

SHORT COMMUNICATIONS

GROWTH AND DEVELOPMENT OF THE BROWN-BACKED HONEYEATER *RAMSAYORNIS MODESTUS* IN NORTH QUEENSLAND

Passerine birds in the humid tropics have smaller clutches, higher egg and nestling mortality and grow more slowly than temperate zone passerines (Ricklefs 1968b). Ricklefs (1976) compared the growth rates of 30 tropical passerine species from Trinidad and Panama with the growth rates of 51 species of temperate-zone passerines and found that on average the former grew 23% more slowly than the latter, and that the variation in growth rate within each group was similar. More recently, growth data on nine tropical passerines from Brazil indicated that these species grew at a daily rate intermediate between the tropical passerines and temperate zone passerines compared above and their growth rate was not significantly different from the average growth rate of temperate zone passerines (Oniki & Ricklefs 1981). Developmental adaptations of tropical passerines and temperate zone passerines apparently differ, and the former group may have more diverse adaptations than the latter (Ricklefs 1976). More study of the growth and development of passerines in the humid tropics is needed before these adaptations can be understood.

This paper presents the results of a study of the growth and development of the Brown-backed Honeyeater *Ramsayornis modestus*, Meliphagidae, done from August to November 1984 near Townsville, Queensland, latitude 19°15'S.

The Brown-backed Honeyeater. The Brown-backed Honeyeater is sometimes called the Melaleuca bird because of its dependence on the bark of *Melaleuca* sp. (paper bark gums or tea trees) for nest material and its frequent use of those trees for nest sites. It builds a roofed pensile nest situated near the end of a branch in trees or tall shrubs. The clutch is usually two eggs (Pizzey 1980), occasionally one. Incubation begins with the second egg and takes about 15 days. Seventy-five hours of nest observation indicate that the nestlings are fed mostly on insects. Both adults feed the young. The results of this study show that the young are 13 days old on average, when they fledge (range 12–15 days, $n = 9$). The average weight of adults is 12.1 g, range 8.5 to 14.0 g (*s.d.* 1.37, $n = 17$). Breeding of the Brown-backed Honeyeater begins in August and continues during the remaining three months of the dry season and well into the wet season.

Co-operative breeding is frequent in the Meliphagidae (Dow 1980) but apparently does not occur in the Brown-backed Honeyeater. The birds are usually observed in

pairs, particularly when several birds are engaged in territorial disputes. During 75 h of observation at six nests only members of the pair fed the young. Occasional strange birds that visited the nest were chased by the pair.

STUDY AREA AND METHODS

The study was done in open *Eucalyptus* — *Melaleuca* woodland in the Townsville Town Common Environmental Park. The climate is tropical with strongly contrasting rain and dry seasons. Median rainfall, based on 34 years of climatic records, is 112.3 cm per year. Seventy percent of the rain (78.9 cm) falls in a 4 month rain season from December through March, the remaining 33.4 cm falls irregularly in the remainder of the year. July, August, and September usually have the least rain. The mean annual temperature, for the same record period, is 24.1°C (minimum 19.5°C, maximum 28.7°C). The monthly mean temperature varies from 19.3° (range 13.7°C to 24.9°C) in July, to 27.6° (range 23.8°C to 31.3°C) in January. The mean daily temperature range for the year is 9.2°C; it is greatest (11.2°C) in the coldest month (July) and least (7.1°C) in February. The climate during the study was average.

Nests were visited in the morning between 0630 and 1000. The nestlings were individually marked and were weighed on an Ohaus triple beam balance accurate to 0.1 g and measurements of several body parts were taken. The bill was measured from the external nares to the tip, and from the corner of the mouth to the tip (gape). The tarsus was measured from the back of the tarsal joint to the distal end of the tarsometatarsus. The manus was measured from the bend in the wing to the end of the fleshy part of the wing. Two flight feathers were also measured, the seventh primary, counted from the proximal end of the series, and one central rectrix. Measurements were taken with a dial caliper, although as the plumage matured the flight feathers were measured to the nearest 0.5 mm with a thin plastic ruler inserted next to the feathers. Details of development and behaviour were noted on each visit. The weight curves were analyzed according to Ricklefs (1967).

Adult dimensions are from ten male and ten female Queensland specimens, combined for comparison with nestling measurements, in the American Museum of Natural History. Measurements were taken as nearly as possible as on the nestlings. The manus was measured from the end of flesh between the two most distal primaries to the bend in the wing.

RESULTS

Growth data were obtained from 21 nestlings, 18 of which were weighed and measured repeatedly, nine for the entire nestling period. Most nestlings (16) were from nests with two nestlings, but two were from nests in which only one nestling was raised.

Plumage development. At hatching (age Day 0) the

Brown-backed Honeyeater nestling is without down and has clear orange-yellow skin. There is no evidence of feather follicles of either down or contour feathers. Day 0 nestlings may have a dark band of melanin pigment in the forearm and manus (alar tract), which marks the developing remex follicles. Projecting filaments, approximately 0.5 mm long, on the ends of the primary feather follicles may pierce the skin late on Day 0. Similar structures were reported on the remiges and rectrices of the Eastern Bluebird *Sialia sialis* (Pinkowski 1975) and on the House Wren *Troglodytes aedon* (Boulton 1927). Boulton considered them to be degenerate neossopiles.

Melanin pigment appears in the alar tract of some nestlings on Day 0. On Day 1 these pigments are general in the alar, spinal and humeral tracts.

Feather follicles are distinguishable on Day 2. Primary and secondary feather follicles (as distinct from their filament tips) emerge through the skin on Day 2. The greater upper primary and secondary coverts emerge on Day 3, beginning at the distal end of each row.

Contour feather follicles begin to emerge through the skin in the spinal and humeral tracts on Day 3, the ventral tract on Day 4 and femoral and crural tracts on Day 4 and 5, and feather follicles also appear on the thigh and crus. The follicles of the capital tract emerge on Day 5 and 6 beginning in the frontal region.

Two rows of filaments are visible on the uropygium on Day 3, and melanin pigments of the rectrix follicles become visible in the skin. Rectrix follicles emerge on Day 5 and 6 along with the follicles on their upper and lower coverts. The feather follicles of the anal circlet become visible on Day 5 or 6, and the follicles of the dorsal pair of feathers emerge through the skin.

Thus by Day 6 feather follicles have emerged from the skin in all tracts, and emergence of feathers from the end of the follicle sheaths begins in most tracts on the same day. This process begins on the spinal, humeral, ventral, femoral and crural tracts, proceeding from posterior to anterior. The primary feathers emerge, followed by the secondary feathers, and simultaneously the greater upper primary and secondary coverts all proceeding proximally to distally. The capital tract feathers emerge on Day 8 beginning in the frontal region. The last feathers to emerge, the rectrices and their upper and lower coverts, emerge on Day 9.

The thorax and abdomen are partly covered by the ventral tract by Day 8 and at nine days of age most of the body feathers are spread. Only on the head, wings, and tail are quills prominent. By Day 12 the thorax and abdomen are concealed by the plumage and the feathers

on the head are emerged and spread except for quills around the eyes and on the front of the head.

Physical development. Newly hatched nestlings can raise their head and gape for food. Their eyes are closed and they void faeces in a mucous faecal sac. The flanges of the bill are a clear pale yellow and they have a small inconspicuous egg tooth. The nestlings continue to void faeces in a faecal sac until they fledge. The bill flanges remain conspicuous and pale yellow during the entire nestling period. The egg tooth was not present after Day 2.

Slits appeared in the eye covering of some nestlings on Day 2. The eyes of most were open on Day 4 and by Day 5 were fully open in all nestlings. Nestlings gaped frequently from Day 0 to Day 8 while being handled and on the scale.

Vocalization was first heard on Day 4 and from Day 6 through Day 9 nestlings commonly called while being removed from the nest. Righting behaviour was first seen on Day 4. Nestlings began to grab the nest lining and struggle when being removed from the nest on Day 7. Nestlings could sit up on the scale on Day 9 and on Day 10 one tried to fly. The first successful flight was on the following day, Day 11, when one nestling flew 0.5 m from the scale to a twig. By Day 13 several nestlings had flown from 0.3 m to 1.0 m.

Weight gain. Seven newly hatched nestlings weighed 1.4 g (range 0.8 to 1.7 g, *s.d.* 0.32) or 11.6 percent of the mean adult weight of 12.1 g. The mean weight of all Day 0 nestlings was 1.7 g (Table I). At fledging, 12.7 days later (range 12 to 15 days), nine nestlings had a

TABLE I

*Daily weights and weight gains of
Brown-backed Honeyeaters.*

Age (days)	<i>n</i>	Mean weight (g)	<i>s.d.</i>	Mean weight change (g)
0	14	1.71	0.38	—
1	14	2.19	0.50	0.5
2	12	3.19	0.71	1.0
3	13	4.3	0.77	1.1
4	16	5.49	0.73	1.2
5	18	6.78	0.78	1.3
6	15	8.15	0.96	1.4
7	15	9.21	0.82	1.1
8	14	9.77	0.80	0.6
9	12	10.15	0.30	0.4
10	12	10.8	0.76	0.6
11	10	11.02	0.60	0.2
12	10	11.01	0.79	0.0
13	4	11.02	1.07	0.0

mean weight of 11.1 g (range 10.1 to 12.6, *s.d.* 0.80) a 7.9 fold increase in weight from hatching. They then weighed approximately 92% of mean adult weight.

The mean daily weight of all nestlings (Table I) reached a peak of 11.0 g on Day 11 and remained more or less constant until Day 13 when most fledged. The mean daily weight increment was 0.4 g from Day 0 to Day 1, increased steadily to 1.4 g on Day 6, and declined to 0.22 g on Day 11.

The growth curve of the Brown-backed Honeyeater, like that of most passerines, conforms to the logistic curve (Ricklefs 1968a). The growth constant (Ricklefs 1967) for the combined sample, is $K = 0.452$. The calculated asymptote is 11.6 g. The age at the inflection of the growth curve (5.2 days) and the days to grow from 10 to 90% of the asymptote of the growth curve ($t_{10-90} = 9.7$ days) indicate moderately rapid development. These growth data can be described by the logistic equation:

$$W = A / (1 + e^{-K(t - t_i)}) \text{ or}$$

$$W = 11.6 / (1 + e^{-0.452(t - 5.2)})$$

where W is weight in grams, e is the base of natural logarithms and t is age in days with Day 0 as the day of hatching, A is the asymptote of the growth curve, K the growth rate constant and t_i the age at the inflection of the growth curve.

Growth of body parts. The tarsus and manus were the only body parts measured that had reached adult size at fledging (Figure 1). The bill grew more slowly than the limbs and was 65% (from nares) and 90% (gape) of adult size on Day 13. The primaries and rectrices were only 61 and 31 percent respectively of adult length at fledging.

A two stage growth pattern is evident when these growth data are inspected on semi-log scale paper. The limb and bill components grew at a rapid and constant rate from hatch to Day 6. After Day 6 limb growth rate gradually slowed until full size was reached, while the bill grew at a reduced but approximately constant rate until fledging. Day 6 also marks the beginning of the decline in daily weight increment and the emergence of feathers from the sheaths. The flight feathers began to grow late (Fig. 1) and grew at a continuously declining rate until fledging.

DISCUSSION

The growth rate of the Brown-backed Honeyeater is above the average of other passerines that have been studied in the humid tropics. Its growth rate, $K = 0.452$ day^{-1} is 1.17 times faster than the mean of 30 tropical

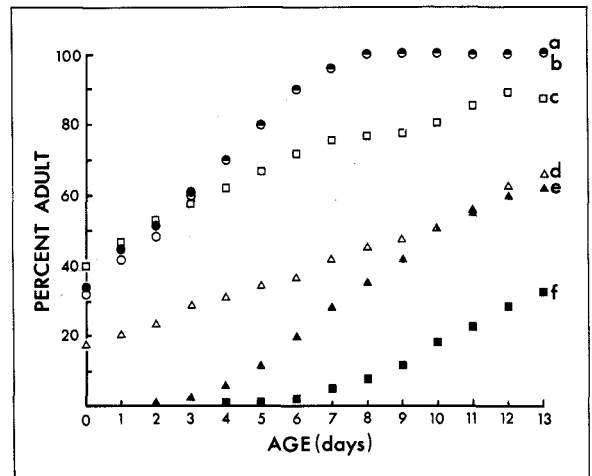


Figure 1. Differential growth of body parts. The curves are the mean length expressed as percent of adult measurements of: a. tarsus, b. manus, c. gape, d. bill, e. seventh primary, and f. central rectrix.

species from Trinidad and Panama (Ricklefs 1976) and almost the same as that of nine tropical passerines studied in Brazil (Oniki & Ricklefs 1981). Compared with the growth rate of 51 temperate zone passerines (Ricklefs 1968a) it is 90 percent as fast. The mean growth rate of the Brazil passerines was not significantly different from the mean growth rate of the sample of temperate zone passerines (Oniki & Ricklefs 1981) and the growth rate of the Brown-backed Honeyeater falls between those two means and within one standard deviation of the growth rate of temperate zone passerines. Thus the Brown-backed Honeyeater appears to grow at a rate indistinguishable from that of passerines in the temperate-zone.

The growth and development of the Brown-backed Honeyeater resembles that of passerines from the temperate and arctic zones that have been studied in some detail (Austin & Ricklefs 1977; Maher 1964; Pinkowski 1975; Ricklefs 1975). During the first half of the nestling period weight gain and growth of all body parts is rapid. By day 6 the nestling Brown-backed Honeyeater has gained 74% of adult body weight, the tarsus is 88% of adult length, the manus is 89% grown and the bill (from nares) is 36% grown. The body feathers are just beginning to emerge from the tips of their sheaths and the flight feathers lag in growth, the primary is only 20% of adult size and the rectrices have just begun to grow. Subsequently, the rate of weight gain and growth rate of all body parts declines. The tarsus and manus reach adult size on Day 8 and Day 9 respectively. The flight feathers continue to elongate until fledging. Full adult size is not reached until after fledging, but I have

no information on post fledging growth of the Brown-backed Honeyeater.

Interspecific comparisons. Compared with the Rufous-winged Sparrow *Aimophila carpalis*, an open nesting fringillid (Austin & Ricklefs 1977), the Brown-backed Honeyeater grows 22% more slowly. On Day 9 when the sparrow leaves the nest only its tarsus is fully grown, it has gained 79% of adult body weight, the manus is 88% grown, its bill is two thirds grown and the primaries and rectrices are 90 and 18% grown. It cannot fly and begins to fly weakly between Day 12 and 17. The Brown-backed Honeyeater on Day 9 has gained 84% of the adult weight, its tarsus and manus are full grown and its bill is 47% of adult size. It noticeably lags behind the Rufous-winged Sparrow only in the development of the primaries and rectrices, which are 42% and 12% of adult length respectively. By Day 9 the honeyeater nestlings are well feathered. They fly on Day 13 when they leave the nest.

The Eastern Bluebird is a cavity nesting turdid, which usually fledges in 19 days (Pinkowski 1975). When it leaves the nest it weighs 27.2 g or 91% of adult weight. Its tarsus is full grown, its primaries are 44% of adult size and its rectrices are approximately 23% grown. Its wing chord is 70 to 75% of adult size and it can fly. On Day 13, however, the age at which most Brown-backed Honeyeaters fledge the Bluebird already weighs 91% of adult weight, its tarsus is full grown but its primaries are only 15% grown. The Brown-backed Honeyeater at that age has also gained 91% of adult weight, tarsus and manus are full sized, the primaries and rectrices are 60 and 32% of adult size and it can already fly.

Thus when overall development is considered in addition to weight gain the Brown-backed Honeyeater appears to be as developed and physically competent at fledging as the Rufous-winged Sparrow at the same age (Day 13), which has a growth rate 22% faster. At fledging the Brown-backed Honeyeater is also considerably more advanced in development than the Eastern Bluebird at the same age, which grows at approximately the same

rate. The problem of some tropical passerines growing more slowly than temperate zone passerines will require detailed studies of growth and development in a number of different taxa as well as more knowledge of the ecology of the nestlings before it will be satisfactorily described and explained.

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REFERENCES

- AUSTIN, G.T. & RICKLEFS, R.E. 1977. Growth and development of the Rufous-winged Sparrow (*Aimophila carpalis*). Condor 79: 37-50.
- BOULTON, R. 1927. Ptilosis of the House Wren (*Troglodytes aedon aedon*). Auk 44: 387-414.
- DOW, D.D. 1980. Communally breeding Australian birds with an analysis of distributional and environmental factors. Emu 80: 121-140.
- MAHER, W.J. 1964. Growth and development of endothermy in the Snow Bunting (*Plectrophenax nivalis*) and Lapland Longspur (*Calcarius lapponicus*) at Barrow, Alaska. Ecology 45: 520-528.
- ONIKI, Y. & RICKLEFS, R.E. 1981. More growth rates of birds in the humid New World Tropics. Ibis 123: 349-354.
- PINKOWSKI, B.C. 1975. Growth and development of Eastern Bluebirds. Bird-banding 46: 273-289.
- PIZZEY, G. 1980. A Field Guide to the Birds of Australia. Sydney: W.A. Collins.
- RICKLEFS, R.E. 1967. A graphical method of fitting equations to growth curves. Ecology 8: 978-983.
- . 1968a. Patterns of growth in birds. Ibis 110: 421-451.
- . 1968b. On the limitation of brood size in passerine birds by the ability of adults to nourish their young. Proc. Nat. Acad. Sci. 61: 847-851.
- . 1975. Patterns in growth of birds. III. Growth and development of the Cactus wren. Condor 77: 34-45.
- . 1976. Growth rates of birds in the humid New World Tropics. Ibis 118: 179-207.

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