

Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

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

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 SwiftletAerodramus spodiopygius assimilis in Fiji and  
Aerodramus spodiopygius chilloensis 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.

Torbarton

Signed M. K. TorbartonDate 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  
TavMASSEY UNIVERSITY  
LIBRARY

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 fedges. 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. Abikoy, 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 Chapman Memorial Fund is acknowledged in appreciation.

## TABLE OF CONTENTS

ABSTRACT. . . . .	. . . . .	ii
INTRODUCTION. . . . .	. . . . .	v
ACKNOWLEDGEMENTS. . . . .	. . . . .	viii
TABLE OF CONTENTS . . . . .	. . . . .	ix
LIST OF FIGURES . . . . .	. . . . .	xii
LIST OF TABLES. . . . .	. . . . .	xiii

### Section 1

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

Abstract. . . . .	. . . . .	1
Introduction. . . . .	. . . . .	2
Description of study areas. . . . .	. . . . .	3
Methods . . . . .	. . . . .	6
Results & Discussion		
Distribution in Fiji & Australia. . . . .	. . . . .	11
The nests . . . . .	. . . . .	13
The nest site . . . . .	. . . . .	14
The breeding season . . . . .	. . . . .	18
The eggs. . . . .	. . . . .	22
Moult in the breeding season. . . . .	. . . . .	30
Incubation. . . . .	. . . . .	31
Sex determination . . . . .	. . . . .	35
Egg loss & replacement. . . . .	. . . . .	36
Extra parental 'co-operation' or 'egg dumping'. . . . .	. . . . .	38
Nestling development. . . . .	. . . . .	39
The nestling period . . . . .	. . . . .	41
Fledging success. . . . .	. . . . .	42
Chick mortality . . . . .	. . . . .	43

TABLE OF CONTENTS Cont.

Adult mortality at nesting caves. . . . .	46
Nest sanitation & ectoparasites . . . . .	48
Feeding of young. . . . .	52
A morphological comparison of six sub-species . . . . .	56
Conclusions . . . . .	60

Section 2

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

Introduction. . . . .	61
Methods . . . . .	63
Results	
Hatching success. . . . .	64
Chick growth. . . . .	65
Fledging success. . . . .	65
Feeding rate. . . . .	69
Discussion. . . . .	72
Conclusion. . . . .	74

Section 3

CLIMATE & INTRA-TROPICAL VARIATION IN CLUTCH SIZE

Introduction. . . . .	75
Methods . . . . .	77
Results	
Hatching success. . . . .	78
Chick growth. . . . .	78
Fledging success. . . . .	84
Feeding rate. . . . .	87
Available food supply . . . . .	88

TABLE OF CONTENTS Cont.

Discussion. . . . .	88
Clutch size and 'competitive' release on islands. . . . .	89
The theory that nest size influences clutch size. . . . .	90
The theory that relates clutch size to predation. . . . .	94
A non clutch-size strategy. . . . .	97
Regulation of clutch size by stability of food supply . . . . .	98
Conclusions . . . . .	103
Section 4	
<u>A NOVEL STRATEGY IN INCUBATION - CHICK INCUBATION</u>	
Introduction. . . . .	105
Methods . . . . .	106
Results . . . . .	107
Conclusions . . . . .	108
Section 5	
<u>DISCUSSION.</u> . . . . .	109
<u>REFERENCES.</u> . . . . .	119
<u>APPENDICES</u>	
Climatological summary table for Fiji & other breeding locations. . .	130
Daily rainfall data for experimental period in Fiji . . . . .	131
Climatological summary table for Chillagoe, Qld.. . . . .	132
Daily rainfall 1985, Chillagoe. . . . .	134
Daily rainfall 1986/87 Chillagoe. . . . .	135
Maximum temperatures at Chillagoe 1985/86 . . . . .	136
The food of the White-rumped Swiftlet in Fiji . . . . .	137
The food of the White-rumped Swiftlet in Queensland . . . . .	153

TABLE OF CONTENTS Cont.

An experimental manipulation of clutch and brood size of White-rumped Swiftlets <u>Aerodramus spodiopygius</u> of Fiji . . . . .	164
A comparison of the flight behaviour of the White-rumped Swiftlet and the Welcome Swallow . . . . .	172
The population status, longevity & mortality of the White-rumped Swiftlet in Fiji. . . . .	185
The significance of the vocalizations of the White-rumped Swiftlet in Fiji . . . . .	216
Breeding of the White-rumped Swiftlet in Fiji . . . . .	225

## LIST OF FIGURES

Location of White-rumped Swiftlet colonies studied in Fiji . . . . .	8
Distribution of <u>chillagoensis</u> and <u>terraereginae</u> . . . . . . . . . . .	9
Location of <u>chillagoensis</u> colonies visited in this study . . . . .	10
Relationship between adult weight and egg weight in swifts & swallows	28
Relationship between feeding rate and nestling periods in swifts . .	57
Mean daily increase in the wing length of chicks in different sized broods .	66
Mean daily increase in chick weight. .	67
Mean daily increase in tarsal length .	68
Wing growth in individuals from broods of all three sizes. . . . .	70
Weight increase in individuals from all three sized broods . . . . .	71
Mean daily increase in wing length of chicks at Chillagoe 1985/6 . .	79
Mean daily increase in weight of chicks at Chillagoe 1985/86 . . . .	80
Mean daily increase in wing length of chicks at Chillagoe 1986/87. .	82
Mean daily increase in weight of chicks at Chillagoe 1986/87 . . . .	83
Average daily change in relative chick weights (3 Dec.1986-23Jan.1987)	85
Average weight increase in chicks 1986/87. . . . . . . . . . . . . . . .	86
Daily weight change in two single broods 1986/87 . . . . . . . . . .	86
Daily weight change in a pair of manipulated chicks 1986/87. . . . .	86

LIST OF TABLES

The size of breeding swiftlet colonies at Chillagoe. . . . .	19
Various apodid and hirundine egg and clutch weights. . . . .	24
Progress of moult in the primary flight feathers . . . . .	30
Length and success of incubation and fledging periods in various swifts and swallows . . . . .	33
The numbers of louse-flies on chicks at 10 day age intervals . . . .	51
Frequency of chick feeding in the Apodidae . . . . .	54
Morphology of four sub-species of the White-rumped Swiftlet. . . . .	58
Synchronization of moult and breeding in Apodidae. . . . .	101