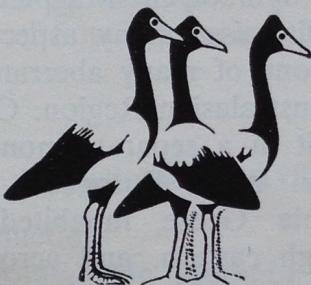


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ECOLOGICAL OPPORTUNITIES AND ADAPTIVE EVOLUTION ON ISLANDS, WITH SPECIAL REFERENCE TO EVOLUTION IN THE ISOLATED FOREST OUTLIERS OF SOUTHERN AUSTRALIA

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INTRODUCTION

Islands have fewer species of land birds than do equivalent mainland areas and their faunas are unbalanced with an incomplete range of taxonomic and morphological types. This is ascribed to (a) their remoteness, so that only a minority of groups reach them and, (b) their small size and lack of physiographic and ecological diversity and, hence, inability to support more species. Recent years have seen much research into island evolution. Notwithstanding this we lack data, or adequate data, on a wide range of basic facets. Included here are divergence rates of island populations; reasons why island populations of some species or groups, but not others, show morphological shifts; the adaptive meaning of these changes; intrapopulation variability and sexual size diversity in island, relative to mainland, populations; frequency with which "congeneric species pairs" diverge on islands; and so on.

Along the southern coastline of Australia are a series of five, broadly equivalent, forest "outliers"—true islands, and forested pockets isolated by arid terrain—that offer unique opportunities for comparative evolutionary studies and for resolving some of the above issues. This paper reviews a continuing series of taxonomic and field studies on these avifaunas.

THE ISOLATED FOREST OUTLIERS OF SOUTHERN AUSTRALIA

The locations and relative sizes of these are shown in Figure 1. Also shown are the water depths separating the islands from the mainland, and the distribution of the 10 inch rainfall isohyet, representing the line of "desert". The characteristics of the outliers are summarized in Table 1.

Pacific sea levels were 100 metres lower during the Pleistocene glacial maxima in the Northern Hemisphere, hence it will be seen that Tasmania and the intermediate islands, plus Kangaroo Island, were broadly connected to the mainland at such times. This would mean four junctions over the last 2-3 million years, although from the Upper Pliocene onwards there could have been up to nine in the opinion of Prof. Rhodes Fairbridge (pers. comm.). Tasmania and King Island finally became separated 12,000-13,000 years ago (Ridpath and Moreau, 1966; Jennings, 1971; Abbott, 1973), and Kangaroo Island 11,000 years ago (Abbott, 1973).

The forests and woodlands of the southwest corner of the continent have also had a history of intermittent separation from, and junction with, those of the southeast. In this case the mechanism has been a northward movement of the rainfall belts which would have moved the intermediate arid barrier

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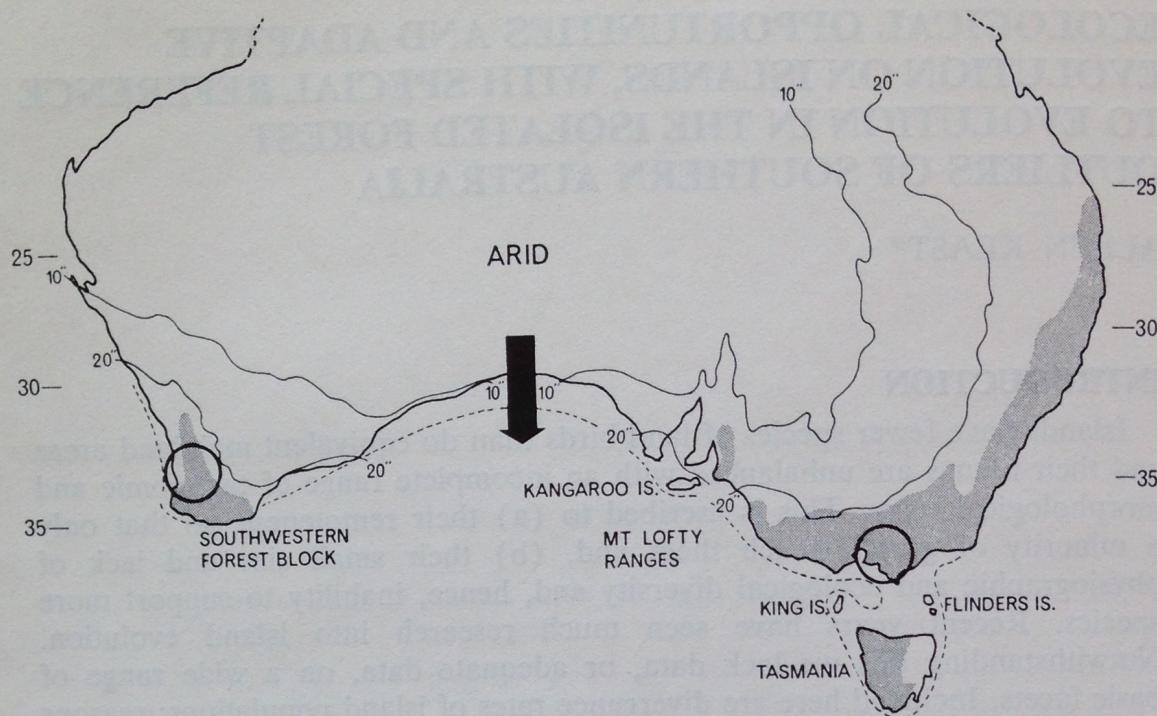


FIGURE 1. The isolated forest-woodland outliers of southern Australia, showing average annual rainfalls in inches, and the 50 fathom line offshore.

to the north. There are good biological data to support series of Pleistocene east-west colonizations across the head of the Great Australian Bight—see Main *et al.* (1958) and others. A minimum of four major south-north climatic sweeps might be postulated, although Fairbridge (1953) has suggested that there could have been up to nine. The current phase of climatic isolation of the southwest extends back to at least 20,000 years, as evidenced by palynological data, studies of sediment grain morphology, and retarded karst development of the limestones, from the centre of the Nullarbor Plain (Martin, 1973 and references contained therein). Cave sediments there (Madura Cave fossil mammal site—see Lundelius and Turnbull, 1973), moreover, indicate a drying about 15,000 years ago and no significant reversal to the present: this same event has been discerned for the Willandra Lakes area (Bowler, 1971). A phase of desiccation beginning 21,000 years ago can be recognized in African lake basins (Butzer *et al.*, 1972).

In later years it has been increasingly demonstrated that glacial maxima in the Northern Hemisphere were *not* matched by wet periods in the south but by dry ones, e.g. Fairbridge (1964), Damuth and Fairbridge (1970), Gibbs (1967), Bonatti and Gartner (1973). This would then mean that times of junction of the Tasmanian forests with the southeastern ones (times of lower sea-level) would not have corresponded with the junctions of the southwestern and southeastern ones.

Tasmania, alone of the five areas, experienced Pleistocene glaciation. During the last glacial maximum it has been estimated that the treeline would have been 900 metres lower (J. L. Davies, quoted by Ridpath and Moreau) though, to judge from the map of Jennings (1971) only 8% of the area of the island was covered by ice. The resultant colder temperatures, however, would have made the island a less desirable habitat for birds.

TABLE 1: Characteristics of the Forest Outliers of Southern Australia

<i>Outlier</i>	<i>Area km²</i>	<i>Distance from Victorian Forests—Woodlands km</i>	<i>Nature of Barrier</i>	<i>Habitats Present</i>	<i>Age of Isolation Year B.P.</i>	<i>Glaciation</i>
Tasmania	40,000	190, but King & Flinders Is. intermediate	sea	wet and dry sclerophyll forest, woodland temperate rain forest, some heathland & moor	12,000–13,000 (Jennings, 1971; Abbott, 1973)	may have covered 10%
King & Flinders Is.	1,000 & 1,300	100–110	sea	forest & woodland	12,000–13,000	no
Kangaroo Id.	4,350	40, but only 20 offshore	sea	forest and mallee	10,000–11,000 (Abbott, 1973)	no
Mount Lofty Ranges	300	100	arid terrain	forest & woodland	??	no
Southwest corner	30,000	1,500	arid terrain	wet & dry sclerophyll forest, woodland, sand heath, mallee adjacent	20,000	no

Hence it would seem likely that most overland colonization occurred during the warming (melting) phase and as the water-gaps were coming into existence.

In the present study all comparisons are made relative to coastal southern Victoria, this being the southern end of the major continental forest-woodland belt. Victoria is diversified altitudinally, contains extensive areas of wet and dry sclerophyll forest, woodlands, and has minor pockets of temperate rain forest. It has also, of course, extensive grassland and marshes.

For a vegetation map of Tasmania see Ridpath and Moreau (1966) and for southwestern Australia see Gardner (1944).

THE PASSERINE AVIFAUNAS OF THE ISOLATED FOREST OUTLIERS OF SOUTHERN AUSTRALIA

Table 2 summarizes the numbers and percentages of breeding passerine species in the various southern forest outliers relative to southern Victoria. Tasmania has 46 (48%) of the Victorian total, King Island 44 (46%), Kangaroo Island 35 (36%), the Mount Lofty Ranges 65 (68%), and the southwest corner 66 (69%). The Mount Lofty figures are high despite the small area of true forest because virtually all the Victorian woodland species occur there. The small Kangaroo Island avifauna would be still smaller were it not for the presence of half a dozen mallee species there, e.g. *Pardalotus xanthopygus*, *Hylacola cauta*. This arid-adapted avifauna is not under consideration here.

TABLE 2: Numbers of Passerine Bird Species Breeding in the Isolated Forest Outliers of Southern Australia Relative to Coastal Victoria
(Numbers after plus sign refer to Mallee species)

<i>Family or Sub-Family</i>	<i>Coastal Victoria</i>	<i>King Id.</i>	<i>Tasmania</i>	<i>Mount Lofty Range</i>	<i>Kangaroo Id.</i>	<i>South-west Corner</i>
Muscicapinae	14	6	6	6	3	8
Pachycephalinae	4	3	3	3	2	3
Campephagidae	4	1	1	3	1	1
Acanthizinae	14	5	6	10	4+1	10+1
Malurinae	3	2	2	2	2	6
Sittidae & Climacteridae	4	—	—	3	—	2
Pardalotidae	4	3	3	2	1+1	2
Meliphagidae	23	9	10	16	9+1	13
Others	26	15	15	20	10	20
Total	96	44	46	65	35	66

One point should be made with respect to this "rich" Victorian avifauna. A dozen or so of the species occurring there (e.g. *Myzomela sanguinolenta*, *Meliphaga lewini*) should probably rightly be thought of as only "marginal" so far south and would probably not persist there if cut off from their main "reservoir" populations to the north. Their exclusion from Tasmania hence might be as much a matter of latitude as isolation.

For previous papers on the avifaunas of the above outliers see Ridpath and Moreau (1966), Keast (1968, 1970), and Abbott (1973, 1974a, 1974b).

THE PARTIAL MAKING UP OF DEFICIENCIES IN SPECIES NUMBERS

Tasmania has three cases of speciation by double invasion and the southwest corner two (Keast, 1961). In each case the members of the pair are today separated on habitat. The forested southwest corner, adjacent as it is to mallee and desert areas, secondarily gains a few species by colonization from these habitats. Thus the honeyeater *Meliphaga virescens* and the warbler *Gerygone fusca*, strictly interior dry-country species in the east of the continent, are here forest dwellers. Other dry-country forms like *Cinclosoma castanotum* penetrate the woodland areas. Again the small honeyeater *Lichmera indistincta*, an inhabitant of the dry interior and mangroves elsewhere, is here also a forest species.

MORPHOLOGICAL SHIFTS IN INSULAR POPULATIONS

The tendency of island populations of species to have longer bills and longer tarsi has been remarked upon repeatedly, e.g. Murphy (1938), Chapman (1940), Amadon (1953), Grant (1965). There is no agreed-upon explanation for this. Grant has suggested that it confers greater ecological versatility, a necessity on biotically depauperate islands.

The southern forest outliers provide an abundance of examples of this phenomenon—see quantification for warblers, muscicapids and meliphagids, in Table 3. In order to discriminate between minor trends and clearcut instances only those cases of bill, tarsus and wing length change which meet two rigid criteria are included: (a) where the mean values of insular and Victorian population differ by at least 5% and, (b) where the percentage of non-overlap between the measurements exceeds 75% (see formula of Mayr, 1968). (For comparison sets of figures are given in brackets for cases where only one of these criteria is met.)

Warblers: Well-defined shifts in wing length occur in 60% of the Tasmanian populations, 8% of the Mount Lofty-southeastern South Australian ones, 14% of those from Kangaroo Island and 33% of the southwestern ones. In the case of bill length the percentage figures are 30, 17, 28 and 25, and for tarsus length 20, 25, 57 and 42.

Muscicapine flycatchers and pachycephalines: Here percentage figures for shifts in wing length are: Tasmania, 11; Mount Lofty, 33; Kangaroo Island, 25; and the southwest corner, 22. For bill length the percentages are: 56, 33, 25 and 33, and for tarsus, 33, nil, 25 and 36.

Honeyeaters: In this ecologically diversified group, containing a wide range of different ecological types, marked shifts in wing length occur in the following percentages of insular populations: Tasmania, 30; Mount Lofty, 9; Kangaroo Island, 13; and southwest corner, 33. Figures for bill length are 40, 9, 63 and 78; those for tarsus length are 50, nil, 25 and 22.

TABLE 3: Insular Relative to Victorian Populations, Shared Species

Percentages in which measurements differ by (1) 5% or more, and (2) where non-overlap exceeds 75%. Figures in brackets refer to additional percentage in which only one of these criteria is met. For numbers of species see Table 4.

	Tasmania	Mount Lofty Ranges	Kangaroo Id.	South-west Corner
	%	%	%	%
WARBLERS				
Wing	60	(8)	14 (14)	33 (17)
Bill	30 (40)	17 (17)	28 (14)	25 (8)
Tarsus	20 (20)	25 (8)	57	42 (8)
MUSCICAPIDS				
Wing	11	33	25	22 (11)
Bill	56	33 (17)	25	33 (22)
Tarsus	33 (11)	(17)	25	56 (22)
HONEYEATERS				
Wing	30 (20)	9	13	33
Bill	40	9 (9)	63	78
Tarsus	50	—	25	22 (11)

CONGENERIC SPECIES PAIRS, DIVERGENCE IN INSULAR POPULATIONS

There is a potential advantage in "congeneric species pairs" diverging morphologically in impoverished insular environments and thus reducing interspecific competition. This has already been described for owls and melithreptid honeyeaters in Tasmania (Keast, 1970).

Congeneric "species pairs" occur in the forest-woodland outliers of southern Australia as follows: *Petroica*, Tasmania and the southwest; *Eopsaltria*, southwest; *Pachycephala*, Tasmania (not including the migratory *P. rufiventris*); *Pardalotus* (throughout); *Acanthiza* (throughout); *Sericornis* (Tasmania); *Malurus*, (Southwest); *Melithreptus* (Tasmania, Mount Lofty Ranges, and southwest Australia); *Phylidonyris* (throughout); and *Anthochaera* (throughout). There are thus some 8 cases of congeneric species pairs in Tasmania, 6 in the Mount Lofty's, 2 in Kangaroo Island, and 8 in the southwest. Tasmania actually has 3 species of *Petroica*, *Acanthiza* and *Pardalotus*. It also has two species of the large-bodied *Strepera* (not discussed here).

In half of the above cases different habitats are occupied by the members of the species pair, and hence, at most, interactions between them can only be partial.

Again using the bill, tarsus and wing as a basis of comparison it is found that significant divergences between congeneric species pairs occur in Tasmania as follows: once in wing length, three times in bill length and twice in tarsus length. However, the *reverse* also occurs (i.e. the difference is greater in species pairs in Victoria), once each in wing and bill, and twice in tarsus length. In the southwest wing length differences are appreciably greater than the Victorian ones in two cases, bill lengths in four and tarsus lengths in two. The reverse applies in three, one and two, cases. It should be

stressed, of course, that bill, tarsus and wing length changes may occur independently of each other, paired, or together. They are listed independently here for convenience only.

MAJOR ADAPTIVE SHIFTS AND SHIFTS IN VERTICAL FEEDING ZONE

The Tasmanian avifauna provides several examples of spectacular adaptive shifts (Keast, 1968, 1970; Abbott, 1973): (1) in the absence of trunk-feeding creepers and nuthatches a honeyeater of the genus *Melithreptus*, one of *Meliphaga*, and a shrike-thrush (*Colluricinclla*), have become part-time trunk feeders and, (2) in the absence of the foliage-gleaning warblers, *Acanthiza lineata* and *A. nana*, and several honeyeaters of the genus *Meliphaga*, warblers of the *Acanthiza pusilla* group (which have invaded the island twice at widely separated intervals) partly occupy the foliage-gleaning niche.

Figure 2 shows diagrammatically a parallel case in the genus *Acanthiza* in southwestern Australia. The five species of the genus occurring in the southeast are separated in their feeding as follows. *A. lineata* and *A. nana* are foliage gleaners, being mainly restricted to forest and woodland, respectively; *A. pusilla* feeds in low shrubbery and saplings; *A. reguloides* in the branches and on the trunk and ground; *A. chrysorrhoa* is predominantly a ground feeder. But *A. lineata* and *A. nana* are absent from the southwest. Now *A. pusilla* and *A. (reguloides) inornata*, become foliage feeders to a significant extent, and spend part of their time in the tree tops. *A. chrysorrhoa*, whilst showing a lesser shift, feeds proportionately more in the branches and foliage of saplings than it does in the east.

Actual figures, for *A. pusilla* and *A. reguloides*, expressed as a percentage, based on 1500 individual observations at four sites in each area and calculated as per Keast (1968), are shown below. The Victorian figures are given first, those for the southwest in brackets.

A. pusilla: outer leaves of trees, 9(23); twigs, 4(9); outer branches, 4(10); inner branches, 3(2); upper trunk, 2(1); lower trunk 2(1); sapling canopy, 38(25); sapling trunks, 2(7); low shrubs, 36(22).

A. reguloides: outer foliage of trees, 5(30); twigs, 6(16); outer branches, 8(4); inner branches, 13(10); upper trunk, 20(10); lower trunk, 8(6); sapling canopy, 2(4); sapling trunks, 16(9); low shrubs, 7(5); ground, 12(6).

SHIFTS IN HABITAT UTILIZATION PATTERNS

Ridpath and Moreau (1966) summarize habitat utilization patterns in Tasmanian birds. No comparable analysis has been published for southern Victoria but any field worker familiar with mainland birds, looking over the Tasmanian list, will recognize cases of greater habitat diversity on the island. For example, in Victoria *Sericornis frontalis* is a sclerophyll forest—rain forest bird but in Tasmania its habitat also embraces woodland and high moor; *Petroica cucullata* is a woodland species in Victoria, its

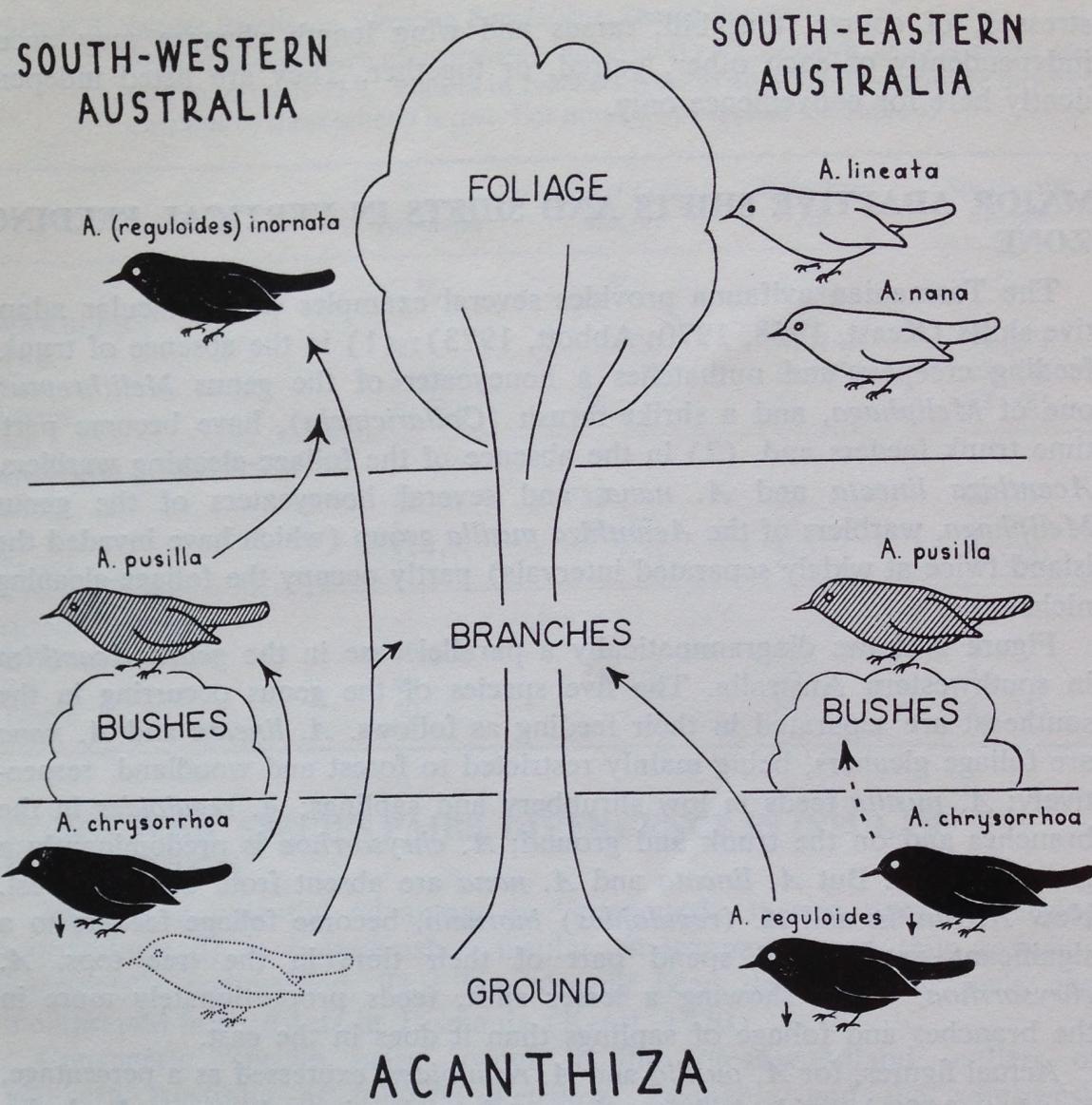


FIGURE 2. Changes in vertical feeding zones in *Acanthiza (regulooides) inornata* and *A. pusilla* in southwestern Australia in response to the absence of the true arboreal foliage-gleaning *A. lineata* and *A. nana* of the eastern forests and woodlands. In both cases a foliage gleaning component is developed. *A. chrysorrhoa* remains largely a ground feeder but now also does more arboreal feeding.

Tasmanian derivative (*vittata*) inhabits woodland and forests; *Meliphaga leucotis* is mainly a coastal scrub inhabitant in southern Victoria, its Tasmanian counterpart (*flavicollis*) largely a eucalypt forest and woodland species.

Striking examples of the phenomenon also occur in the southwest, e.g. *Phylidonyris novaehollandiae* is mainly a *Banksia* heathland species in the east, but here it is a dominant forest, as well as heathland species (Serventy and Whittell, 1962; writer's observations). *Stipiturus malachurus* is here a dry inland, as well as coastal, thicket species (Keast, 1958). The area interior dwelling *Meliphaga virescens* and *Gerygone fusca*, are also forest dwellers in the southwest.

As might be expected Kangaroo Island and the Mount Lofty pockets are too small to provide significant cases of habitat shift.

VARIABILITY IN INSULAR RELATIVE TO MAINLAND POPULATIONS

Van Valen (1965) and Van Valen and Grant (1971), have reasoned that increased morphological variation may be correlated with increased ecological diversity in island populations. Abbott (1973), however, stresses that this need not be expected and that, by contrast, the biotic impoverishment of islands could actually exert an evolutionary influence in three partly opposing ways:

- (1) fewer competitors might mean a wider range of ecological opportunities, which in turn might be reflected in greater variability in adaptive characters such as the bill and tarsus, as Grant (1971) has suggested;
- (2) if habitat and food type diversity is less on islands morphological variability might, by contrast, be reduced and,
- (3) if those species present simply utilize the food made available by the absence of competitor species morphological shifts may not be expected.

Abbott sought to test whether or not the isolated populations of bird species in Tasmania and the Bass Strait Islands did, in fact, show greater variability by making 46 statistical comparisons of bill length, and also of tarsal length, in mainland and island populations. He found that the insular populations were not more variable.

In the present studies variability of wing, bill and tarsus in each insular population of each species has been compared with that of the mainland Victoria populations by means of standard deviations and coefficients of variation, and using the F-test and procedure recommended by Lewontin (1966). The work is based on the measurement of about 5,000 skins. In only one or two cases in the resultant 400 comparisons did an island population show significantly greater variability than its mainland counterpart. This fully corroborates Abbott's findings; that insular bird populations are not more variable than the mainland ones.

INCREASED SEXUAL SIZE DIMORPHISM IN INSULAR POPULATIONS

A potential mechanism for minimizing *intraspecific* food competition in the biotically impoverished insular situation, and thereby enabling the species to maintain higher population numbers would be for the minor morphological differences that characterize the sexes to become exaggerated, and thus partly channelling the males and females towards different resources. This phenomenon has been described in island woodpeckers (Selander, 1966) and occurred in classic form in the New Zealand huia.

Table 4 summarizes the sexual differences in wing, bill and tarsus lengths for the Victorian, and all insular populations, of warblers, muscicapid flycatchers and meliphagids based on means and using the same statistical tests as in the previous section.

It will be seen that, whilst there are some differences, they are neither sufficiently regular in occurrence, marked in degree, nor consistent in direction as to represent a significant evolutionary trend. Sexual differentiation is more marked in meliphagids than in the other groups.

TABLE 4: Sexual Size Dimorphism, Victorian and Insular Populations Compared

Percentages in which measurements differ by (1) 5% or more and, (2) where non-overlap exceeds 75%.

	<i>Victoria</i>	<i>Tasmania</i>	<i>Mount Lofty Ranges</i>	<i>Kangaroo Id.</i>	<i>South-west Corner</i>
WARBLERS					
No. of Species	12	10	12	7	12
Wing	% 25 (25)	% 10 (20)	% 33 (25)	% 28 (14)	% 17 (17)
Bill	8 (8)	20 (10)	— (16)	— (14)	25 (33)
Tarsus	8	10	8	14	8
MUSCICAPIDS					
No. of Species	12	9	6	4	9
Wing	% 33 (25)	% 11 (33)	% — (17)	% 25 —	% 44 (22)
Bill	8	11 (22)	—	—	44 (11)
Tarsus	16	— —	—	(25)	22
HONEYEATERS					
No. of Species	11	10	11	8	9
Wing	% 64 (9)	% 30 (10)	% 45 (18)	% 63 (12)	% 78 (11)
Bill	36 (18)	40 (20)	36 (9)	50 (12)	66 (11)
Tarsus	18 (9)	30 —	27 (18)	38	22

THE EVOLUTIONARY ECOLOGY OF THE SOUTHERN INSULAR AVIFAUNAS, INTEGRATION

How does insular avian evolution in these southern Australian situations compare with that on islands elsewhere and does their study lead to any significant increase in our knowledge of evolutionary processes on islands? Obviously, apart from the unique species radiations of the Hawaiian Islands and Galapagos, they provide classic examples of virtually the full range of island phenomena.

The first ecological change that occurs when a species successfully establishes on a depauperate island is a broadening of feeding zones and habitat utilization patterns: this is the well-known "ecological release" phenomenon. In its initial stages this broadening is not accompanied by morphological changes (see, for example, the Bermudan situation, as described by Crowell, 1962). Eventually the new selective pressures will initiate adaptive morphological changes in the colonizers. These, theoretically, should continue until they are optimal. The bird populations of these Australian islands provide a large number of examples of all the stages in the succession, in different combinations, and involving different species. Such adaptive structures as bill, tarsus, toe and wing length are involved. Ultimately, these morphological changes may become as great, or greater than, those separating congeneric species on the mainland.

Just what do these changes in bill, tarsus, etc., length mean ecologically? In some cases they are evolving towards some of the morphological features of missing species whose role they are usurping. Only a minority can be

explained in this way, however. We are thus, for the present, left with Grant's suggestion (1965, 1968) that these changes confer greater ecological versatility. Obviously the subject requires much more study. Why, again, do the divergence rates vary widely in different species?

One important features of these Australian studies, is in fixing a time on how long these various evolutionary changes have taken to develop: they are very well established at 11,000-13,000 years.

It must be stressed, at this point, that some of this differentiation, specifically that at the "species level" and in those cases of speciation by double invasion, must stem from the earlier phase, or phases, of insular isolation. Doubtless, however, the bulk of the differentiation achieved *prior* to the last period of protracted land junction would have been wiped out by contact with mainland populations at this time.

Island faunas, like those elsewhere, evolve to a state of balance whereby all ecological opportunities are utilized. Since insular avifaunas are impoverished in terms of numbers of species, and some basic taxonomic groups are absent, the end point of the reshuffling process will be different to the original mainland one, and is likely to differ from island to island. There is not the space here to give this theme the attention it merits but the marked difference between the species occupying the trunk-feeding niche in Victoria and Tasmania is a striking example. This reshuffling applies, of course, not only to the avifauna as a whole but to combinations of species within habitats.

The two largest insular areas, Tasmania and the southwest corner, are also "refuge areas" in the true sense. This is assured by their position, physiography, and size. Throughout each period of isolation they have obviously supported a diversified avifauna. With each junction they have received colonizers from the main southeastern continental forest-woodland block. Since there has presumably been at least four periods of isolation and four periods of colonization why have they not built up more diversified avifaunas? Why have they not the full spectrum of species of the southeastern mainland forests? It can only be that these insular areas are limited in the numbers of species that they can support.

The considerable similarities, in numbers of species, divergence levels, and evolutionary patterns, between the southwest corner and Tasmania, despite the differing breadths of barrier isolating them (1500 and 190 km), and greater ease with which birds should be able to penetrate to the latter, and ages of isolation (20,000 and 13,000 years), further emphasizes that the important factors effecting insular differentiation lie *within* the island ecosystem.

Two other important findings are that the Australian insular populations are *not* more variable than the mainland ones, and that increased sexual size, or character, dimorphism is not a major device for minimizing intraspecific competition.

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