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DO NEW HOLLAND HONEYEATERS *PHYLIDONYRIS NOVAEHOLLANDIAE* BREED REGULARLY IN SPRING AND AUTUMN?

In general, birds breed when food resources are sufficient for young to be raised successfully (Lack 1950). In temperate regions, most species start laying in spring and have young in late spring and early summer, the period when food is assumed to be most abundant. In the Northern Hemisphere there are some species that may have an additional laying period in autumn, separated from spring breeding by moult and gonadal regression. This second breeding season is usually attributed to the renewed sexual activity that follows the refractory period (Immelmann 1971). In unusually mild years some species succeed in raising young (e.g. European Starling *Sturnus vulgaris*, Immelmann 1971).

In temperate Australia, members of one family of birds appear to breed regularly in autumn and in spring. Australian honeyeaters (Meliphagidae), particularly the nectarivorous genus *Phylidonyris*, are described as breeding at any time of the year with peaks of breeding activity in spring (July-October) and autumn (February-May; Bell 1966; Recher 1971, 1977; Ford 1980). These conclusions are based largely on observations which have been collected over large areas and over many years (e.g. Recher 1977; Ford 1980). Such broad surveys may be misleading and not represent the periods of breeding activity that occur within a single area or population of birds. Such analyses may also obscure the frequency with which honeyeaters breed in autumn. Ford (1980) notes that the incidence of autumn breeding seems frequent in some years and rare in others. Rooke (1979), in a three-year study near Helena Valley, WA, found that pairs of New Holland Honeyeaters *Phylidonyris noveahollandiae* produced up to four clutches of eggs each spring, but only once did a pair produce eggs in autumn.

In this paper I document breeding by New Holland Honeyeaters in two areas in Victoria during a three year period. In one area the birds bred only in spring, while in the other they bred in autumn and spring of each year. The two areas were the Royal Botanic Gardens

Annexe at Cranbourne, 40 km SE of Melbourne and Golton Vale, 265 km NW of Melbourne. Cranbourne consisted of coastal heath with emergent eucalypts, while Golton Vale was a sclerophyll woodland with a heathy understorey. Further information on the vegetation of these areas can be found in Gullan (1978) and Paton (1985a). I visited Cranbourne about six days a month between September 1975 and June 1978, and Golton Vale for six days every 6-8 weeks, between August 1976 and October 1978. During these trips I noted any breeding by New Holland Honeyeaters and made detailed observations, including time-budgets, of colour-banded individuals. In addition I mist-netted and weighed birds at intervals of 3-4 (Cranbourne) and 6-8 (Golton Vale) weeks and scored their moult and breeding condition (e.g. brood patches for females). In both areas there was a year-long cycle of flowering plants and carbohydrate food sources, and many individual New Holland Honeyeaters were permanent residents, switching from one resource to the next as each came into bloom (Paton 1980, 1982a, 1985a).

At Cranbourne and Golton Vale, New Holland Honeyeaters bred as monogamous pairs, with individuals usually breeding with the same mate in consecutive years, unless their mate disappeared (Table I). Occasionally females changed mates and bred with another bird, even though the previous male still resided in the original area. Male New Holland Honeyeaters defended the nectar sources used by the pair, while the female built the nest, incubated the eggs and brooded the young. Females developed extensive brood patches just prior to, and during, incubation. Brood patches subsided after incubation, but the abdomen remained bare of feathers long after breeding, and was often scratched. Both sexes fed nestlings and fledgelings, and fledgelings reached independence when about 40 days old, or about four weeks after leaving the nest. At this age fledgelings were no longer fed by their parents, but were still often present near the breeding area. Pair-bonds were not maintained outside the breeding

periods, but males often remained near the breeding area, if there was sufficient nectar to support them.

New Holland Honeyeaters depended on nectar or similar carbohydrates (manna, honeydew) for energy

and spent most of their foraging time collecting these resources at both sites (Paton 1980, 1982a). They also spent a few minutes per day catching small flying insects to satisfy protein and nutrient requirements (Paton 1982a). Young were fed on nectar and insects, also in

TABLE I

Breeding by individual New Holland Honeyeaters at Cranbourne and Golton Vale between 1976 and 1978. The table gives for each male, the female with whom he bred, and the number of clutches she laid in each season when this was known. Individuals are identified by three letters representing coloured rings or as marked (numbered band only) or unmarked. An asterisk indicates that the female was caught with a brood patch in that season but where and with whom she was nesting were not known.

Breeding season	Cranbourne				
	autumn 76	spring 76	autumn 77	spring 77	autumn 78
male : female					
OWW : GBG	1	1	1	2	1
ONR : OWN	1	1	1	2	
OBO : OOW	1	1	1		
OON : GON	1				
unmark		1			
BWW			1	1	
WGY : RYY		1	1	1	1
ORB : unmark	1		1		
mark		1			
BON : unmark			1		1
OOW				1	
ROY : unmark		1			1
mark			1	2	
WBG : unmark			1	1	1
YNB : unmark			1		
mark				1	
OGN					1
GBO : unmark				1	1
OGY : GRG				1	1
RRY : mark		1			
unmark				1	
GYW : YYN				1	
mark					1
ROB : WRG		1	1		
Unknowns					
WOB	*	*	*		
WBW	*	*	*		
GGG	*		*	*	

Breeding season	Golton Vale		
	spring 76	spring 77	spring 78
male : female			
NYR : NRR	*	2	1
NGW : ROW		2	1
NBB : WRN		2	1
NON : WNO		2	1
NRO : RBY	*	1	
GWB			1
WRB : unmark		1	
GYB			1

proportion to their energy and nutrient requirements (Paton 1979, 1982a).

At Cranbourne there were two distinct periods of breeding activity in each year, one in autumn and one in spring (Fig. 1). Furthermore, the same individuals bred in consecutive autumns and springs. Table I lists data for 25 individuals, eight of which bred in both seasons for at least two consecutive years.

At Golton Vale breeding took place only in spring (Fig. 1). No individuals were seen performing breeding activities (e.g. song flights by males, nest-building by females), no females were caught with brood patches and no fledgelings were seen during autumn (Feb - May) at this site.

Breeding seasons in both areas coincided with the periods when the nectar supply was sufficiently rich to

enable the birds to satisfy the energy requirements of their young and themselves (Paton 1982a, 1985a). The most energetically demanding time occurs during late nestling and early fledgeling stages, when each parent must collect double the amount of energy needed by a non-breeding bird (Paton 1982a). In both areas resources were sufficient to enable breeding in spring but only at Cranbourne were resources sufficient during autumn. At Golton Vale non-breeding birds spent 80-90% of the day collecting carbohydrates during autumn, and even then some lost weight (Paton 1982a, 1985a). Thus resources at Golton Vale were not sufficient to allow breeding in autumn. Non-breeding birds at Cranbourne only had to spend about 40% of the day foraging in autumn, so resources were sufficient to enable birds to breed.

No breeding occurred in either area during summer when the birds were moulting (Paton 1982b). Adults commenced a complete moult immediately after breeding in spring, and autumn breeding usually did not begin until remigial moult was complete (Paton 1982b). Moult places additional demands on the energy and protein requirements of these birds (Paton 1982b), so a cessation of breeding during summer was expected. Some females arrested the moult of their remiges to breed during autumn at Cranbourne, completing the moult after autumn breeding (Paton 1982b). Rarely did breeding and moult overlap in individuals, and then only during the initial or late stages when just a few feathers were being replaced (see Paton 1982b for details). I have no information on whether the gonads regress between spring- and autumn-breeding.

Differences in the commencement of breeding in spring from one year to the next (Fig. 1) were due mainly to variations in the weather. Cold, rainy weather delayed the early stages of breeding such as nest building (Paton 1979). In 1977, July and August were drier than in 1975, 1976 and 1978, days were warmer and breeding commenced two to four weeks earlier. Differences in the timing of autumn breeding between years at Cranbourne reflected differences in the timing of breeding in the previous spring. If spring breeding finished late, then breeding in the following autumn was also late. Adults needed to moult between these breeding periods and this took a similar amount of time each year (Paton 1982b).

New Holland Honeyeaters usually laid only a single clutch of eggs in autumn at Cranbourne even if the nest and eggs were destroyed early in a breeding attempt. Usually a single clutch was laid in spring though in 1977 several pairs laid a second clutch and some raised two broods at both sites. Clutch sizes averaged 2.0 eggs in both autumn (5 clutches) and spring (12 clutches) at Cranbourne and were not significantly different from

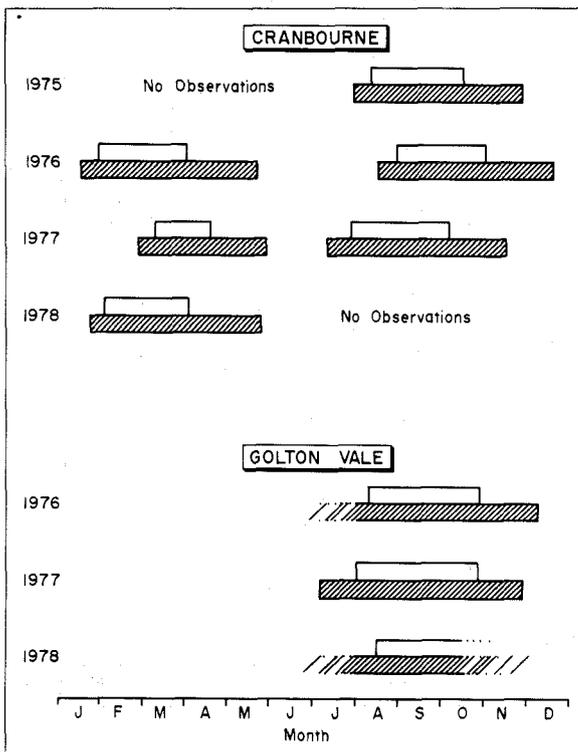


Figure 1 Breeding seasons of New Holland Honeyeaters at Cranbourne and Golton Vale. Hatched areas show the period between the first signs of nest-building to the last fledgeling reaching independence, while the blank areas show the period when eggs were laid in each population. Observations were insufficient to provide exact dates for commencement of nest-building at Golton Vale in 1976 and 1978, and observations ceased in this area in mid-October 1978.

those at Golton Vale (2.2 eggs, 26 clutches, Paton 1979). For many pairs I was able to determine the number of young raised to independence, and so could calculate the annual productivity of breeding pairs in each area. At Cranbourne, New Holland Honeyeaters produced an average of 3.2 independent young per pair per year (data based on seven pairs and ten pair-years), while at Golton Vale New Holland Honeyeaters produced 2.8 independent young per pair per year (production of nine pairs in 1977). Individual New Holland Honeyeaters were more productive at Cranbourne, where two breeding seasons occurred per year, than at Golton Vale. The figures for Golton Vale were collected in 1977 and may overestimate the average annual production. In 1977 several birds produced two clutches (Table I), and the average clutch size was 2.40 ± 0.51 (s.d., $n = 15$) eggs, which was significantly larger than the clutch size for 1976 and 1978 combined (1.91 ± 0.30 (s.d., $n = 11$) eggs; t-test, $p < 0.01$). The higher reproductive effort in 1977 reflected a greater abundance of nectar. Both the density of flowers (6.2 vs 9.5 flowers/plant) and the nectar content of flowers (30 vs 50 joules/flower) were higher in 1977 than in 1978 (Paton 1979, 1985a).

In conclusion, individual New Holland Honeyeaters bred regularly in spring and autumn at Cranbourne where an adequate source of energy (nectar or manna) occurred at both times. At Golton Vale, they bred only during spring. My observations on individuals in these two populations do not support the general statement that these honeyeaters can breed at any time of the year.

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