An experimental manipulation of clutch and brood size of White-rumped Swiftlets *Aerodramus spodiopygius* of Fiji

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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 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 maximizing their clutch size in respect to the quantity of food that is immediately available during the breeding season. However, they also recognize that parents may be maximizing 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 (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 $0{\cdot}43 \pm 0{\cdot}18$ ($\bar{x} \pm$ s.e., $n = 9$), while the manipulated ones hatched an average of $0{\cdot}61 \pm 0{\cdot}12$, ($n = 20$); (Median test; $\chi^2_1 = 0{\cdot}28$, n.s.). Pairs with a natural clutch size of two hatched, on average, $1{\cdot}18 \pm 0{\cdot}15$, ($n = 34$) and the manipulated twos, $1{\cdot}0 \pm 0{\cdot}26$, ($n = 6$) ($\chi^1_2 = 0{\cdot}6$, n.s.).

The combined hatching success of single-egg clutches was $0{\cdot}52 \pm 0{\cdot}09$ ($n = 29$) and that of the combined two-egg clutches $1{\cdot}15 \pm 0{\cdot}14$ ($n = 40$), showing a clear advantage to the two-egg clutch ($t_{65} = 3{\cdot}81$, $P < 0{\cdot}001$). The manipulated three-egg clutches had an average clutch hatching of $1{\cdot}22 \pm 0{\cdot}17$ ($n = 27$), which was not significantly larger than that of the two-egg clutches ($t_{55} = 0{\cdot}33$, 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 $0{\cdot}43 \pm 0{\cdot}11$ chicks ($\bar{x} \pm$ s.e., $n = 24$). Those with a brood of two raised $0{\cdot}92 \pm 0{\cdot}15$ ($n = 25$) and those with a brood of three raised $1{\cdot}09 \pm 0{\cdot}3$ ($n = 11$).

These data show that a pair with a brood of two rear significantly more young than those with a brood of one, ($t_{44} = 2{\cdot}57$, $P < 0{\cdot}01$), while those with a brood of three do not rear significantly more than those with broods of two ($t_{15} = 0{\cdot}59$, n.s.).

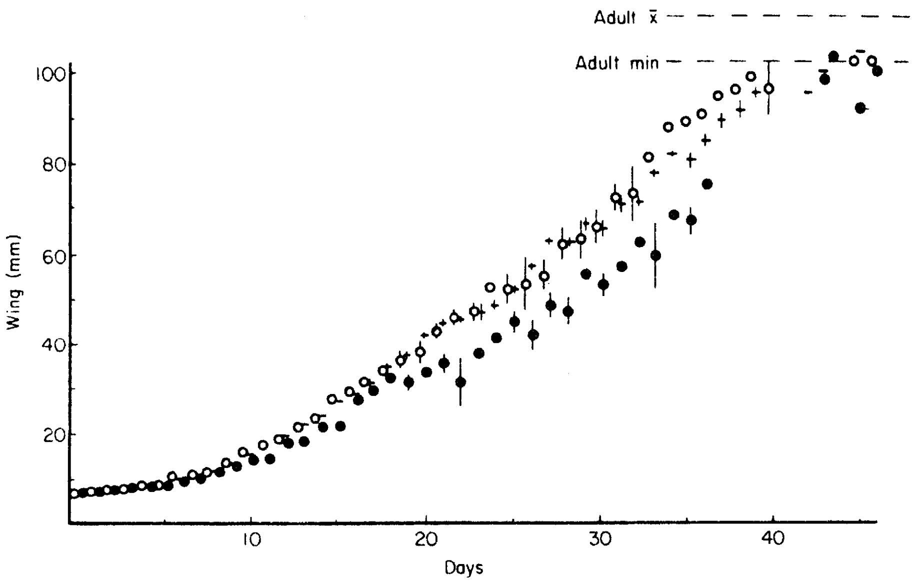

Figure 1. Mean daily increase in the wing length of White-rumped Swiftlet chicks in different sized broods: the means for broods of one are represented by hollow circles, broods of two by horizontal bars and broods of three by solid circles. Standard errors of the means (vertical lines) for chicks in 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.

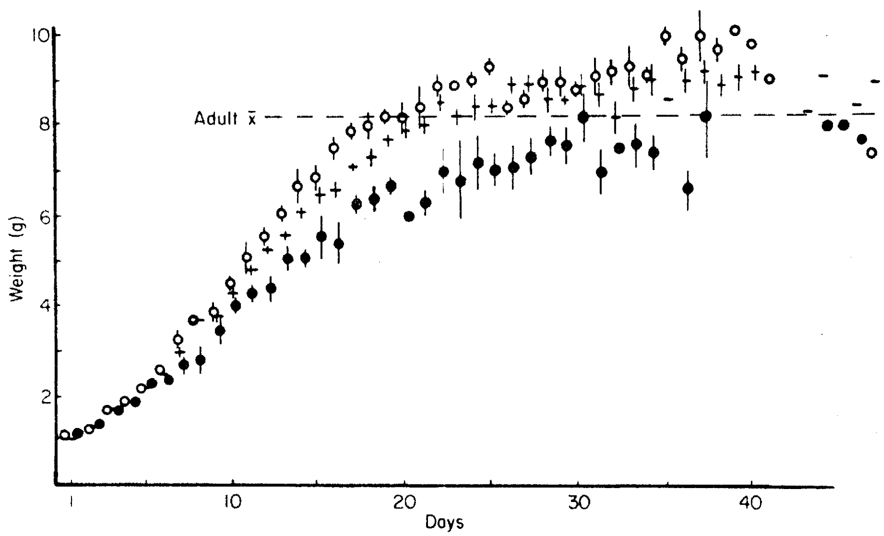

Figure 2. Mean daily increase in White-rumped Swiftlet chick weight: the means for broods of one are represented by hollow circles, broods of two by horizontal bars and broods of three by solid circles. Standard errors of the means (vertical lines) for chicks in broods of three rarely overlap those for 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.

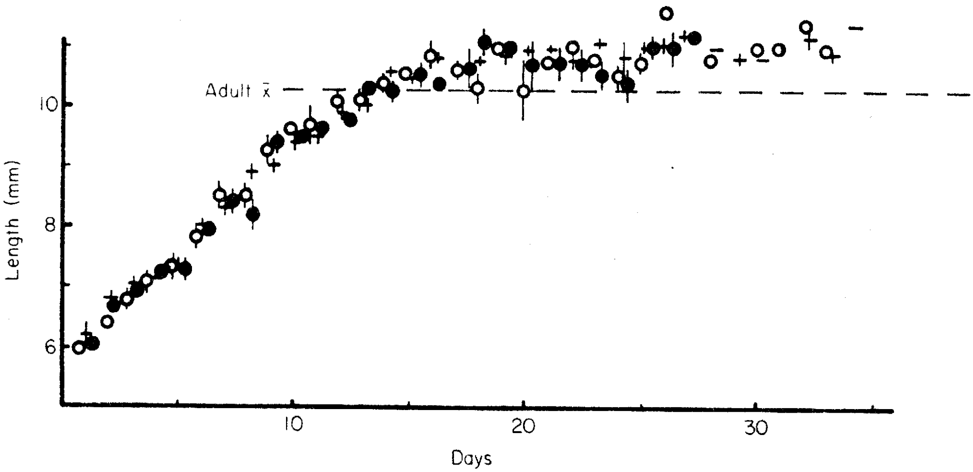

Figure 3. Mean daily increase in tarsal length of White-rumped Swiftlets: the means for broods of one are represented by hollow circles, broods of two, horizontal bars and broods of three by solid circles. The consistent overlap between the standard errors (vertical lines) of chicks from all three clutch 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.

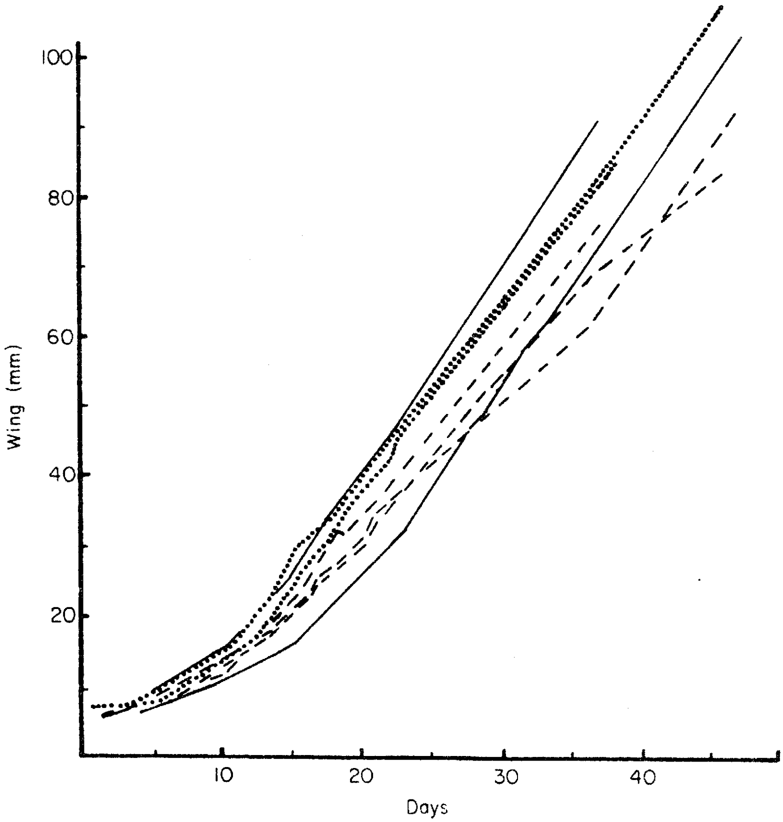

Figure 4. Wing growth of White-rumped Swiftlet individuals from broods of all sizes. Chicks from single broods are represented by continuous lines, those from broods of two by dotted lines, and those from broods of three by discontinuous lines.

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

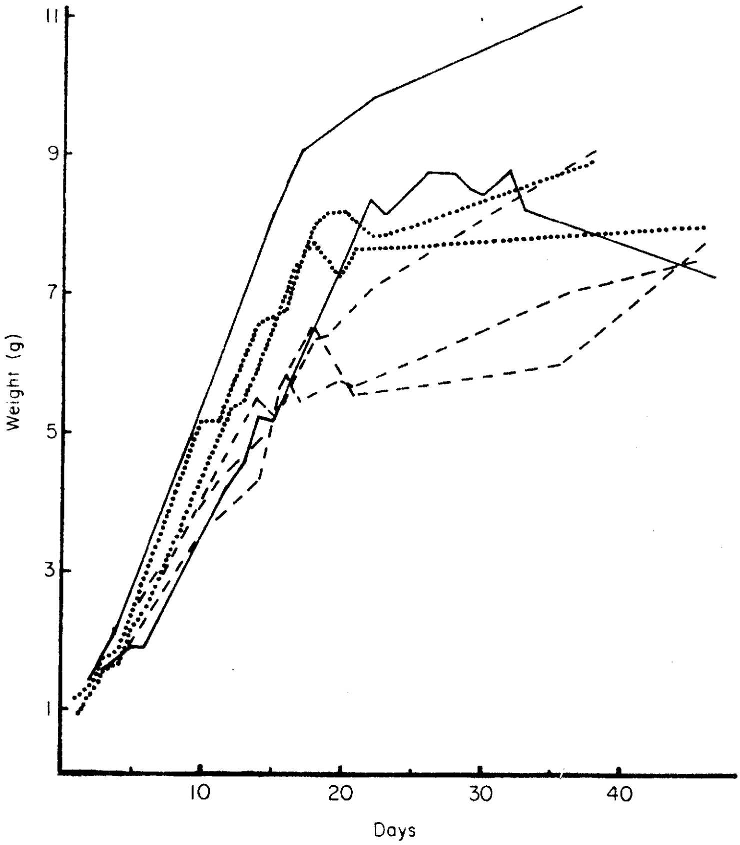

Figure 5. Weight increase in White-rumped Swiftlet individuals from all three sized broods. Chicks from single broods are represented by continuous lines, those from broods of two, by dotted lines and those from broods of three by discontinuous lines.

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.

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