Adaptive Evolution and Shifts in Niche Occupation in Island Birds[1]

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ABSTRACT

Adaptive evolution in island birds is investigated with special reference to the birds of Tasmania, a continental island 26,000 square miles in area that lies 140 miles off southern Australia. The avifauna is a typical insular one being numerically impoverished (only 43 species of passerine birds compared with 89 in equivalent habitats on the adjacent mainland), and lacking certain "basic kinds" of birds (e.g., true trunk feeders are absent). The study emphasizes shifts in vertical feeding zones and in morphological attributes associated with perching and feeding (e.g., bill, tarsus, hallux). The findings are as follows: 1. A series of island species have moved into the vacant trunk feeding and underexploited arboreal, foliage-gleaning, adaptive zones; 2. these are species that, on the adjacent Australian mainland, already feed to some slight extent in these zones; 3. the shifts invariably involve a broadening of, or increased diversity in, feeding; 4. there is a broad redivision of ecological roles and adaptive niches on the island; vacant niches are eliminated, and a new state of integration and balance is achieved within the avifauna.

INSULAR AVIFAUNAS ARE numerically impoverished, in terms of numbers of species, relative to those of the larger landmasses. Whole taxonomic groups, and basic ecological types, of birds are missing in some cases. This absence applies even to the avifaunas of large, biotically fairly diverse, islands.

Various intriguing ecological questions are posed. Do some adaptive zones, or ecological niches, remain empty in these cases? Are the vacant roles secondarily filled by other species? If so, what ecological and morphological adaptations do they make? What happens when a well-adapted new colonizer finds an unoccupied, or semivacant, niche? Finally, is there a comprehensive (and possibly periodic) reshuffling or redivision of ecological roles by the members of insular avifaunas so that all ecological opportunities are realized, and a new state of balance achieved?

An investigation of these aspects forms the basis of the present paper. The avifauna[2] considered is that of the island of Tasmania. This continental island lies about 140 miles to the south of Victoria, Australia, has an area of 26,000 square miles, and includes a wide range of avian habitats. It has only about half the number of species of breeding land and freshwater birds found in equivalent vegetation formations in southern Victoria. For small passerines the relative figures are 43 and 89 (table 1).

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[2] Binomials and authorities for birds under discussion are arranged in familial groups in table 4.

ECOLOGICAL ATTRIBUTES OF BIRD SPECIES

In any fauna cohabiting species differ from each other ecologically in a variety of ways. These specializations not only fit their owners for particular roles but serve to minimize interspecific competition and permit the coexistence of large numbers of species. The most important differences are:

1. Habitat specialization, or restriction to a specific vegetation type. A good Australian example is provided by honeyeaters of the genus *Meliphaga* where different species occupy, respectively, mangroves, rain forest, sclerophyll (eucalypt) forest, woodland, river margins, mallee, and savannah grassland (fig. 7 in Keast 1961).

2. Specialization for feeding at different levels, as shown by Colquhoun and Morley (1943), Hartley (1953), Gibb (1954), and Keast (1968). This amounts to dividing the living space into a series of vertical zones and up to 10 of these can be recognized, for example: leafy canopy, twigs, upper branches, inner branches, upper trunks, low shrubs, and so on (see table 2). Whilst some bird species range widely through several of these levels most feed predominantly in only a couple (examples in Keast 1968).

3. Eating different foods, or similar foods in different proportions.

4. Having different diurnal and/or seasonal patterns of feeding, i.e., foraging ranges, wintering grounds, etc.

Of these, zonal feeding lends itself to analysis more readily than others, and is the aspect treated in detail by me. Comparative food studies, by con-

TABLE 1. *Passerine avifaunas of southern Victoria and Tasmania compared.*

	Southern Victoria	Tasmania
	Numbers of species	
Muscicapidae		
Muscicapinae (true flycatchers)	8	3
(robins)	7	4
Pachycephalinae (thickheads)	4	3
Falcunculinae (shrike-tits)	2	———
Cinclosomatinae (quail-thrushes)	1	1
Turdinae (thrushes)	1	1
Malurinae and Sylviinae (warblers)	22	12
Campephagidae (cuckoo-shrikes)	4	1
Artamidae (wood-swallows)	1	1
Sittidae (nuthatches and creepers)	4	———
Dicaeidae (pardalotes)	4	3
Zosteropidae (white-eyes)	1	1
Meliphagidae (honeyeaters)	23	10
Motacillidae (pipits)	1	———
Alaudidae (larks)	1	1
Estrildidae (finches)	3	1
Oriolidae (orioles)	1	———
Grallinidae (magpie-larks)	1	1
Total	89	43

trast, are difficult in that they necessitate the killing of large numbers of birds for stomach analysis. Extensive data on habitat preferences in Tasmanian birds have been assembled by Ridpath and Moreau (1966) and can be used for making some comparisons with mainland birds. No attempt is made here to discuss feeding patterns, although the prominence of seasonal migration in Tasmanian birds is noted.

MORPHOLOGICAL INDICATORS OF WAY OF LIFE AND ECOLOGICAL NICHE IN PASSERINE BIRDS

The leg, toes, bill, and wing are relatively plastic morphological features in birds and reflect minor shifts in feeding and perching habits (literature reviewed in Keast 1968). Whilst by no means fully analyzed, several correlations have been demonstrated. The leg (usually the tarsus only is measured) is relatively long in terrestrial birds, and those that do part of their feeding on the ground. It is short in birds that habitually cling to vertical trunks because of the need to hold the body close to the tree. The tarsus is likely to be relatively shorter in large birds than small ones, reflecting the need for proportionately greater support (Dilger 1956). Amongst small arboreal species those foraging on flimsy twigs and thin branches have shorter tarsi than those making greater use of rigid perches (Dilger 1956, Grant 1966). Finally, in any progressive evolutionary modification of the hind limb the most distal segments change more rapidly than the proximal ones (Osterhaus 1962). Examples of the toes lengthening with increased trunk feeding are given in Keast (1968), and will be seen with the transition to semiterrestrial feeding in the robin, *Petroica rodinogaster,* in table 2.

The bill of a bird reflects its diet. It is long in nectar-feeders and those that probe for food in the ground, or in fissures in the bark. It functions, in insectivorous species, as a pair of fine tweezers for seizing or lifting off prey. Little attempt has been made to correlate bill form with the kind of insects eaten, but the bill is very small and short in species that, like the Australian *Pardalotus,* habitually eat scales.

Island populations of birds very commonly have bills longer than their mainland counterparts. The reason for this has been the subject of some discussion, and various explanations have been advanced. The most logical is that of Grant (1965), inspired by the researches of Kear (1962) with finches, that an enlarged bill is more efficient for dealing with a wider range of food items. The inference thus is that a greater versatility is advantageous on islands which, because of over-all biotic impoverishment, are likely to have relatively fewer species of insects than the mainland.

Wing length and shape increases slightly with the acquisition of migratory habits, and this change is seen in the Tasmanian population of *Zosterops lateralis.* It can be used, however, as an indication of over-all size since aerodynamic considerations keep the ratio between wing length and body weight relatively constant (Amadon 1943).

METHODOLOGY, FEEDING-ZONE DETERMINATIONS

Feeding-zone studies in Tasmania and southern Australia were carried out during the breeding seasons of 1967 and 1968. This time was chosen because the birds' demands on the environment were considered to be greatest then. The methods outlined in Keast (1968) were used. The forest was divided into 10 vertical "feeding zones," as shown in table 3, and the relative amounts of feeding carried out by each species in each of these zones were then determined quantitatively at a series of widely spaced sites (nine in the case of Tasmania). It was found

TABLE 2. *Robins* (Eopsaltria *and* Petroica, *Muscicapinae*) *of the wet sclerophyll* (Eucalyptus) *and temperate rain forests, southern Victoria and Tasmania.*

Species	*Eopsaltria australis*	*Petroica rosea*	*Petroica rodinogaster*
	Victoria	Victoria	Tasmania
	Areas of feeding activity (percent)		
Aerial hawking	———	15	8
Canopy	———	30	12
Twigs	———	20	5
Branches outer	———	25	23
Branches inner	10	10	20
Trunks upper	10	———	———
Trunks lower	5	———	———
Ground	75	———	32
Total feeding actions recorded	490	325	355
Number individuals on which feeding data obtained	35	19	26
Total minutes of observation	175	95	135
	Measurements of body appendages (mm, adult ♂)		
Wing length	78–88 (85)	65–69 (66)	65–70 (68)
Bill length	9.9–11.6 (10.7)	7.6–8.5 (8.0)	8.2–9.2 (8.6)
Tarsus length	19.6–21.9 (20.8)	13.8–14.8 (14.4)	17.4–18.8 (18.2)
Hallux plus claw length	14.2–15.9 (15.2)	9.3–10.3 (9.8)	10.8–12.1 (11.3)
Tail length	59–69 (64)	53–60 (57)	53–57 (54)
Number of individuals	10	9	10

to be more efficient to take numbers of feeding actions (pecks) as the criterion, rather than time spent in the zone. Bias was minimized by standardizing observations at 30 seconds per individual bird and a maximum of 4 minutes per flock, in the case of gregarious species.

Morphological data were obtained by standard taxonomic methods using museum specimens. Measurements are given for adult males only. The major museums housing Australian material were visited (see Acknowledgements), and the size of the samples reflects the availability of material.

TASMANIA, HISTORY AND VEGETATION REGIONS

Ridpath and Moreau (1966) have recently assembled a well-documented account of what is known of the geological history of Tasmania, and what follows is a summary of this. The island area is 26,000 square miles. It lies 140 miles off the coast of Victoria, but intermediate islands reduce the maximum water gap to half this. Bass Strait is known to have existed in the Miocene (Jennings 1959), but its history thereafter is uncertain. It is today less than 70 metres deep in the east, and 100 metres deep in the west (fig. 1). Since at the height of the Pleistocene glaciations Pacific sea levels fell by about 100 metres, Tasmania was presumably connected with the mainland four times. Local geological data, however, provide no evidence on this one way or the other (J. N. Jennings, quoted by Ridpath and Moreau 1966). It is estimated, however, that Tasmania was broadly connected for most of the last glaciation, from about 70,000 until some time after 18,000 years ago. The final severance may have been as recent as 12,000 years ago.

During the last glaciation a highland ice sheet covered about 2000 square miles of Tasmania (Jennings and Banks 1958), and the timberline probably extended to only 300–375 feet above sea level, some 900 feet lower than today (J. L. Davies, quoted by Ridpath and Moreau 1966). Conditions would then have been relatively rigorous for the avifauna. About 18,000 years ago, however, a progressive warming began. In the later stages this must not only have initiated a shift in the distribution of vegetation but encouraged the southward colonization of birds.

Today some 14 vegetation categories are recognizable in Tasmania, and, in their treatment of avian habitats, Ridpath and Moreau (1966) have considered avian distribution relative to these. The formations may, however, be grouped into about five major categories from the viewpoint of their supporting subfaunas: marshes and wet heathland, savannah woodland-grassland, dry sclerophyll (eucalypt) forest, wet sclerophyll (eucalypt) forest, and

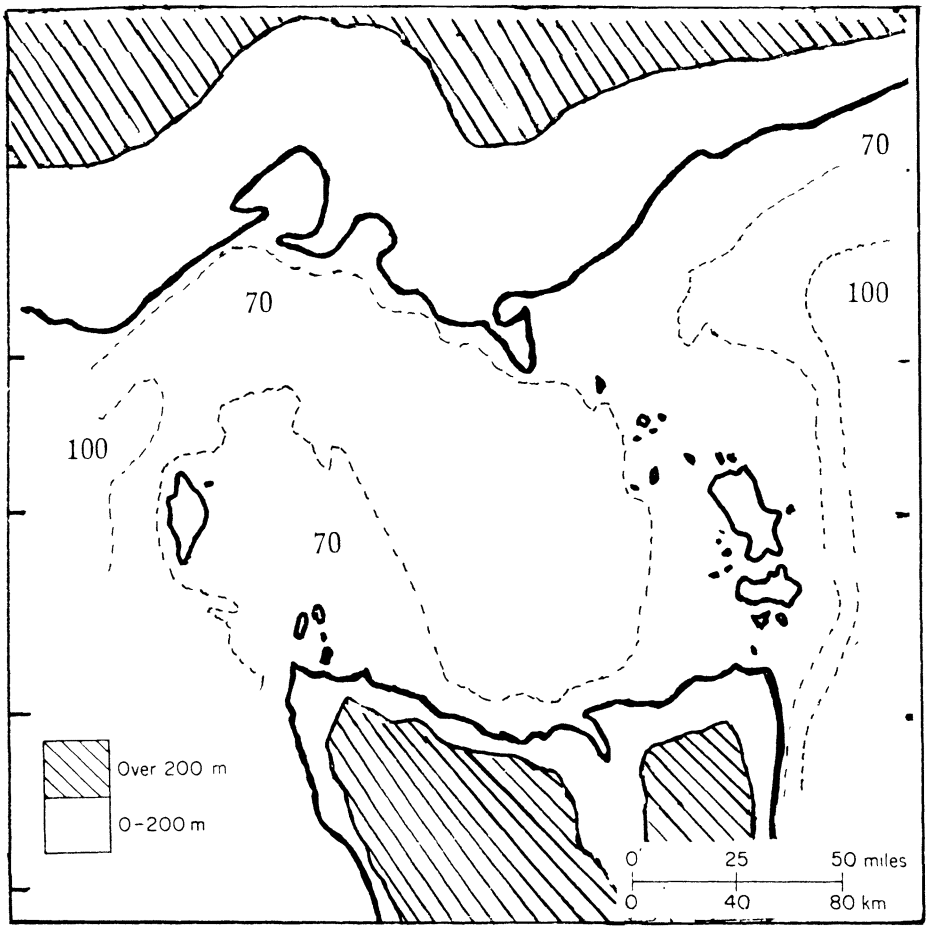


FIGURE 1. Bass Strait to show the 70- and 100-cm contour lines and intermediate islands. Tasmania and Victoria were presumably in contact during each of the four Pleistocene glaciations when Pacific sea levels are estimated to have fallen by about 100 m. (Figure redrawn from Ridpath and Moreau 1966, which is an adaptation of that of Jennings 1959.)

temperate (*Nothofagus*) rain forest. All these vegetation formations cover extensive areas of the adjacent mainland, although temperate rain forest is restricted to scattered pockets.

Endemism in the plants of Tasmania is moderate, about one-sixth of the species being restricted to the island. Twelve of the 25 species of *Eucalyptus* are endemic (Jackson 1965). *Nothofagus* rain forest represents an old habitat that for much of the Tertiary covered southern Australia. It is relict today. The wet sclerophyll forests contain a distinctive eucalypt, *Eucalyptus simmondsii* Maiden. One of the dominant trees of this formation is the 200- to 250-ft-high *E. regnans* F. Mueller. The dry sclerophyll forest contains six endemic eucalypt species (out of the 12 occurring). This circumstance suggests a longer evolutionary history than that of the wet sclerophyll forest. Notwithstanding the differences, however, knowledge of the soil, rainfall, and temperature requirements of the contemporary forest types suggests that all probably existed through the last glaciation. This conclusion would indicate that there has been no major evolution of new avian habitats, just shifts in relative extent of each.

AVIFAUNAS OF TASMANIA AND ADJACENT MAINLAND OF AUSTRALIA COMPARED

Tasmania has a little more than half the breeding land and freshwater birds of the adjacent mainland of Australia, if the avifaunas of equivalent habitats are compared. The extent of the discrepancy varies with the group. The island is nearly as rich in quails, pigeons, most categories of water birds, and hawks, as the adjacent mainland. Ibis and most

of the herons are seasonal visitors only, as in southern Victoria. The island has, however, only three of six species of owls, and three-quarters as many parrots (13 against 17). The disparity is greatest in small passerines (table 1), with 43, as against 89 species. There are only seven species of Muscicapinae (flycatchers), compared with 15; 12 of warblers (Malurinae and Sylviinae), as against 22; one campephagid compared with four; and 10 Meliphagidae (honeyeaters) compared with 23. Trunk-feeding creepers and nuthatches (Sittidae), with four species in southern Victoria, and Falcunculinae, with two species on the mainland, are totally absent. It is passerines, accordingly, that are emphasized in the present study.

Tasmania has about a dozen species of birds (passerines and non-passerines) that have reached the level of morphological differentiation characteristic of species. There are three examples of speciation by double invasion, in *Acanthiza* (see discussion in Mayr 1942) and *Sericornis* (Malurinae), and *Pardalotus* (Dicaeidae). These increase the faunistic diversity to a slight extent.

ECOLOGICAL AND MORPHOLOGICAL CONSEQUENCES OF AVIFAUNAL IMPOVERISHMENT

1. FLYCATCHER AND ROBIN (MUSCICAPID) ADAPTIVE ZONE.—The members of the Muscicapinae occupy a range of niches. Two main groups are discernible. Typical flycatchers catch insects in the air and obtain other prey from the branches and ground. Robins lack the aerial component. The two groups are different morphologically and behaviorally. Flycatchers are animated, restless, quick-moving birds that sweep to and fro, and commonly startle hidden prey into revealing itself. Robins are somewhat dumpy, staid birds that sit motionless on a lookout point, and from there pounce down onto prey. They are quiet and unobtrusive in their feeding.

The Tasmanian forests have two flycatchers, the arboreal *Myiagra cyanoleuca,* inhabiting mostly higher and more open situations, and the small fan-tailed *Rhipidura fuliginosa,* feeding at all levels. Both occupy the same habitats and adaptive zones as on the mainland. *R. fuliginosa* does not venture into open situations to utilize the niche of the absent *R. leucophrys,* which might be expected.

The dry sclerophyll forests, woodlands, and open country of Tasmania lack flycatchers. This absence is curious because three species, *R. leucophyrs, Seisura inquieta,* and *Microeca leucophaea,* are particularly common and widespread in these habitats on the mainland. The first two obtain much of their prey near the ground and have special hovering, insect-flushing forms of behaviour. In Tasmania their niches are presumably partly usurped by robins of three species: *Petroica phoenicea, P. multicolor,* and *P. vittata. P. phoenicea* is much more common in Tasmania than on the mainland, and large numbers spend much of the year feeding in woodlands and paddocks (Sharland 1958). *P. multicolor* has a very broad habitat range in Tasmania, being common in savannah woodland as well as in forest (Ridpath and Moreau 1966). On the mainland the former habitat is occupied by a related species, *P. goodenovii.* Plovers (*Lobibyx novae-hollandiae, Zonifer tricolor*) are common in open situations in Tasmania (Sharland 1958, p. 50) and presumably eat some of the insects that would otherwise be taken by flycatchers. Aerial feeding in the Tasmanian woodlands is carried out by migratory swallows (two species), and the artamid, *Artamus cyanopterus.* These species, which all occur on mainland Australia, feed higher than *Rhipidura* and *Seisura,* but not necessarily above the level of *Microeca.*

A different adaptive situation occurs in the rain forest and wet sclerophyll forests. On the mainland such forests are occupied by the common and predominantly ground-feeding, 5½-inch-long, yellow robin, *Eopsaltria australis,* and the less common, arboreal, 4½-inch-long, rose-breasted robin, *Petroica rosea* (table 2). The "robin niche" is thus divided two ways. There is only one robin in the Tasmanian forests, the five-inch-long *P. rodinogaster,* a species so similar morphologically to *P. rosea* that if a few did not breed alongside the latter in Victoria it would rank only as a race (Keast 1961). Zonal feeding studies (table 2) show a striking shift on the part of *P. rodinogaster* to occupy an adaptive zone that is a combination of that of the two mainland species. It has a terrestrial component to its feeding of 32 percent, which is lacking in *P. rosea,* and comes to 75 percent in *Eopsaltria.* (See also the account of Sharland 1958, relating to the ground-feeding habits of *P. rodinogaster.*)

Morphological studies show that *P. rodinogaster* has a markedly longer tarsus than *P. rosea* (26 percent on mean measurements), and a long hallux (15 percent). This finding accords well with what would be expected from the shift in feeding habits.

2. ADAPTIVE ZONES OF PACHYCEPHALINAE, FALCUNCULINAE, AND TURDINAE.—The basic feeding zones of the medium-sized, insectivorous Pachycephalinae are the branches, twigs, and leaves of tall shrubs and trees. Tasmania has two species of *Pachycephala* (body length 6½–7½ inches) com-

pared with three on the mainland. The insular populations apparently occupy niches similar to those of mainland birds. The larger and more versatile shrike-thrush, *Colluricincla harmonica* (length 9½ inches), has, however, undergone a major ecological shift, and now has a pronounced trunk-feeding component to its feeding. It has also evolved a bill 35 percent longer than in the Victorian population (tables 7 and 8 in Keast 1968).

The Falcunculinae, absent from Tasmania, are represented by two common genera in southern Victoria. *Falcunuculus* (length seven inches) obtains its insects from the twigs, branches, and trunk (see table 7 in Keast 1968), whilst the forest-dwelling, terrestrial, 11-inch-long *Psophodes* feeds amongst the undergrowth, fallen leaves, and rotting logs of the forest floor. Both thrive in cold and wet mountain forests on the mainland, and it is difficult to explain their absence from Tasmania other than by failure to reach the island. The feeding zone of *Falcunculus* in Tasmania is presumably usurped by a combination of species, vide the 6½-inch-long *Melithreptus validirostris,* 8½-inch-long *Meliphaga flavicollis,* and four-inch-long *Acanthiza pusilla* (discussion in Keast 1968). That of *Psophodes* is probably partly taken over by the two, five-inch-long *Sericornis* (only one in southern Victoria) and the 11-inch-long thrush, *Oreocincla lunulata,* that also occurs on the mainland. The success of the introduced European blackbird, *Turdus merula,* in the forests of Tasmania suggests, however, that the adaptive zone is not fully exploited.

3. WARBLER (MALURINAE AND SYLVIINAE) ADAPTIVE ZONES.—The 3½- to 5½-inch-long, insectivorous warblers occupy some four adaptive zones. In southern Australia there are:

a. Foliage gleaners (*Acanthiza*) and the mainland *Smicrornis* and *Gerygone;*

b. Undergrowth and low shrub fossickers that also feed on the ground: these are mainly forest inhabitants (*Sericornis, Malurus*);

c. Dry sclerophyll forest-woodland ground feeders (the mainland *Chthonicola* and *Aphelocephala*), and;

d. Reedbed-wet heath-moorland shrub dwellers (*Megalurus, Acrocephalus, Stipiturus, Cisticola, Calamanthus*).

The island has a total of 12 species of warblers, the adjacent mainland of Victoria 22.

Tasmania has nearly the full quota of birds in the last category. The third category with two mainland species is, by contrast, absent. Their niches, if such truly exist in Tasmania, are probably partly utilized by the *Petroica* robins.

The island is deficient in forest undergrowth fossickers, with genera such as *Hylacola, Pycnoptilus,* and *Dasyornis* being absent. *Malurus cyaneus* is widespread both on the island and mainland. Two species of *Sericornis* occur (one in Victoria), derived from two invasions of the mainland *S. frontalis* type at widely separate intervals. The older invader, *S. magnus,* is confined to shrinking areas of rain forest where, apparently, it is steadily being compressed by the later colonizer, *S. (frontalis) humilis.* The latter occurs in an unusually wide range of habitats for a member of the genus, presumably a response to the fewer competitors. Ridpath and Moreau (1966, p. 367) record it as frequenting the margins of swamps, heathlands, and forests of all kinds.

The two Tasmanian *Sericornis* have, respectively, smaller and larger bills than the mainland form, vide: *S. magnus,* 9.5–10.5 mm (mean 9.8); *S. humilis,* 11.0–12.3 mm (11.7); *S. frontalis,* 10.0–11.1 mm (10.5). The large bill of *S. humilis* should certainly equip it for handling the food items eaten on the mainland by the larger *Pycnoptilus* and *Dasyornis.* At the same time the divergent bills of the two insular species support the thesis of Schoener (1965) that closely related species pairs on islands minimize interspecific competition by exaggerating their morphological differences.

The foliage-gleaning group of warblers is also deficient in Tasmania. The forests and woodlands of coastal Victoria support four species of *Acanthiza,* but Tasmania has only two, excluding the part terrestrial feeder, *A. chrysorrhoa,* that is common to both. The mainland *A. lineata* and *A. nana* are almost exclusively canopy feeders, *A. pusilla* feeds mostly amongst the leaves of saplings and low shrubs, whilst *A. reguloides* is versatile, feeding at all levels in the forest (table 3). Only the *A. pusilla* group occurs in Tasmania. It has given rise, by two invasions, to two species now occupying different habitats, the former being largely confined to the rain forests, the latter living mainly in the sclerophyll forests and woodlands (R. H. Green, pers. comm.; Ridpath and Moreau 1966; writer's observations).

In the absence of the true canopy feeders of the mainland both Tasmanian thornbills have acquired a canopy-feeding component. Counts reveal figures of 30 percent for tree canopy and 50 percent for sapling canopy in *A. ewingi,* and 22 and 25 percent for *A. pusilla diemenensis* (table 3). The latter feeds at heights of up to 100–150 ft in the tops of the tallest eucalypts, which it never does on the mainland. Nevertheless, it still spends part of its time in low shrubs, and 17 percent of the feeding actions recorded were in this zone. It also feeds

TABLE 3. *Arboreal thornbills of the genus* Acanthiza (*Sylviinae*), *zonal feeding and measurements of body appendages, forest and woodland species of southern Victoria and Tasmania.*

Species	*A. lineata* (Victoria)	*A. nana* (Victoria)	*A. reguloides* (Victoria)	*A. pusilla* (Victoria)	*A. pusilla* (Tasmania)	*A. ewingi* (Tasmania)
	Areas of feeding activity (percent)					
Canopy	68	45	6	8	22	30
Twigs	2	5	6	4	2	2
Branches outer	3	15	8	4	16	2
Branches inner	1	———	12	3	9	6
Trunks upper	1	———	20	2	8	6
Trunks lower	1	———	7	2	6	———
Sapling canopy	21	35	6	40	25	50
Sapling trunks	———	———	17	———	2	2
Low shrub	3	———	6	35	17	———
Ground	———	———	12	———	———	———
Total feeding actions recorded	965	564	568	1265	1078	598
Number of individuals on which feeding data obtained	79	43	59	98	89	59
Total minutes observation	159	105	118	145	135	126
	Measurement of body appendages (mm, adult ♂)					
Wing length	51–54 (52)	49–51 (50)	51–55 (53)	46–52 (50)	50–56 (54)	52–57 (54)
Bill length	6.9–7.3 (7.2)	6.9–7.5 (7.3)	8.0–8.5 (8.3)	6.8–7.7 (7.4)	8.8–10.0 (9.3)	7.8–8.3 (8.0)
Tarsus length	16.5–16.8 (16.5)	15.6–16.6 (16.2)	15.2–16.4 (15.8)	18.2–19.3 (18.8)	18.0–19.2 (18.6)	19.7–20.9 (20.4)
Hallux plus claw length	8.9–9.9 (9.5)	8.8–9.9 (9.1)	9.7–10.7 (9.9)	9.5–10.4 (9.9)	10.2–11.3 (10.7)	9.0–11.0 (10.3)
Tail length	36–38 (37)	33–38 (35)	34–39 (36)	38–45 (41)	39–44 (42)	45–50 (48)
Number of individuals	10	9	11	11	10	10

extensively on the trunks and branches of the trees, thus usurping also the feeding zone of *A. reguloides*. *A. pusilla* presents a striking case of increased ecological versatility.

Both Tasmanian species of *Acanthiza* have longer bills than the mainland *A. pusilla*. The increase is particularly marked in *A. pusilla diemenensis*, being 25 percent on mean length. This species also has a longer hallux (8 percent). These trends are away from the morphological characteristics of the mainland foliage-gleaning *A. lineata* and *A. nana*, which have both short bills and legs. The adaptations would thus seem to be not toward foliage-gleaning but toward more diverse ecological roles. This finding supports the thesis of Grant (1965) that longer bills and legs in island birds may be linked with increased ecological versatility.

4. CAMPEPHAGID ADAPTIVE ZONE.—Cuckoo-shrikes (Campephagidae) are medium-sized to large-bodied birds (length 10–13 inches) that feed on the larger insects of the branches and leaves (*Coracina* and *Edolisoma*), or mainly from the ground (*Lalage sueurii*).

Only one arboreal species, *Coracina novae-hollandiae*, occurs in Tasmania, three in southern Victoria. The insular population is characterized by a short bill (length, 16.8–18.3 mm, mean 17.4 mm), compared with the mainland one (length 18.3–19.9 mm, mean 18.9 mm). The bill lengths of the other mainland species are: *C.* (*papuensis*) *robusta* (15.7–16.8 mm, mean 16.0); *C.* (*Edolisoma*) *tenuirostris* (17.0–18.5 mm, mean 17.8 mm). The intermediate-sized bill of the Tasmanian *C. novae-hollandiae* suggests an adaptation for occupying the roles of all three mainland species (Keast 1958).

5. ADAPTIVE ZONES OF THE HONEYEATERS (MELIPHAGIDAE).—The Meliphagidae (10 species in Tasmania, 23 in southern Victoria) may be arbitrarily

TABLE 4. *Binomials with authors for birds discussed.*

Charadriidae
- Lobibyx novae-hollandiae (Stephens)
- Zonifer tricolor (Vieillot)

Strigidae and Tytonidae
- Ninox novae-seelandiae (Gmelin)
- N. connivans (Latham)
- N. strenua (Gould)
- Tyto novae-hollandiae (Stephens)
- T. tenebricosa (Gould)
- T. alba (Scolpoli)

Muscicapinae
- Rhipidura fuliginosa (Sparrman)
- R. leucophrys (Latham)
- Myiagra cyanoleuca (Vieillot)
- Seisura inquieta (Latham)
- Microeca leucophaea (Latham)
- Petroica multicolor (Gmelin)
- P. rodinogaster (Drapiez)
- P. rosea Gould
- P. phoenicea Gould
- P. vittata (Quoy and Gaimard)
- Eopsaltria australis (Shaw)

Pachycephalinae
- Colluricincla harmonica (Latham)

Turdinae
- Oreocincla lunulata (Latham)
- Turdus merula Linne

Malurinae and Sylviinae (Acanthiainae)
- Malurus cyaneus (Latham)
- Sericornis frontalis (Vigors and Horsfield)
- S. humulis Gould
- S. magnus (Gould)
- Acanthiza chrysorrhoa (Quoy and Gaimard)
- A. reguloides Vigors and Horsfield
- A. lineata Gould
- A. nana Vigors and Horsfield
- A. pusilla (Shaw)
- A. ewingi Gould

Campephagidae
- Coracina novae-hollandiae (Gmelin)
- C. robusta (Latham)
- C. tenuirostris (Jardine)
- Lalage sueurii Vieillot

Artamidae
- Artamus cyanopterus (Latham)

Dicaeidae
- Pardalotus striatus (Gmelin)
- P. punctatus (Shaw)

Zosteropidae
- Zosterops lateralis (Latham)

Meliphagidae
- Melithreptus gularis (Gould)
- M. validirostris (Gould)
- M. affinis (Lesson)
- Meliphaga lewini Swainson
- M. fusca Gould
- M. chrysops (Latham)
- M. leucotis (Latham)
- M. penicillata Gould

grouped into three categories: a. short-billed, small-bodied (five- to eight-inch-long), predominantly insectivorous species (*Meliphaga, Melithreptus*); b. longer-billed, small-bodied, largely nectarivorous ones (*Phylidonyris, Acanthorhynchus, Gliciphila*), and c. large-bodied (length, 11–16 inches) species (*Myzantha, Anthochaera*). Tasmania has nearly the full component of the two latter categories. The real deficiencies lie in short-billed species. There is only one species of *Meliphaga,* instead of eight. This species, *M. flavicollis,* is common and a very versatile feeder, taking food at all levels in the trees and shrubs (table 4 in Keast 1968). It also occupies a wide range of habitats, occurring in heath, dry and wet sclerophyll forest, subalpine forest, and orchards (Ridpath and Moreau 1966, p. 365).

Tasmania has two species of *Melithreptus* compared with three in southern Victoria. The large one, *M. validirostris,* has changed strikingly from its mainland counterpart, *M. gularis,* in having strongly entered the adaptive zones of the absent trunk-feeding and fissure-probing Sittidae and Falcunculidae. In association with this development, it has evolved a significantly longer bill and stronger tarsus and hallux (fig. 3 and tables 3 and 4 in Keast 1968). The smaller *M. affinis,* by contrast, has the shortest bill in the genus (fig. 4), an adaptation that possibly fits it better for a foliage-gleaning role (Keast 1968).

The two Tasmanian *Melithreptus,* thus, also show character divergence.

6. FOLIAGE-GLEANING BIRDS OF TASMANIA AND SOUTHERN VICTORIA COMPARED.—The differences between these two avifaunas in terms of foliage-gleaning, insectivorous birds are summarized pictorially in figure 3. As noted, Victoria has three species of four-inch-long thornbills (*Acanthiza*), Tasmania two. The former has three species of short-billed 3¼-inch-long pardalotes (*Pardalotus,* Dicaeidae), the mainland two. The extra Tasmanian species result from a double invasion by *P. punctatus* stocks. Tasmania lacks all the true canopy-feeding members of *Meliphaga;* the Victorian forests and woodlands have at least four: *M. chrysops, M. penicillata, M. fusca, M. lewini.* Each has one foliage-gleaning *Melithreptus.*

Figure 3 brings out clearly how "making good" the Tasmanian "deficiencies" in foliage-gleaners involves the interplay of several unrelated groups.

7. TRUNK-FEEDING, BARK-PROBING BIRDS OF VICTORIA AND TASMANIA COMPARED.—The birds occupying this adaptive zone in Victoria, three partly allopatric *Climacteris,* one *Neositta,* and *Falcunculus,* are shown pictorially in figure 4, along with the species that have secondarily invaded this vacant zone in Tasmania. Five species are involved, those shown here plus *Acanthiza pusilla.* In *Melithreptus validirostris* the branch- and trunk-feeding component averaged 67 percent, compared with 29 percent in the mainland *M. gularis,* whilst it was 49 percent in *Meliphaga flavicollis,* compared with 15 percent in *M.*

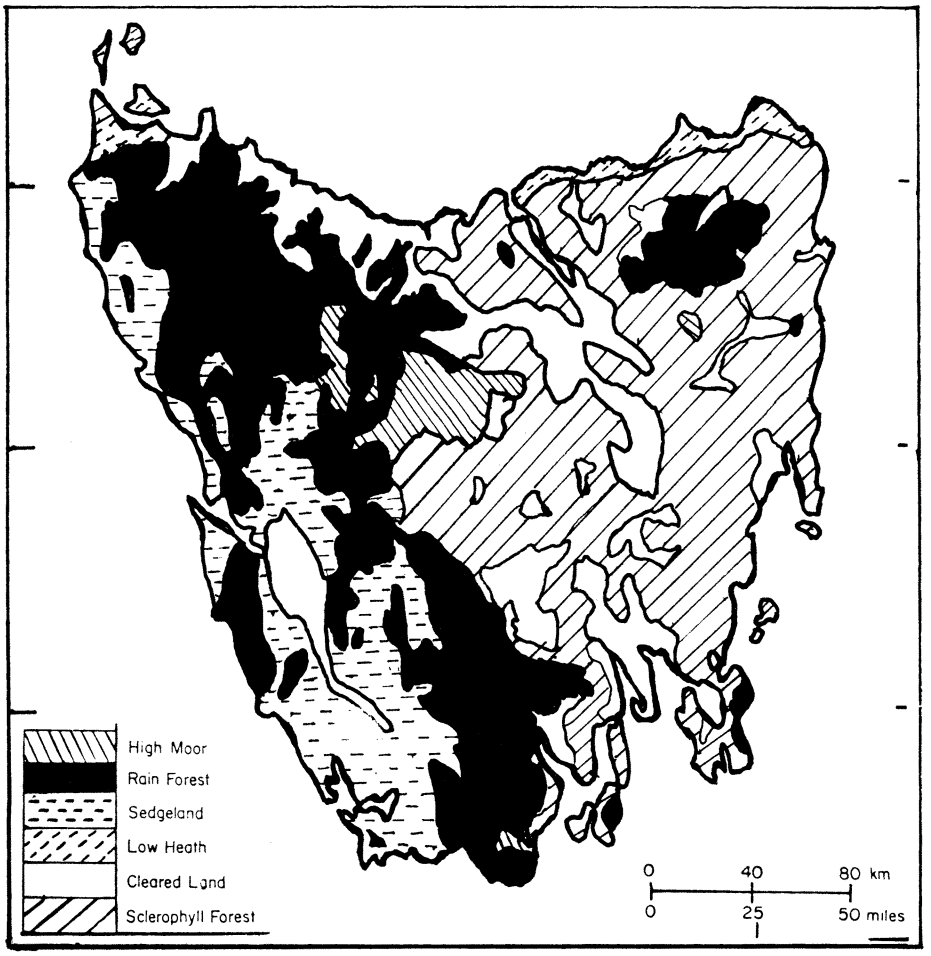
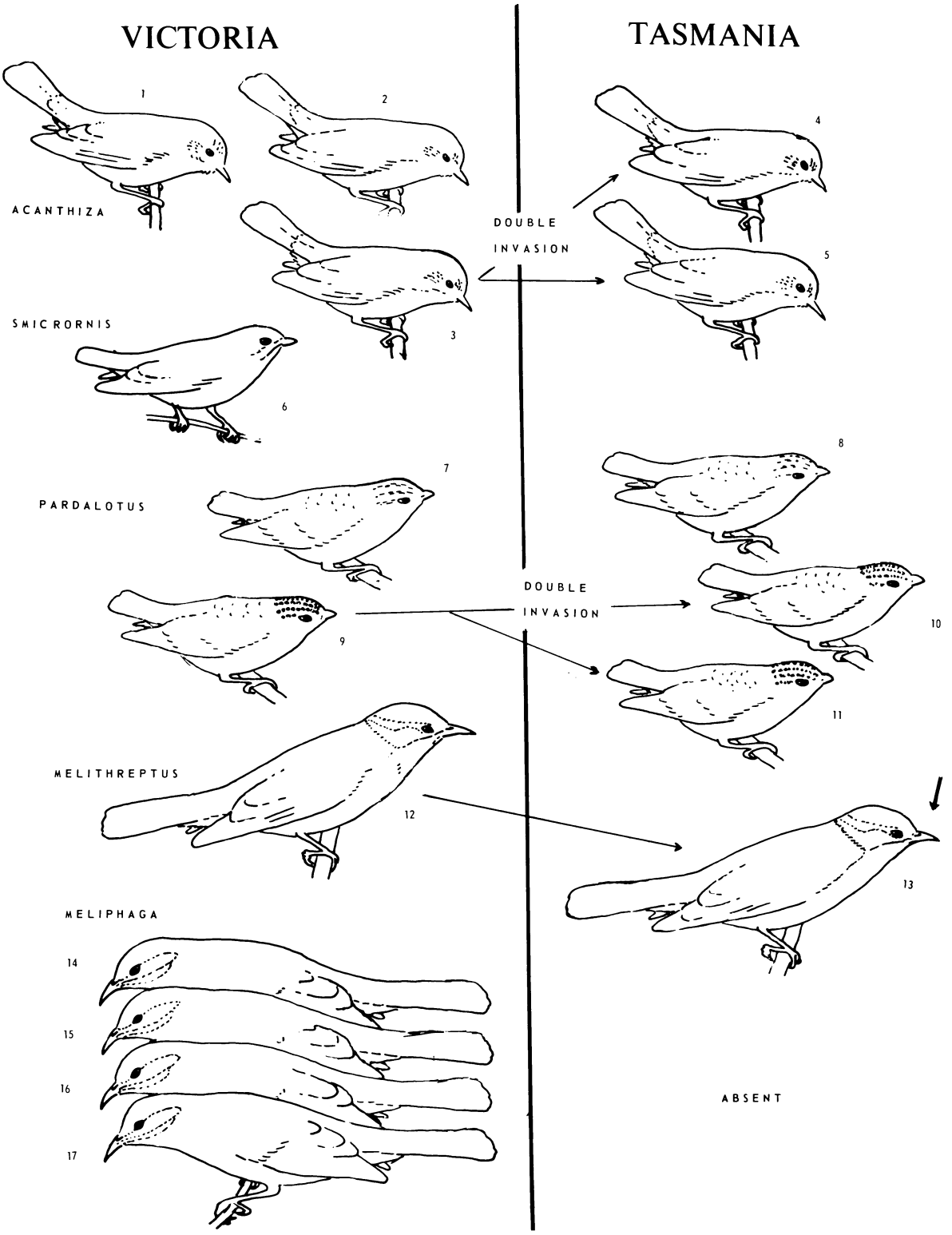


FIGURE 2. The major vegetation formations of Tasmania. (Redrawn from Ridpath and Moreau 1966, which is an adaptation from Davies 1964.) The most important forest habitats, in terms of supporting avian subfaunas, are temperate (*Nothofagus*) rain forest, wet sclerophyll (eucalypt) forest, and dry sclerophyll forest-woodland. The latter two are grouped here. Clearing for agriculture up to now has been limited in Tasmania.

leucotis (tables 3 and 7 in Keast 1968). In the insular *Colluricincla harmonica* it totalled 26 percent of the feeding effort, compared with 7 percent in the mainland populations of this species. The writer was able to gather little data on the frequency of the habit in *Sericornis magnus* because of its rarity, but Sharland (1958) and Ridpath and Moreau (1966) both attest to its trunk-feeding tendencies. Data for *Acanthiza pusilla* are given in table 3.

Three aspects might be stressed with respect to this secondary trunk-feeding in Tasmania. First, the same species take part in the habit throughout the island, and no observer can be long in the field without recording it. It was remarked upon in *Colluricincla* and *Meliphaga* 60 years ago (Littler 1903). A succession of observers has remarked upon mistaking *Melithreptus validirostris* for a tree-creeper, from its trunk-clinging habits. Sharland (1958) also discusses the prominence of bark-feeding in this species. Second, all the species that bark-probe have evolved some morphological adaptations that better fit them for it. This finding confirms that the habit is not recent. Third, none of the species has, in the process, abandoned feeding in its former zones. In each case diversification is the rule. This diversification, and fewer competitors, probably explains the visibly higher population levels of *Melithreptus validirostris* and *Meliphaga flavicollis* in Tasmania, relative to their mainland counterparts.

8. NOCTURNAL PREDATORS: OWL ADAPTIVE ZONES. —Tasmania has two common species of owls, the large *Tyto novae-hollandiae* and the small *Ninox novae-seelandiae*. *Tyto alba* occurs but is rare and marginal, being amongst the first species to perish in hard winters (Sharland 1958). Southern Victoria,



by contrast, has six species of owls. As shown by the wing-length measurements for males given in Mees (1964), these species represent successively larger body sizes, vide: *Ninox novae-seelandiae,* 231–248 mm; *N. connivans* (inhabiting woodland), 303–325 mm; *Tyto tenebricosa* (in rain forest), 295–320 mm; *T. novae-hollandiae,* 298–333 mm; and *Ninox strenua,* 398–420 mm.

The Tasmanian population of *N. novae-seelandiae* is conspicuously small in body size, the wing length of the males being 198–222 mm. The second species there, *Tyto novae-hollandiae,* however, is characterized not only by increased size but by exaggerated sexual size dimorphism, vide, wing of males, 319–343 mm; those of females, 360–387 mm.

The ecological significance of these changes is presumably twofold. Interspecific competition between the species is reduced by their size differences being exaggerated. Within *T. novae-hollandiae,* the dimorphism between males and females must favor the selection of prey of slightly different sizes, with a consequent reduction in intraspecific competition. This kind of phenomenon has been noted by Lack (1947) in large hawks, and must be advantageous in a faunistically impoverished insular fauna.

SHIFTS IN HABITAT PREFERENCE AND PATTERNS OF ENVIRONMENTAL UTILIZATION IN TASMANIAN BIRDS

Subjects such as shifts in habitat preference and patterns of environmental utilization require proper study. The three cases of the double invaders (*Acanthiza, Sericornis,* and *Pardalotus*), in which the members of each pair are separated or partly separated on habitat grounds, might be noted. These represent a finer division of the habitat than occurs in each species group on the mainland. In *Sericornis* and *Pardalotus,* however, the later invader appears now to be replacing the earlier one in its particular habitat. This development could mean simply that the later invaders in each case are more progressive or that the present habitat subdivision is too fine.

There are a few cases of Tasmanian populations of species occupying a wider range of habitats than their mainland counterparts, e.g., *Petroica multicolor, Sericornis humilis,* and *Meliphaga flavicollis.* Analysis will doubtless reveal others.

South–north seasonal migration is somewhat more developed in Tasmania than Victoria, and thus reflects the limitations of the island as a wintering ground for certain species. The difference is, however, relative since the proportion of migratory species progressively decreases from south to north on the mainland. Included in the species, some or all of whose members leave Tasmania before winter, are: two species of parrot, a kingfisher, four cuckoos, two swallows, a flycatcher, three robins, a woodswallow, a cuckoo-shrike, a reed-warbler, a pardalote, and a white-eye.

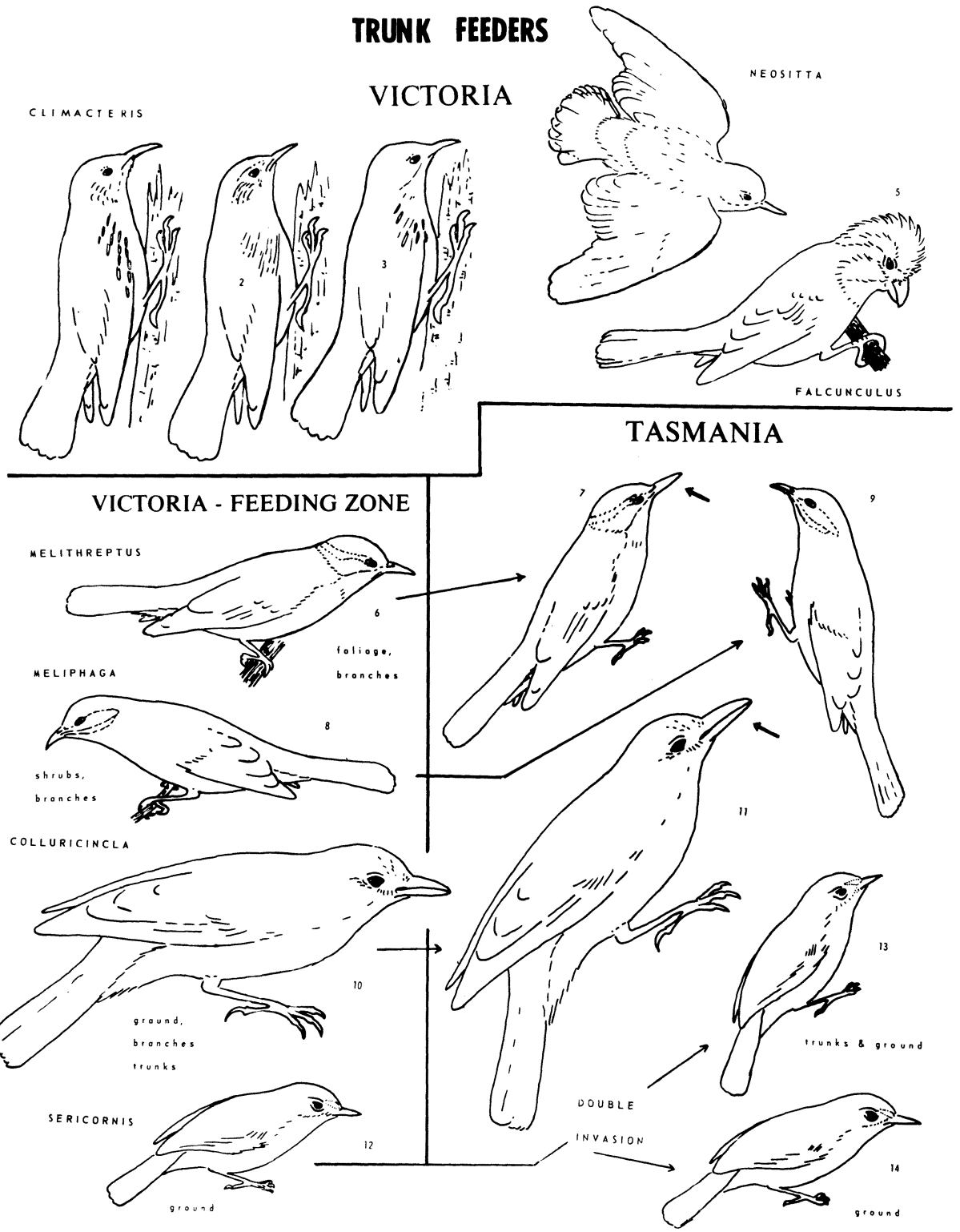
ADAPTIVE EVOLUTION RELATIVE TO FAUNISTIC IMPOVERISHMENT IN THE INSULAR AVIFAUNA OF TASMANIA

The Tasmanian avifauna throws considerable light on some of the questions posed with respect to insular faunas.

1. There are, or rather were, a large number of vacant niches in Tasmania. Included here are whole adaptive zones, e.g., the trunk-feeding zone. Other major gaps, that have now been secondarily filled, are a ground-feeding, rain-forest robin niche, a bark-feeding warbler niche (as per the mainland *Acanthiza reguloides*), and some arboreal, foliage-gleaning niches. Additional evidence of former vacant niches comes from the three cases of double invasion, where a single mainland species has been able to become established twice.

2. At the same time it is wrong to suppose that the number of vacant niches, or opportunities for species, in Tasmania is equal to the number of absent species (89 minus 43 equals 46 in the case of passerines). There is considerable evidence that the island has not the same carrying capacity for numbers of species as southern Victoria: a. various species, including *Rhipidura leucophyrs*, reach the island from time to time but fail to become established; b. many species, including those belonging to a wide range of families, are migratory, leaving

FIGURE 3. The arboreal foliage-gleaning birds of southern Victoria and Tasmania compared (equivalent habitats). Victoria has three, four-inch-long warblers of the genus *Acanthiza* (*A. lineata, A. nana, A. pusilla*). Tasmania has two, these having been acquired by a double invasion of *A. pusilla* stock. They are, however, largely allopatric, one frequenting mainly rain forest, and the other eucalypt forest. The monotypic, short-billed *Smicrornis* is absent from the island. Tasmania has, however, three species of 3½-inch-long *Pardalotus* (Dicaeidae), two of which were acquired by a double invasion. Southern Victoria has only two (excluding the Tasmanian *P. striatus,* some members of which overwinter on the mainland). Each area has one member of the short-billed meliphagid genus, *Melithreptus* (length, five inches). The Tasmanian member, *M. affinis,* has the shortest bill in the genus, and it is suggested that this may be a response to the paucity of short-billed foliage-gleaners on the island. Southern Victoria has four species of short-billed, foliage-gleaning *Meliphaga* (body lengths, 6–7 inches), Tasmania none.



the island before winter; c. many species apparently occupy the niches of 2 or 3 mainland species, e.g., *Coracina novae-hollandiae, Acanthiza pusilla;* d. there are at least three cases (*Sericornis, Melithreptus,* the owls) where closely related species pairs show character divergence, which can be interpreted as a device for lessening interspecific competition between them.

3. Strictly speaking, of course, fewer species, and the absence of particular species per se, does not prove fewer niches. Some species may, because of the distance involved and poor flying powers, have been unable to colonize the island, but would thrive there if they could. A species may reach the island occasionally but be unable to withstand a severe winter. A colonizer may find its food unavailable all year, or partly usurped by a resident species. The extinction of a species cannot readily be made good in Tasmania because there is not a reservoir of birds immediately to the north. Lastly, because of the small size of the island, and the absence of isolating barriers within it, the local proliferation of species, by speciation, has probably been impossible in recent geological times.

4. Although the present study reveals much on the utilization of vacant niches in Tasmania, it also raises many questions. For example, what happens to the niche of the shrub and undergrowth, forest-dwelling *Psophodes, Pycnoptilus,* and *Dasyornis,* in Tasmania? Why is there no species utilizing the flycatcher niche in the island's dry sclerophyll forests and woodlands? Is such a niche simply not available? Or is it, in fact, utilized marginally by such diverse and unrelated groups as robins, plovers, and wood-swallows?

5. What kinds of bird species move into a vacant adaptive zone? If the trunk-feeders of Tasmania can be taken as an example, it is the species that already have some tendencies to feed in that zone. Thus, the mainland relative of *Melithreptus validirostris, M. gularis,* already carries about 29 percent of its feeding there. The figures for the mainland *Meliphaga leucotis* are 15 percent; *Colluricincla harmonica,* 7 percent; and *Acanthiza pusilla,* 4 percent.

6. What is the mechanism whereby a species adapts to a new feeding zone or ecological niche? Presumably, when a species that occasionally feeds in a zone suddenly finds a continued and abundant source of food there, because of the absence of other species, it is encouraged to feed there with greater consistency. The new zone is probably exploited inefficiently at first. But a selection pressure is set up for more effective body structures. Eventually this is achieved, and the species is now consolidated in its new role. One might speculate as to what would happen to the Tasmanian trunk-feeders if, for example, *Climacteris* treecreepers suddenly became established on the island. Since none of the insular trunk-feeders has developed the specialized short legs, or unique abilities of this group to run or hop rapidly up vertical surfaces, they would probably find themselves at a competitive disadvantage. Retention of generalized features (which equip them for diverse roles on the island) would now prove an advantage. They could survive in their other feeding zones, unless the now-restricted niche was not capable of supporting them.

7. Does an island fauna, initially deficient, eventually reach a state of integration and balance with all the major adaptive zones being utilized? This is obviously so in the case of Tasmania. Proof that a fauna, in part at least, evolves as a unit comes from the diversity of unrelated species that have combined to exploit the insects of the canopy, on the one hand, and those of the trunks, on the other.

8. How long has the present state of "balance" in Tasmania taken to evolve? This cannot be answered. Certainly the late-Pleistocene avifauna must have been altered, if not decimated, by the temperature and habitat changes associated with the last glaciation. Recolonization must have been accelerated with the return to warmer temperatures, and been interrupted about 12,000 years ago by the formation of the sea barrier. Presumably, however, there has been a continuing dribble of colonizers across Bass Strait ever since. Probably most, if not all, of the distinctive Tasmanian species, rain-forest, wet-forest, and dry-forest ones, antedate the sea barrier. Some, presumably, antedate the last glaciation. Attempts to age faunal segments by ageing their habitats prove fruitless, and only speculations can be made from

FIGURE 4. The trunk-feeding and bark-probing birds of southern Victoria and Tasmania compared. The three specialized genera occupying this adaptive zone in Victoria are absent from the island, vide the six- to seven-inch-long *Climacteris* (three species, partly allopatric), and the 4½-inch-long *Neositta* (both Sittidae), plus the seven-inch *Falcunculus* (Falcunculinae). In Tasmania five species have secondarily entered the zone: *Melithreptus validirostris* (five inches), derived from the mainland *M. gularis; Meliphaga flavicollis* (eight inches), whose mainland relative is *M. leucotis;* the shrike-thrush *Colluricincla harmonica* (10 inches); the warbler *Sericornis magnus* (five inches); and the warbler *Acanthiza pusilla* (four inches), which is not shown here. The main feeding zones of the mainland stocks are indicated. Morphological adaptations to the new roles include a 19 percent longer bill in *Melithreptus,* a 35 percent longer one in *Colluricincla*—see arrows—and a 25 percent longer one in *Acanthiza.* Percentage differences are based on the means.

the birds themselves. Whilst it is obvious that *Nothofagus* rain forest is very old, it cannot be said, for example, whether the ancestors of *Sericornis magnus* and *Acanthiza ewingi,* inhabitants of this habitat, reached the island during the last, or an earlier, land connection. Possibly they entered the beech forests of Tasmania only 70,000 years ago at the beginning of the last glaciation, and remained in them throughout the glacial period. Again, it cannot be stated whether their later-arriving, eucalypt forest relatives, *Sericornis humilis* and *Acanthiza pusilla diemenensis,* entered Tasmania with the expansion of these forests at the end of the glaciation, or across Bass Strait at a later date.

SUMMARY

Evolutionary and ecological phenomena associated with the numerically impoverished insular avifauna of Tasmania are analyzed. This fauna contains only 43 passerines compared with 88 in equivalent habitats on the adjacent continental mainland, and lacks basic taxonomic categories, e.g., the trunk-feeding Sittidae and Falcunculinae. Procedures followed are analyses of feeding-zone specializations, made in the field, and studies of body morphology, using museum specimens.

The vacant trunk-feeding and underexploited arboreal, foliage-gleaning, adaptive zones are analyzed in detail. It is found that series of unrelated species fill the former zone in Tasmania, and that the ones that do this are those that marginally or occasionally feed on trunks on the mainland. They are species that thus already have some tendencies to feed in the zone. In the case of the arboreal, foliage-gleaning zone, some proliferation of species is achieved by two cases of speciation by double invasion, in the *Acanthiza pusilla* and *Pardalotus punctatus* groups.

Broadly speaking, vacant niches are exploited by species from adjacent feeding zones. They acquire a more diversified ecology by so doing. Thus, in the absence of a rain forest and wet sclerophyll forest, ground-feeding robin, a species (*Petroica rodinogaster*) whose mainland relative (*P. rosea*) is an arboreal feeder, develops a significant ground-feeding component (and acquires longer legs in the process). The warbler, *Acanthiza pusilla,* that feeds in the foliage of saplings and low shrubs on the mainland, now acquires a high canopy component to its feeding in the absence of the mainland *A. lineata,* and a branch-feeding one, in the absence of *A. reguloides.* Diversified feeding may be linked to an increase in bill or tarsus length, as suggested by Grant (1965). It may also, apparently, be associated with the absence of a longer-billed or larger-bodied species. There are also one or two cases of the adaptation involving a shorter bill, e.g., in the insular *Coracina novae-hollandiae,* the bill is intermediate in length between those of the three mainland members of the genus.

Evolutionary and ecological adjustments in Tasmania involve not only individual zones, niches, and species, but the whole avifauna. There is a redivision of ecological roles, a broadly based reintegration, and a new state of "balance." An attempt is made to date these changes, by ageing the major vegetation zones or avian habitats, and from birds themselves, without much success. The more distinctive endemic species and races undoubtedly antedate the postglacial isolation of the island, when sea levels rose, and probably antedate the glaciation itself. The glacial period, when about one-thirteenth of the island was covered by ice, and temperatures must have been severe, presumably eliminated many bird species. Temperatures were already warming and habitats expanding, however, prior to the isolation of the island about 12,000 years ago. Many of the major elements probably reached Tasmania at that time, and there has undoubtedly been a dribble of new colonizers ever since. This would have required continued, if minor, faunistic readjustments to the present day.

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