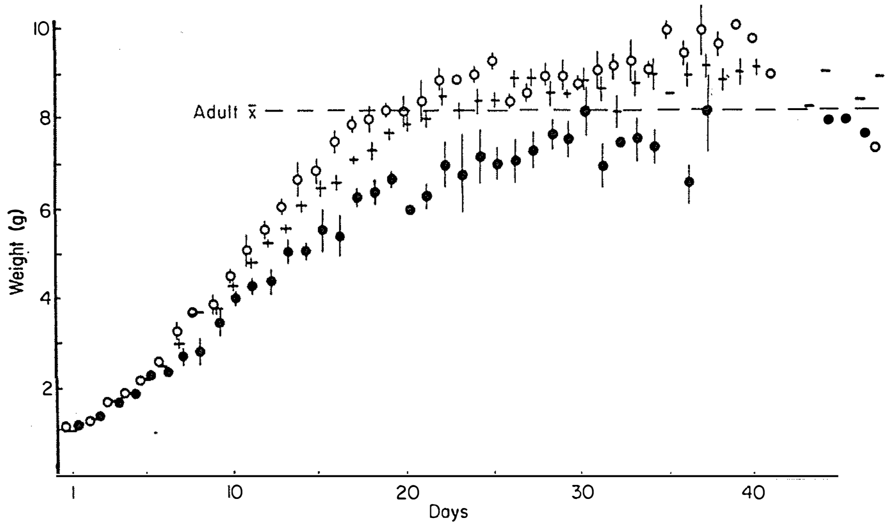


Figure 2. Mean daily increase in White-rumped Swiftlet chick weight: the means for broods of one are represented by hollow circles, broods of two by horizontal bars and broods of three by solid circles. Standard errors of the means (vertical lines) for chicks in broods of three rarely overlap those for chicks from single or double broods after the tenth day. Although $n = 118$, not all chicks were measured each day, hence the unevenness of the growth curves.

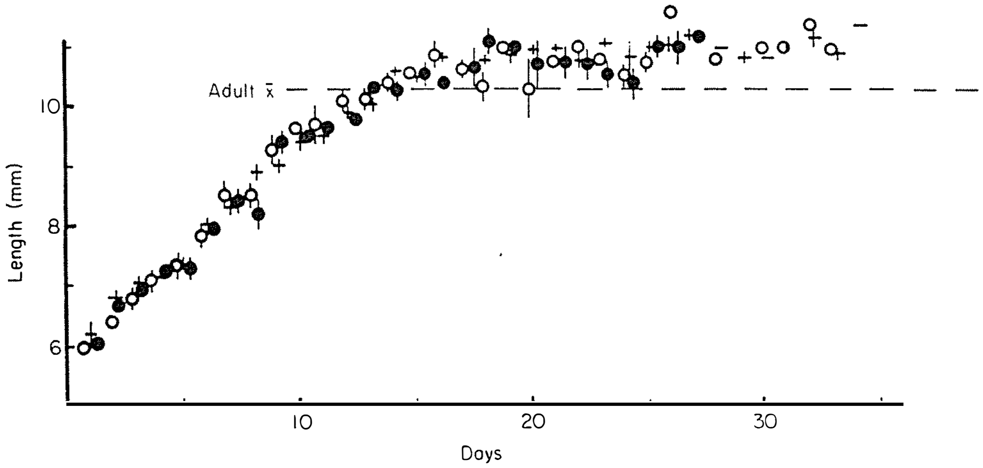


Figure 3. Mean daily increase in tarsal length of White-rumped Swiftlets: the means for broods of one are represented by hollow circles, broods of two, horizontal bars and broods of three by solid circles. The consistent overlap between the standard errors (vertical lines) of chicks from all three clutch sizes indicates the small effect food supply has on tarsal growth.

Because average growth curves conceal certain characteristics of the individual growth curve and in particular the variation within a brood, the progress for a selection of individuals has been plotted in Figures 4 and 5. It will be noticed that even in the brood of three (and this was true for all other broods of three) death was not preceded by a drop in weight as in the Common Swift in wet summers (Lack & Lack 1951) and sometimes in the smaller siblings of the Edible-nest Swiftlet *Aerodramus fuciphagus* (Langham 1980).

Feeding rate

The four full-days observation on a sample of the manipulated nests demonstrated that the average of 2·9 ± 0·34 visits ($\bar{x} \pm$ SE, $n = 11$) to broods of three was significantly greater (Median test, $X^2_1 = 4{\cdot}97$, $P < 0{\cdot}05$) than the 2·2 ± 0·1 visits ($n = 18$) to broods of two. The 2·1 ± 0·01 visits ($n = 18$) to broods of one was not significantly different (Median test), $X^2_1 = 0{\cdot}8$, n.s.) from the number of trips to broods of two. The feeding rate per chick (1·0 feed each) in broods of three was not significantly different ($t_{27} = 1{\cdot}1$) to the feeding rate (1·1 feeds each) per chick in broods of two.

During the day's observation in 1981 a simultaneous collection of data was made on 20 undisturbed nests. These were not part of the manipulation experiment, and were so high as to be out of reach. An average of 2·8 ± 0·26 feeding visits were made to these nests. As these nests undoubtedly contained both one- and two-chick broods they can be compared to the combined average of 2·17 ± 0·06 visits to manipulated broods of one and two chicks. Because the difference is significant ($t_{34} = 2{\cdot}36$, $P < 0{\cdot}05$), the possibility arises that my presence was reducing the number of feeding visits made by parents whose chicks were being regularly handled. Such an effect would be equal in all sized clutches and so not affect the comparison between different-sized clutches. However, birds nesting at greater heights might be older, have closer feeding ranges and/or have some other benefit that will increase their capacity to provide for their brood.

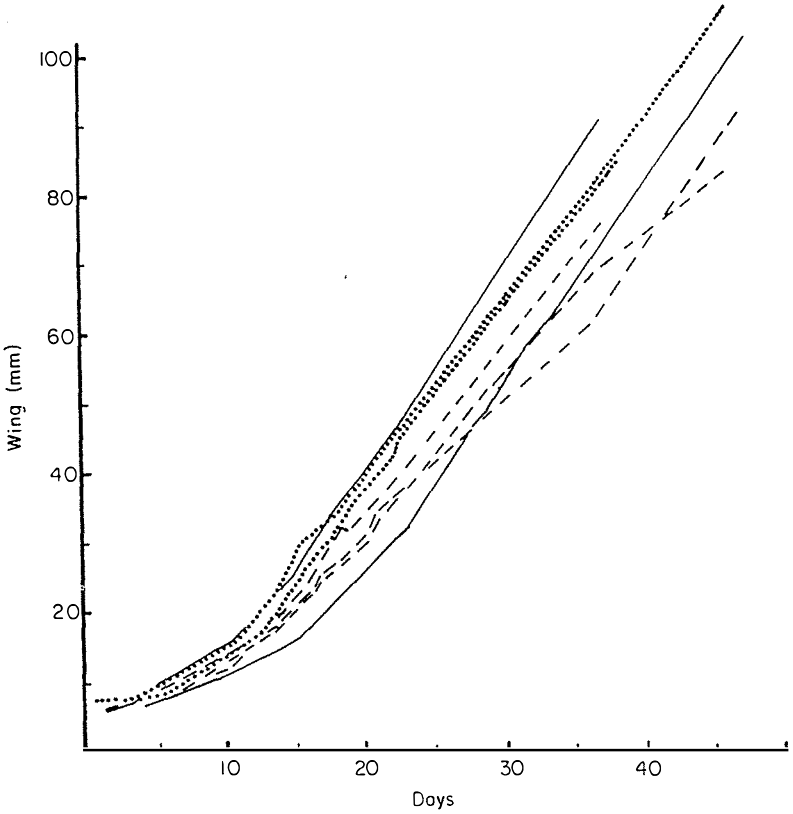


Figure 4. Wing growth of White-rumped Swiftlet individuals from broods of all sizes. Chicks from single broods are represented by continuous lines, those from broods of two by dotted lines, and those from broods of three by discontinuous lines.

Conclusions

Despite the apparently favourable weather for gathering food, the three chicks in artificially enlarged broods experienced significant delays in wing growth and weight increase. Such results are inconclusive because survival studies following brood manipulation of the Puffin *Fratercula arctica* (Harris 1982) and the Blue Tit *Parus caeruleus* (Nur 1984a,b) show that such a delay does not necessarily reduce the future survival of either chicks or parents. This should be particularly true in the Apodidae where chicks are adapted to withstand long periods without food.

Because broods of three were fed significantly more than broods of two, it appears that the White-rumped Swiftlet of Fiji is not maximizing its harvest of the available food supply during the breeding season. Even though the feeding rates to broods of two and three were not significantly different, parents could not hatch significantly more chicks when given a third egg, or fledge significantly more chicks when given a third chick. It is clear that parents are maximizing the number of fledglings thay can raise. The inability to rear three chicks may mean that food boluses are smaller when the feeding rate increases, thus preventing significantly more chicks fledging from the larger broods.

Although this swiftlet is not maximizing its harvest of the available food supply, this does not mean that they are reducing annual production in order to optimize their life-long production. However, the effort saved by not working at its maximum

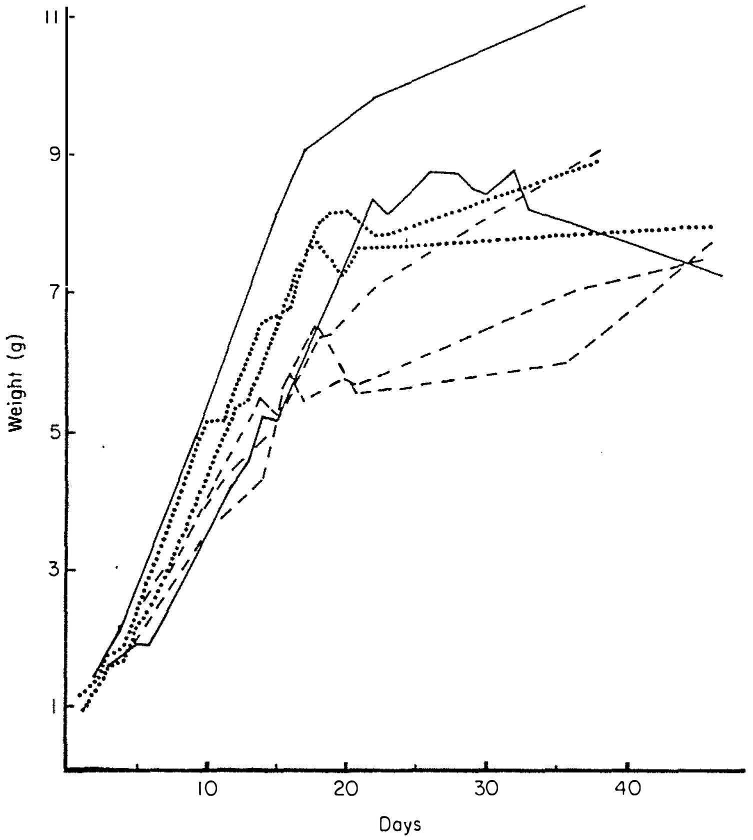


Figure 5. Weight increase in White-rumped Swiftlet individuals from all three sized broods. Chicks from single broods are represented by continuous lines, those from broods of two, by dotted lines and those from broods of three by discontinuous lines.

food-gathering capacity may help to explain why the White-rumped Swiftlet is a long-lived species for its size (Tarburton in prep.).

The helpful advice and criticism given by Dr Edward Minot in preparing this paper as part requirement for a Ph.D. degree from Massey University is gratefully acknowledged.

Ashmole, N.P. 1961. The biology of certain terns. D.Phil. thesis (Oxford): cited by Lack & Moreau 1965.

Ashmole, N.P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103b: 458–473.

Charnov E.L. & Krebs, J.R. 1974. On clutch-size and fitness. Ibis 116: 217–219.

Gadgil, M. & Bossert, W.H. 1970. Life historical consequences of natural selection. Am. Nat. 104: 1–24.

Goodman, D. 1974. Natural selection and a cost ceiling on reproductive effort. Am. Nat. 108: 23–31.

Harris, M.P. 1982. Seasonal variation in fledging weight of the Puffin *Fratercula arctica*. Ibis 124: 100–103.

Lack, D. 1947. The significance of clutch size. Ibis 89: 302–352, 90: 25–45.

Lack, D. 1956. Swifts in a tower. London: Methuen.

Lack, D. & Lack, E. 1951. The breeding biology of the Swift *Apus apus*. Ibis 93: 501–546.

Langham, N. 1980. Breeding biology of the Edible-nest Swiftlet *Aerodramus fuciphagus*. Ibis 122: 447–460.

Murphy, G.I. 1968. Pattern in life history and the environment. Am. Nat. 102: 391–403.

Nur, N. 1984a. The consequences of brood size for breeding Blue Tits I. Adult survival, weight change and the cost of reproduction. J. Anim. Ecol. 53: 479–496.

Nur, N. 1984b. The consequences of brood size for breeding Blue Tits II. Nestling weight, offspring survival and optimal brood size. J. Anim. Ecol. 53: 497–517.

PIANKA, E.A. & PARKER, W.S. 1975. Age specific reproductive tactics. Am. Nat. 109: 453–464.

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

WILLIAMS, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Nat. 100: 687–692.

WINKLER, D.W. & WALTERS, J.R. 1983. The determination of clutch size in precocial birds. Current Ornith. 1: 33–68.

Department of Botany and Zoology, Massey University, Palmerston North, New Zealand

APPENDIX 5

Bird Behaviour 6: 72-84

A Comparison of the Flight Behaviour of the White-rumped Swiftlet and the Welcome Swallow

M. K. Tarburton
Department of Botany and Zoology, Massey University
Palmerston North, New Zealand

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

A number of physical and behavioural characters are used to compare the flight of the White-rumped Swiftlet *Aerodramus spodiopygius* with that of the Welcome Swallow *Hirundo neoxena*. Although the Swiftlet conserves energy by gliding more and having a slower wing beat, it also reaches higher speeds and altitudes and spends more time in flight each day than the Swallow. The published morphological data on other members of the swift and swallow families are compared to test the predictive value of two manoeuvrability indices (36). I believe that the indices are invalidated by problems of allometry and so cannot be used to compare birds of different sizes. An improved index formula is suggested.

White-rumped Swiftlet *Welcome Swallow* *Manoeuvrability* *Allometry* *Flight moult*

Introduction

White-rumped Swiftlets *Aerodramus spodiopygius* can fly continuously for up to 16 hours (pers. obsev.), and must therefore be well designed for flight. But for what type of flight are they best equipped? Because up to 30,000 White-rumped Swiftlets may live in one cave (64), an ability to forage widely is probably important. Lack (41) suggested that the wings of the Apodinae are adapted for high speed; and certainly high speed flight would allow a large population to disperse rapidly to distant foraging areas. But can wings adapted for high speed, also be adapted for manoeuvrability? Circumstantial evidence suggests that high speed and manoeuvrability can be combined. Hespenheide (38) believed that the relative scarcity of flies in the diets of birds is a result of the flies' speed and agility. White-rumped Swiftlets have a large proportion of flies in their diet (60, 64). This fact and the smaller size of the Swiftlet than a number of swallows (Table 1) suggests that Lack (41) was incorrect in postulating that swallows are better designed than the smaller swifts for catching tiny insects. One way of assessing the flight speed and manoeuvrability of swifts and swallows is to make interspecific morphological and behavioural comparisons, both within and between the Apodinae and the Hirundines.

Hails (35) has shown that two martins, *Progne subis* and *Delichon urbica*, a swallow *Hirundo rustica* and the Common Swift *Apus apus* all have similar flight capacities in terms of energetics. When metabolic estimates were made (in cal.g.$^{-1}$ hr^{-1}), each species was shown to be, not only similar to one another but also similar to the Golden Plover *Pluvialis dominica*, Rock Dove *Columba livia*, three larids and two anatids, though each was more efficient than a number of other birds. However, because the energetic cost of flight per gram of the birds weight, decreases with increasing body weight, comparisons will only be valid when either the metabolic rate of flight is compared with the resting metabolic rate of the same species or flight costs are compared between species of similar weight. Either way, the Apodidae and the Hirundines have the lowest flight costs of any birds measured so far (Table 2).

In order to fly, birds must expend energy in three ways (54): to generate lift, to overcome drag caused by non-lifting parts (parasitic drag), and to overcome the drag created by movement of the wings. The Hirundines and Apodines have morphological characteristics that tend to reduce the energy required for each of these activities (35). Firstly, these birds have relatively long wings and weigh little compared with their wing area (i.e. they have a low loading); thus they generate lift more easily than do birds of similar size. Secondly, the streamlined head, short neck and tapered abdo-

TABLE 1
MANOEUVRABILITY INDICES OF SOME SPECIES OF APODIDAE HEMIPROCNIDAE AND HIRUNDINIDAE

Species	Wing mm	Tail Outermost Rectrix	Weight g	Sample Size	Wing Index	Tail Index	References
White-rumped Swiftlet *Aerodramus spodiopygius*	112.0	44.7	8.19	102	13.68	5.46	A
White-bellied (Glossy) Swiftlet *Collocalia esculenta*	102.0	40.4	8.28	–	12.32	4.87	36
Mossy-nest Swiftlet *Aerodamus vanikorensis*	124.0	53.8*	10.99	37	11.28	4.90	3,58,69,B
Neotropical Palm Swift *Reinarda squamata*	112.5	69.5	10.36	4	10.86	6.71	C
Edible-nest Swiftlet *Aerodramus fuciphagus*	116.0	50.6	10.80	8	10.74	4.69	44,63
Old World Palm Swift *Cypsiurus parvus*	129.2	50.6	10.80	421	9.4	7.79	12
Wire-tailed Swallow *Hirundo smithi*	112.0	M 74	12.7	–	8.82	5.83	
		F 51.5	12.7	6	8.82	4.1	26,48
Eastern Rough-winged Swallow *Psalidoprocne orientalis*	104.5	83.0	11.9	3	8.78	6.97	47
Black-nest Swiftlet *Aerodramus maximus*	131.9	47.9	15.9	21	8.30	3.01	37,63
Boehm's Swift *Neafrapus (Mearnsia) boehmi*	121.7	–	15.3	–	7.95	–	26,69
Welcome Swallow *Hirundo neoxena*	110.0	67.5	13.92	6	7.90	4.85	A
Sabines Spinetail *Rhaphidura sabini*	120.9	–	16.6	79	7.28	–	10
Bank Swallow *Riparia riparia*	105.5	48.0	14.6	249	7.23	3.29	46,62
Band-rumped Swift *Chaetura spinicauda*	102.6	–	14.2	19	7.23	–	61
Pacific Swallow *Hirundo tahitica* Malaysia	–	–	14.75	35	6.98	3.08	36
Fiji	109.1	46.6	17.8	11	6.13	2.62	A
Mangrove Swallow *Tachycineta albinia*	99.0	41.3	14.5	7	6.83	2.85	57,C
Short-tailed Swift *Chaetura brachyura*	122.0	31.0*	18.3	240	6.67	1.69	18
Grey-rumped Swift *Chaetura cinereiventris*	101.5	–	15.71	83	6.46	–	18,61
Lesser-striped Swallow *Hirundo (Cecropis) abyssinica*	110.7	97.0	17.2	5	6.44	5.64	26,47
Caffer Swift *Apus caffer*	141.8	74.0	22.1	229	6.42	3.35	9,26,47
Barn Swallow *Hirundo rustica*	125.0	87.0	19.5	10	6.41	4.56	47
Vaux Swift *Chaetura vauxi*	115.0	–	18.11	174	6.35	–	2,19
Chestnut-collared Swift *Cypseloides rutilus*	124.0	40.0*	20.2	45	6.14	1.98	18
Fork-tailed Swift *Apus pacificus*	180.0	80.0	29.6*	–	6.08	1.75	32,56
House Martin *Delichon urbica*	112.0	58.5	19.8	7	5.66	2.95	47

TABLE 1 (continued)

		Species mm	Wing Outermost	Tail g	Weight Size	Sample Index	Tail Index	References
Horus Swift								
Apus horus		152.2	58.0	27.37	140	5.56	2.12	9.18,47
Chimney Swift								
Chaetura pelagica		128.0	37.6	23.6	1805	5.42	1.59	27,30,C
Pallid Swift								
Apus pallidus		170.1	–	36.7	7	4.63	–	52
House Swift								
Apus affinis	Asia	–	–	–	–	4.29	1.54	35
	Africa	131.0	44.5	27.2	–	4.82	1.64	17,47
White-throated Swift								
Aeronautes saxatalis	F	138.5	55.7	32.3	18	4.29	1.72	4
	M	140.4	56.8	34.2	22	4.11	1.66	
Common Swift								
Apus apus		173.0	72.0	42.7	35	4.12	1.70	43,47
African Bearded Swift								
Apus barbatus		172.0	74.5	42.28	89	4.07	1.76	5
Bradfield's Swift								
Apus bradfieldi		171.7	63.3	43.0	82	4.00	1.47	5,6,
Grey-breasted Martin								
Progne chalybea		131.0	61.5	33.5	–	3.91	1.84	18,71
Black Swift								
Cypseloides niger		170.0	57.5	45.6	12	3.73	1.28	C
Mosque Swallow								
Cecropis senegalensis		143.5	95*	40.7	–	3.53	2.33	26,47
San Geronimo Swift								
Panyptila santiheronymi		183.7	86.9	56.65	9	3.24	1.53	1,16,59,C
Chapins Spinetail								
Chaetura melanopygia		167.4	49.4	52.0	7	3.22	0.95	45
Mottled Swift								
Apus equatorialis		203.1	87.5	93.08	28	2.18	0.94	7,12
Alpine Swift								
Apus melba	S.W. Angola	199.8	–	76.0	20	2.63	–	8
	Spain	222.6	–	87.0	10	2.56	–	52
	S.W. Africa	202.6	85.5	91.0	15	2.23	0.94	8
	Russia	220.0	–	102.5	28	2.15	–	23
	Uganda	226.2	–	127.6	19	1.77	–	8
White-collared Swift								
Streptoprocne zonaris		197.0	–	98.1	19	2.01	–	19,71
White-throated Needletail								
Chaetura caudacuta	F	200.0	88.0+	113.7	4	1.76	0.77	51
	M	200.0	88.0+	122.2	11	1.64	0.72	51
white-naped ~~Chestnut-collared~~ Swift								
Streptoprocne semicollaris		228.0	81.7	C175.0	–	1.30	0.47	18,C
Philippine Needletail								
Chaetura celebensis		219.0	64.0	179.6	22	1.22	0.36	50

* Based on mean or mode and therefore probably an under or overestimate

A This paper

B American Museum of Natural History

C Los Angeles County Museum of Natural History

TABLE 2

ESTIMATES OF METABOLISM DURING FLIGHT FOR A VARIETY OF AVIAN SPECIES

Species		Body Weight (g)	Metabolism ($J\ g^{-1}\ hr^{-1}$)	Source
Sooty Tern	*Sterna fuscata*	187.0	92	Flint & Nagy 1984
Mallard	*Anas platyrhynchos*	1000.0	152	Dolnik & Gavrilov 1973
American Black Duck	*Anas rubripes*	1026.0	152	Berger *et al* 1970
Common Swift	*Apus apus*	40.5	156	Lyuleeva 1970
Great Black-backed Gull	*Larus marinus*	800.0	156	Dolnik & Gavrilov 1973
Ring Billed Gull	*Larus delawarensis*	410.0	180	Berger *et al* 1970
House Martin	*Delichon urbica*	19.0	168}	Keskpaik 1968
	Delichon urbica	20.5	180} 181	Lyuleeva 1970
	Delichon urbica	17.81	194}	Hails 1979
Laughing Gull	*Larus artricilla*	350.0	188	Tucker 1972
Golden Plover	*Pluvialis dominica*	140.0	220	Johnston & McFarlane 1967
Pigeon	*Columba livia*	384.0	224	Lefebvre 1970
Barn Swallow	*Hirundo rustica*	18.99	236	Hails 1979
	Hirundo rustica	17.8	259	Lyuleevva 1970
Purple Martin	*Progne subis*	51.0	264	Utter & Lefebvre 1970
Budgerigar	*Melopsittacus undulatus*	35.0	388	Tucker 1968
Blue-throated Bee-eater	*Merops viridis*	33.8	421	Bryant *et al* 1984
Loggerhead Shrike	*Lanius ludovicianus*	48.6	488	Weathers *et al* 1984
Pacific Swallow	*Hirundo tahitica*	14.1	581	Bryant *et al* 1984
Common Rosefinch	*Carpodacus erythrinus*	60.0	640	Berger *et al* 1970
Bullfinch	*Pyrrhula pyrrhula*	29.5	654	Dolnik & Gavrilov 1973
Chaffinch	*Fringilla coelebs*	22.5	608} 656	Dolnik & Gavrilov 1973
	Fringilla coelebs	22.0	704}	Dolnik & Gavrilov 1973
Brambling	*Fringilla montifringilla*	23.3	630	Dolnik & Gavrilov 1973
Costa's Hummingbird	*Calypte costae*	3.0	792	Lasiewski 1963
Purple Carib Hummingbird	*Eulampis jugularis*	8.3	820	Hainsworth & Wolf 1969
Siskin	*Carduelis spinus*	12.5	820	Dolnik & Gavrilov 1973
Glittering-throated Emerald Hummingbird	*Amazilia fimbriata*	5.5	824	Berger & Hart 1974
Savannah Sparrows	*Passerculus sandwichensis*	19.1	992	Williams & Nagy 1984

men and tail reduce the energy required to overcome parasitic drag. Lastly, the sickle-shaped wings and high wing aspect ratio (wing span to wing area) of Hirundines, Hemiprocnidae (Crested or Tree Swifts) and Apodidae results in reduced profile drag. This last characteristic is unexpected as it would seem logical for larger than average wings to create larger than average wing drag when in motion.

If these characteristics can be used to demonstrate the efficiency of swallows, swifts and tree-swifts over other birds, they can also be used for comparisons within and between the three orders.

In the second assumption we have the naive expectation that a measure of length is linearly related to weight or volume. For example, when the data for wing length and weight from Table 1 are graphed as in Figure 1 it is clear that a straight line does not provide a good fit. Thus the wing index used by Hails and Amirrudin (36) is very dependent on the weight of the bird (Figure 2). However, as with most allometric problems the relationship between weight and wing length is better described by a power function i.e., an equation of the form $y = a X^b$. The curve in Figure 1 is of this form and is the least squares fit to the power function, $y = 55.0 X^{0.29}$ ($R^2 = 0.93$; df = 50; $P<0.001$). An index of manoeuvrability based on wing length might employ this power function and could take the form of wing length / wing length predicted from weight. Predicted wing length equals 54.95 $(\text{weight})^{0.29}$ based on the data in Table 1. This could be improved to give symmetry about the mean by taking the log of this ratio i.e., wing index = lg (wing length / predicted wing length). This new index may be used to compare all members of the Apodidae and Hirundinidae regardless of their weight (Figure 3). The new index in effect allows an examination of deviations from the general relationship between wing length and weight for a number of species. It is worthwhile noting that almost all of the Hirundines are found in the lower left corner of the graph indicating that after adjustment for allometry, hirundines have a smaller wing than apodines.

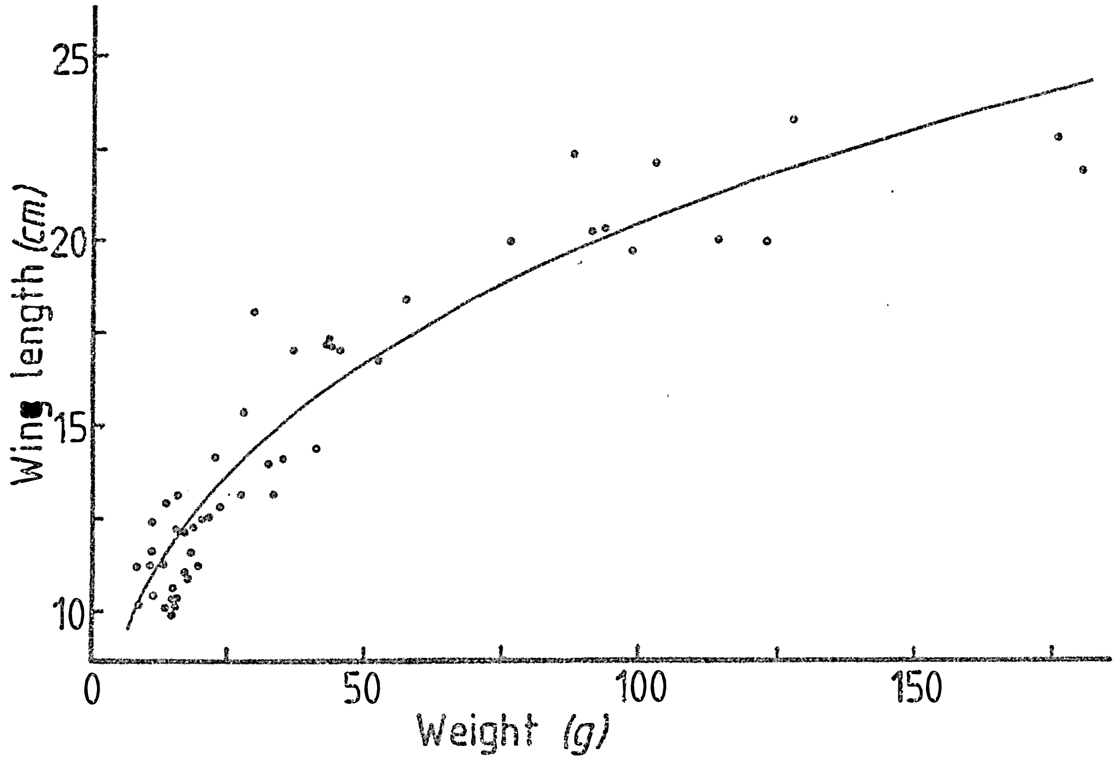


Figure 1. The relationship between wing length and weight in those swifts and swallows given in Table 1.

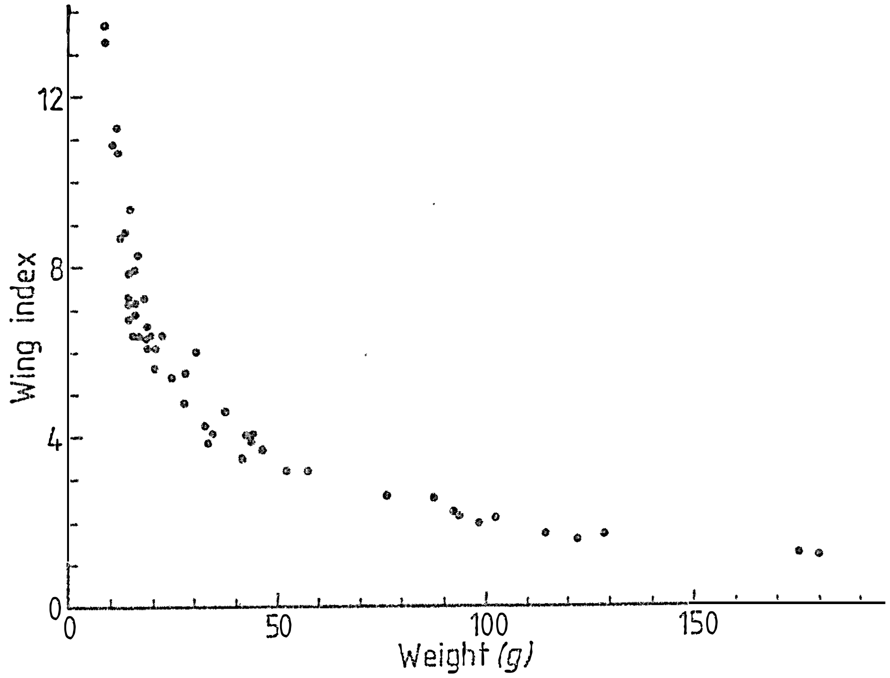


Figure 2. The relationship between the wing index used by Hails and Amirrudin (36) and the weight of the swifts and swallows given in Table 1.

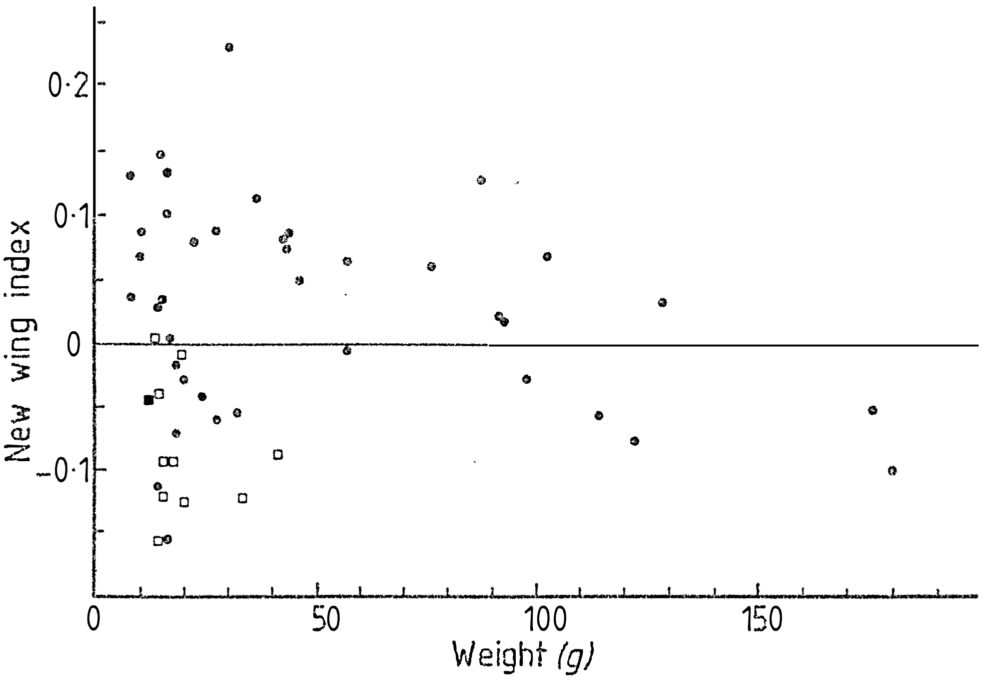


Figure 3. The new wing index plotted against the weight of the swifts and swallows given in Table 1.

TABLE 3
FLIGHT BEHAVIOUR

	Wing Beats per second $\bar{X} \pm$ S.E.	n	Length of Glide (seconds) $\bar{X} \pm$ S.E.	n	Length of Wing-beat Sequence (seconds) $\bar{X} \pm$ S.E.	n
White-rumped Swiftlet						
Circuit Feeding	4.7 ± 0.20	33	1.17 ±0.09	35	1.84 ± 0.16	35
High Movement	4.7 ± 0.14	50	10.36 ±2.1	45	4.40 ± 0.70	45
Welcome Swallow						
Circuit Feeding	5.71 ± 0.14	31	1.51 ± 0.15	30	17.55 ± 1.8	44
High Movement	5.79 ± 0.29	16	1.0	6	39.84 +	6

Other Flight Behaviour. During feeding flights gliding is undoubtably important, for as Pennycuick (55) points out, it is achieved at a much lower cost than Flapping flight. Hails (35) has calculated that the swifts and house martins, which glide the most, have a flight cost saving of 72%; whereas swallows, which glide the least, have only a 62% saving over other birds of similar size. I have tested these findings in the field by comparing the flight behaviour of the White-rumped Swiftlet with that of the Welcome Swallow. The results are shown in Table 3.

The average length of time in each glide for the Swallow (1.5 s) and the Swiftlet (1.2 s) was not significantly different (t =1.94; df=63; P<0.05). However, since the time spent flapping by Swallows (17.6 s) is considerably longer than that spent flapping by Swiftlets (1.8 s), it is clear that the Swiftlet glides more than the Swallow when feeding. Two other factor also show that the Swiftlet conserves energy better than does the Swallow. Firstly, feeding Swallows have a significantly faster wing-beat rate (0.57 s) than the feeding Swiflets (0.47 s) (t = 3.8; df = 34; P<0.001). Secondly Swallows rest from flying by perching for an average of 3.0 min after an average flight time of 2.45 min, compared with the Swiftlet, which does not perch or rest at all through the day (in the non-breeding season). Even in the breeding season parents take only one to three rests (lasting one to 20 min) at their nest.

Methods

Comparisons between the White-rumped Swiftlet and Welcome Swallow were based largely upon two manoeuvrability indices used by Hails and Amirrudin (36) to compare the White-bellied Swiftlet *Collocalia esculenta,* House Swift *Apus affinis* and Pacific Swallow *Hirundo tahitica.* These authors use the long wings and tail as well as the light weight of the White-bellied Swiftlet to explain not only its reduced energetic costs but also its greater manoeuvrability, which allows the Swiftlet to forage much closer to vegetation than other swifts. The first manoeuvrability index (tail index) is the ratio of the outer (longest) rectrix length to body weight and is attributed by Hails and Amirrudin (36) to Waugh (68) and Bryant and Westerterp (14). The second index (wing index) is the ratio of the wing length to weight. For both indices the higher the index the greater the manoeuvrability.

For this study indices were derived from measurements of live White-rumped Swiftlets caught in Fiji, of skins of the Pacific Swallow in the National Museum of New Zealand and of live Welcome Swallows caught at Longburn, New Zealand. All other measurements were taken from published data or from museums as shown in Table 1. Those tail measurements marked with an asterisk were based on the mean tail length and so slightly underestimate the length of the outer rectrix in species with forked tails and overestimate the length of the outer rectrix in species with only slightly bifurcated tails.

Other features of flight that were measured were (i) average length of time of a sequence of wing beating, (ii) number of beats per flapping sequence, and (iii) average length of a glide. Single beats were ignored because they appeared to be used for manoeuvring rather than propulsion, and also because they were below my reaction time to record with a (Casio C-80) stopwatch. All three measures were determined for feeding flights and travel fights. During feeding flights, the birds flew in feeding circuits that approximated circles with a diameter range of about four to 50m. During travel flight, the birds usually flew at greater altitudes (30-130 m for the Swiftlets, 10-40 m for the Swallows) and were moving to or from their feeding areas. Although the Swiftlet travel flights were measured close to the Nasinu caves, 15 km north of Suva, in Fiji, feeding circuits en route to feeding areas were not uncommon and these were included in the data for travel flight.

Results and Discussion

Manoeuvrability in Flight. In applying the manoeuvrability indices to 40 additional species of Hirundines and Apodines, I have found that there is considerable variation (Table 1). Hails and Amirrudin's (36) assertion of high manoeuvrability in the White-bellied Swiftlet is substantiated to the extent that as measured by the tail index, their manoeuvrability is higher than that of most swifts. However, the same index shows that the White-rumped Swiftlet is even more manoeuvrable, while the wing index indicates greater manoeuvrabilities among four swiftlets. Thus it is no longer possible to claim that the White-bellied Swiftlet's manoeuvrability is exceptional in the Apodidae.

For the wing index the White-rumped Swiftlet had the highest manoeuvrability rating, but for the tail index two palm swifts and three swallows were given the highest rating. This inconsistency between the two indices leads one to question their validity. In using the indices we make two assumptions, both of which are possible sources for error. The first is that each index actually measures manoeuvrability, and the second is that each index overcomes the allometric problem of comparing species of different weights.

One way of testing the first assumption would be to compare the manoeuvrability indices with the proportion of prey in the diet that is difficult to catch. The difficulty of capturing each type of prey could be determined by comparing the proportion of each type in the diet with its availability where and when the bird forages. This procedure has been considered elsewhere (64), where it was shown that flies, which are said to have high manoeuvrability (38), are equally likely to dominate in sampled diets of birds with high or low manoeuvrability indices. However, to determine whether species with low indices take only those fly species that lack manoeuvrability will require further study.

During travel flight, differences between species were even greater. The Swiftlet beats 4.7 times a second and the Swallow 5.8 times a second. The Swiftlet glides for much longer (10.4s) than the Swallow (1.0s), but beats for much shorter periods (4.4s) than the Swallow (39.8s). A Swiftlet that started flapping overhead rarely flew out of sight in the same flapping sequence, whereas Swallows in travel flight usually did so.

Visual differences in the flight of the two species were obvious. Wetmore (70) noted that swifts generally fly higher than the smaller swallows. The White-rumped Swiftlet, which is smaller in size to both the Pacific *Hirundo tahitica* and Welcome Swallow, feeds from 10 cm to 130 m above the ground. This is considerably higher than the altitudes at which the two swallows feed (from nearly zero over water to 30m).

A second difference is that when gliding both swallows hold their wings slightly closed and close to the body, whereas Swiftlets hold their wings well away from the body resulting in the characteristic sickle-shaped curve. Mayr (48) used this character to separate swiftlets from swallows in the south-west Pacific. The sickle-shaped curve of the Swiftlet is accentuated by the pointed wing tips where the first primary is 8mm shorter than the second primary as well as having an emarginated inner web. Lack (42) suggested that the short first primary (which he found to be 5mm shorter than the second in other species of swiftlets) and the wing slot (caused by the feather emargination) help give greater control in slow flight.

A third difference is the amplitude of the wing beat. Both the Pacific and Welcome Swallow almost always use large amplitude strokes, whereas the Swiftlet only uses such strokes in tight manoeuvres and slow flight, especially in caves.

A fourth difference occurs when feeding flight is in a straight line: both swallows exhibit a regular undulation but the Swiftlet does not. Rather, swiftlets change altitude irregularly, sometimes pulling up to a halt to catch prey and then diving down again to gain airspeed. The tail is often fully spread in this activity and its considerably larger area than that of the swallows' forked tail must aid in performing the manoeuvre.

Fifthly, deviation to the side is infrequent and gradual in both swallows, but not the Swiftlet. A gliding Swiftlet may quickly drop one wing to swerve sideways; or if the insect prey is further to the side the bird may rapidly twist the body and tail to bring the momentarily gaping mouth in line with the prey.

A further difference is that only Swiftlets fly in total darkness. Audible clicks are used to guide their way in the dark.

Both species of swallows and the Swiftlet sometimes put on a burst of rapid wing beating to alter altitude in pursuit of prey. At times the Swiftlet will turn such sequences into impressive power dives, reminiscent of the larger swifts. By contrast, descriptions of the feeding flight of some swift species include comments on their lack of manoeuvrability. For example, White-throated Spinetails feeding on a grasshopper swarm in Queensland (15) were never seen to make a second attempt to catch the same grasshopper for the swift would rather select another target 'more or less on the bird's line of flight' and Philippine Spinetails feeding on bees, near their hives (50) had such 'straight' flight that the local people regularly caught the birds by swinging pole-mounted fish nets into their flight paths.

Another problem for aerial feeding birds is heat production. Ricklefs (57) found that on sunny afternoons the Three Swallow *Iridoprocne bicolor* only slightly reduced its foraging in its temperature habitat; whereas the closely related, tropical Mangrove Swallow *Tachycineta albilinea,* drastically reduced its midday foraging regularly. Ricklefs (57) demonstrated that the radiational heat absorbed by a bird in the middle of the day approached that generated by its metabolism during flight and thus caused problems of regulating its temperature. That there is reduction in insect abundance and size around midday (38) could also contribute to the Mangrove Swallow's relative inactivity; but Ricklefs (57) noted that sympatric flycatchers feed most frequently during the middle of the day. Since the White-rumped Swiftlet does not stop flying in the heat of the day, it's greater flight efficiency presumably not only allows it to catch highly manouevrable prey, unobtainable by most other aerial predators, but also allows it to do so right through the heat of the tropical day.

Another aspect of flight efficiency in the Apodidae can be seen in Bryant's (13) observations on the habit of leg trailing during flight in 17 Malaysian birds. He showed that the Pacific Swallow and Red-rumped Swallow *Hirundo striolata* both increase their amount of leg trailing around midday, evidently for the purpose of dissipating excess heat. Two Apodidae, the White-vented Needletail *Hirundapus cochinchinensis* and House Swift *Apus affinis* and one Hemiprocnid, the Crested Swift *Hemiprocne longipennis,* did not show an increase in leg trailing during the hottest part of the day.

Several physiological processes have also been shown to help facilitate efficient flight in the Apodidae. For example, the Common, Alpine and Pallid Swifts have larger erythrocytes with greater oxygen affinity than passerines (52). Their haematological values and ratios of heart to body size are equal to those of montane birds living at altitudes above 2500m. Because the breast muscles of the swifts are smaller (15.6 to 19.7% of body weight) than those of the Pigeon *Columba livia* (26.5%), they make more efficient use of the haematological adaptations. This efficiency has been demonstrated by comparing the energy used in flight by the Common Swift, four Hirundines and four other birds of similar weight (Table 2). The Swift used 39.0 cal.g^{-1} hr^{-1} which is 5.4 times its average metabolic rate while roosting (Sleeping Metabolic Rate), whereas the other birds averaged 152 cal. g^{-1} hr^{-1} which is 12 times their SMR.

Although these physical and physiological features work together to reduce the energetic needs of the White-rumped Swiftlet their habit of flying longer than the diurnal period, without rests, means that in a day's flying they probably do not save as much energy in a day when compared with the Hirundines. The gross daily energy consumption of the Common Swift is 30.7 kcal, whereas that of the House Martin and Barn Swallow is 17.0 kcal and 17.4 kcal per day (25). When these energy expenditures are corrected for differences in body size, by dividing them by the body weight of each bird (Table 1), the comparisons still show an advantage to the Swift. The Common Swift consumes 0.72 kcal g^{-1} d^{-1}, the House Martin 0.86 kcal $g^{-1}d^{-1}$, and the Barn Swallow 0.89 kcal $g^{-1}d^{-1}$. However, some of this advantage will result from the reduced thermoregulatory costs of the Swift due to its larger body size than the two Hirundines.

Speed of Flight. The flight speeds attainable by swifts are both breathtaking and legendary. The Needletailed Swift *Chaetura caudacuta* has been described as one of the fastest-flying birds in the world, feeding and cruising at 50 to 130 km/h (31). The same bird has been described as the fastest bird in the Soviet Union with level flight speeds of up to 170 km/h (29). However, two other swifts have also been described as the world's fastest birds: the Brown-throated Needletail *Chaetura gigantea* with reputed speeds of up to 200 mph (33) and the Philippine Spinetail Swift *Chaetura celebensis*(22) with reputed speeds of well over 100 mph. The flight speed of the White-rumped Swiftlet can also be impressive, particularly when they are entering or departing through the opening of the caves used for roosting and nesting. In Fiji this Swiftlet usually increases its speed as it flies through the cave entrance. Why these bursts of speed were made at the entrance puzzled me until I realized that the cave entrance was where Barn Owls

Tyto alba lulu sometimes preyed upon the Swiftlets. The Owls apparently still find the concentration of swiftlets rewarding enough to periodically hunt at cave entrances. Similar behaviour has been reported for a small colony (24 nests) of Mottled Swifts *Apus aequatorialis* in Rhodesia (21) that occupied a cave whose entrance was patrolled by a pair of nesting falcons.

The entrance to the Waterfall Cave at Nasinu was suitable for marking off a 10m horizontal section through which White-rumped Swiftlets could be timed and 92 birds were timed through this section. The slowest took 1.51 s and the fastest 0.34 s. The average speed was 45 km/h; the slowest 24 km/h; and the fastest 106 km/h. Most birds appeared to fly even more quickly in their dives towards the cave entrance, but the difficulty of timing them there was not overcome.

Six Welcome Swallows timed across 119 m of paddock on their way to their evening roost ranged in speed from 41 to 66 km/h. Their average speed of 53.6 km/h was greater than the average flight speed of the Swiftlets. The maximum Swallow speed, however, which I estimated to be close to their maximum, was well below the maximum speed of the Swiftlets. This suggested many Swiftlets fly well below their maximum speed even when flying through predator patrolled areas.

My data (including Table 4) for moult in the White-rumped Swiftlet is similar to that of the Black-nest Swiftlet except that it starts earlier, in September or October instead of November or December. Moult in the primaries is accompanied by a burst of nest building and probably by enlargement of gonads as four out of six moulting birds found dead or accidentally killed were found to have enlarged gonads. The moult is reasonably synchronized, between individuals, symmetrical between right and left wings, and centrifugal (starting with the innermost or first primary). However, as Table 4 shows, 62% had not commenced moulting by December and 36% were still moulting their last (tenth) primary in June. No birds were found moulting primaries in August. The designated primary in the table was either missing or was the smallest regenerating feather in the tract. Sometimes two feathers were regenerating simultaneously (the outermost always being the least mature), but in only one bird were three growing at the one time. Wing coverts were found to be moulting in December, April and June. Tail feathers were found to be moulting in June, and head feathers in September.

Few tropical birds moult and breed at the same time though some show considerable overlap. Payne (53) looked at 1,050 specimens of tropical African birds and found that only 13% of 190 species showed overlap or synchronous moult and gonadal or breeding activity.

The only other moult data for swiftless that I can find in the literature relates to the Mossy-nest Swiftlet from Sumatra, where Wells (69) found two of five specimens were moulting their tenth primary. Although these birds had regressed gonads, a few nests contained eggs, hence synchrony is ruled out, though overlap would still be possible.

The martin genus *Progne* shows similar variation to *Aerodramus*. The tropical, northern and southern species all breed and moult at different times of the

TABLE 4

MOULT IN THE PRIMARIES

	Aug	Oct	Dec	Feb	Apr	Jun
Number Examined	130	13	65	55	44	50
Number not in moult	130	13	40	33	22	32
Number in moult						
P1	–	–	4	1	–	–
P2	–	–	10	1	–	–
P3	–	–	3	1	–	–
P4	–	–	5	–	–	–
P5	–	–	2	–	–	–
P6	–	–	–	5	–	–
P7	–	–	–	6	–	–
P8	–	–	1	3	1	–
P9	–	–	–	5	5	–
P10	–	–	–	–	16	18

year. The exception, *P.M. Modesta*, is endemic to the Galapagos Islands where it breeds while actively moulting (28).

Sleeping on the Wing. The Common Swift has been recorded as sleeping on the wing (41). The evidence includes an observation at night by a pilot of a group of Swifts and observations of groups heading out to sea at nightfall. Snow (61) suggests that the White-collared or Cloud Swift *Cypseloides (Streptoprocne) zonaris* may also sleep on the wing at times. Wattling (68) similarly believes that White-rumped Swiftlets sleep on the wing, but he gives no evidence. My banding and recapture data indicate that the population is larger than that found roosting in Dry Cave, Nasinu on any one night, and therefore it is possible that non-roosting birds may have spent the night on the wing.

The results of a Swedish experiment further demonstrate that swifts do not often fly at their fastest speeds. Altimeters, capable of measuring and recording frequent air pressure readings, were placed on Common Swifts that were then released 405 km from their nests. As well as showing that the homing birds reached altitudes of up to 3600 m and in clear weather held an average altitude of 2300 m, the altimeters showed that the birds spent an average of 12 h flying (34). This means the birds averaged less than 34 km/h if they flew in a straight line.

Moult of Flight Feathers. Moult of the flight feathers could conceivably affect flight performance in the Apodidae. Because of their total dependence on aerial feeding and small size it is to be expected that they would display some strategies for reducing the disadvantages of moulting. Many temperate birds solve the problem of moult affecting flight by having distinct and separate times of the year for breeding and moulting, thereby reducing the amount of energy required at any one time. This does not mean that all temperate zone swifts have a common moult and breeding cycle. The Lacks (43) noted that 'It is remarkable that of the two swifts breeding in central Europe, *A. apus* migrates a few days after breeding and moults in winter quarters, whereas *A. melba* undergoes a nearly complete moult before leaving the breeding colonies'. In West Africa the Sabines Spinetail *Raphidura sabini* commences moult shortly after laying; but the Stumpy-tailed Spinetail *Neafrapus cassini* moults at any time of the year, and moulting itself is no indication of an individual's breeding condition (6).

The swiftlets, which are all tropical, show even greater diversity. The Edible-nest Swiftlet showed no seasonal pattern in the number of primary flight feathers replaced over a seven month period (44). Moult in the Edible-nest Swiftlet was arrested in some breeding birds, and apparently resumed at the innermost primary as well as at the position where primary moult was halted. In the Black-nest Swiftlet, however, the progress of moulting the flight feathers was orderly, synchronized and annual (49). Moult of the primaries in the Black-nest Swiftlet started in November or December and was not interrupted in breeding birds though complete body moult took seven months. Two of five specimens of the Mossy-nest Swiftlet were found to be moulting tenth primaries, yet all five had regressed gonads.

Acknowledgements

I wish to thank Edward Minot for constructive advice during the preparation of this paper; I also thank Mary Lecroy (American Museum of Natural History), Charles T. Collins (University of California), Kimball Garrett (Los Angeles County Museum) and N. Hyde (National Museum of New Zealand) for measuring swifts and swallows.

References

1. **Arnold, K.A. and T.C. Maxwell.** 1970. The Great Swallow-tailed Swift *(Panyptila sactihieronymi)* from the state of Guerrero, Mexico. *Condor* **72**: 108.
2. **Baldwin, P.H. and N.K. Zaczkowski.** 1963. Breeding biology of the Vaux Swift. *Condor* **65**: 400-406.
3. **Becking, J.H.** 1971. The breeding of *Collocalia gigas*. *Ibis* **113**: 332-334
4. **Behle, W.H.** 1973. Clinal variation in White-throated Swifts from Utah and the Rocky Mountain region. *Auk* **90**: 299-306.
5. **Brooke, R.K.** 1970. Geographical variation and distribution in *Apus barbatus, A. bradfieldi and A. niansae* (Aves; Apodidae). *Durban Museum Novitate* **8**: 363-374.
6. **Brooke, R.K.** 1971. Breeding of swifts in Ethiopian Africa and adjacent islands. *Ostrich* **42**: 5-36.
7. **Brooke, R.K.** 1971. Taxonomic notes on some lesser known *Apus* swifts. *Bulletin of the British Ornithological Club* **91**: 33-36.
8. **Brooke, R.K.** 1971. Geographic variation in the Alpine Swift *Apus (Tachymarptis) melba* (Aves; Apodidae). *Durban Museum Novitate* **9**: 131-143.
9. **Brooke, R.K.** 1971. Geographic variation in the swifts *Apus horus* and *Apus caffer* (Aves: Apodidae). *Durban Museum Novitate* **9**: 29-38.

10. **Brooke, R.K.** 1971. Taxonomic and distributional notes on the African Chaeturine. *Bulletin of the British Ornithologists Club* **91:** 76-79.

11. **Brooke, R.K.** 1972. Geographical variation in Palm Swifts *Cypsiurus spp. Durban Museum Novitate* **9:** 216-231.

12. **Brooke, R.K.** 1973. Distributional and biological notes on the Mottled Swift in Rhodesia. *Ostrich* **44:** 106-110.

13. **Bryant, D.M.** 1983. Heat stress in tropical birds? behavioural thermoregulation during flight. *Ibis* **125:** 313-323.

14. **Bryant, D.M. and K.R. Westerterp.** 1979. Energetics of foraging and free existence in birds. *Proceedings of the 17th International Ornithological Congress* (Berlin).

15. **Cameron, A.C.** 1968. Feeding habits of the Spine-tailed Swift. *Emu* **68:** 217-219.

16. **Carr, M.H. and J.C. Dickinson Jr.** 1951. The San Geronimo Swift in Honduras. *Wilson Bulletin* **63:** 271-273.

17. **Chih-tung, K.** 1973. Preliminary studies in the breeding behaviour of the House Swift. *Acta Zoologica Sinica* **19:** 293-304.

18. **Collins, C.T.** 1968. The comparative biology of two species of swifts in Trinidad, West Indies. *Bulletin of the Florida State Museum* **11:** 257-320.

19. **Collins, C.T.** 1972. Weights of some birds of north-central Venezuela. *Bulletin of the British Ornithologists Club* **92:** 151-153.

20. **Collins, C.T. and R.K. Brooke.** 1976. A review of the swifts of the genus *Hirundapus* (Aves: Apodidae). *Contributions in Science; Los Angeles County Museum* **282:** 1-22.

21. **Cooke, P.** 1965. Breeding of Mottled Swift *Apus aequatorialis* (Von Muller) in the Matapos Hills, S. Rhodesia. *Ostrich* **36:** 38-39.

22. **Delacour, J. and E. Mayr.** 1946. *Birds of the Philippines.* New York: Macmillan.

23. **Dementyev, G.P., N.A. Gladcov, E.S. Ptushenko, E.P. Spangenburg and A.M. Sudilovskaya.** 1951. *Birds of the Soviet Union. Volume 1.* (English translation: Israeli program for scientific translations, Jerusalem).

24. **Dolnik, V.R. and V.M. Gavrilov.** 1973. Energy metabolism during flight of some passerines. In *Bird Migrations, Ecological and Physiological Factors.* Edited by B.E. Bykhovskii. New York: Halstead Press.

25. **Dolnik, V.R. and L.I. Kimzhevskaya;** 1981. Time and energy budgets during the nest period in the swift *(Apus apus)* and swallows *(Delichon urbica, Hirundo rustica). Zoologicheskii Zhurnal* **59:** 1841-1851.

26. **Donnelly, B.G.** 1974. Vertical zonation of feeding swallows and swifts at Kariba, Rhodesia. *Ostrich* **45:** 256-258.

27. **Dunning, J.B.** 1984. Body weights of 686 species of North American birds. *Western Bird Banding Association Monograph No 1.*

28. **Eisenmann, E.** 1959. South American migrant swallows of the genus *Progne* in Panama and northern South America: with comments on their indentification and molt. *Auk* **76:** 528-532.

29. **Ferguson-Lees, I.J.** 1960. Studies of less familiar birds. 107. Needle-tailed Swift. *British Birds* **53:** 431-433.

30. **Fischer, R.B.** 1958. The breeding biology of the Chimney Swift *Chaetura pelagica* (Linnaeus). *New York State Museum and Science Service Bulletin* **368:** 431-433.

31. **Frith, H.J.** Editor. 1976. *Readers Digest Complete Book of Australian Birds.* Sydney: Readers Digest.

32. **Gibson, D.D.** 1981. Migrant birds at Shenya Island Aleutian Islands Alaska. *Condor* **83:** 65-77.

33. **Gooders, J.** 1975. *The Great Book of Birds.* New York: Dial Press.

34. **Gustafson, T., B. Lindkvist, L. Gotborn and R. Gyllin.** 1977. Altitudes and flight times for swifts *Apus apus* L. *Ornis Scandinavia* **8:** 87-96.

35. **Hails, C.J.** 1979. A comparison of flight energetics in hirundines and other birds. *Comparative Biochemistry and Physiology* **63a:** 581-585.

36. **Hails, C.J. and A. Amirrudin.** 1981. Food samples and food selectivity of White-bellied Swiftlets *(Collocallia esculenta). Ibis* **123:** 328-333.

37. **Harrisson, T.** 1976. The food of *Collocalia* swiftlets (Aves; Apodidae) at Niah Great Cave in Borneo. *Journal of the Bombay Natural History Society* **71:** 376-393.

38. **Hespenheide, H.A.** 1975. Selective predation by two swifts and a swallow in Central America. *Ibis* **117:** 82-99.

39. **Keskpaik, J.** 1968. Heat production and heat loss of swallows and martins during flight. *Easti nsv teaduste akadeemia toimetised.* XVII *(Kaoide Biologia)* **2:** 179-190.

40. **Kuroda, N.** 1936. *Birds of the Islands of Java* **2:** 374-385.

41. **Lack, D.** 1956. *Swifts in a Tower.* London: Methuen.

42. **Lack, D.** 1957. The first primary in swifts. *Auk* **74:** 385-386.

43. **Lack, D. and E. Lack.** 1951. The breeding behaviour of the swift. *British Birds* **45:** 185-215.

44. **Langham, N.***1980.* Breeding biology of the Edible-nest Swiftlet *(Aerodramus fuciphagus). Ibis* **122:** 447-460.

45. **Lockwood, G., M.P. Lockwood and M.A. Macdonald** 1980. Chapin's Spinetail Swift *Telacanthura melanopygia* in Ghana. *Bulletin of the British Ornithologists Club* **100:** 162-164.

46. **Lyuleeva, D.S.** 1970. Energy of flight in swallows and swifts. *Dok Akad Nauk Tadzhik SSR* **190:** 1467-1469.

47. **McLachlan, G.R. and R. Liversidge.** 1978. *Roberts Birds of South Africa.* Cape Town: John Voelcker.

48. **Mayr, E.** 1945. *Birds of the South-west Pacific.* Hertsfordshire: Wheldon and Wesley.

49. **Medway, Lord.** 1962. The swiftlets *(Collocalia)* of Niah Cave, Sarawak part I. Breeding Biology. *Ibis* **104:** 454-466.

50. **Morse, R.A. and F.M. Laigo.** 1968. The Philippine Spinetailed Swift, *Chaetura dubia* McGregor as a Honey Bee predator. *Philippine Entomologist* **1:** 138-143.

51. **Neufeldt, I. and A.I. Ianov.** 1960. Some notes on the biology of the Needle-tailed Swift in Siberia. *British Birds* **53:** 431-433.

52. **Palomeque, J., J.D. Rodriquez, J.D. Palacios and J. Lanas.** 1980. Blood respiratory properties of swifts. *Comparative Biochemistry and Physiology* **67a:** 91-95.

53. **Payne, R.B.** 1969. Overlap of breeding and moulting schedules in a collection of African birds. *Condor* **71:** 140-145.

54. **Pennycuick, C.J.** 1969. Mechanics of bird migration. *Ibis* **111:** 525-556.

55. **Pennycuick, C.J.** 1972. *Animal Flight.* London: Edward Arnold.

56. **Rand, A.L. and E.T. Gilliard.** 1967. *Handbook of New Guinea Birds.* London: Weidenfeld and Nicolson.

57. **Ricklefs, R.E.** 1971. Foraging behaviour of Mangrove Swallows at Barro Colorado Island. *Auk* **88:** 635-651.

58. **Ripley, S.D.** 1980. A new record of the Sooty Swiftlet *Collocalia vanikorensis* from New Ireland. *Bulletin of the British Ornithologists Club* **100:** 238.

59. **Selander, R.K.** 1955. Great Swallow-tailed Swift in Michoacan, Mexico. *Condor* **57:** 123-125.

60. **Smyth, D.M.** 1980. Notes on the diet of the Grey Swiftlet *(Aerodramus spodiopygius). Sunbird* **11:** 20-21.

61. **Snow, D.W.** 1962. Note on the biology of some Trinidad swifts. *Zoologica* **47:** 129-139.

62. **Stoner, D.** 1936. Studies on the Bank Swallow *(Riparia riparia riparia)* (Linnaeus), in the Oneida Lake region. *Roosevelt Wildlife Annals* **4:**127-233.

63. **Stresemann, E.** 1931. Notes on the systematics and distribution of some swiftlets *(Collocalia)* of Malaysia and adjacent subregions. *Bulletin of the Raffles Museum* **6:** 83-101.

64. **Tarburton, M.K.** 1986. The food of the White-rumped Swiftlet in Fiji. *Notornis* **33:** 1-16.

65. **Tucker, V.A.** 1968. Respiratory exchange and evaporative water loss in the Budgerigar. *Journal of Experimental Biology* **48:** 67-87.

66. **Utter, J.M. and E.A. Lefebvre.** 1970. Energy expenditure for free flight by the Purple Martin *(Progne subis). Comparative Biochemistry and Physiology)* **35:** 713-719.

67. **Waugh, D.R.** 1978. Predation strategies in aerial feeding birds. Unpublished Ph.D. thesis, University of Stirling.

68. **Wattling, D.** 1982. *Birds of Fiji, Tonga and Samoa.* Wellington: Millwood Press.

69. **Wells, D.R.** 1975. The Moss-nest Swiftlet *(Collocalia vanikorensis)* Quoy and Gaimard in Sumatra. *Ardea* **63:**148-151.

70. **Wetmore, A.** 1957. Species limitation in certain groups of the swift genus *(Chaetura). Auk* **74:** 383-385.

71. **Zimmer, J.T.** 1955. A review of the genus *(Progne). American Museum Novitates* **1723:** 8.

(Accepted: 3 January 1986)

Corella 11 : 97-110.

THE POPULATION STATUS, LONGEVITY & MORTALITY OF THE WHITE-RUMPED SWIFTLET IN FIJI.

M.K. TARBURTON

Dept. of Botany & Zoology, Massey University,
Palmerston North, New Zealand.

Received

The population size of the white-rumped Swiftlet _Aerodramus spodiopygius_ in five Fijian caves has been estimated by up to five methods. The averages of these methods for 1974 are: Dry Cave, 413; Waterfall Cave, 20 994; Ono Cave, west entrance, 345; east entrance, 21 888; Waiyala Cave, 8 430; Cikobia-i-lau, 210. The largest annual average estimated population was 32 526 for Waterfall Cave in 1975. Although the population of Dry Cave declined between 1974 and 1984 the recapture rate of marked birds remained high. These data show an average survival rate of 64 per cent, though a survival rate of 73 per cent (which is determined when data taken in the abnormal years of 1976 and 1982 are deleted), may be more realistic. The higher rate, which gives an adult further life expectancy of 3.2 years is higher than most passerines, some seabirds and one other species of swift. Higher adult life expectancies have been shown for four other swift species. Juvenile mortality is shown to be too high to replace the adult population and it is reasoned that human interference in Dry cave is responsible for the high juvenile mortality. Adult mortality is low and arises from predation and accidents caused by conspecifics. The current longevity record holder in this study is at least 12 years old.

INTRODUCTION

It might be assumed that if a population is large, its survival is not threatened, but without census data only guesses can be made as to its long term viability.

Knowing something of the stability of the population upon which manipulation (Tarburton 1987) and longevity studies were made, could help in the interpretation of the results of those experiments. The ability of the swiftlets to obtain adequate food for themselves and their chicks is the basis of both studies. In the former, the growth rate of chicks in artificially enlarged broods of three was compared with the growth rates for single chicks and those in broods of two young. It was reasoned that a population in balance with its food supply would not be able to gather enough food to feed an additional chick. On the other hand it has been suggested that for the Lesser Black-backed Gull Larus fuscus (Harris & Plumb 1965) and the North Atlantic Gannet Sula bassana (Nelson 1964), the ability to raise broods artificially larger than normal was at least in part facilitated by an increased food supply resulting in a period of considerable population growth prior to and during the time the manipulation experiments were being conducted. Alternatively, a population that is either stable or in decline, as a result of a limiting food supply is unlikely to be able to raise a larger brood than that normally produced.

In this paper the population trends in two Fijian (18°S 179°E) caves where manipulation experiments and longevity studies were conducted, are determined. The populations of these and three other Fijian caves are estimated and the locality of the nesting sites are mapped for four of the caves. Together five caves on two islands (Nasinu Caves [Waterfall Cave and Dry Cave], Ono Cave, and Waiyala Cave are on the island of Viti Levu, while Ono-i-Lau Cave is on the island of Ono-i-Lau), were incorporated into the study. The further life expectancy of adults is calculated and that measure, survivorship and longevity are discussed in relation to the stability of each population and are compared with those for a range of other birds. Finally, causes of mortality are identified and their relative importance discussed with a view to preserving these South Pacific populations of the White-rumped Swiftlet.

METHODS

The location of the five Fijian caves visited in this study are shown in Figure 1. All caves are in limestone and although Ono Cave has several levels of development none has reached the stage of collapse that allows light to enter internal passages or chambers. The majority of nest and roost sites are in the totally dark portions of each cave. The cave on Ono-i-lau is the only one without running water and it and Dry Cave are the only two that do not pass completely through the base of a hill to provide a second entrance.

Dry and Waterfall Caves were the most frequently visited in the course of this and other studies with a total of 59 visits to Waterfall Cave and 45 to Dry Cave. Ono cave was visited 10 times while Waiyala and the cave on Ono-i-Lau were visited once.

Five methods of estimating population size have been used in this paper. Counting the sleeping birds late at night, once they had ceased entering the cave, was the first method of census and is only possible with small populations in small caves. Thus this was only feasible in Dry Cave Nasinu and the sole cave on Cikobia-i-Lau. This method of estimating a population assumes that all birds that roost and breed in a particular cave enter it each night. To check this, estimates made by direct counting in Dry Cave were compared with a nest count and two capture-recapture analyses; Jolly's Stochastic method and the Modified Peterson method (Begon 1979). As the Peterson method does not allow for deaths, the number of marked birds estimated by this method was reduced at the end of each year by 29 per cent, being the estimated annual mortality rate for each of the first two years after banding.

In the Waterfall Cave, very few recaptures were made so the Schnabel method as well as those of Petersen and Jolly were applied to the recapture data and each result compared with the nest count.

In the larger caves the swiftlet populations were estimated by counting nests, most of which remained intact and were used from year to year. The sampled area in the Waterfall Cave at Nasinu contained just over three birds to each nest. An assumption was made that a ratio of three birds to each nest, held for all parts of the cave as well as for other caves; the larger ones being censused within a week of completing the Waterfall Cave census.

RESULTS

CAVE POPULATION AND POPULATION TRENDS

Dry Cave, Nasinu

Data from the Dry Cave alone are sufficiently comprehensive to be analysed by Jolly's Stochastic method. The results of this probablistic method are shown in Table 1. The raw capture and recapture data and preliminary computations are shown as Appendices 1, 2 and 3.

The four estimates made in 1974 using Jolly's method indicate an average population of 397 ± 51 ($\bar{x}$ ± SE). Close to this estimate is that of the Modified Petersen estimate of 430 ± 32. The two estimates for 1975 average 339 ± 79 which is similar to the Petersen estimate of 346 ± 56. The 11 recaptures made in 1976 provide an estimated population of 305 ± 37 using Jolly's method and 204 ± 28 from Petersen's method. These estimates differ considerably but both indicate a marked decline. This decline has continued, as the nest and bird count data in Table 2 indicate. Nests declined from 163 in 1974 to 49 in 1983. Bird counts indicated that the population declined from 200 in 1974 to 90 in 1983 but was maintained at 94 in 1986. Nest positions in the cave are shown in Figure 1.

Table 1
Population estimates of the Dry Cave population

Sample Date	Jolly's Estimates $\hat{M}_i$	n	$\hat{N}_i$ ± SE	$\hat{O}_i$	$\hat{B}_i$	Modified Petersen $\hat{N}_i$ ± SE
8 Aug 74	0	48	– –	–	–	– –
18 Aug 74	54.75	72	438 ±158	0.47	233	389 ±115
4 Sep 74	106.46	115	515 ±100	0.54	238	522 ±118
27 Oct 74	178.2	36	356 ± 78	0.91	330	387 ± 90
19 Dec 74	143.72	34	279 ± 57	0.90	29	420 ±201
23 Nov 75	155.85	58	418 ± 78	0.93	30	401 ±157
4 Dec 75	155.87	19	260 ± 55	0.96	11	290 ±115
10 Jun 76	157.87	91	138 ± 12	0.78	36	219 ± 70
13 Jun 76	254.82	91	378 ± 44	0.90	39	322 ± 52
7 Oct 76	213.66	60	214 ± 25	0.93	16	308 ± 59
14 Oct 76	157.86	16	335 ± 98	0.95	18	340 ±154
17 Oct 76	196.96	43	234 ± 28	0.98	6	132 ± 45
22 Oct 76	174.62	18	221 ± 41	1.04	-8	163 ± 57
25 Oct 76	213.2	9	237 ± 75	1.00	1	90 ± 46
29 Oct 76	191.5	12	244 ± 61	0.99	3	63 ± 34
7 Nov 76	312.0	88	463 ± 82	0.92	38	153 ± 52
9 Nov 76	421.0	15	561 ±300	0.99	7	235 ± 70
11 Nov 76	271.11	43	328 ± 94	0.98	8	220 ± 33

Key:

$\hat{M}_i$ = number of marked birds at risk.

n = sample size.

$\hat{N}_i$ = population size on day i.

$\hat{O}_i$ = stochastic survival rate.

$\hat{B}_i$ = additions between i and i+1.

Table 2
Population of Dry Cave, Nasinu

	No of Nests	Nests x 2	Nests x 3	Jolly's Estimate ± SD	Mod. Petersen ± SD	Bird Census
1974	163	326	489	430 ± 51	430 ± 32	200
1975	-	-	-	339 ± 79	346 ± 56	-
1976	142	284	426	305 ± 37	204 ± 28	88
1978	-	-	-	-	-	91
1979	-	-	-	-	-	94
1980	-	-	-	-	-	82
1981	61	122	182	-	-	-
1983	49	98	147	-	-	90
1986	-	-	-	-	-	94

Table 3
Population of Waterfall Cave

	Nests	3 x Nests	Modified Petersen±SE	Schnabel±SE	Jolly	Average of all estimates
1974	3 660	10 980	22 266± 5 273	26 040±2 121	24 688	20 994±3 428
1975	-	-	45 032±14 868	30 753±2 844	21 792	32 526±6 767
1976	7 370	22 110	37 045±12 613	32 890± 965	29 143	30 292±3 170
1981	7 140	21 420	-	-	-	-

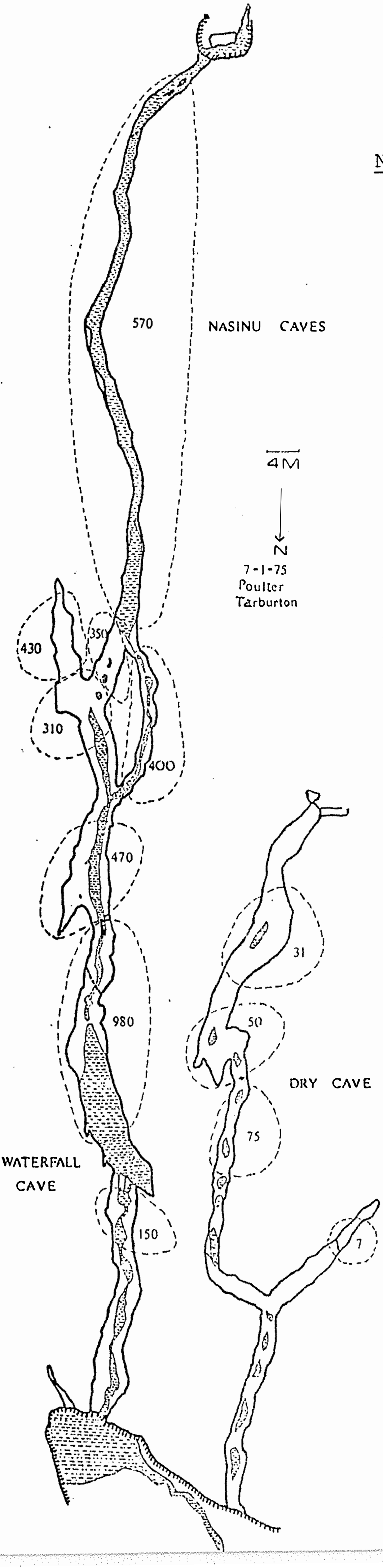


Fig. 1.
Nasinu Caves

Waterfall Cave, Nasinu 9 Mile

Although 2 545 birds were banded in the Waterfall Cave, the population is so large that it was the fifth evening visit before any recaptures were made. The average number of recaptures thereafter was 5.8 from an average sample size of 192. This recapture rate was so low that population estimates using Jolly's method ranged from 11 332 to 408 165 having standard errors of 5 692 to 445 128. The resulting average of 91 054 ± 41 796 (± SE) seems less realistic than the average derived by using only those estimates with standard errors less than the means. These averaged 25 690 ± 6 078 and are more in line with the Petersen and Schnabel estimates shown in Table 3. (Computations for Schnabel's method are shown in Appendix 4). The final column of this Table is an average of all methods used in estimating the population and indicates a population increase between 1974 and 1975 but no significant change into 1976.

As no bands were recovered from this cave after 1976 (not an unexpected result with only about 8 per cent of the population marked), the 1981 nest count is the only method for assessment of the population size at the time the manipulation experiment was run (470 birds were caught in an effort to make recaptures). This estimate indicates that the 1981 population was similar in size to that of 1976 and 1975, though the occurence of intervening fluctuations cannot be disproved. Nest numbers and positions are shown in Figure 1.

Ono Cave, Wailotua

The west entrance to this large cave has only a small colony. There were 115 nests in 1975, giving an estimated population of 345. This is much smaller than the 1 211 given by the average of five Modified Petersen estimates. This is probably explained by a high level of band loss as a result of the band being placed on the tarsus during the first few trips. Bands were subsequently placed on the tibia, once recaptures revealed that the hind toe does not prevent bands from sliping down over the other three toes and presumably in some cases slipping off the leg completely. No birds were ever found flying the 390 m between the closest west and east colonies, but as in the Nasinu Caves, a small level of exchange may have taken place through the separate entrances.

The population at the east end of the cave had 3 455 nests giving it an estimated size of 10 365 birds. Nest positions in the cave are shown in Figure 2. The Modified Petersen estimate was 17 909 ± 7 202, from four recaptures in a total catch of 167. Another estimate when only one recapture was made in a catch of 138 birds was 37 909 ± 24 432. A subsequent capture of 298 birds made no recaptures. Perhaps this disparity is due to some birds staying out at night, though the small sample sizes (<3%), in this case may also influence the accuracy.

Waiyala Cave

Only one visit was made to this cave (February 1975) and the best estimate of its population size is made from the count of 2 800 nests giving 8 430 birds. The position of these nests is shown in Figure 3.

Cikobia-i-Lau

Seventy nests were counted on 7 January 1976 making an estimated population of 210 birds.

SURVIVAL AND FURTHER LIFE-EXPECTANCY

It is in the context of a declining swiftlet population in Dry Cave that the data from 502 banded birds have been used to determine survivorship and further life-expectancy of adult birds and hence the results should be regarded as conservative. Of the 446 banded adults,

Fig. 2.
Ono Cave, Wailotua.

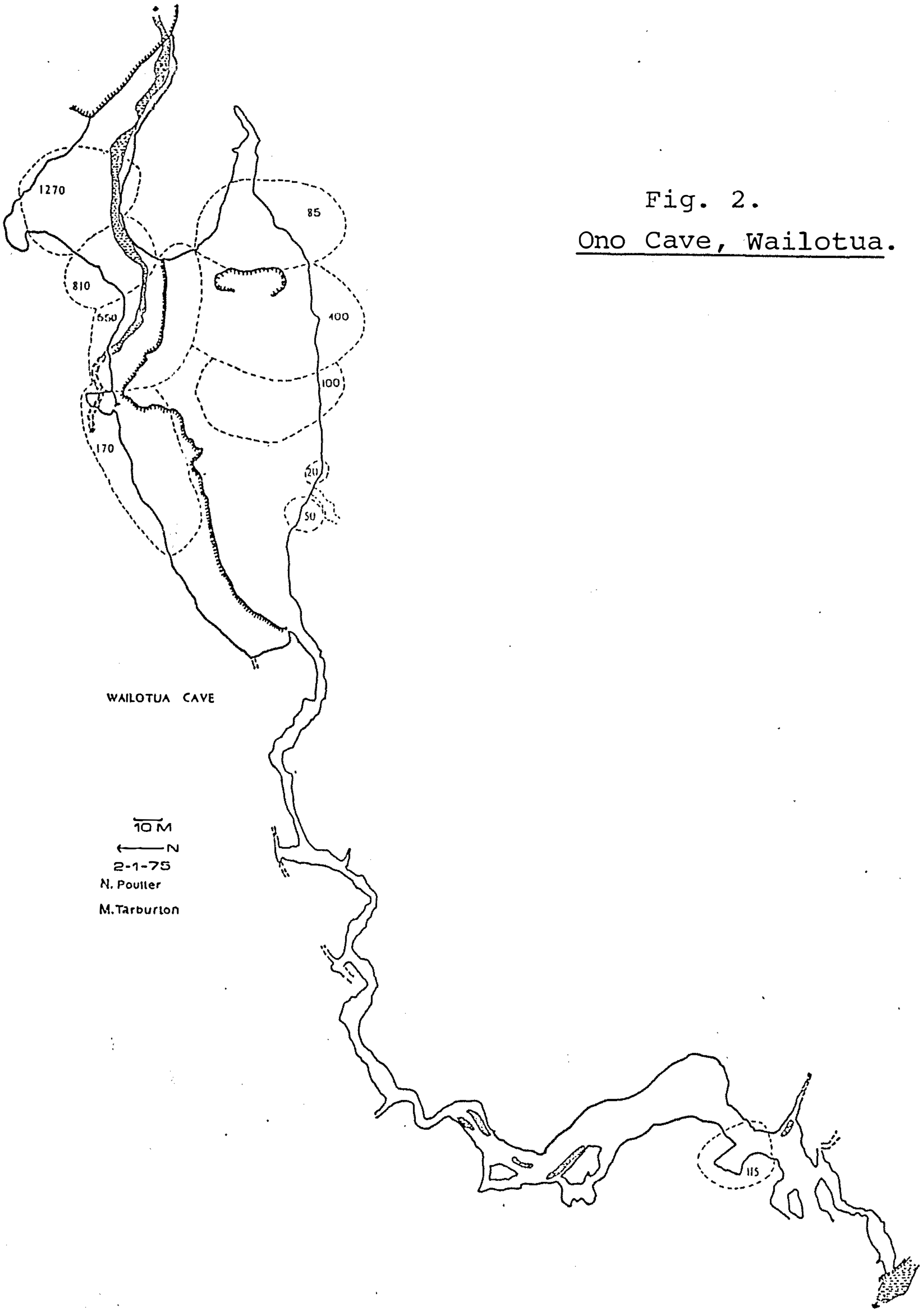
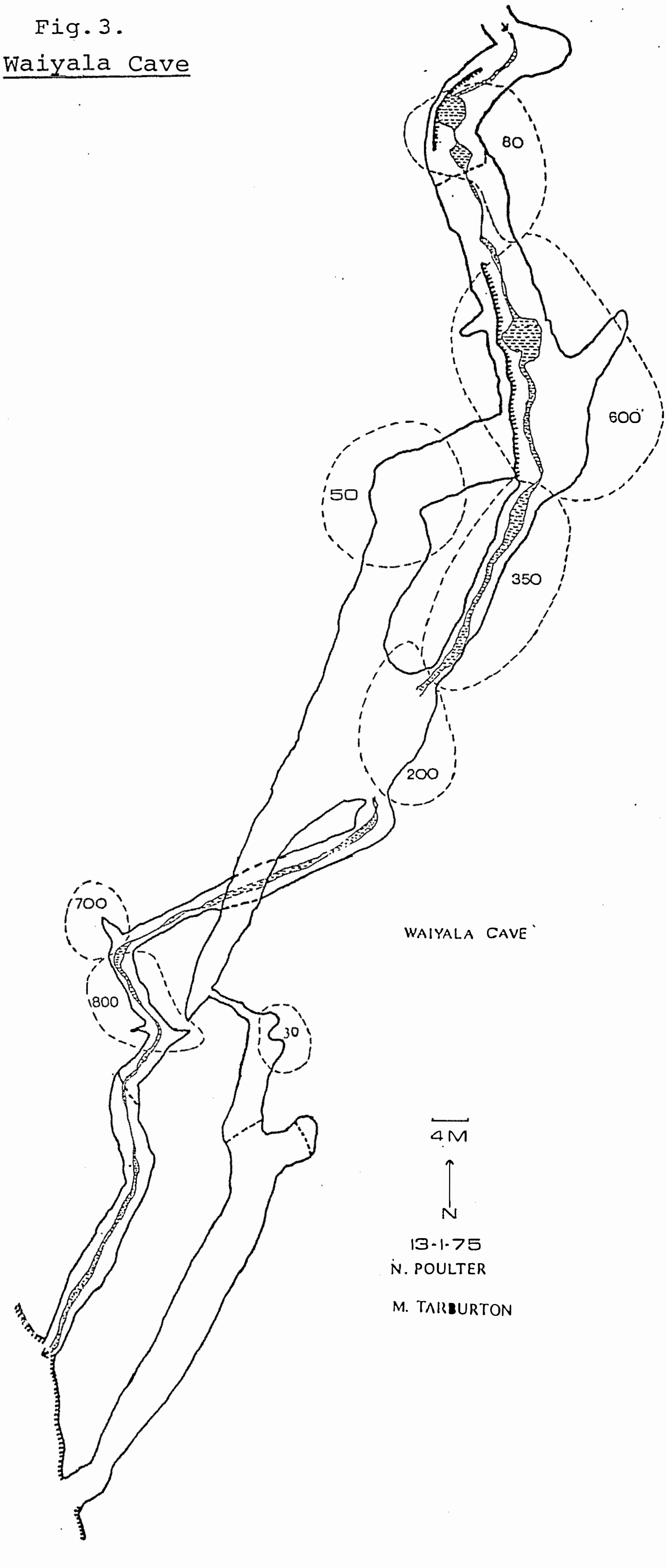


Fig. 3.
Waiyala Cave



261 were subsequently recaptured. This represents a recapture rate of 59 per cent and contrasts with the nestling recapture rate of 17 per cent. Four adults were recaptured 11 times; one was captured nine times; three, eight times; four, seven times; 11, six times; 22, five times; 18, four times; 41, three times; 42 twice and 115 only once.

The 788 recoveries of these 261 birds show a range of annual adult survival of 41 to 77 per cent and an average of 64 per cent. The lowest annual survival was that of 1976, the year that the Dry Cave population had the most visits by me and to my knowledge the most disturbance from other people. Nevertheless none of 99 clutches observed in the manipulation experiment (Tarburton 1987) were deserted and no chicks from the 130 observed in the same experiment died of starvation.

Even though the two Nasinu caves were only 18 m apart few birds made the short transfer. On each banding visit to Dry Cave more than half the birds present were captured, yet only three of the 2 545 birds banded in Waterfall Cave were found among them.

Thirty-five of 48 birds taken from Dry Cave and released at Fulton College, 21 km to the north, on 10 June 1976, were subsequently recaptured at Dry Cave. This represents a recapture rate of 73 per cent which is identical to the average adult recapture rate for this population. Hence my handling of birds, whether breeding or non-breeding does not cause desertion of the breeding cave.

When the data for all nine years are used the expected further adult life expectancy is determined to be 2.3 years. When the data for 1976 and 1982 are excluded, the expected further adult life is estimated to be 3.2 years.

DISCUSSION

There has been some discussion of the accuracy of Lack's method for population analysis. For example Piper et al (1981) found estimates on

Table 4
Survivorship of adult birds in Dry Cave
as at 1-9-83

	No Banded Birds Present	No Still Present 1 Year Later	% Survival
1974	69	52	75
1975	119	91	76
1976	160	66	41
1977	88	65	74
1978	65	44	68
1979	44	34	77
1980	34	23	68
1981	23	17	74
1982	17	10	59
1974-1982	629	402	64%

Further adult life expectancy for all years $= \frac{2-m}{2m} = \frac{1.64}{0.72} = 2.3$ years
(m = mortality)

Further life expectancy excluding the poor years of 1976 and 1982
$= \frac{1.73}{0.54} = 3.2$ years

vultures using Lack's method were lower than those of Haldane and Piper which allow for the incompleteness of data from bands yet to be recovered. Yet Seber (1972) states that it can be shown mathematically that the methods of Haldane and Lack still hold if the recoveries are ignored for an initial period of any length. In this longevity study banded swiftlets were not counted as present unless they were recovered subsequent to the 1 September following their initial recapture. As all eggs hatch before the end of February all birds would be at least seven months old before being included in the calculations. These data then should be reasonably accurate and in any case are comparable with the data for the other species mentioned, as the same method was used to determine their mortality. As all of the Apodid species have similar feeding and breeding ecologies, comparisons within the family should be reasonably valid.

The adult recapture rate of 59 per cent in this study contrasts with the recapture rate of 2.1 per cent for adult Common Swifts <u>Apus apus</u> in Britain between 1909 and 1969 (Spencer 1971). However a Russian study on the Common Swift (Kashentseva 1982) had better returns than the total British banding scheme. Between 1950 and 1979, 4.1 per cent of juveniles and 40.1 per cent of adults were recaptured from 667 banded swifts. Both the Russian study and this study have much higher returns than normal, recovery rates of all bird species banded in Britain and America, being usually less than 4 per cent (Botkin & Miller 1974).

That frequent or severe human disturbance and low survival may be related is suggested by several authors finding that disturbance causes avoidance of the site of capture by up to one third of the Common Swift population (Lack 1956). Lack qualified this statement by adding that some birds taken from their nests for banding and measuring deserted but when the birds were banded on the nest desertion was very uncommon.

It might be reasoned that birds deserting one of the two Nasinu Caves as a result of being disturbed would be more likely to go to the other cave as the two caves are only 18 m apart, whereas the next nearest cave is 10 km away. From the proportion of birds banded in the Waterfall Cave and caught in Dry Cave it is estimated that six birds banded in the Waterfall Cave would have subsequently been caught in the Dry Cave if all birds present had been captured at the time of each visit. If it is assumed that the same percentage move in the reverse direction and that there is no movement between the caves before the birds are handled for banding, then only one of the 502 birds banded in the Dry Cave will have transfered to the Waterfall Cave.

However the observable effect of disturbance in the two caves may not be equal. The Waterfall Cave is quite large in cross-section (most birds are out of reach of a hand-net), is long (178 m) and has two entrances. Birds banded and released in the Waterfall Cave may just relocate within that cave and would thus be rarely recaptured in the Dry Cave. Dry Cave on the other hand is small in cross section (all nests and most birds can be reached by the hand-net), is short (90 m) and has only one entrance. This means that in Dry Cave a greater percentage of birds will be caught or otherwise disturbed at each visit, than is the case in the Waterfall Cave. If birds from Dry Cave relocated in the Waterfall Cave there would be little chance of their recapture and hence little chance of determining whether members of the Dry Cave population were deserting more frequently due to their greater disturbance.

It is also possible that some birds may change caves periodically whether disturbed by humans or not. If this is the case the three birds banded in Waterfall Cave and retrapped in Dry Cave can be used to estimate the total movement of swiftlets from the Waterfall Cave to the Dry Cave. The retrapped birds are counted as six to allow for that (almost) half of the birds present each visit that were not caught. The

2 545 birds banded in the Waterfall Cave make 8.4 per cent of the estimated total population of 30 292. Thus 71 birds are likely to have moved from the Waterfall Cave to Dry Cave. However unless a greater percentage move in the reverse direction we can still only account for one bird moving from the Waterfall Cave as a result of 'random' movement, for almost all birds in the Dry Cave were banded by the end of 1976.

The above reasoning assumes random movement, but that this does not always exist in swifts is shown by the regular use of two chimneys during the northward movements of Chimney Swifts (Chaetura pelagica) in Texas whereas only one of the chimneys is used during their southward movements in autumn (Michael & Chao 1973). That swiftlets caught in Dry Cave may sometimes sleep elsewhere cannot be discounted.

Since the Dry Cave allows for a far higher percentage capture of birds present than does the Waterfall Cave, this activity itself possibly creates greater disturbance with more birds leaving the cave after human activity in it. A small post-disturbance exodus is possible, as each of the methods used for estimating the population and shown in Table 2 give consistently higher estimates through the 1970's than the numbers of birds found to be in the cave. But there are other possibilities.

It is likely that some birds were still to return after the time of the visit. I have recorded arrivals as late as 2230 hours, the latest I have made observations. The rate of arrival at that time of night is however very low, though it may continue for some time as Medway (1961) has recorded Black-nest Swiftlets Aerodramus maximus returning as late as 0310 hours. That birds may delay their return to the roost is substantiated by the first reported night feeding for the White-rumped Swiftlet. Jim Pierce who is familiar with this swiftlet told me of its feeding on insects flying around fluorescent lights at the Williamstown mining camp 25-30 km south-west of Mungana, Queensland. These swiftlets were seen feeding amongst the bats for an hour or so after sunset on at least two nights in September 1985.

Some birds may stay in the field. Several Fijians have told me swiftlets will sleep in the coil of a young banana leaf. Another Fijian whom I consider reliable, once saw a swiftlet enter such a banana leaf during the day and leave it a short time later. The Fijian belief, that they sleep in the roll of a young banana leaf may have developed from sightings such as this. After all, the Fijian belief that the swiftlet has no legs appears to have developed from the observation that the birds never land on tree branches.

Watling (1982) suggests some swiftlets probably sleep on the wing but no supporting evidence is given. I presume the view is simply a transfer of Lack's report that the Common Swift sometimes sleeps on the wing.

That alternative sleeping places may exist does not, however, mean that they are used, nor does it mean that they are used more when the birds are disturbed frequently at their normal roost site in the cave. However such possibilities do allow for the discrepancy between the population estimates and the number of birds counted.

My high recapture rate for all adults (including those held overnight and taken some distance away), caught in Dry Cave suggests my handling of the birds was not causing a significant decline in the population. However, disturbance through nest destruction, which is quite possible in Dry Cave, (due to other persons visiting it) could cause a population decline in three ways. Birds having to rebuild their nests could experience greater physiological stress, resulting in higher mortality. Birds losing their nests and clutch or brood may be more likely to abandon the colony. This has been suggested to explain the persistent decline of Black-nest Swiftlets in Madai Cave (Sabah, Malaysia), where the nests are harvested for human consumption (Dalton

1977). Finally, replacement nests may not be as large or as strong as the original nest, resulting in higher egg or chick losses from the eggs, chicks and/or nests falling to the ground. Replacement nests in the Edible-nest Swiftlet *Aerodramus fuciphagus* are inferior in this way, (Gibson-Hill 1948), though the effect on breeding success is not known.

If we consider the disturbances of 1976 and 1982 to be abnormally excessive and so delete the data for these years, we obtain an average adult survival rate of 73 per cent instead of 64 per cent. The consequent average mortality of 27 per cent (range 16-32 per cent) means the White-rumped Swiftlet does considerably better than the Barn Swallow *Hirundo rustica* (63 per cent) and 12 other passerines (41-72 per cent) but less than the Alpine Swift *Apus melba* (18 per cent), and the Common Swift (20 per cent) (all in Lack 1954). Two other studies on the Common Swift found mortalities to be between that which Lack found for the Common Swift and those found in this study. In the USSR mortality was 24.4 per cent (Kashentseva 1982), and in Britain it was 21 per cent. Two other swifts also have lower mortality than the White-rumped Swiftlet. These are the White-throated Swift *Aeronautes saxatalis* of the United States, which has an annual mortality of about 20 per cent (Collins 1973) and the Chestnut-collared Swift *Cypseloides rutilus*, which in Trinidad has 15-17 per cent mortality (Collins 1974). While the recapture rate for the White-tipped Swift *Aeronautes montivagus* in Venezuela (Collins unpub.) is about 65 per cent, Collins work on this species leads him to believe that the real figure is about 82 per cent. It appears that both a disturbed bird and its mate are likely to lose the nest site and leave the colony, hence avoiding recapture (Collins, pers. comm.). If this is correct, (as is to be expected, for larger birds tend to live longer), the only swift with higher mortality than the White-rumped Swiftlet is the Chimney Swift of the United States, which has an annual mortality of 38 per cent (Henny 1972). The

White-rumped Swiftlet has lower mortality than 15 other non-passerines, including two seabirds and is only bettered from those non-passerines given in Lack (1954) by the Royal Albatross Diomedia epomophora and the Yellow-eyed Penguin Megadyptes antipodes which have annual mortality rates of 3 per cent and 10 per cent respectively.

Both estimations for further adult life expectancy (2.3 years and 3.2 years), appear reasonable, when compared with 1.1 years for the Barn Swallow, 4.6 and 5.6 years for the Common Swift, (Magnusson & Svardson 1948; Weitnauer 1947). However because of the declining population in Dry Cave even the life expectancy of 3.2 years should correctly be regarded as conservative.

Just how conservative an adult life expectancy of 3.2 years is, can be estimated by calculating the number of years it would take for parents to replace themselves with breeding offspring at variously selected mortality rates. By using the annual fledging success data (1.1 chicks per pair per year) from the stable population of the Waterfall Cave and the 80 per cent survival rate of adult European and American swifts, it would take 2.3 years for parents to replace themselves. With 74 per cent survival (the average of Fijian swiftlets without the two abnormally poor years) replacement would take 2.5 years. With 64 per cent survival (the average of all years for fijian swiftlets) replacement would take 2.9 years. Clearly each of these replacement rates could be achieved in the 3.2 years of further adult life estimated from the declining population of Dry Cave. However as juvenile mortality is usually higher than adult mortality, lower survival rates than those used should be expected. The proven first year survival of 21.25 per cent (from 74 banded chicks) in the declining Dry Cave population would require 8.6 years to replace parents and can be regarded as below the minimum of that in a stable population. If we raise the juvenile survival to 50 per cent the parents would be replaced in 3.6 years, which is the average longevity of the adult Common Swift in Russia (Kashentseva 1982).

The Common Swift also has an adult mortality similar to that of the White-rumped Swiftlet, and so (assuming no net migration gain or loss) if the same ratio of juvenile to adult mortality holds for the swiftlet, 50 per cent mortality between fledging and breeding may be realistic. If it is realistic, then disturbance of the birds by the suspected destruction of their nests and contents in Dry Cave has considerably reduced juvenile survival and has led to the decline observed in that population.

Maximun Recorded Longevity

At the time of writing (March 1986) the oldest recorded bird from the 502 banded in Dry Cave was 013-69752 banded on 4 September 1974 and last recaptured on 27 February 1986, 137 months having elapsed. As the bird was an adult when banded it would have been at least 12 years old at the time of recapture. Two other adult birds have been recaptured 112 months after banding, making them at least nine years old when last recorded.

There are few longevity records for Apodidae with which to compare this record for this species. The oldest recorded Chimney Swift was 13 years (Hight 1953). The record for the Alpine Swift is 16 years (Rydzewski 1962) and 21 years for the Common Swift (Rydzewski 1962). The oldest recorded Common Swift in the Russian study is 11 years (Kashentseva 1982) and in a Czechoslovakian study 12 years 11 months and 21 days (Beklova 1976). The records for two swallows in this last study show that they only live about half as long as the Apodidae. The longest records for Hirundine longevity are seven years for the Barn Swallow and six years five months for the House Martin _Delichon urbica_.

Mortality and its causes

Because the survivorship of the White-rumped Swiftlet is here shown to be greater than most other similarly sized land-birds studied so far, it naturally follows that its mortality will be low compared to theirs. Adult mortality was shown to average 27 per cent for seven years. If the years (1976 & 1982) showing abnormally high mortality are included the average mortality for the nine years rises to 36 per cent. It can be reasoned that the practice of being airborne all day and of roosting and breeding in what may be thought of as the safe environment of a cave would help reduce mortality. However mortality remains, and some observations and discussion regarding its causes will help clarify whether the feeding, roosting and nesting habits do enhance longevity, not only for this species but possibly also for other species having similar ecological habits.

That man has little direct effect on the mortality of this bird outside the caves is evidenced by the fact that whereas numerous bands from those I have placed on similar numbers of other bird species in Fiji have been returned, none of the 4 554 swiftlets I banded in Fiji were ever recovered away from the caves they use for nocturnal roosting and breeding. The small size of this swiftlet means man is not interested in it as a food source. Though some indigenous Fijians are very good at collecting birds by throwing stones at them I have heard only once of their collecting a swiftlet in this manner. The extreme difficulty I had in trying to mist-net this swiftlet in the field also demonstrated that their keen eye sight and rapid manoeuvrability make them much harder for man to capture than most land birds.

Even the caves offer protection from man when the birds are roosting. Indians are reticent to enter caves for fear of snakes and Fijians rarely enter alone, giving as their reason that the devil lives there. However when a group of Fijians do go in to catch the free-tailed fruit-bat for food, numbers of swiftlets may also perish. In Ono Cave at Wailotua village in the Wainibuka Valley, bamboo is burnt to drive the bats (and birds) into small dead end passages and if this is done when swiftlets are present, numbers of swiftlets may also perish.

Apart from man the White-rumped Swiftlet in Fiji has few predators. A Pacific Python Enygrus bibranii, a little over a metre in length was found sleeping on a rock below nests in the eastern end of Ono Cave. It would be unreasonable to expect that pythons would feed on anything but chicks and eggs that fell from nests. American Cockroaches Blattaria americanus and large fresh-water eels do the same, though the cockroaches also feed on the saliva that glues the nests to the wall. Although cats are reported (Clunie 1984), to bat them down when flying low, most birds feed over the forest where such a fate is not likely.

The Barn Owl Tyto alba does take adult and nestling swiftlets. It was said to be responsible for the abandonment of several score of nests placed in the twilight zone of the upper entrance (south end) of the Waiyala Cave (see map). Many eggs lay on the guano below the nests and villagers from Waiyala said they had seen the Barn Owl chasing swiftlets in this entrance. I have found a Barn Owl feather in the entrance to Waterfall Cave and Clunie (1972) has seen a Barn Owl catching swiftlets at the entrance to a cave in Navosa. I have picked up several freshly dead and concussed birds from the stream in the entrance of Waterfall Cave. However, they were probably victims of head-on collisions in the zone where the birds fly their fastest, though the possibility that they were struck by a Barn Owl could not be ruled out. Even in Europe where there are abundant data for avian predation on the Common Swift the diurnal predators take few swifts compared to other species. The Common Swift forms only one percent of the prey of the Sparrowhawk Accipiter nisus, one and a half percent of the prey of the Peregrine Falcon Falco peregrinus and two and a quarter percent of the prey of the Hobby Falco subbuteo (Lack 1956). Clunie (1972b, 1976) has shown that swiftlets comprise only a small portion of the diet of the Fijian Peregrine Falcon.

In short, the low mortality rate of the White-rumped Swiftlet results from the inability of terrestrial predators to reach them and the limited effect of aerial predators on their numbers. (Neither Barn Owls nor Peregrine Falcons flock at cave entrances). So apart from periodic interference from man, the availability of food appears to be the main regulator of Fijian populations of the White-rumped Swiftlet. As no chicks starved in the manipulation experiment, even in the artificially enlarged broods of three (Tarburton 1987), pressure from a lack of food does not appear to be critical in a normal brood situation and one is left with the likelihood that a period when available food is low such as in a prolonged cyclone, and/or a period of excessive human interference may individualy or in unison increase mortality.

It is probably predatory pressure from Barn Owls that has encouraged the majority of swiftlets to nest beyond the twilight zone in the five Fijian caves I have examined. That swiftlets increase their speed at cave entrances (Tarburton 1986), supports this view. This view is contrary to Watling's (1982) statement that most nests are built in the twilight zone of caves. In Waiyala only 4 per cent of nests were in the twilight zone, the rest in total darkness. In Dry cave only 1 per cent and in Waterfall cave only about 27 per cent were in the twilight zone. At Ono Cave, 36 per cent of nests were in the twilight zone but none of the nests in the cave on Cikobia-i-Lau were in the twilight zone. The position where twilight gives way to total darkness is shown as a dotted line across the passage on each map.

Death may result from the activity of conspecifics. I found five adults dead at their nests. Their wings had been glued by saliva to their neighbours nest. This presumably happened while they slept but the hardened saliva held them suspended in the air when they attempted to fly, thus preventing them from feeding. Two other birds had not been long in the same predicament and were rescued. This problem is clearly caused by high density nesting.

CONCLUSIONS

Population size of the White-rumped Swiftlet in Fiji correlates with island size, except that a small colony may be found even on the largest island if it is close to another colony. Because most nests are in total darkness and on overhanging cave walls and roofs, brooding birds, eggs and chicks are safe from most natural predators. Handling of the birds or their young does not cause desertion, but the marked decline in the population of Dry Cave, where all nests can be reached by humans is thought to have occured as the result of willful destruction of nests eggs, chicks and possibly adults by man. The other small colony in this study is not under threat as the villagers on Ono-i-Lau protect the site and the birds. The large colonies are not considered to be in danger either, as most nests are out of easy reach and there is little interest in catching such small birds.

The factors that have made the Dry Cave population vulnerable to human predation have also brought higher percentages of band retraps in this longevity study than in all other studies on Apodids. It is concluded that my activity in collecting the data that show an expected further adult life of 3.2 years has not significantly reduced the birds survival and that the estimate is close to reality. However the lower than expected juvenile survival is attributed to the destruction of eggs and young by other visitors to the cave.

ACKNOWLEDGEMENTS

The helpful advice and criticism of earlier drafts of this paper given by Dr. Ed. Minot of Massey University is gratefully acknowledged. I also wish to thank the following persons for valuable assistance in the field: M. & A. Ahkoy, A. Currie, C. Grieve, P. Hoffman, T. Kabu, R. Litster, T. Osborne and J. Wells.

REFERENCES

Begon, M. (1979). Investigating Animal Abundance - Capture-recapture for Biologists. Edward Arnold, London.

Beklova, M. (1976). Contribution to the characteristics of population dynamics of certain hemisynanthropic species of birds in Czechoslovakia. Zool. Listy 25: 147-155.

Botkin, D.B. and Miller, R.S. (1974), Mortality rates and survival of birds. Amer. Nat. 108: 181-192.

Clunie, F. (1972a). Fijian Birds of Prey. Fiji Museum, Suva.

Clunie, F. (1972b). A contribution to the natural history of the Fijian Peregrine. Notornis 19: 302-322.

Clunie, F. (1976). A Fiji Peregrine (Falco peregrinus) in an urban-marine environment. Notornis 23: 8-28.

Clunie, F. (1984). Birds of the Fiji bush Fiji Museum. Suva.

Collins, C.T. (1973). Notes on survival and band wear in White-throated Swifts. West. Bird Bander 48: 20-21.

Collins, C.T. (1974). Survival rate of the Chestnut-collared Swift. West. Bird Bander 49: 10-13.

Dalton, K. (1977). Letter from Kuching. Far East Econ. Rev. 21, Oct. p.62.

Gibson-Hill, C.A. (1948). The Malaysian Swiftlets. Malayan Nat. J. 3: 190-200.

Harris, M.P. and Plumb, W.J. (1965). Experiments on the ability of Herring Gulls (Larus argentatus) and Lesser Black-backed Gulls (L. fuscus) to raise larger than normal broods. Ibis 107: 256-257.

Henny, C.J. (1972). An analysis of the population dynamics of selected avian species with special references to changes during the modern pesticide era. Bureau of Sport, Fish. and Wildl., Res. Rep. 1: 1-99.

Hight, G.L. (1953). Longevity record for Chimney Swift (Chaetura pelagica). Bird Banding 24: 109-110.

Kashentseva, T.A. (1982). Age-related structure of the Swift (Apus apus) population in Oka reserve, Russian S.F.S.R., U.S.S.R. Vestn, Zool. 0(3): 44-48.

Lack, D. (1954). The Natural Regulation of Animal Numbers. Oxford University Press, London.

Lack, D. (1956). Swifts in a Tower. Methuen, London.

Lack, D. and Arn, H. (1947), Die bedeutung der gelegrobe beim Alpensegler. Orn. Beob. 44: 188-210.

Magnusson, M. and Svardson, G. (1948), Livslangd hostornsvalor (Micropus apus (L)). [Age of Swifts (Apus apus)]. Var Fagelvard 7: 129-144.

Medway, Lord. (1962). The swiftlets (Collocalia) of Niah Cave, Sarawak part 2. Ecology and the regulation of breeding. Ibis 104: 228-245.

Michael, E.D. and Chao W.H. (1973). Migration and roosting of Chimney Swifts in east Texas. Auk 90: 100-105.

Piper, S.E., Mundy, P.J. and Ledger, J.A. (1981). Estimates of survival in the Cape Vulture (Gyps coprotheres). J. Anim. Ecol. 50: 815-825.

Rydzewski, W. (1962). Longevity of ringed birds. Ring 3: 147-152.

Seber, G.A.F. (1972). Estimating survival rates from bird band returns. J. Wildl. Manag. 36: 405-413.

Spencer, R. (1971). Report on bird ringing for 1969. Brit. Birds, 65: 137-186.

Tarburton, M.K. (1986). A comparison of the flight behaviour of the White-rumped Swiftlet and the Welcome Swallow. Bird Behaviour 7:72-84.

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

Watling, D. (1982). Birds of Fiji, Tonga and Samoa. Milwood press, Wellington.

Weitnauer, E. (1947). Am neste des mauerseglers, (Apus apus apus)(L.). Ornith. Beobachter 44: 133-182.

Appendix 1.
Raw Data for use in Jolly's Population Estimate of the Dry Cave Population

Time of release of marked birds (j)

Number of Marked Birds Recaptured (m_{ij})

Date	Day_i	n_i	r_i	18 Aug '74	4th Sep '74	27 Oct '74	19 Dec '74	23 Nov '75	4th Dec '75	10 Jun '76	13 Jun '76	7th Oct '76	14 Oct '76	17 Oct '76	22 Oct '76	25 Oct '76	29 Oct '76	7th Nov '76	9th Nov '76	11 Nov '76	20 May '78
8 Aug 74	1	-	48																		
18 Aug 74	2	71	71	8																	
4 Sep 74	3	115	115	8	15																
27 Oct 74	4	37	36	2	6	10															
19 Dec 74	5	34	34	3	1	11	2														
23 Nov 75	6	58	58	3	5	5	4	4													
14 Dec 75	7	19	19	0	1	4	0	3	3												
10 Jun 76	8	90	90	1	2	9	8	6	10	7											
13 Jun 76	9	91	89	6	4	7	1	2	11	5	25										
7 Oct 76	10	60	60	0	2	3	0	2	2	1	15	17									
4 Oct 76	11	16	16	0	0	0	0	0	1	0	3	1	2								
17 Oct 76	12	43	41	2	2	2	2	2	3	1	6	3	10	3							
22 Oct 76	13	18	18	0	1	1	0	1	1	0	1	2	1	2	4						
25 Oct 76	14	9	9	1	0	0	0	1	0	0	1	3	0	1	0	1					
29 Oct 76	15	13	12	0	0	0	0	0	1	0	2	0	1	2	2	1	1				
7 Nov 76	16	88	88	0	0	3	1	1	2	0	3	8	15	3	9	6	2	6			
9 Nov 76	17	15	15	0	0	0	0	0	0	0	0	2	1	0	2	1	0	0	5		
11 Nov 76	18	45	43	1	1	6	1	1	0	0	4	5	2	3	3	2	0	1	6	0	
20 May 78	19	92	92	0	1	1	1	0	5	2	5	3	4	1	5	2	2	1	13	3	9

KEY

n_i = number captured on day i, r_i = number marked & released on day i, m_i = number of marked recaptures on day i.

Appendix 2

Preliminary Computations for Jolly's Estimate of the Dry Cave Population

Day, i	r_i	m_i	y_i	z_i
1	48	–	35	–
2	71	8	41	27
3	115	23	62	45
4	36	18	20	89
5	34	17	22	93
6	58	21	40	93
7	19	11	16	122
8	90	43	76	97
9	89	61	45	98
10	60	42	36	103
11	16	7	14	132
12	41	36	27	106
13	18	14	13	116
14	9	8	5	114
15	12	10	8	121
16	88	59	24	69
17	15	11	3	82
18	43	37	9	49
19	92	58	–	–

KEY

r_i = number of marked birds released on day i(Appendix 1)

m_i = number of marked birds recaptured on day i.

z_i = number of birds marked before day i, but not recaptured until after day i.

y_i = number of r_i individuals subsequently recaptured.

Appendix 3.

Results Using Jolly's Estimate of the Dry Cave Population.

Sample	$\hat{M}_i$	$\hat{N}_i$	SE $\hat{N}_i$	$\hat{O}_i$	$\hat{B}_i$
1	0				
2	54.76	438	158	0.47	233
3	106.45	515	100	0.54	238
4	178.20	356	78	0.91	330
5	143.72	279	57	0.90	29
6	155.85	418	78	0.93	30
7	155.87	260	55	0.96	11
8	157.87	158	12	0.78	36
9	254.82	378	44	0.90	39
10	213.66	214	25	0.93	16
11	157.86	333	98	0.95	18
12	196.96	234	28	0.98	6
13	174.62	221	41	1.04	-8
14	213.20	237	75	1.00	1
15	191.50	244	61	0.99	3
16	312.00	463	82	0.92	38
17	421.00	561	300	0.99	7
18	271.11	328	94	0.98	8

KEY

$\hat{M}i$ = the estimated number of marked birds at risk on day i.

$\hat{N}i$ = the estimated population using the modified Petersen formula

$$\hat{N}_i = \frac{\hat{M}_i(n_i+1)}{(m_i+1)}$$

$\hat{O}i$ = the estimated stochastic survival rate

$\hat{B}i$ = the estimated additions between i and i + 1

SE $\hat{N}i$ = the standard error of the estimate, for method of estimation see Begon (1979).

Appendix 4

Computation for estimates of Population in Waterfall Cave - Schnabel's Method.

Date	A No. Trapped	No. Newly Marked & Released	B No. Already Marked in Population	A x B	(A x B)	C No. Recap--tures	C	Estimate of Population $\frac{(A \times B)}{C}$
7 APR 74	27	27	0					
8 AUG 74	83	83	27					
18 AUG 74	165	165	110					
4 AUG 74	129	129	275					
27 OCT 74	121	121	404	48 884	48 884	2	2	24 442
26 DEC 74	264	264	525	138 600	187 484	6	8	23 436
29 DEC 74	299	299	789	235 911	423 395	6	14	30 243
								26 040±2 121
22 JUN 75	164	164	796	130 544	448 090	7	18	24 894
16 JUL 74	235	235	1031	242 285	690 375	6	24	28 766
23 NOV 75	75	75	1106	82 950	773 325	1	25	30 933
4 DEC 75	202	201	1307	264 014	1 037 339	2	27	38 420
								30 753±2 844
10 JUN 76	237	237	1270	300 990	1 089 368	8	31	35 141
13 JUN 76	208	208	1478	307 424	1 396 792	13	44	31 745
23 SEP 76	182	182	1660	302 120	1 698 912	11	55	30 889
7 OCT 76	127	126	1786	226 822	1 925 734	2	57	33 785
								32 890± 965

NOTE This commonly used method estimates the size of a population by taking the sum of all birds captured (A), mutiplied by the number of birds already marked (B), and dividing that by the sum of the number of marked birds captured. Like many methods Schnabel's assumes that the population is stable.

Notornis 35:·

APPENDIX 7

VOCALIZATIONS OF THE WHITE-RUMPED SWIFTLET IN FIJI

INTRODUCTION

Following the discovery that some swiftlets have the ability to echonavigate in complete darkness (Medway 1959, Novick 1959), those species with the ability, were separated from the genus *Collocalia* (Medway & Pye 1977), to form what has become the larger genus *Aerodramus*. The White-rumped Swiftlet *A. spodiopygius* was placed in this genus, as Pecotich (1974), had recorded that *A. s. terraereginae* and *A. s. chillagoensis* produced the echolocatory "click" call. Subsequently this call and two other calls used by *chillagoensis* were described (Roberts *et al* 1976).

This paper records four new calls for the species. Three of these are from *A. s. assimilis* and one from *chillagoensis*. It is confirmed that two of the previously described calls from *chillagoensis* are given by *assimilis*. Although 66 visits totalling over 300 hours, were made to five separate cave nesting colonies, the call given by Queensland birds at cave entrances (Roberts *et al* 1976) was not heard. The "chirrup" call is probably the "twittering" calls currently being described in the common literature on the birds of Fiji (Mercer 1966; Watling 1982; Clunie 1984).

Three of the calls described here have recognizably different functions, while two infrequently used calls will be more difficult to ascribe a function. Two of the calls were heard outside of the cave as well as inside. Three calls have only been heard inside caves and one has only been heard outside.

METHODS

Onometopoeic transcriptions of the calls were made during four separate days of continuous watching to determine chick feeding rates, and during ten hours of watching adult feeding behaviour. Additionally two one hour visits were made to tape-record calls and similar transcriptions with qualifying descriptions were made from these. Narrow band sonagrams were made from these recordings using a digital Sona-graph 7800 (Kay Elemetrics Corp.). Dry Cave (in which the tape recordings were made) and Waterfall Cave are at Nasinu 9 Mile, nine miles north of Suva. Ono Cave is in the Wainibuka Valley, 40 miles north-west of Suva and Waiyala Cave is in the Sigatoka Valley 25 miles north of Sigatoka.

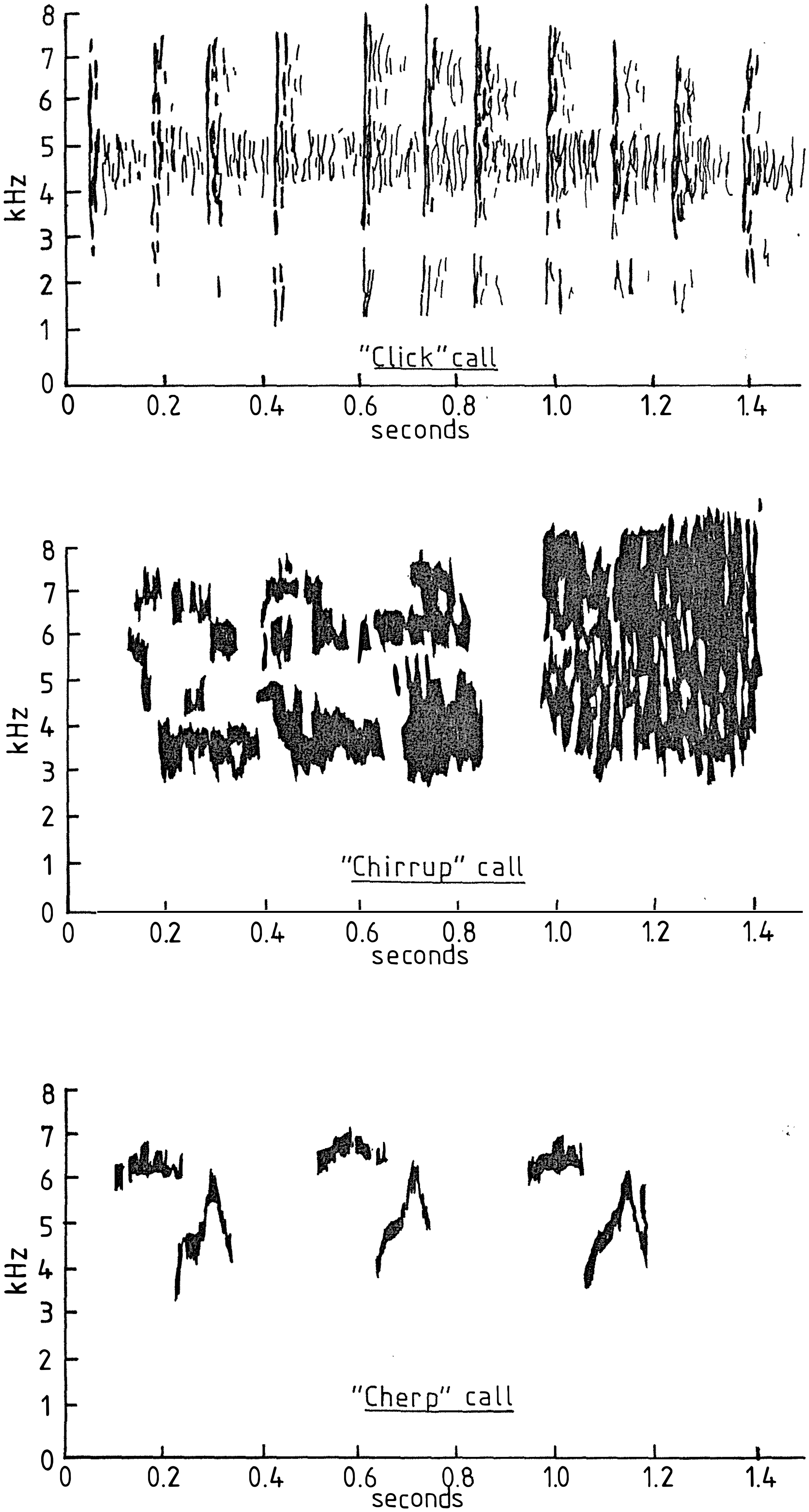
RESULTS

Echolocatory "click" call

The most commonly produced call of the White-rumped Swiftlet is a distinctive "click". This call is used frequently in the twilight zone of the cave they use for roosting and breeding. The call is used continuously by birds flying in total darkness, as the call is used for echonavigation. The "click" call is rarely given by birds while clinging to the wall or being handled, and even then, it is accompanied by a flapping of the wings, as Harrisson (1966) found in the Mossy-nest Swiftlet (Aerodramus vanikorensis). This call is characterised by a sharp wave front and rapid decay. Most energy is concentrated between four and five kHz, though it ranges from one to eight kHz and on one sonagram a harmonic was visible at 14 to 15 kHz.

The repetition rate of this call varies. From sonagrams for two birds the time from the commencement of one "click" to the begining of the next varied between 0.09 seconds and 0.173 seconds. Further evidence of variation comes from counting calls from live birds and recorded calls. The mean rate was 4.0 ± 0.23 per second ($\bar{x} \pm$ SE, n = 22, range 1.4 - 5.9). Birds flying swiftly along the narrow passage of Dry Cave, Nasinu, or those just frightened from their roost, appeared to call at a faster rate than those making repeated short flights from the

Figure 1 Sonagrams of adult calls



wall in an effort to locate their nest. In Dry Cave it was evident that there was variation between individuals in the pitch of the call.

In the larger caves, such as Ono, Waiyala, and Waterfall Caves, the cacophony just after sunset, resulting from many hundreds of flying birds giving the "click" call, is so great that one wonders how the call could ever have echolocatory usefulness. However, even when several thousand roosting birds were put to flight, the birds still managed to move through the cave, though movement was slower.

The "click" call of a fledgling on its first flight is higher in pitch and noticeably quieter than that of the adult. However this "thinner" call is adequate in preventing juveniles from colliding with the cave wall and the sound of adult birds appears to help guide them towards the entrance instead of into other sections of the cave.

The "chirrup" call

The second adult call gives the impression of being more highly pitched than the "click" call. However the sonagram shows that the frequencies of this call do not reach any higher than those of the "click" call.

The most common form of the call is "chirrup, chirrup", though I have heard "giddy up, giddy up" and "gar-p". The call is used much less frequently than the "click" call and occurs most often upon the arrival of a bird at the nest. It is normally uttered by the bird already at the nest, as if in agonistic challenge or threat, to the new arrival and yet at the same time given to help identify itself as an aid to the orientation of the incoming bird.

If the incoming bird replies and both birds vocalize this call simultaneously, the result is a sharp vocal exchange or squabble, best described as a screech (shown on the right of the sonagram), which sometimes leads to a brief fight and the new arrival flying away. The "chirrup" call is not used often when feeding. I heard it only once, when a second bird joined in the 25 m diameter feeding circuit of the original bird. The call is used by birds wheeling around, above the entrance to a cave and is usually associated with a pair of birds involved in an aerial chase.

In Queensland the call used by chillagoensis in such aerial pursuits is a long "tweet-tweet-tweet-tweet-tweet-tweet", "peer-peer-tweet" or a "tweer-tweer" that sounds like the scream that the Fijian "chirrup" call sometimes ends with.

The "shree-ee" call

A call more shrill than any other call was given by chillagoensis when a flock had been dispersed from above a cave entrance by a Brown Goshawk Accipiter fasciatus. Some minutes later the flock reassembled above the goshawk occasionally giving a high pitched "shree-ee" call which I have not heard at any other time. I do not have a recording of this call.

The "cherp" call

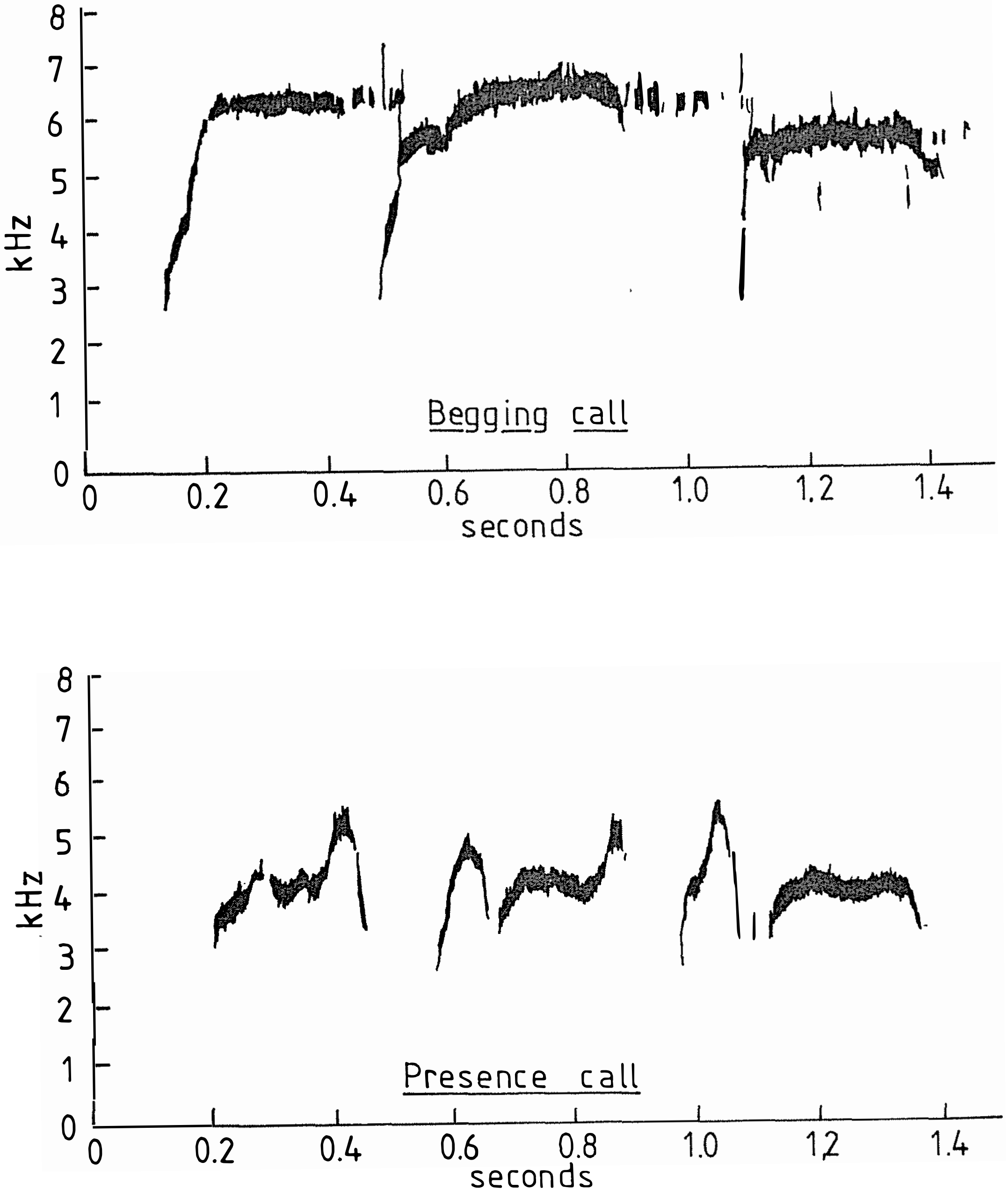
This is the least common of the three adult calls given by assimilis. I have only heard it in the total darkness of a cave and then only rarely. It was given by a roosting or recently landed bird. The call was a mellow yet fast "cherp, cherp, cherp", much softer than the "chirrup" call.

The chick begging call

Starting as a plaintive whisper then becoming a demanding "cheep" and culminating in a full fledged raspy call, each of the stages in this call only become louder and more harsh with age. Alternatively, the call may start suddenly, close to full volume.

Begging, which accompanies this call is contagious and is often triggered by the begging of nearby chicks, the landing of an adult near by, or the close passage of an echolocating bird.

Figure 2 Sonagrams of chick calls



The chick "presence" call

This call is a single soft "cheep", "chip" or "peep" that is given (or at least noticeable) on occasion when the cave is quiet. Whether it is some form of sub-song or just making one's presence felt, I do not know. The pattern on the sonagram shows its similarity to the "cherp" call of adults.

DISCUSSION

Echolocatory "click" call

The echolocatory "click" call is termed the "rattle call" by Medway (1959, 1962a,b, 1966, 1967) and by Medway and Wells 1969), and has been proposed as the basis for separation of those swiftlets with the call into the genus Aerodramus Oberholser (Medway & Pye 1977).

With these calls, White-rumped Swiftlets are able to detect rods down to 6.3 mm diameter (Griffin & Thompson (1982, Smyth & Roberts 1983). These authors agree that the "click" call is not sufficiently perceptive to be used for nocturnal feeding, as the majority of swiftlet prey is below the size the birds can detect with the low frequency of these calls. The advantage of low frequency calls is that they do not attenuate as quickly as high frequency calls (Pye 1983). These findings do not mean that swiftlets cannot feed at night. In situations where artificial illumination is sufficient, The White-rumped Swiftlet (Tarburton 1987), the Indian Edible-nest Swiftlet Aerodramus unicolor (Ali & Dillon 1970), the Alpine Swift Apus melba (Freeman 1981) and the Chimney Swift Chaetura pelagica (Cottam 1932), have each been observed feeding around lights at night.

The ability of the White-rumped Swiftlet to echonavigate in the dark not only means that the birds may nest in relatively safe sites, but it also means they can feed in rich feeding areas far from their nests during dawn and dusk, the times when aerial insects are the most abundant (Hespenheide 1975; Tarburton 1986). I have observed birds probably 20 km from their roosting caves, feeding actively until last light. I have also recorded birds coming into their caves as late as 2230 hours. That most of the birds had left the caves by 0430 hours that morning means that their echonavigational ability allows them to make the most of the tropical day. The ability to echonavigate saves White-rumped Swiftlets from the problem that Common Swifts (Apus apus) have of not being able to reach their nests or chicks if they arrive at the nest site a few minutes after dark (Lack 1956).

The echolocatory call is not only used for echolocatory purposes. It is sometimes given by adults feeding in bright light and so is presumed to have additional function. I have never heard a lone, feeding bird use it, but it may be heard soon after one feeding bird starts to chase another. This context suggests the call has a communication function and the differences I could detect between birds in the quietness of Dry Cave suggests that identification of individuals may be one function. It may be this call, that some mistake for the "clapping" or clicking of the birds bill as it persues insects (Mercer 1966, Watling 1982, Clunie 1984).

The "click" call is a double click similar to that in terraereginae (Roberts et al. 1976, Smyth & Roberts 1983). There is a pulse at each end of the "click" so that it sounds "cli-ik", but is so fast that the two pulses are barely perceptible. The syringeal procedure for making this double click has now been determined, (Suthers & Hector 1982). In effect the birds transform a longer squeek-like vocalization into two brief clicks by momentarily closing the syrinx in the centre of the call. The authors suggest that by so generating the brief clicks the swiftlets have created a sonal signal with a greater bandwidth, which having abrupt rise-decay times should improve target range determination based on measurement of the pulse-echo interval.

Swiftlets using paired clicks, 20 ms or so apart, gain information additional to determining target range, for upon reflection not only the pitch but also the time interval between the clicks will be changed by the doppler shift, allowing target velocity to be determined (Pye 1983). This should enable the birds to avoid other birds or bats that might be flying in the same airspace.

The importance of this call can be seen in the location of the majority of nests. Most nests and roost sites in Fiji and Chillagoe are protected from a number of potential predators by being in total darkness.

The "chirrup" call

It is evident that, in saying "their cry is a high pitched twittering which also appears to act as a type of sonar when the birds are flying in and out of the dark caves", Mercer (1966), is confusing the "chirrup" call with the function of the "click" call. Watling (1982) also talks of a high pitched twitter, most commonly heard when used for echolocation in the dark caves. At least Clunie (1984), leaves out the high pitched portion of the description when he writes of their using a twittering call to echo-sound in the caves.

The "chirrup" call appears to serve as a greeting, helping to identify individuals. If the incoming bird is not the mate, the call may develop into a threatening scream. In the Common Swift the threat and greeting calls are also very similar, though Lack (1956) found that the position of the head during vocalization was distinctive.

The "cherp" call

It is possible that this call corresponds with the plaintive piping call of the Common Swift, given by the loser of a fight over a nest site or a mate (Lack 1956).

The chick begging call

Similar calls in the Chimney Swift (*Chaetura pelagica*) are triggered by any disturbance (Amadon 1936).

ACKNOWLEDGEMENTS

The helpful advice and criticism given by Drs. Edward Minot of Massey University and Hugh Ford of the University of New England in preparing this communication is gratefully acknowledged. Special thanks are also due to the Wildlife Division of C.S.I.R.O. Australia for running the sonagrams shown in figures 1 and 2.

REFERENCES

ALI, S.; DILLON, R.S. 1970. Handbook of the birds of India & Pakistan: 4. frogmouths to pitta's. Bombay.

AMADON, D. 1936. Chimney Swifts nesting in a barn. Auk 53: 216-217.

CLUNIE, F. 1984. Birds of the Fiji bush. Suva. Fiji Museum.

COTTAM, C. 1932. Nocturnal habits of the Chimney Swift. Auk 49: 479-481.

FREEMAN, H.J. 1981. Alpine Swifts feeding by artificial light at night. British Birds 74: 149.

GRIFFIN, D.R.; THOMPSON, D. 1982. Echolocation by cave swiftlets. Behav. Ecol. Sociobiol 10: 119-123.

HARRISSON, T. 1966. Onset of echolocation clicking in Collocalia swiftlets. Nature 212: 530-531.

HESPENHEIDE, H.A. 1975. Selective predation by two swifts & a swallow in Central America. Ibis 117: 82-99.

LACK, D. 1956. Swifts in a tower. London. Muthuen.

MEDWAY, L. 1959. Echo-location among (Collocalia). Nature 184: 1352-1353.

MEDWAY, L. 1962a. The swiftlets (Collocalia) of Niah Cave, Sarawak part 1. Breeding Biology. Ibis 104: 45-66.

MEDWAY, L. 1962b. The swiftlets (Collocalia) of Java & their relationships. J. Bombay Nat. Hist. Soc. 59: 1-8.

MEDWAY, L. 1966. Field characters as a guide to the specific relations of swiftlets. Proc. Linn. Soc. Lon. 177: 151-177.

MEDWAY, L. 1967. The function of echonavigation among swiftlets. Anim. Behav. 15: 416-420.

MEDWAY, L.; Wells, D.R. 1969. Dark orientation by the Giant Swiftlet (Collocalia gigas). Ibis 111: 609-611.

MEDWAY, L.; PYE, J.D. 1977. Echolocation & the systematics of swiftlets. In Stonehouse, B. & C. Perrins. Evolutioary Ecology. London. Macmillan.

MERCER, R. 1966. A field guide to Fiji birds. Suva. Fiji Museum.

NOVICK, A. 1959. Acoustic orientation in the cave swiftlet. Biol. Bull. 117: 497-503.

PECOTICH, L. 1974. Grey swiftlets in the Tully River Gorge and Chillagoe caves. Sunbird 5: 16-21.

PYE, J.D. 1983. Echolocation and countermeasures; In Lewis, B. Bioacoustics, comparative approach. pp. 407-429. London. Academic Press.

ROBERTS, J.R.; SMYTH, D.M.; SPAIN, A.V. 1976. Preliminary studies on acoustic orientation in Collocalia spodiopygia. Search 7: 97-98.

SMYTH, D.M.; ROBERTS,J.R. 1983. The sensitivity of echolocation by the Grey Swiftlet (Aerodramus spodiopygius). Ibis 125: 339-345.

SUTHERS, R.A.; HECTOR, D.H. 1982. Mechanisms for the production of echolocating clicks by the Grey Swiftlet, (Collocalia spodiopygia). J. Comp. Physiol.; a sens Neural Behav. Physiol. 148: 457-470.

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

TARBURTON, M.K. 1987. The population Status, longevity and mortality of the White-rumped Swiftlet in Fiji. Corella 11: in press.

WATLING, D. 1982. Birds of Fiji, Tonga & Samoa. Wellington. Millwood Press.

M.K. TARBURTON. Department of Botany & Zoology, Massey University,
Private Bag, Palmerston North, New Zealand.