THE HONEYEATERS OF KANGAROO ISLAND

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Kangaroo Island is the third largest of Australia's islands (4,500 sq. km) and has been separated from the neighbouring Fleurieu Peninsula for 10,000 years (Abbott 1973). A mere 14 km separates island from mainland; but the island has a distinct avifauna and lacks many of the mainland species. This paucity of species has been attributed to extinction after isolation and failure to recolonise (Abbott 1974, 1976), and to lack of suitable habitat (Ford and Paton 1975).

Nine species of honeyeaters are resident on Kangaroo Island. The Purple-gaped Honeyeater *Lichenostomus cratitius* (formerly *Meliphaga cratitia)* was described as a distinct subspecies by Mathews (1923-24); and Keast (1961) mentions that six other species differ in a minor way from mainland populations and may merit subspecific status. These are all given subspecific names by Salomonsen (1967).

In the present paper I discuss morphological and ecological differences between populations of several species of honeyeaters from Kangaroo Island and the Fleurieu Peninsula respectively, and speculate on how these differences originated.

DIFFERENCES IN PLUMAGE

The Kangaroo Island population of Purple-gaped Honeyeater was described as larger and brighter than the mainland population by Mathews (1923-4). Brightness of plumage is a very subjective characteristic, and in my opinion Purple-gaped Honeyeaters on Kangaroo Island are, if anything, duller than mainland ones.

Condon (1951) says that the gape of this species is invariably yellow on Kangaroo Island instead of lilac, although he later comments that lilac-gaped individuals do occur on the island (Condon 1969). The "gape" which Condon discusses and which gives the bird its

name is, strictly, a wattle, a flange of engorged skin extending back from the gape *(sensu stricto)*. Terrill (in Rix 1943) showed that the yellow wattle was an immature character, as the wattles of four birds captured near Monarto in late spring changed from yellow to purple by the following winter. Even if the yellow wattle is an immature characteristic, it is still possible that the Kangaroo Island population differs from the mainland one in that the development of the purple wattle is delayed or even suppressed entirely in some birds. The retention of immature characteristics is shown by other species or populations of birds on islands. Male Darwins Finches, Geospizinae, of the Galapagos Islands show a progressive loss of the black adult male plumage and retention of the grey-brown female and immature plumage. In Tasmania the endemic Forty-spotted Pardalote *Pardalotus quadrigintus* closely resembles an immature Spotted Pardalote *P. punctatus* from which it presumably evolved.

I have noted the wattle-colour of Purple-gaped Honeyeaters mist-netted in Flinders Chase National Park, Kangaroo Island, and at Braendler's Scrub, Monarto, in the Murray Mallee between September, 1974 and July, 1976. The numbers of individuals with wattles of each colour from the two areas are given in Table 1a. The proportions of the two colours are the same in both areas; so the yellow wattle is probably an immature characteristic which is not retained longer on Kangaroo Island than on the mainland. This is consistent with Terrill's observations, but there is another possible explanation. Fuscous *L. fuscus* and White-plumed Honeyeaters *L. penicillatus* show a change during the year in the colour of their oral flange, which is mostly dark in late winter and spring, and pale in summer and autumn. The colour may indicate breeding condition if it is dark in breeding birds and pale in non-breeding ones (Dow 1973, 1975, and Lane 1974). The same may be true of the wattle in the Purple-gaped Honeyeater, with yellow indicating not only an immature but also a non-breeding adult. Recapture of a bird showing the appropriate colour-change (purple to yellow) would be necessary to confirm this. The numbers of birds with yellow and purple wattles in each season are shown in Table 1b. More birds with yellow wattles were caught in summer and autumn than in winter and spring ($p < 0.05$, X_1^2 test). Although the breeding season of this species is not well known, it is possible that wattle-colour is related both to age and breeding condition.

None of the other species of honeyeaters on Kangaroo Island differ in plumage from the mainland populations.

DIFFERENCES IN STRUCTURE AND ECOLOGY

I have sufficiently large samples of measurements of five species of honeyeaters from Kangaroo Island and the mainland for statistical analysis (see Table 2). Only small numbers of Tawny-crowned *Phylidonyris melanops* and White-eared Honeyeaters *Lichenostomus leucotis,* and Red Wattlebirds *Anthochaera carunculata* were measured, showing no apparent differences between island and mainland populations.

Purple-gaped Honeyeaters on Kangaroo Island have slightly shorter beaks and longer wings than the mainland population (t test, $p < 0.05$). They have also undergone an ecological change, as they occupy forest, woodland and mallee-heath habitats on Kangaroo Island, but only mallee-heath on the mainland (Ford and Paton 1976). The increased range of habitat on Kangaroo Island may result from the absence of the Yellow-faced *L. chrysops* and White-plumed Honeyeaters which occupy forest and woodland habitats on the mainland. As both of these species have shorter beaks than the Purple-gaped Honeyeater, the reduced beak length of the Latter species on Kangaroo Island may be the result of Character Release (convergence in morphology towards an absent competitor, see Grant 1972).

The Brown-headed Honeyeater *Melithreptus brevirostris* on Kangaroo Island has a significantly longer beak and wing, and is heavier than on the mainland. Keast (1968a) suggests that this is due to an increased amount of bark-feeding by this species on Kangaroo Island, in the absence of bark-feeding tree creepers *Climacteris* and sittellas *Daphoenositta.*

This increase in size, especially of the bill, and development of the tree-creeper-like feeding ecology is shown to an even greater extent by the Strong-billed Honeyeater *M. validirostris* of Tasmania (Keast 1968a, Thomas m.s., and pers. obs.). Keast (1968a) regards the Black-chinned Honeyeater *M. gularis* as the ancestor of the Strong-billed; but, in my opinion, the Brown-headed Honeyeater, particularly on Kangaroo Island, far more closely resembles the Strong-billed in its behaviour and calls. In addition the Brown-headed Honeyeater occurs throughout southern Victoria and on the Bass Strait islands, whereas the Black-chinned occurs only to the north of Melbourne in Victoria.

In the New Holland Honeyeater *Phylidonyris novaehollandiae,* in both sexes of the Crescent

Honeyeater *P. pyrrhoptera,* and in the Eastern Spinebill *Acanthorhynchus tenuirostris,* there are slight differences in measurements between island and mainland samples. However these show remarkably consistent trends in these three species. The island populations all have significantly longer beaks than the mainland ones; they all have shorter wings (significant in all except female Spinebills); and are all slightly lighter than their mainland counterparts (significant in all except male Crescent and female Spinebills). Campbell (1905) described the first two as subspecies because of their longer beaks. He gave the Spinebill a subspecific name because it was smaller and paler than Victorian birds, but does not say how many individuals of each species were measured. Paton (pers. comm.) says that Spinebills from coastal Victoria have beak lengths similar to those of the Mount Lofty Ranges, but that those from mountain regions have longer beaks and are similar to more northern samples (Disney et al. 1974). The biogeographical laws of Bergmann and Allen state that animals of one species become larger and have shorter extremities in colder regions. This is contrary to what has happened on Kangaroo Island, which is cooler than the Fleurieu Peninsula and yet these three species of honeyeaters are smaller and have longer beaks. Keast (1968b) showed that nomadic or migratory species of honeyeaters tend to have longer wings than more sedentary species. Perhaps the more maritime climate of Kangaroo Island leads to a more predictable food supply and less necessity for movement among the honeyeaters. Certainly in the autumn and early winter of 1976, when food was scarce on the mainland, honeyeaters were finding sufficient food on Kangaroo Island to breed.

The change in beak lengths of the New Holland, and Crescent Honeyeaters and Spinebill is particularly interesting, as this character is closely related to the feeding ecology of a species.

Populations may diverge for genetic reasons alone: when their numbers are low the population as a whole only contains a sample of the genes of a larger population. The smaller the sample the more the average for a morphological characteristic is likely to differ from that of the original population. This seems an unlikely explanation for this distinctness of the Kangaroo Island populations, because, at present anyway, they must number some tens of thousands of individuals of each species. Also the similarity of the trends in these three species suggests a common directional force rather than random genetic drift.

Interspecific competition is often considered as a force bringing about changes in island populations of birds. A species may change morphologically or ecologically when a potential competitor is absent. This change is usually but not always shown as a convergence towards the absent competitor, or a divergence away from it when the two species are present together. This phenomenon of character displacement is discussed at length by Grant (1972). Although competition, or lack of it, may have been important in changes in the Purple-gaped and Brown-headed Honeyeater, all of the long-beaked honeyeaters of the neighbouring mainland occur on Kangaroo Island (3 species of *Phylidonyris,* 2 *Anthochaera* and 1 *Acanthorhynchus);* so there would seem little opportunity or necessity for convergence or divergence as a result of increased or reduced competition. Another reason for changes on islands, probably the most obvious but often over-looked one, is that the environment on the island is different from that on the mainland. If Kangaroo Island is considered broadly there are two main habitats; a rather stunted dry sclerophyll forest with *E. baxteri* and *E. cosmophylla,* and a mallee-heath with *E. diversifolia* and *E. rugosa,* habitats also found on Fleurieu Peninsula and the lower Murray Mallee respectively. On Kangaroo Island there are also limited areas of tall woodland with *E. cladocalyx, E. fasciculosa* and *E. huberiana* similar to, but taller than, that found on Eyre Peninsula.

On the mainland the most important sources of nectar for honeyeaters are *Eucalyptus* (especially *E. leucoxylon*) with 53% of the 2,900 observations of all species of honeyeaters feeding on nectar, some heaths such as *Astroloma conostephioides* (10% of all records) and *Banksia* (10% of all records) (Ford and Paton, in prep.). *Eucalyptus* appears to be far less important on Kangaroo Island and *Correa* (3 species), *Adenanthos* and *Banksia* seem to be the major nectar sources (pers. obs. and McWilliams 1973, Honours thesis, Department of Zoology, University of Adelaide). It is very hard to observe honeyeaters feeding on the flowers from low bushes on Kangaroo Island because the vegetation is so dense. A more representative picture of which flowers the birds are feeding on can be gained from collecting and identifying pollen from birds caught in areas where a range of plants is flowering. In Table 3 I have compared the numbers of individuals of each species carrying pollen of a range of species of plants on the mainland (from Paton and Ford, 1977) and Kangaroo

Island. The data from the mainland are not strictly comparable, as birds were captured close to specific flowering trees or bushes to collect evidence that birds transfer pollen of a particular species of plant, rather than being captured in an area where a wide range of plants was in flower, as on Kangaroo Island. This would tend to underestimate the most important plants, such as *Eucalyptus,* so that the difference between island and mainland is probably greater than suggested by the results.

The Table shows the importance of *Correa, Adenanthos* and *Banksia,* and less emphasis on *Eucalyptus,* on Kangaroo Island relative to the mainland. Longer-beaked birds could be more efficient at feeding on the tubular flowers of *Adenanthos* and especially *Correa,* and also possibly on *Banksia* which has long stiff styles on the inflorescences. Also *Correa* flowers appear to have slightly longer corollas on Kangaroo Island (mean anther to nectary distance = 30.0 mm, range 27-33 mm, sample size of 20) than on the mainland (range 22.6-27.2 mm, Paton and Ford 1977). Paton (pers. comm.) suggests that the longer-billed Spinebills of mountain regions of Victoria feed to a large extent on *Correa* which has a very long tubular corolla.

CONCLUSIONS

The Kangaroo Island population of the Purple-gaped Honeyeater does not differ from the mainland population in the colour of the wattle, but is slightly different in wing and bill length. Changes in ecology of the island population, especially in choice of habitat, probably result from the absence of competitors, in the form of other members of the genus. Further study of the wattle-colour would be interesting to see if it depends on age, season or both, and also to see if Kangaroo Island does have a larger proportion of birds with yellow wattles. The Brown-headed Honeyeater has diverged more than the other honeyeaters on Kangaroo Island in both morphology and ecology; it is larger, has a longer beak and feeds more on insects taken from bark than on the mainland. This is most likely to result from the absence of other bark-feeding birds on Kangaroo Island.

The New Holland and Crescent Honeyeaters and Eastern Spinebill differ slightly between island and mainland, and would seem to merit the term "minor isolates" applied to them by Keast. Populations are large, tending to discount genetic drift as a reason for these changes; and most potential competitors are present in both places. A change in their ecology, namely a greater emphasis on tubular and bottle-brush rather than open flowers, could account for the increased beak lengths of these species. A slight reduction in wing length might be the result of less necessity for local movements on the island.

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TABLE 1

The numbers of Purple-gaped Honeyeaters with yellow or purple wattles: (a) caught on Kangaroo Island and the mainland, and (b) caught in each season of the year.

(a)	Yellow	Purple
Kangaroo Island	8	37
Mainland	4	20

$X^2_{(1)} = 0.01$, not significant

(b)	Yellow	Purple
Summer (Dec-Feb)	1	2
Autumn (Mar-May)	10	28
Winter (Jun-Aug)	0	9
Spring (Sep-Nov)	1	18

$X^2_{(1)}$ winter-spring vs summer and autumn $= 6.34$ $p < 0.01$

TABLE 2

The mean, standard error and sample size for beak length, wing length and weight in five species of Honeyeaters from Kangaroo Island and the neighbouring mainland.

			Beak length (mm) mean ± S.E. (no)	Wing length (mm)	Weight (gm)
Brown-headed Honeyeater		K.I.	14.3 ± 0.22(20)	72.1 ± 0.53(19)	17.0 ± 0.37(14)
		main.	* 12.9 ± 0.13(29)	*67.3 ± 0.49(29)	* 13.9 ± 0.30(22)
Purple-gaped Honeyeater		K.I.	14.3 ± 0.17(40)	81.8 ± 0.53(40)	19.7 ± 0.35(36)
		main.	* 15.0 ± 0.20(19)	* 80.0 ± 0.51(24)	20.3 ± 0.74(16)
Crescent Honeyeater	M	K.I.	18.9 ± 0.13(38)	69.2 ± 0.28(38)	14.7 ± 0.36(14)
		main.	* 18.2 ± 0.19(38)	* 70.8 ± 0.45(32)	15.4 ± 0.32(32)
	F	K.I.	17.2 ± 0.15(32)	62.3 ± 0.28(32)	11.9 ± 0.37(15)
		main.	* 16.7 ± 0.18(22)	* 63.9 ± 0.29(22)	* 12.9 ± 0.27(19)
New Holland Honeyeater		K.I.	20.7 ± 0.12(82)	74.0 ± 0.43(82)	19.6 ± 0.40(36)
		main.	* 19.6 ± 0.10(86)	* 75.9 ± 0.40(86)	* 21.0 ± 0.26(53)
Eastern Spinebill	M	K.I.	23.8 ± 0.15(58)	63.8 ± 0.28(58)	10.6 ± 0.17(33)
		main.	* 23.1 ± 0.25(14)	* 67.1 ± 0.33(14)	* 11.5 ± 0.46(10)
	F	K.I.	21.0 ± 0.24(35)	59.1 ± 0.42(35)	9.4 ± 0.17(26)
		main.	* 20.0 ± 0.37(10)	59.5 ± 0.45(10)	9.3 ± 0.43(6)

* indicates a significant difference between the means from the two areas, $p < 0.05$.

TABLE 3

Numbers of birds of each species from which pollen samples were taken, carrying pollen from a range of flowers on Kangaroo Island and the mainland.

	Adenanthos		Banksia		Correa		Eucalyptus		Grevillea		Others	
	K.I.	main.	K.I.	main.	K.I.	main.	K.I.	main.	K.I.	main.	K.I.	main.
Purple-gaped	4		7		6	3	1	2		5		3
Brown-headed	2	1	3	3		1		4		1		3
Crescent	14	3	17	24	10	7	3	8		2	1	20
New Holland	34	13	26	68	18	53	8	59	4	25		84
Tawny-crowned	1	1	1	1		10		5		10		3
Eastern Spinebill	22	1	17	11	25	11	2	4			2	13
Red Wattlebird	1		4	9	3	5		4		3		3
TOTAL	78	19	75	116	62	90	14	86	4	46	3	129
%	*33*	*4*	*32*	*24*	*26*	*19*	*6*	*18*	*2*	*10*	*1*	*26*