# Determinants of clutch size in the tropics; with reference to the White-rumped Swiftlet

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**Summary** – A series of experiments involving clutch and brood-size manipulation, supplemental feeding and nest enlargement were conducted on White-rumped Swiftlets (*Aerodramus spodiopygius chillagoensis*) nesting in savannah habitat in Queensland Australia, so that the birds' reproductive performance might be compared with that of *A.s.assimilis* (Tarburton 1987a) which nests in the tropical rainforests of Fiji. These experiments show that nest-size, predation, synchrony of moult and breeding, and 'competitive release' are each inadequate to explain why the subspecies in the Queensland savannah has a smaller clutch than the subspecies in the rainforests of Fiji. While an inadequate food supply prevents Queensland birds from raising two nestlings at a time it is clear that current interpretations of food limiting theories are inadequate to explain why birds of the Queensland savannah produce a smaller clutch than their conspecifics in rainforests.

## Introduction

It has long been established 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 and Moreau 1965, Skutch 1967, 1976, Lack 1968, Ricklefs 1970, 1980). While most researchers are agreed that the larger clutch of savannah birds is an adaptive response to a lower population density (Klomp 1970), there is a variety of views as to what controls clutch size.

Lack's theory (particularly as modified by Ashmole 1961, 1963) is widely accepted and probably applies to the tropics more than most theories. This theory proposes that birds achieve 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 surviving pair in the following breeding season. Having more food than those in a stable environment consequently allows for larger clutches. Skutch (1949, 1967), Cody (1966) and Ricklefs (1980) also reason that high mortality in the non-breeding season would at least be a factor in increasing the clutch size in birds from more seasonal regions of the tropics.

It has been suggested (Winkler and Walters 1983) that studies of exceptions to this widely supported trend should be especially instructive in determining

ultimate causes. Because *A. s. chillagoensis* from the savannah environment of Chillagoe, Queensland, Australia, 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.

Several proximate factors that could be looked at in this species and that have been related to the ultimate determination of clutch size are rainfall, nest-size, predation and competitive release on islands. This paper looks at these proximate factors as they affect this swiftlet's ability to raise nestlings in both regions. Latitude and therefore day length is controlled in this study for both study areas are at the same latitude. As the same species is involved in both studies the chance of interspecific variation is eliminated. The purpose is to help determine what it is that ultimately controls clutch size.

## Methods

A sample of nests in Gordale Scar Pot (CH 187) and Guano Pot (CH 146) in the Chillagoe (CH) district of North Queensland was used for controls and for manipulation experiments. Methods used are similar to those used in Fiji (Tarburton 1987a), except that because the only natural clutch is one, it was necessary to manipulate only clutches and broods of two. Only a few single broods were exchanged. 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. An additional experiment was run simultaneously. It involved enlarging eight nests by gluing a length of 6 mm manila rope along the rim of the nest and to the wall with cyanoacrylic acid ester glue. This made nests as deep, as long and as wide as Fijian nests which normally accommodate two nestlings. In the text all means of measurements are followed by standard errors.

The 1985/6 breeding period is considered a good season with abundant rain and insects while the 1986/7 breeding season is considered to have been a poor season with low rainfall and insufficient food supply. The rain that fell during December and January of the good season represented 152 percent of the average rainfall for this period and this correlated with a much higher density of available insects than was found in the poor season (Tarburton 1994), when for the most part only 35 percent of the average rainfall was recorded. In the dry season very little saliva was used in nest contruction and nests fell apart earlier, possibly contributing to the higher loss of chicks which were slower growing in the dry year. Having a good and a poor season has allowed for a clearer assessment of the birds' ability to feed an extra nestling under both abundant and scarce food supply situations.

# Results

## Hatching Success

The hatching success of single-egg and two-egg clutches for both the good (1985/86) and the poor (1986/87) seasons at Chillagoe and the comparable results for Fiji are shown in Table 1. The percentage of single-egg clutches hatching in the good season at Chillagoe is not significantly different (Median test, $X^2 = 0.24$, n.s.) from the hatching success in the poor

season and so the results may be pooled. The pooled average is not significantly different (median test, $X^2 = 0.03$ n.s.) from the hatching rate of single-egg clutches in Fiji. The hatching success of two-egg clutches in the good season at Chillagoe is obviously significantly better than the hatching rate for single egg clutches but was not significantly different (Median test, $X^2 = 1.44$, n.s.) from the hatching rate for two-egg clutches in Fiji. Similarly in the poor season at Chillagoe the hatch rate of twin eggs is not significantly different (Median test, $X^2 = 1.25$, n.s.) from the hatching rate in the good season and not significantly different (Median test, $X^2 = 3.11$, n.s.) from the Fijian hatching rate.

## Nestling 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) nestling were dropping significantly behind those in normal sized broods. Average adult wing length was not reached before birds fledged although the minimum adult wing length was reached by most before fledging.

In the poor season of 1986/7 the occurrence of a significant difference between the average wing length of broods of one and two young was delayed until the tenth day (Figure 3). Figure 3 also shows that the wings of nestlings from single broods grew significantly faster in the good year than in the poor year. In all the manipulated two-nestling broods one nestling died and the survivor's wings took an average of 10 days longer than those in one-nestling broods to reach minimum adult length.

The weight of nestlings 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 nestlings in single-nestling and two-nestling 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 nestlings increased significantly above that of the two-nestling broods. Comparing these measurements with those for *assimilis* nestlings from one and two-nestling broods, which were not significantly different until the 12th day, it is clear that *chillagoensis* is much less able to cope with an extra nestling. Single nestlings reached minimum adult weight by the 17th day whereas

Table 1. Hatching success in the White-rumped Swiftlet.

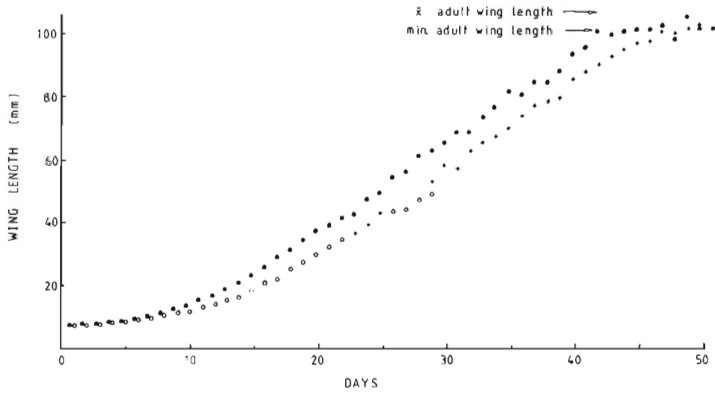| Sample | Clutch size | Mean ± S.E. | n |
|---|---|---|---|
| Chillagoe 1985/86 | 1 | 0.69 ± 0.06 | 58 |
| Chillagoe 1986/87 | 1 | 0.06 ± 0.06 | 69 |
| Chillagoe both yrs | 1 | 0.64 ± 0.06 | 127 |
| Fiji | 1 | 0.52 ± 0.09 | 29 |
| Chillagoe 1985/86 | 2 | 1.80 ± 0.09 | 10 |
| Chillagoe 1986/87 | 2 | 0.80 ± 0.40 | 6 |
| Fiji | 2 | 1.15 ± 0.14 | 40 |

Figure 1. Mean daily increase in wing length of chicks at Chillagoe 1985/6.
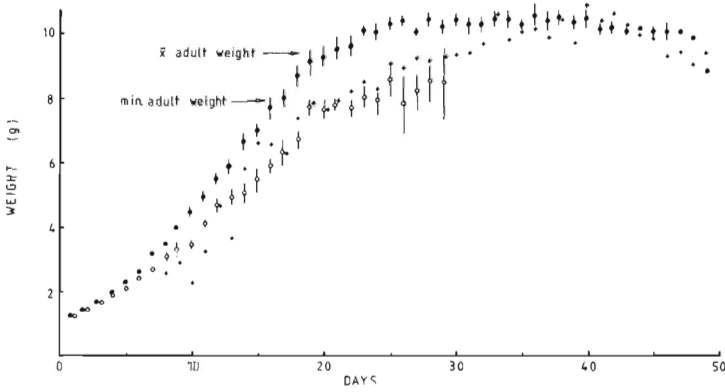


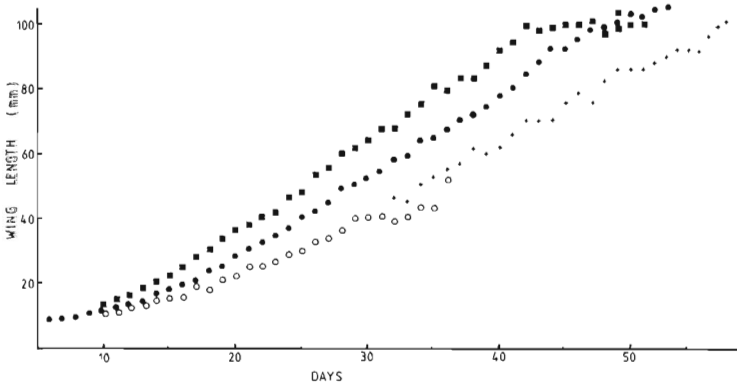Figure 2. Mean daily increase in weight of chicks at Chillagoe 1985/6.



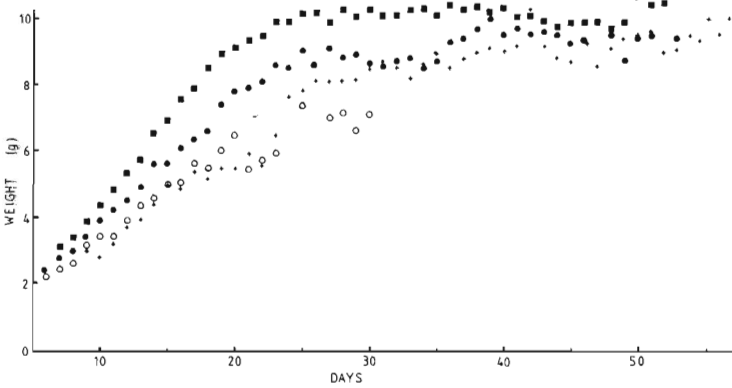Figure 3. Mean daily increase in wing length of chicks at Chillagoe 1986/7.



Figure 4. Mean daily increase in weight of chicks at Chillagoe 1986/7.

surviving nestlings from two-nestling 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, nestlings 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 nestling reached average adult weight.

The long-lasting effect of insufficient food for nestlings in two-nestling broods is shown by the longer time taken by them to reach maximum weight when compared with single-brood nestlings. Another useful measure for making comparisons in nestling growth is the time taken to reach an asymptote (Bradley *et al.* 1984). During the good season single-brood nestlings took 23 days to reach an asymptote whereas the survivors of the two-nestling broods took 35 days to reach the same level. Wing growth in these two-nestling brood survivors was also delayed, taking 47 days to reach 100 mm, whereas single-brood nestlings took only 43 days to reach the same wing length.

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

## Fledging success

The fledging success for the different sized broods is shown in Table 2. In the good season, *chillagoensis* parents with a brood of two did not raise significantly (Median test, $\chi^2 = 0.02$, n.s.) more nestlings than those with broods of one. The fledging success of single broods was also not significantly different (Median test, $\chi^2 = 0.02$, n.s.) from that raised from single broods in Fiji.

However, in not one case in either the poor or good year at Chillagoe were both nestlings from a two-nestling brood successfully fledged. In the poor season *chillagoensis* with broods of one raised significantly fewer (Median test, $\chi^2 = 5.97$, P<0.02) than those raised from single-nestling broods in the good season. In the poor season *chillagoensis* with two-nestling broods raised significantly more (Median test, $\chi^2 = 3.92$, P< 0.05) than those raised from single nestling broods in the same season.

Only one nestling fledged from each of the two-nestling broods (n = 8) 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. The individual growth curves of nestlings from single-nestling broods (Fig. 6b) show greater deviation in response to rain than the deviations for nestlings from two-nestling broods (Fig, 6c) when compared to the average growth curve (Fig. 6a). However, the decline in the weight of nestlings dying by starvation is very clear in the individual growth curves for nestlings from two-nestling broods Fig. 6c). Some nestlings that died did not show weight declines because they fell, or were pushed from their nests while still in good health.

## Nest size

One hundred *chillagoensis* nests from Gordale Scar Pot and Guano Pot had an average size of 49.9 ± 0.49 x 42.7± 0.47 x 11.9± 0.42 mm and a volume index of 25.4 cm³. Thirty-six nests from Fiji averaged 50.0±0.7 x 49.7 ±0.7 x 21.1± 1.0 with an average volume index of 52.4 cm³.

## Feeding rate

By observing a sample of natural and manipulated broods at Chillagoe for one whole day in each season, the data shown in Table 3 were obtained. In the good season the average number of feeding visits per day, to nests with two nestlings was not significantly greater (Median test, $\chi^2 = 0.67$, n.s.) than the number of visits to nests with broods of one. In the poor season it was similarly demonstrated that the average

Table 2. Fledging success in the White-rumped Swiftlet.

| Sample | Brood size | Mean ± S.E. | n |
|---|---|---|---|
| Chillagoe 1985/86 | 1 | 0.69 ± 0.06 | 25 |
| Chillagoe 1985/86 | 2 | 0.56 ± 0.18 | 16 |
| Fiji | 1 | 0.43 ± 0.11 | 27 |
| Chillagoe 1986/87 | 1 | 0.31 ± 0.12 | 12 |
| Chillagoe 1986/87 | 2 | 0.71 ± 0.11 | 11 |

Table 3. Feeding rate (average number of visits per brood per day) in the White-rumped Swiftlet.

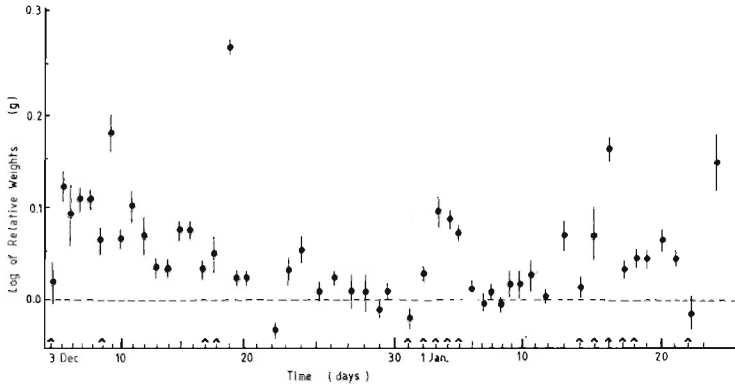| Sample | Brood size | Mean ± S.E. | n |
|---|---|---|---|
| Chillagoe 1985/86 | 2 | 4.7 ± 0.67 | 3 |
| Chillagoe 1985/86 | 1 | 5.2 ± 0.30 | 20 |
| Fiji | 1 | 2.8 ± 0.30 | 20 |
| Chillagoe 1986/87 | 1 | 2.7 ± 0.30 | 3 |
| Chillagoe 1986/87 | 2 | 3.0 ± 0.70 | 6 |

Figure 5. Average daily change in relative chick weights (3 Dec. 1986 - 23 Jan. 1987).
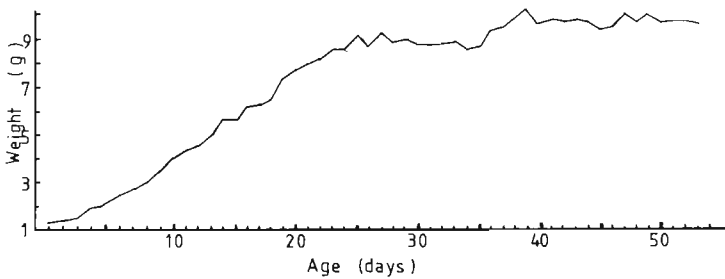


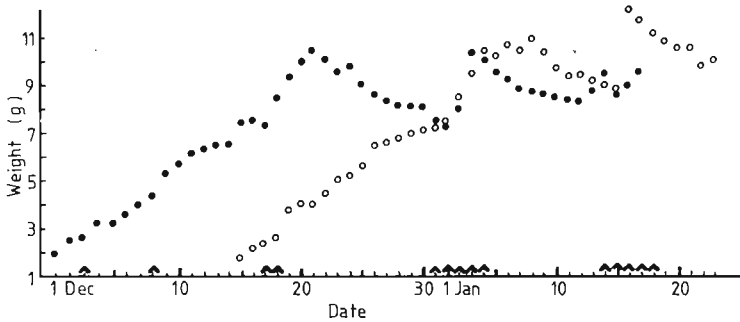Figure 6a. Average weight increase (1986/87).



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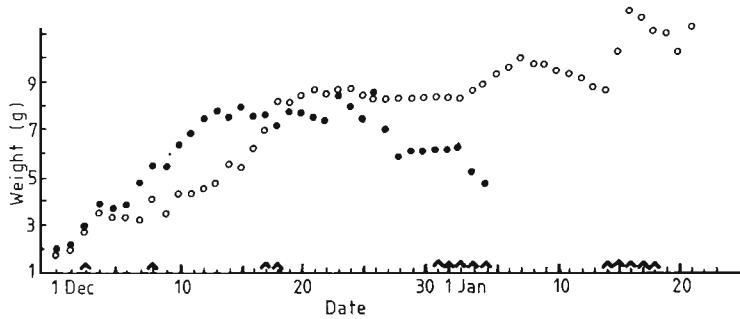


Figure 6c. Daily weight change in a pair of manipulated chicks

number of visits to nests with two nestlings was not significantly greater (Median test, $X^2=0.39$, n.s.) than the number of visits to nests with one nestling. However, the number of visits to broods of one in the poor season was significantly (Median test, $X^2 = 4.2$, P< 0.05) fewer than during the good season. The number of visits to two-nestling broods in the poor season was not significantly (Median test, $X^2 =0.5$, n.s.) less than in the good season. The number of visits to single broods of *chillagoensis* in the good

season was significantly greater (Median test, $X^2=6.1$, P< 0.05) than that of feeding visits to single broods of *assimilis*. In the poor season, however, the number of visits to single broods of *chillagoensis* was not significantly greater (Median test, $X^2 = 0.02$, n.s.) than the number of feeding visits to single broods of *assimilis*.

## Available food supply

The average number of insects (95± 29) (x ± s.e.) caught in the sweep net samples of available prey in Fiji was significantly more ($t_{52} = 3.0$, 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 ($t_{10}=2.1$, e < 0.05) than that caught there in the good year.

Catching more than the average number of insects in the sweep net was significantly (Median test,$X^2 = 6.55$, P< 0.02) more likely than not, 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 also significantly (Median test, $X^2=6.55$, P< 0.02) 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 relationship ($X^2=2.3$, n.s.) between whether swiftlets were feeding in the area sampled with the sweep net and whether or not rain had fallen (or the irrigation sprinklers used), in the previous 24 hours.

## Discussion

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

Despite one season at Chillagoe and two in Fiji which were apparently favourable for gathering food, neither *chillagoensis* nor *assimilis* (Tarburton 1987a) were able to raise significantly more nestlings 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-nestling broods in the poor season at Chillagoe can be explained by the supplementary feeding given to most twins, but not to nestlings in single-nestling 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 dutches 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. All of these hypotheses assume that the founding individuals were not already genetically constrained to producing one egg at some locations.

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 for islands there is yet to be a full accounting of factors controlling breeding strategies such as clutch size. Other evidence for additional 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 other factors thought to contribute to the regulation of clutch size are predation and nest size *per se*. Both deserve a closer look as data are available for six subspecies of the White-rumped Swiftlet and three subspecies of the Caroline Swiftlet to test whether these are factors for 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, this cannot apply to the White-rumped Swiftlet which nests in the totally dark sections of caves, making 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. These areas have roosting bats in them infrequently and predation of birds or bats by the Ghost Bat is rare at Chillagoe.

That some of the swiftlet nests and their nestlings 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 nestlings, 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 (*Parus caeruleus*) and House Sparrows (*Passer domesticus*) the saving in metabolic energy made by individuals in broods larger than average when the environment was at 15°C was not made at 20°C (O'Connor 1975). As *assimilis* and *chillagoensis* nestlings 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 nestling 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 nestling 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 (Møller 1982). So we may well ask does the size of the nest vary in the White-rumped Swiftlet?

The smallest nests measured so far are thirty nests from the Tully Falls Cave in coastal Queensland (Pecotich 1974). These were built by *A.s. terraereginae* and averaged 56 x 45.5 mm in length and width and 3 mm in depth, giving a volume index of 7.6 cm³. The next largest are the nests of *chillagoensis* with the largest of all being the nests from Fiji. The measurements show that the nests of *assimilis* attain a much larger volume through being much deeper than the nests 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?

## 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 coastal Queensland, where '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 with the average

of 2,785 nests for five Fijian caves (Tarburton 1987b), 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, at least at the individual level. My discovery of seven 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) and four found by other caving club members, brings the number of Chillagoe colonies that were active during the time of this study to 34. This number of colonies and there are surely more is greater than is known for any simaarly sized 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 with 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: 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.rukenis*) 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 generally 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 them) 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 lighted locations. This, however, is not the case. *A. s. terraereginae* generally nests in lighted 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 produce two-egg clutches and do so regardless of whether the nests are concealed by darkness or not. On Bougainville Island *A. s. reichenowi* has been found nesting in abandoned mine shafts and under a dead leaning tree (Haddon 1981). In Tonga, *A. s. townsendi* produces its two-egg clutches in sea caves where some nests are only 3 m from the entrance (M. Potts pers. comm.). In New Caledonia *A. s. leucopygia* also appears to nest in twilight situations (Hannecart and Letocart 1980).

## A multiple clutch strategy

One means that both Queensland subspecies may use to overcome the restrictions of 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 Dunk Island swiftlets 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

nestlings. Thus it takes a pair of Queensland swiftlets two and a half months to raise a single brood. 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.* 1980) 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 is no 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, as these birds are almost totally restricted to breeding in their natal colony (Tarburton 1987b).

## 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 correlated with rainfall (Lack 1956, Hespenheide 1975, Emlen 1982). This, in conjunction with Ricklefs' (1980) modification of Lack's hypothesis (that clutch-size is related directly to the resources available duing 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 in Fiji) 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.

Rainfall data from both the dry and wet sides of New Caledonia indicate low variance (39% and 24% respectively), which is consistent with the fact that on this island this species produces a clutch of two (Hannecart and Letocart 1980). Rainfall for seven Samoan stations (excluding those on the wet south-east margin), averaged 14%. This high variance is consistent with the clutch size of one on these islands (Whitmee 1875). These data indicate that the margin between high and low variance is between 14% and 24%.

Savannah is not the only example of a harsh climate (one having extremes). 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 savannah 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 K-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 4 confirm these relationships. Swifts commence moult after laying or after the fledging of their nestlings. 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.

That synchronous moult and breeding restricts brood size in this species is unlikely for both *assimilis* and *chillagoensis* moult while breeding. This means that the only remaining variable between the subspecies that is likely to affect clutch size is the food supply. Because daily growth rate varies with food supply, which 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.

Because the average number of insects caught in the sweep net samples of available prey in Fiji was significantly more than the average number caught during the good year at Chillagoe, and because the average number of insects caught in the sweep net at Chillagoe in the poor year was significantly less than that caught there in the good year, it is clear that it is variation in the abundance of food and not an inability on the part of the bird to collect more food that restricts this swiftlet to raising only one nestling even in a good season at Chillagoe.

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

Table 4. Synchronization of moult and breeding.

| Species | Synchronous | Discreet | Moult after laying | Clutch size | Climate | Source |
|---|---|---|---|---|---|---|
| *Apus apus* | | X | | 2.3 | temp. | Lack and Lack 1951 |
| *Apus melba* | | X | | 3/4 | temp. | Lack and Arn 1947 |
| *Apus berliozi* | | X | | 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 1971b |
| *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 1962 |
| *Aerodramus spodiopygius* | X | | | 1/2 | trop. | Tarburton 1986 |

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 was not significantly correlated to whether rain had fallen (or the irrigation sprinklers had been used) in the previous 24 hours. This lack of correlation is probably due to the birds moving to forage in different areas after several days of rain.

It was the generally low level and high variability in food supply rather than an inability of the parents to obtain food that restricted clutch size to one. If the food was available the parents on those islands were able to collect sufficient for two nestlings. When rain ended a dry period even in the poor season, their nestlings gained weight rapidly (up to one third adult weight in one day). In the good season parents fledged their single broods in the same time as did Fijian birds with single broods. 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 nestlings than they did in the good season.

## Conclusion

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 White-rumped Swiftlet is an exception, for *chillagoensis* is unable in its savannah environment to raise an artificially enlarged brood of two, whereas *assimilis* normally raises two in the more uniform climate of Fijian rainforest.

This paper has shown that a number of theories are unable to explain this phenomenon. Because enlarging nests did not increase the fledging rate, nest size is not effective in controlling clutch size in *chillagoensis*. Because predators cannot reach the nests of *spodiopygius*, the number of nestlings 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 (Hespenheide 1975). In other words, food is the limiting factor that prevents *chillagoensis* from raising two nestlings at one time. Nevertheless 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 nestlings within a season. This is examined in Tarburton and Minot (1987). 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 nestling had significantly shorter wings than those in natural broods of one by the eighth day, while the average weight of the same nestlings fell significantly behind that of the two-nestling broods earlier than *assimilis* nestlings from artificially enlarged broods. This is taken to indicate the greater difficulty *chillagoensis* has in collecting adequate food for two nestlings.

That *chillagoensis* made significantly fewer feeding visits to nestlings in the poor season than in the good season and that two-nestling broods were not fed significantly more often than single-nestling broods in either the poor or good season, indicates that this bird is struggling to adequately feed one nestling in a poor season and cannot feed two nestlings even in a good season. The correspondence between 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 suggest that a lack of available food was the major cause preventing *chillagoensis* from fledging significantly more nestlings from manipulated two-nestling broods than from natural single-nestling broods. So it is the reliability as well as the quantity of food that determines clutch size in the White-rumped Swiftlet in the tropics.

**Riassunto** – In ambiente di savana nel Queensland australiano si sono effettuati esperimenti di manipolazione del numero di uova e di nidiacei, con nutrizione artificiale e ingrandimento del nido di *Aerodramus spodiopygius chillagoensis*.
Le condizioni riproduttive così create sono paragonabili a quelle affrontate dalla sottospecie *A. s. assimilis* che nidifica nelle foreste pluviali di Fiji.
Questi esperimenti hanno dimostrato che la dimensione del nido, la predazione, la sincronia di muta e di nidificazione non sono parametri in grado di spiegare il motivo per cui la sottospecie di savana del Queensland ha una dimensione della covata minore rispetto alla sottospecie di Foresta a Fiji. Anche se carenze di cibo possono impedire alle coppie del Queensland di allevare due nidiacei, occorre notare che le attuali interpretazioni teoriche sulle disponibilità alimentari non possono spiegare covate minori dei loro conspecifici della foresta pluviale.

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