A Novel Strategy of Reproduction in Birds

The breeding biology of birds has been extensively studied and it would seem that every conceivable pattern 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 & Burger 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 over 100 years. Here we report a new strategy of reproduction, incubation by nestling birds. This strategy is used in tropical Australia by white-rumped swiftlets, *Aerodramus spodiopygius*. In this population a single egg is incubated by the adults and a second egg is incubated by the first nestling before it fledges. This behaviour reduces both the time spent incubating by adults and the interval between successive nestlings. Nestlings do not incubate in other populations of this species where a single clutch of two eggs is incubated by the parents. Hence the behaviour appears to be ecologically facultative.

We studied the breeding of two populations of cave-nesting white-rumped swiftlets, one in Chillagoe, Queensland, Australia and the other near Suva, Fiji. In Fiji, pairs incubated two eggs and reared two young per year (Tarburton 1986). To test whether broods of three could be reared successfully an extra egg or nestling was added to 27 nests. These artificial broods of three young were not reared successfully although parents increased their feeding rate (Tarburton 1987). At Chillagoe, nests contained only a single egg. All 17 artificial broods of two were unsuccessful. Thus in both populations the swiftlets are laying a clutch of the most productive size.

However, at Chillagoe in 86% ($N=140$) of nests with a nestling near the age of fledging, the nest also contained an egg being incubated by the nestling. Each of these 140 incubating nestlings was removed from its nest to check the contents. When each was returned it resumed a typical incubating posture by settling over the egg. This behaviour was indistinguishable from that of incubating adults. Thus, the presence of an egg in the nest was sufficient stimulus to release incubation behaviour in the nestling. However, given the small size and shape of the nest cup there was little scope for alternative behaviour by the nestlings.

The brood patches of adults and nestlings appeared to be the same. They were lightly feathered with down and not highly vascularized. The incubation period was for adult-incubated eggs $26{\cdot}9 \pm 0{\cdot}2$ days ($\bar{X} \pm$ SE, $N=32$) and $26{\cdot}8 \pm 0{\cdot}5$ days ($N=8$) for nestling-incubated eggs, so the effectiveness of incubation by nestlings did not differ significantly from that of adults. Nestlings with eggs did all the incubating during the day. At night the adults roosted at the nest but again it was probably the nestlings that did the incubation.

In Australia the timing of laying the second egg was such that it did not hatch before the incubating chick fledged. The mean nestling period was $46{\cdot}9 \pm 2{\cdot}2$ days ($\bar{X} \pm$ SD, $N=13$). The mean age of a chick at the laying of the second egg was 32 days (range 23–47 days, $N=18$). When the incubating chick fledged the adults completed any remaining incubation. Without incubation by nestlings, at least 148 days would be required to rear two nestlings, one at a time, from egg to fledgling, at a single nest. This assumes an incubation period of 27 days, a nestling period of 47 days and no time between the fledging of the first chick and laying of the second egg. Incubation of the second egg by the first nestling makes it possible to save more than 3 weeks in the time needed to rear two young.

Despite the differences in incubation strategies the annual production of swiftlets in Fiji and Australia was similar. A breeding pair produced

$1{\cdot}1 \pm 0{\cdot}11$ ($\bar{X} \pm$ SE, $N = 39$) fledged young in Fiji and $1{\cdot}0 \pm 0{\cdot}15$ ($N = 27$) fledged young in Queensland.

The incubation of eggs by nestling swiftlets at Chillagoe raises some intriguing questions. How do nestlings perform what is typically a breeder's behaviour? Hormone changes are normally associated with incubation behaviour in adults (Follett 1984; Brown 1985) but little is known about the hormone levels in the young. Certainly an incubating nestling will not have been through the same hormonal cycle as an adult. Ultimately the incubation by nestlings should be linked to their gain in inclusive fitness relative to the cost of incubating. There would seem to be very little energetic cost to incubating a single egg at the constant ambient temperature of 23°C inside the Chillagoe caves. Unlike an adult, a nestling has no conflicting behavioural activities. 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 do the Chillagoe birds rear two young in succession rather than two simultaneously as in Fiji? And why don't the young swiftlets develop faster? The answer to both questions appears to rest ultimately on food. The abundance of insect food for the swiftlets is correlated with rainfall. In the rainforest near Suva the annual rainfall is 3200 mm and the ratio of the mean rainfall in the driest month to the mean rainfall in the wettest month is 1:2·6. The corresponding figures for the Chillagoe savanna are 855 mm rainfall and a ratio of 1:54. Insect food at Chillagoe is only abundant just after the erratic rains of the 3-month rainy season. As a result the food supply at Chillagoe is smaller and more variable, both within and between seasons, than in Fiji. In fact, the food supply for most swifts and swiftlets appears more variable than for many other bird species. One or two slowly developing nestlings do not require food at as fast a rate and can better withstand several days without food as compared with a larger brood of quickly developing young. By comparison, songbird nestlings of similar size develop in less than one-third the time required by swiftlets but require a high rate of feeding throughout the nestling period (Lack 1968). A long incubation period for birds in general (Lack 1968) and swifts in particular (Tarburton & Minot, unpublished data) appears to be a developmental constraint resulting from a long nestling period. Incubation by the first nestling is one way around this developmental constraint and the ecological constraint of a limited breeding season.

It is possible that this breeding behaviour will be found in other species. If so it is likely that the circumstances will include (1) a habitat where the food supply severely limits the number of young that can be reared at one time and where survival during the non-breeding season is low, (2) conditions suitable for breeding which last long enough to feed two nestlings in succession, and (3) no post-fledging parental care.

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