

Hybrid Zones in Australian Birds

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Summary

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Geographic patterns in positions of 79-87 avian hybrid zones and 12 parapatric contacts in Australia are analysed in the context of past climates, palaeo-refugia, mechanisms of origin, and temporal stability. No hybrid zone occurs in rain-forest species and differentiated vicariant forms of these are generally separated by unsuitable tracts of sclerophyll forest or savanna woodland. Most hybrid zones occur in semi-arid and sub-humid species. The zones appear to have originated by secondary contact of differentiated vicars rather than by parapatric divergence, because most lie between refugia postulated on the basis of late Pleistocene climates; their widths are generally in accord with those predicted from dispersion rates. The evidence suggests that most, if not all, hybrid zones were formed when expansion of isolates from refugia became possible following the marked improvement in climate at the close of the severe arid phase of about 17 000 y before present. The persistence of hybrid zones since then and their widths offer no support for the concept of reinforcement of previously acquired differences in recognition (signalling) systems. Where a hybrid zone coincides closely with the boundary of a presumed refuge, a semi-arid form has differentially expanded towards its subhumid counterpart.

Introduction

Hybrid zones are regions of steep genetic and phenotypic intergradation between relatively uniform contiguous populations (Mayr 1963; Short 1969; Ford 1974a). Prior to the work of Cain & Currey (1963), Clarke (1966), Jain & Bradshaw (1966) and Endler (1973, 1977), zoologists almost universally accepted such zones as being produced only when vicariant differentiates came into recontact following breakdown of the geographical barrier between their former refuges. Nowadays, the view is also held that steep morphological changes across geographical fronts may arise *in situ*, through the action of selection caused by an environmental gradient, without the intergrading populations ever having been isolated. Accordingly, primary and secondary zones of intergradation are often considered to be difficult to distinguish (Endler 1977). One way of ascertaining the major mode of hybrid zone formation is to analyse their geographical positions on a continental basis. The delimitation of the majority of hybrid zones in Australian birds now provides an opportunity to do this.

The refuge area concept, entailing an allopatric mechanism of speciation and the close association of many bird species with certain vegetation types, has generally been advanced to explain distribution patterns and speciation sequences in Australian birds (Gentilli 1949; Serventy 1951; Keast 1961; Ford 1974b). If hybrid zones represent thwarted stages of the speciation process in which differentiated vicars prematurely rejoin before acquiring different sets of recognition signalling-systems (Paterson 1982), the general geographic positions of hybrid zones would tend to cluster across the former barriers (Endler 1982a, 1982b).

However, a random pattern in the locations of hybrid zones would tend to eventuate if climatic and physical gradients were the real determinants, especially on the Australian continent where the temperature gradients run generally north-south and rainfall has a concentric zonation, because such 'hybrid zones' could arise anywhere.

Many hybrid zones have been discovered in Australian birds (Ford 1974a,b,c, 1975a,b, 1977a, 1978a,b,c,d, 1979a,b, 1980a,b, 1983a,b, 1985a, 1986) since summaries were given by Keast (1961), Ford (1974a) and Meise (1975). All were reassessed and delimited in this study, which was designed to elucidate their origin and significance. I found it necessary to assemble criteria for identifying hybrid zones, to discuss hypotheses on hybrid zones in birds, and to examine palaeo-climatic data in the context of its relevance to the refuge-area concept. Some parapatric contact zones between related species are also discussed.

Characteristics of hybrid zones

Irrespective of whether hybrid zones are primary or secondary phenomena, the following criteria have been used, either separately or in various combinations, to identify them:

- Morphological intermediacy and increased variability of the hybrid populations (Mayr 1963; Schueler & Rising 1976).
- Steep or stepped intergradation over a fairly short distance and relatively little geographical variation elsewhere (Ford 1986).
- Congruence of steps in several clines or characters

associated with unlinked loci (Barton & Hewitt 1981, 1985; Ford 1982b; Barton 1983).

- Increased allozyme heterozygosity in the hybrid zone (Corbin 1981).
- Incidence of novel allelic variants resulting from intragenic (intracistronic) recombination (Watt 1972; Sage & Selander 1979).
- Pronounced chromosomal heterozygosity in the hybrid zone and relative uniformity elsewhere (White 1978; Key 1981).
- Reduced fitness of hybrid (heteromorphs) as measured by reproductive success (Littlejohn 1981). In birds this is generally inferred from phenotype frequencies in hybrid zones.

Avian hybrid zones in Australia have generally been analysed on morphological criteria. Thorpe (1984) proposed a cladistic method for determining whether a hybrid zone was formed by primary or secondary contact, i.e. the parental or parapatric forms would conform to a linking of anagenetically divergent clades or lineages if contact was secondary, but the method does not seem suitable for avian populations at the intraspecific level unless the species consists of several distinct populations and there is a suitable outgroup for rooting the clades. Generally, avian species in continental Australia cannot be divided into a sufficient number of readily separable sub-populations.

Origins of hybrid zones

On the basis that speciation or gross divergence is an allopatric process, hybrid zones represent secondary intergradations, whereas on the basis of the parapatric and stasipatric models of speciation, such zones arise *in situ*. Parapatric differentiation could occur by means of differential adaptation of adjacent populations in different environments produced by a substrate or habitat boundary (Mayr 1963; Clarke 1966; Jain & Bradshaw 1966; Ford 1974a; Endler 1977; Templeton 1981). It has been asserted by Endler (1973, 1977) and Bush (1975, 1981) that many hybrid zones arise through parapatric differentiation and that many allopecies with abutting ranges represent parapatric speciations.

The essential difference between the allopatric and parapatric models of differentiation between populations is the amount of gene flow necessary to prevent divergence (Futuyma & Mayer 1980). A neutral locus is prevented from diverging by genetic drift by an extremely low rate of immigration (Crow & Kimura 1970) but, in the face of selection, gene flow rates need to be much higher to preserve genetic uniformity. A cline (a gradient in character across a geographical region) can arise through selection whether or not there is gene flow. The interaction between gene flow and selection in moulding clinal variation in a continuously distributed population is now fairly well understood (Nagylaki 1965; Endler 1973, 1977; Slatkin 1973, 1975; May *et*

al. 1975). If the average distance of migration (gene flow rate) is long (compared with the distance over which the selection pressure difference in the environment is operative), gene flow will tend to swamp the effects of selection and so clinal variation (primary intergradation) will be gradual. However, if the gene flow rate is relatively weak compared with the selection gradient, gene (allele) frequencies and associated character states may change abruptly whether or not the environment changes sharply, so forming a stepped cline.

Barrowclough (1980a, 1980b) investigated gene flow in avian populations. Dispersal distances varied from about 340 to 1700 m per y in most continuously distributed populations; effective populations sizes (breeding individuals per deme) varied from 175 to 7700, which was considered relatively large; and genic variation between populations was very small. Barrowclough & Shields (1984) used chromosomal variation to verify the effective population size in birds. Pronounced clinal divergence in the form of a stepped cline is unlikely in such almost panmictic populations unless selection is extremely potent.

As demonstrated experimentally (Endler 1973, 1977), stepped clines may simply involve a selective gradient acting on a single diallelic locus even in circumstances where there is gene flow. Steepening occurs because on one side of a critical or threshold point in the environment one homozygote is favoured while the other homozygote is favoured on the other side. Further steepening may be effected by the pleiotropic action of modifier genes. However, though stepped clines involving a single character or gene locus may be primary or secondary, the concordance of several stepped clines involving unlinked loci or independent characters appears to be *prima facie* evidence for secondary hybridisation (Futuyma & Mayer 1980; Ford 1982b, 1985a; Barton 1983).

Barton & Hewitt (1981, 1985) considered ways by which primary clines could become concordant. Independent clines could accumulate where there is a density trough, for this would tend to prevent further shifting. Clines would also tend to form together if the genome is well co-adapted, especially if the relevant loci are linked or are responding to the same environmental selection. Also, if the initial cline retards gene flow across a critical region, new incompatible differences may tend to accumulate in the same region. Impedence to gene exchange by a set of coincident clines may promote further divergence involving weakly selected genes (Barton 1983; Barton & Hewitt 1985). It seems, however, that the genetic population structure of birds is not conducive to parapatric divergence and parapatric speciation (Templeton 1980, 1981; Barrowclough 1983). Stepped clinal differentiation is more probable in species fragmented into small semi-isolated demes (Wright 1978) than in those having an integrated population structure.

The development of complex zones of intergradation in Australian birds has not been explained in terms of the parapatric or clinal model (Keast 1961; Ford 1974a, 1985a) except for two examples. First, Hughes (1982) suggested that the hybrid zone between the magpies *Gymnorhina tibicen* and *G. t. leuconota* in south-eastern Australia was a primary cline involving two morphs, though previously Burton & Martin (1976) considered it originated by secondary contact. These magpies differ mainly in back colour, male *leuconota* being completely white on the back and *tibicen* having a black mantle, and Hughes (1982) gave a plausible explanation for this in terms of two diallelic loci on different autosomal chromosomes, with alleles coding for black dominant over white. Nevertheless, because two unlinked loci are involved, and these presumably arose by duplication in one chromosome and subsequent relocation by chromosomal rearrangement, the hybrid zone appears to represent secondary hybridisation. Secondly, intergrades between the miners *Manorina melanotis* and *M. flavigula* in south-eastern South Australia led H. Ford (1981) to suspect that these forms were simply clinal variants, although Serventy (1953) had previously suggested that they had evolved allopatrically. New evidence (Schodde 1981; Joseph 1986) indicates that they were formerly isolated by unsuitable terrain and that widespread clearing has facilitated genetic swamping of *melanotis* by the advancing *flavigula*, which favours more open woodland.

The existence of steep zones of intergradation between strikingly different subspecies of birds on small oceanic islands could be construed as strong evidence for parapatric differentiation. Pratt (1980) has described intra-island variation in the monarchine flycatcher *Chasiempis sandwichensis* on Hawaii. This species exhibits an unusually high degree of colour variation on this island of 10 458 km² but not on nearby Kauai and Oahu where it also occurs. There are three main geographic forms on Hawaii and these are connected by very steep zones of intergradation. The flycatcher does not disperse much and presumably has undergone local adaptation to factors involving thermoregulation and concealment against predators. Another interesting case concerns the White-eye *Zosterops borbonica* on Reunion Island (Gill 1973), which has an area of only 2590 km². This White-eye has steep clines in colour morph frequencies and geographical differentiates are quite distinct. Both Reunion and Hawaii have a range of environmental extremes and diverse habitats produced by mountainous terrain and climate diversity. In the case of *Z. borbonica*, Gill (1973) postulated that these conditions led to isolation of populations and to their subsequent differentiation, the present-day patterns representing mainly secondary contacts following destruction of much of the original vegetation by man over the last 250 years. In *C. sandwichensis*, however, Pratt (1980) considered that intergradation was a primary phenomenon but the possibility of it being secondary cannot be dismissed because lava extrusions have repeatedly broken up forest habitats on

Hawaii. Another possible example is the hummingbird *Trochilus polytmus* on Jamaica (11 784 km²) (Gill *et al.* 1973) but this has been disputed by Schuchmann (1978) who considered it actually consists of two species that diverged in allopatry. On the island of Grenada, the Bananaquit *Coereba flaveola* exhibits a cline in two colour morphs (yellow and black) but the yellow morph apparently emigrated from a nearby island (Wunderle 1981). Thus, in all cases of strong intro-differentiation in birds on small islands, evidence for a parapatric mode is, at the most, equivocal.

Though hybrid zones between different karyotypic populations are well known in various animal and plant groups (e.g. morabine grasshoppers *Morabinae*, pocket gophers *Thomomys* and some lizards) none are known in Australian birds. Chromosomal rearrangements may impart post-mating isolation by disturbing chromosomal pairing and segregation during meiosis but there is no evidence that such chromosomal variation in birds is a cause of divergence (Shields 1982) or indeed a cause of exomorphological differences (Lande 1979). Karyotypic changes that are partly or fully heterotically deleterious are only likely to become fixed in an avian population by drift in a peripatric population (Lande 1979; Slatkin 1981). Consequently, hybrid zones maintained by negative heterosis between chromosomally distinct avian populations would arise by secondary contact.

Because there is no substantial evidence that hybrid zones in birds arise from other than secondary contact, in the following sections the view is accepted that hybrid zones represent secondary contacts. A curious aspect regarding theoretical assertions to the contrary is the general treatment of individuals in populations as simply consisting of a collection of genes and as having no behaviour. Birds are fairly complex creatures with a repertoire of traits that include recognition and signalling systems. The contention that hybrid zones may arise *in situ* is tantamount to displacement or reinforcement in recognition signals (whether or not they are morphological or behavioural), but conclusive experimental and observational evidence for this is lacking (Moore 1957; Paterson 1978, 1981, 1982; Lambert *et al.* 1984).

Stability of hybrid zones

On the basis that steep hybrid zones in birds generally arise through secondary contact between vicariants, there are three principal explanations for their existence and characteristics: (1) the ephemeral-zone hypothesis (Sibley 1957, 1961; Corbin & Sibley 1977); (2) the dynamic-balance or stable-zone hypothesis (Mayr 1963; Bigelow 1965); and (3) the ecotone superiority hypothesis (Moore 1977). According to the first explanation, hybridisation leads either to the development of anti-hybridisation mechanisms as specific-mate recognition signals are reinforced

(Remington 1968) or to complete intergradation as gene exchange proceeds between the two populations (Fig. 1). This hypothesis would be supported if the hybrid gradient steepened or lessened over a period of time. The idea that isolating mechanisms acquired in allopatry may be reinforced or perfected through selection against hybrids is an appealing notion. In fact Rohwer (1972), Ayala (1975) and Bush (1975, 1981) apparently believed that reinforcement forms part of the basic framework of the allopatric mode of speciation but they ignored the implications of negative heterosis (Paterson 1978; Harper & Lambert 1983) and that complete reproductive isolation can be achieved in allopatry.

Evidence for reinforcement of premating isolation (or reproductive character displacement) is weak (Grant 1972, 1975; Paterson 1978, 1982; Slatkin 1980) and there is no substantiated example based on quantitative data in the Australian avifauna (*pace* Schodde 1981, p. 406). Presumed instances of reproductive character enhancement in birds are apparently misinterpretations of interspecific hybridisation induced by restricted mate choice when a species expands into a region occupied by a close relative; for the incidence of interbreeding often declines as the population of the invader increases. The example of apparent reinforcement between the western and eastern subspecies of the North American oriole *Icterus galbula* reported by Corbin & Sibley (1977) and Corbin & Ferguson (1979) was not confirmed by later work in a nearby region (Rising 1983). If two parapatric forms are effectively isolated by post-mating barriers, it seems reasonable that premating isolation may strengthen simply as a result of divergence between the two populations because of differential selection (Ford 1974a). As demonstrated by Paterson (1982) and Lambert *et al.* (1984) and initially noticed by Bigelow (1965), antihybridisation mechanisms are unlikely to evolve in a narrow hybrid zone because of the swamping effect of dispersal from the non-overlapping areas. Rather, as emphasised by Paterson (1978, 1981, 1982), if hybrids were less fit than parental forms, the cause of the reduced fitness would be eliminated by natural selection. If reinforcement does not occur, then neither does parapatric speciation.

The second concept of hybrid zones is that there is a dynamic balance between gene flow (from the allopatric portions of the ranges of the parental forms into the hybrid zone) and elimination of hybrids because of their relative unfitness caused by disharmonious gene combinations (i.e. intrinsic selection) (Mayr 1963, p. 378). The width of the hybrid zone depends on the degree of maladaptiveness of the hybrids (Barton & Hewitt 1981). In the absence of extrinsic selection, such a hybrid zone would move towards the less vagile or less numerous parental form until trapped by a region of low population density (Moore & Buchanan 1985). Hybrid zones maintained in a state of equilibrium by the opposing forces of gene flow and intrinsic selection

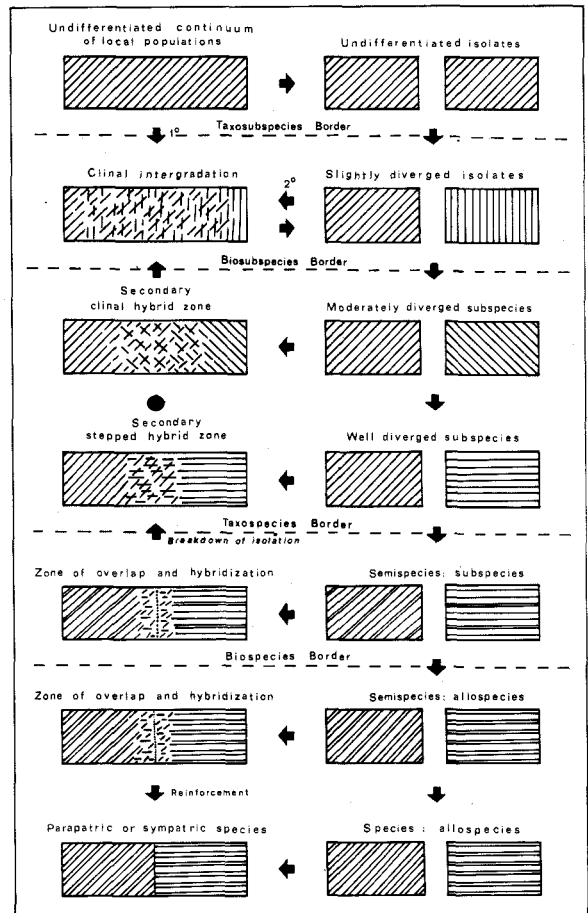


FIGURE 1 Sequential stages in parapatric and allopatric divergence of vicariant populations, and processes involved in clinal intergradation, hybrid-zone formation, reinforcement of mate-recognition signals, and speciation in birds. Arrows indicate pathways. (Modified from Ford 1974a.)

act as hybrid sinks and so should be expected to occur in regions of low density (Barton 1980; Barton & Hewitt 1981). The idea of such hybrid zones arising from an interaction between two homeostatically balanced epigenetic systems is somewhat negated by the fact that breeding experiments suggest that stabilising selection is the main mode of preserving phenotypic uniformity (Lande 1980). Nevertheless, if the hybrids are completely infertile and reinforcement is an unlikely event, hybridisation may persist.

Thirdly, hybrid zones coinciding with an ecotone between contiguous habitats could conceivably be maintained by the adaptive superiority of hybrids (heterozygotes) in the intermediate habitat (Moore 1977). According to this concept, hybrids are not favoured outside the intermediate

habitat. A hybrid zone maintained by ecotonal superiority is unlikely to steepen, flatten or shift unless climatic changes alter the ecotone.

Past climates, refuge areas and barriers

Pleistocene climates in Australia were reviewed by Bowler *et al.* (1976), Rognan & Williams (1977), Galloway & Kemp (1981, 1984) and Kershaw (1981, 1985). It is now generally accepted that there were arid to pluvial oscillations, and aridity rather than pluviality correlates with glaciation (Galloway 1965; Bowler 1976, 1982). Because a concentric zonation of climatic regions pervaded the Australian continent from about 2.5 million years BP (before present), the amplitude of successive climatic cycles has progressively increased and the last glacio-aridity of 25 000 to 15 000 y BP was the severest (Bowler 1975, 1976, 1982). At the peak of this aridity, which occurred towards the end of the last glaciation, increased continentality brought about by lower sea-levels was characterised by simultaneous activity of sief (longitudinal), parabolic and lunette dunes, and widespread dessication of lakes in the present semi-arid zone as well as in the arid zone (Fig. 2). Dramatic evidence for a greatly expanded arid core during the last phase of low sea-level is provided by the occurrence of inundated sief dunes in Spencer Gulf, King Sound, Exmouth Gulf and off the North-West shelf (Fairbridge 1961; Jessup 1968; Jennings 1975; Wyrwoll 1979) and the now stabilised systems south to Esperance, the 90-Mile Plain and Kangaroo Island (Beard 1982; Bowler 1982) and north to at least Newcastle Waters. Associated with these cyclic changes in climate were changes of great magnitude in the vegetation systems (Singh 1981). The severity of the last arid period obliterated earlier distribution patterns, e.g. the extinction of the formerly widely distributed Tasmanian Native-hen *Gallinula mortierii* on mainland Australia (Baird 1984).

Range contractions (causing isolation of and facilitating divergence between populations) and expansions (leading to secondary contacts) would have been cyclically induced by the climatic oscillations. Contractions would have been towards refuge areas. Keast (1961) postulated that the major refuges in Australia during long-term phases of aridity coincided with present-day regions of high rainfall around the continental periphery and the uplands in the centre (Fig. 3). Geographical barriers between refuge areas were inhospitable or low rainfall salients with open vegetation stretching from the continental interior to the coast, especially where the ocean projected inland as a large gulf (e.g. Spencer Gulf, Gulf of Carpentaria). Keast recognised eight major and several minor coastal centres of isolation and these were reconstructed according to the present coastline. During the past periods of prolonged glacio-aridity, the coastal configuration was quite unlike the present, for Australia was broadly joined to New Guinea and Tasmania. The significance of lower sea levels on the nature of geographical barriers has received little attention.

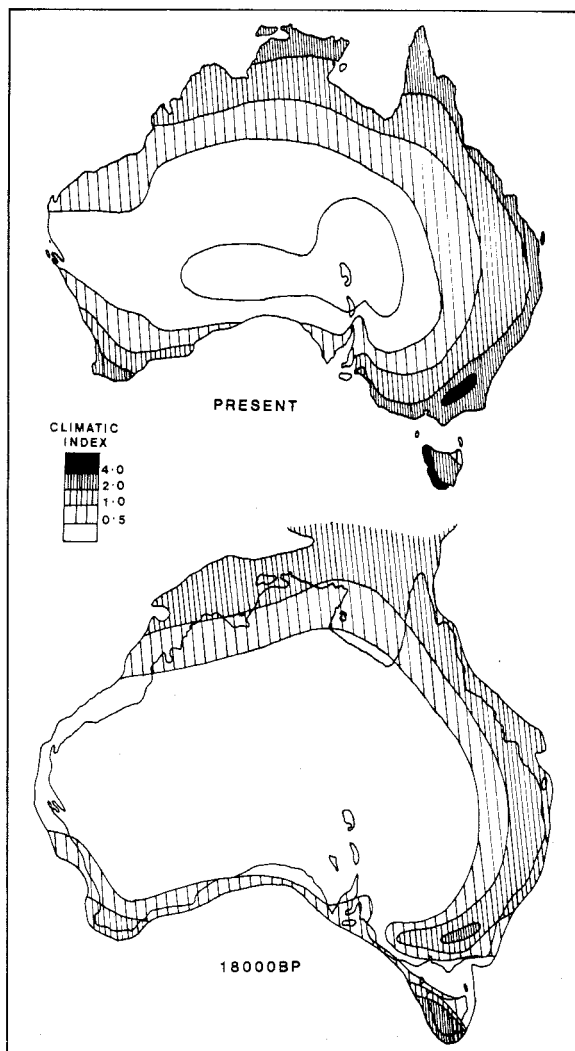


FIGURE 2 Hydrologic zonation of Australia at present and at the glacial maximum using the climatic index of Prescott based on precipitation and evaporation ratios ($I = P/E^{0.7}$). (Modified from Nix & Kalma [1972] and Bowler [1982]).

Figure 4 illustrates the positions of major geographic barriers during the peak of the aridity of around 17 000 y BP. The positions of these barriers are approximately the same as those postulated on the basis of the present Australian coastline but the Eyrean and Carpentarian barriers have markedly altered. In glacio-arid times, when the Nullarbor Plain was presumably more inhospitable than now, an extensive coastal plain vegetated with mallee projected south of the Nullarbor cliffs between Eyre Peninsula and south-western Australia (Parsons 1968, 1970; Ford 1971b; Nelson 1981), and possibly into the latitudes of rain-bearing

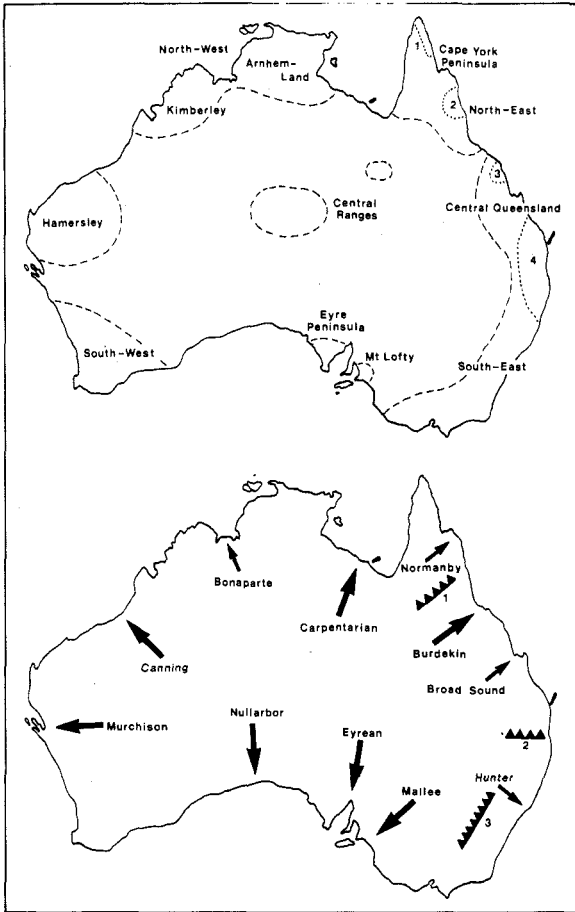


FIGURE 3 Refuge areas and geographic barriers. In the top map, numbers 1 to 4 denote rain-forest refuges. In the lower map, 1 to 3 indicate highland barriers: Burdekin-Lynd Divide, McPherson Range and Blue Mountains to Snowy Mountains chain (Ford [1986] modified from Keast [1961]).

Island) coalesced into a single refuge of greatly reduced size. If faunal connections were possible to the west of this palaeo-refuge, they may not have been so to the east because dune fields in extreme arid times were simultaneously active all the way from the Simpson Desert, through the Eyre and Frome basins and Ninety-Mile Plain to the north-western fringe of the Bassian Plain. Elsewhere on the Bassian Plain, there was predominantly an open vegetation of grassland-shrubland (Hope 1984). Thus, one arm of the Eyrean Barrier actually incorporated the Mallee Barrier and extended to the Bassian Plain. The concept and name of the Eyrean Barrier was first introduced by Ford & Parker (1974) and discussed by Ford (1974b) who indicated that it now consists of a dry salient stretching northward from Spencer Gulf, through the Lake Eyre Basin to and beyond Simpson Desert. Serventy (1953, 1972) believed that the barrier formerly involved in splitting semi-arid and arid faunal elements in this region was Lake Dieri, a greatly expanded Pleistocene Lake incorporating Lake Eyre and Lake Frome. However, the palaeo-Eyrean Barrier was an extremely formidable arid barrier and it is doubtful that this palaeo-lake would have been a significant barrier to birds.

Because the severest barrier for semi-arid avian populations in southern Australian during the peak of the last glaciation was on the eastern side of the Mt. Lofty-Kangaroo Island refuge, some western forms with hybrid zones in the region of the Ninety-Mile Plain may have had distributions extending all the way from south-western Aus-

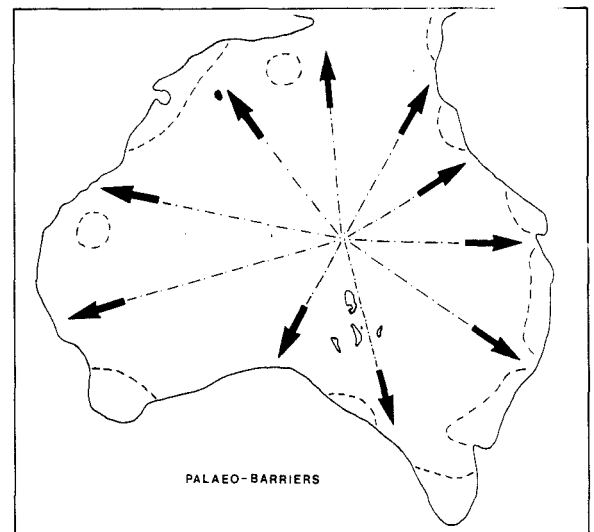


FIGURE 4 Radial pattern of major isolating barriers to birds at the peak of the last glaciation. Coastal refuges are enclosed by dashed lines. Note the amalgamation of refuges in South Australia, the alignment of the Eyrean barrier towards the Bassian Plain, and the changed nature of the Carpentarian Barrier.

ing fronts. Because large gulfs in the South Australian coast were then non-existent, faunal traffic of all least semi-arid avian elements may have been possible along the mallee corridor. Significantly, there are only two examples of subspeciation in mallee-heath inhabitants on opposite sides of the Nullarbor Plain (those between the whipbirds *Psophodes n. nigrogularis* and *P. n. leucogaster* and the emu-wrens *Stipiturus malachurus westernensis* and *S. m. intermedius*); all other mallee birds on Eyre Peninsula are subspecifically identical to those on the western side of this Plain (Ford 1971b), though subspecific identity in some cases may have arisen from an eastward recolonisation of Eyre Peninsula from the south-west refuge or vice versa. At the peak of the last glaciation, the refuges in South Australia (Eyre Peninsula, Yorke Peninsula, Mt. Lofty Range and Kangaroo

tralia, along the palaeo-Roe plain of the Great Australian Bight to the Mt. Lofty area. Consequently, when the eastern arm of the Eyrean Barrier (now the Mallee Barrier) ameliorated some 15 000 y BP, western populations like *Daphoenositta chrysoptera pileata*, *Pachycephala pectoralis fuliginosa* and *Pardalotus striatus substriatus* may have merely expanded eastward from the palaeo-South Australian refuge rather than all the way from west of the Nullarbor Plain as has been previously suggested. It should also be pointed out that wet-country avian populations isolated in the palaeo-South Australian refuge would have been more prone to extinction than those in the south-western and south-eastern refuges on account of its relatively small area. The taxonomic similarity of most wet-country avian populations in the Mt. Lofty refuge with those in eastern Australia may therefore be due to recolonisation during the minor pluvial of 8000 to 5000 y BP (Ford 1981).

Another barrier that underwent dramatic change was the Carpentarian, which now consists mainly of open grassland plains about the head of the Gulf of Carpentaria and, in the case of humid adapted species, the gulf itself. Prior to the Holocene transgression, the Gulf was mostly dry land and the Torres Strait bridge stretched continuously to New Guinea. Nevertheless, the whole region was fairly arid at 20 000-15 000 y BP (Fig. 2; Nix & Kalma 1972) and many north-western avian elements were probably displaced further westward than now, though there may have been some connections along the northern edge of the Torres bridge. In conclusion, therefore, the nature of barriers during the peak of the last aridity differed from those envisaged for the present climatic regime but the relative positions of barriers were approximately unchanged.

Avian hybrid zones in Australia

Figure 5 shows the positions of hybrid zones in Australia. Most coincide with the positions of past and present barriers (Appendix), which is suggestive of vicariant populations having expanded more or less equal distances from their

refugia. The greatest number of contacts coincide with the Carpentarian, Burdekin-Lynd, Burdekin, McPherson and Mallee barriers. Secondary contacts in lower south-west of Western Australia have been produced by a westward expansion of eastern vicariants, either from the south-eastern or palaeo-South Australian refuge (Keast 1961; Ford 1974b; Serventy & Whittell 1976), whereas many of the contacts in the eastern Mallee belt are due to eastward expansions of either south-western or palaeo-South Australian isolates (Keast 1961; Ford 1974b, 1986; Schodde 1981). In differential expansions, the drier adapted form has invariably dispersed the greater distance (e.g. the dry country forms *Daphoenositta chrysoptera pileata*, *D. c. leucoptera*, *Barnardius z. zonarius*, *Microeca leucophaea assimilis*). No random pattern is indicated, which would be the case if the majority of them arose by a parapatric or clinal mechanism.

The barriers with which the majority of hybrid zones coincide are still formidable barriers to many avian populations, especially humid-adapted ones. Table 1 summarises isolations and discontinuities between neighbouring coastal refuge areas. This table illustrates that there are many isolates in these refugia, which supports the concept that taxa involved in hybrid zones once had been confined to these refugia (*cf.* Endler 1982a,b).

Habitats of hybridising taxa are given in Table 2. By far the majority of taxa are woodland (semi-arid to sub-humid) inhabitants, and it is these taxa that have spread from their refuge areas since the climate improved around 12-15 000 y BP. This greater number is a function of three factors: woodland supports more avian species than any other habitat in Australia (Keast 1961); woodland habitats cover the greatest area in Australia (Keast 1961); and production of woodland inhabitants has been more prolific in Australia than for any other habitat type (Brereton & Kikkawa 1963). There are no hybrid zones between rainforest forms, reflecting the fact that tracts of rainforest and their avifaunal elements are generally separated by wide barriers. The reverse is true in New Guinea and the Amazonian basin.

TABLE 1 Isolation and discontinuities between neighbouring coastal refuge areas.

| Barrier | Vicariant isolates | | Allospecies | Non-vicariant isolates | | Total |
|-------------|--------------------|------------|-------------|------------------------|-----------|-------|
| | Undifferentiated | Subspecies | | Anti-clockwise | Clockwise | |
| Canning | 18 | 21 | 1 | 24 | 82 | 146 |
| Capentarian | 30 | 35 | 8 | 10 | 53 | 136 |
| Normanby | 9 | 18 | 9 | 18 | 37 | 91 |
| Burdekin | 21 | 15 | 5 | 23 | 5 | 69 |
| Mallee | 22 | 3 | 0 | 29 | 1 | 55 |
| Eyrean | 25 | 7 | 1 | 42 | 3 | 78 |
| Nullarbor | 40 | 15 | 1 | 17 | 9 | 82 |
| Murchison | 2 | 4 | 5 | 29 | 55 | 95 |

Anticlockwise non-vicars are populations occurring only on the anticlockwise side of the geographic barrier and *vice versa* for clockwise non-vicariants.

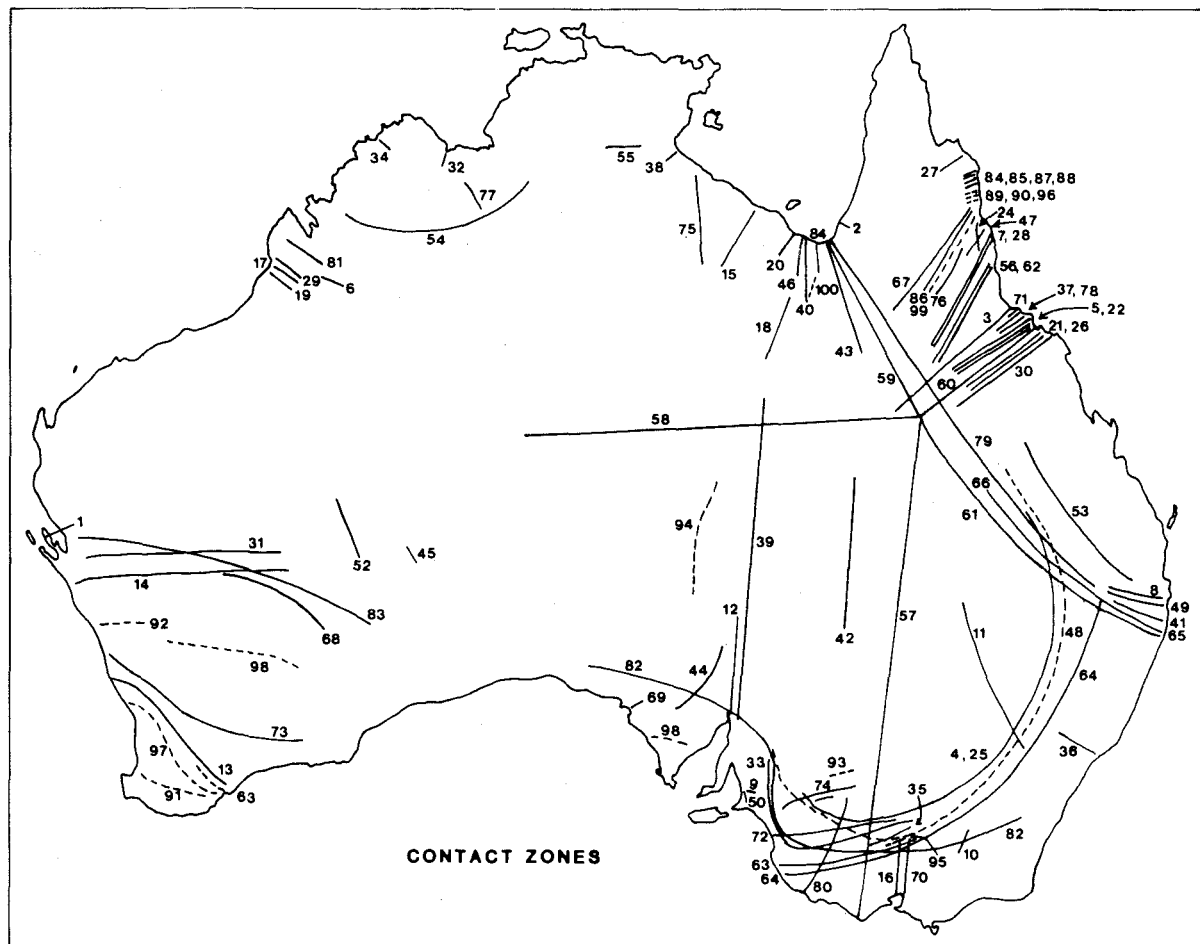


FIGURE 5 Hybrid zones and parapatric contact zones in Australian birds. Continuous lines denote the 50% transitions of hybrid zones between subspecies and dashed lines, parapatric contacts between allopecies. Hybrid zones: 1. *Haematopus f. fuliginosus* & *H. f. ophalmicus*, 2 *Butorides striatus stagnatilis* & *B. s. macrorhynchus*, 3 *Vanellus m. miles* & *V. m. novaehollandiae*, 4 *Falco b. berigora* & *F. b. occidentalis*, 5 *Petrophassa s. scripta* & *P. s. peninsulæ*, 6 *P. p. plumifera* & *P. p. ferruginea*, 7 *Platycercus a. adscitus* & *P. a. palliceps*, 8 *P. eximius* & *P. adscitus*, 9 *P. e. elegans* & *P. e. subadelaidae*, 10 *P. e. elegans* & *P. e. flaveolus*, 11 *Northiella haematogaster* & *N. h. haematorrhous*, 12 *Barnardius b. barnardi* & *B. b. zonarius*, 13 *B. b. zonarius* & *B. b. semitorquatus*, 14 *B. b. zonarius* & *B. b. occidentalis*, 15 *Calyptorhynchus m. magnificus* & *C. m. macrorhynchus*, 16 *C. f. funereus* & *C. f. xanthonotus*, 17 *Cacatua roseicapilla kuhli* & *C. r. assimilis*, 18 *C. s. sanguinea* & *C. s. gymnopsis*, 19 *C. s. sanguinea* & *C. s. westralensis*, 20 *C. g. galerita* & *C. g. fitzroyi*, 21 *Cuculus v. variolosus* & *C. v. dumetorum*, 22 *Centropus p. phasianinus* & *C. p. melanurus*, 23 *Chrysococcyx minutillus russatus* swarm 24 *Ninox novaeseelandiae* boobook & *N. n. lurida*, 25 *Podargus s. strigoides* & *P. s. brachypterus*, 26 *P. s. phalaenoides* & *P. s. strigoides*, 27 *Ceyx a. azurea* & *C. a. ruficollis*, 28 *Dacelo n. gigas* & *D. n. minor*, 29 *D. l. leachii* & *D. l. clifforti*, 30 *Coracina p. papuensis* & *C. p. stalkeri*, 31 *C. n. novaehollandiae* & *C. n. subpallida*, 32 *Microeca f. flavigaster* & *M. f. tormenti*, 33 *M. l. leucophaea* & *M. l. assimilis*, 34 *Pachycephala m. melanura* & *P. m. spinicauda*, 35 *P. p. pectoralis* & *P. p. fuliginosa*, 36 *P. p. pectoralis* & *P. p. ashbyi*, 37 *Colluricincla megarrhyncha rufogaster* & *C. m. "parvissima"*, 38 *C. m. parvula* and *C. m. rufogaster*, 39 *C. h. harmonica* & *C. h. rufiventris*, 40 *C. h. harmonica* & *C. h. brunnea*, 41 *Myiagra r. rubecula* & *M. r. yorki*, 42 *Cinclosoma c. cinnamomeum* & *C. c. castaneothorax*, 43 *Pomatostomus t. temporalis* & *P. t. rubecula*, 44 *Aphelocephala l. leucopsis* & *A. l. whitei*, 45 *A. l. whitei* & *A. l. castaneiventris*, 46 *Gerygone o. olivacea* & *G. o. rogersi*, 47 *G. palpebrosa personata* & *G. p. flava*, 48 *Acanthiza p. pusilla* & *A. p. apicalis*, 49 *Sericornis f. frontalis* & *S. f. laevigaster*, 50 *S. f. osculans* & *S. f. rosinae*, 51 *Sericornis f. fuliginosus* & *S. f. campestris*, 52 *Malurus s. splendens* & *M. s. callianus*, 53 *M. l. lambewri* & *M. l. assimilis*, 54 *M. l. assimilis* & *M. l. rogersi*, 55 *M. l. assimilis* & *M. l. dulcis*, 56 *M. m. melanoccephalus* & *M. m. cruentatus*, 57 *Daphoenositta c. chrysoptera* & *D. c. pileata*, 58 *D. c. pileata* & *D. c. leucoptera*, 59 *D. c. leucoptera* & *D. c. striata*, 60 *D. c. striata* & *D. c. leucocephala*, 61 *D. c. leucocephala* & *D. c. chrysoptera*, 62 *Climacteris p. picumnus* & *C. p. melanota*, 63 *Pardalotus punctatus* & *P. xanthopygus*, 64 *P. striatus ornatus* & *P. s. substriatus*, 64 *P. striatus ornatus* & *P. s. substriatus*, 65 *P. s. ornatus* & *P. s. melanoccephalus*, 66 *P. s. substriatus* & *P. s. substriatus* & *P. s. melanoccephalus*, 67 *P. s. melanoccephalus* & *P. s. uropygialis*, 68 *P. s. substriatus* and *P. s. murchisoni*, 69 *Zosterops lateralis gouldi* & *Z. l. halmaturina*, 70 *Z. l. halmaturina* & *Z. l. familiaris*, 71 *Lichenostomus v. versicolor* & *L. v. fasciularis*, 72 *L. l. leucotis* & *L. l. novaenoriae*, 73 *Manorina f. flavigula* & *M. f. obscura*, 74 *M. f. flavigula* & *M. f. melanotis*, 75 *Poephila b. bichenovii* & *P. b. annulosa*, 76 *P. c. cincta* & *P. c. atropygialis*, 77 *P. a. acticauda* & *P. a. hecki*, 78 *Sphecotheres viridis flaviventris* & *S. v. vielloti*, 79 *Artamus cinereus melanops* & *A. c. albiventris*, 80 *Strepera v. versicolor* & *S. v. melanoptera*, 81 *Cracticus n. nigrogularis* & *C. n. picata*, 82 *Gymnorhina t. tibicen* & *G. t. leuconota*, 83 *G. t. tibicen* & *G. t. dorsalis*, 84 *Chlamydera n. nuchalis* & *C. n. orientalis*. Some possible hybrid zones: 85 *Ninox c. connivens* & *N. c. galei*, 86 *Melithreptus g. gularis* & *M. g. laetior*, 87 *Emblema t. temporalis* & *E. t. minus*, 88 *Strepera g. graculina* & *S. g. magnirostris*. Some parapatric contacts: 89 *Turnix varia* & *T. olivii*, 90 *Alectura l. lathamii* & *A. l. purpureicollis*, 91 *Calyptorhynchus funereus latirostris* & *C. b. baudinii*, 92 *Cacatua sanguinea* & *C. pastinator*, 93 *C. sanguinea* & *C. tenuirostris*, 94 *Psophodes cristatus* & *P. occidentalis*, 95 *Sericornis cautus* & *S. pyrrhopygius*, 96 *Sericornis beccarii* & *S. magnirostris*, 97 *Malurus elegans* & *M. pulcherrimus*, 98 *M. lamberti assimilis* & *M. pulcherrimus*, 99 *Lichenostomus fuscus* & *L. flavescens*, 100 *Poephila acuticauda* & *P. cincta*.

Several hybrid zones and secondary contacts involving vicariant pairs in forest and woodland/mallee respectively occur in south-eastern Australia where the mallee and open woodlands adjoin forests on the inland margin of the Great Dividing Range (e.g. that between the south-eastern *Pachycephala p. pectoralis* and the western *P. p. fuliginosa*). A similar set occurs in south-western Australia (e.g. that between the forest-dwelling *Barnardius z. semitorquatus* and the woodland inhabiting *B. z. zonarius*).

Endler (1982a, 1982b) made two predictions concerning hybrid zones that originate by populations rejoining after expanding across barriers from former refugia: contact zones should be concentrated between rather than in the former refugia; and the widths of contact zones should be broader the greater the dispersal rate of the species. The first prediction is satisfied for hybrid zones in Australian birds. The second prediction is harder to test.

Most vicariant pairs of hybridising taxa in Australia were presumably isolated by the last severe arid period, especially between 18 000 to 16 000 y BP. Isolation would have diminished as the climate improved thereafter, especially during the minor pluvial of the period 8000-5000 y BP. The time since secondary contact for species breeding in their post-juvenile year may be calculated from the equation $T = (W/1.68D)^2$ (Endler 1977) where W is the cline width for an adaptively neutral locus measured between phenotypic values of 20% and 80% of the pure forms, D is the root-mean-square dispersal (gene-flow) distance and T is the number of generations since secondary contact. Unfortunately there is little information on average dispersal distances in Australian birds but Barrowclough (1980a, 1980b) has suggested this is about 1 km/y in passerine birds of temperate climatic regions. Using these data, Ford (1982b) indicated that the time of secondary contact between the yellow-breasted and grey-breasted figbirds *Sphecotheres viridis* in the Burdekin region of coastal Queensland

accords well with the estimated time of breakdown of this barrier to sub-humid zone birds. Using the same data on the depth of the hybrid zone between the white-backed and black-backed magpies *Gymnorhina tibicen* in south-eastern Australia (Burton & Martin 1976), a contact age of 8000 y is obtained. For the hybridisation between the white-vented and black-vented forms of the Black-faced Woodswallow *Artamus cinereus* along the spine of the Great Dividing Range in north-eastern Australia (Ford 1978d), a time of 28 000 y is obtained but the mean dispersal distance in this species is probably in excess of 1 km/y. Unfortunately, widths of hybrid zones over the 20%-80% transition between parental phenotypes have seldom been determined in Australia, so more effort should be expended towards this need. Bird-banders could also direct more attention to determining average dispersal rates rather than to novel or extraordinary values. Notwithstanding the paucity of accurate estimates of secondary contact times, the vast majority of hybrid zones appear to be quite old, yet probably not older than the last glacial arid period.

The persistence of hybrid zones in birds for very long periods has previously been noted (Short 1969, 1972; Selander 1971). A similar phenomenon is being found in other groups. Key (1981) gave a very good example in the morabine grasshopper *Vandiemenella*, which has a disjunct hybrid (tension) zone between two chromosomal races on Kangaroo Island and the opposite mainland. The break in the hybrid zone coincides with Backstairs Passage, which formed about 10 000 y BP when the island became separated by the post-glacial transgression in sea level. The long duration of hybrid zones could be viewed as a state of suspended evolution and may provide support for the Stationary Model of phenotypic evolution (i.e. evolutionary changes are promoted by abiotic changes whereas evolutionary stasis reigns during periods of environmental stability) (Strenseth & Maynard Smith 1984).

As judged on the age of hybrid zones in Australian birds, there appears to be no evidence that differences in specific-mate recognition signals (visual and acoustic characters) have been reinforced since secondary contact in hybridising taxa. In fact, persistence of hybridisation indicates that critical distinctions in signalling systems are quite lacking despite apparently strong morphological differences between many hybridising taxa.

Hybrid zones of long duration are not in accord with the ephemeral-zone hypothesis, which predicts either complete and gradual blending of the taxa or reinforcement of differences leading to full speciation. However, because the rate of introgression may be slow (Barrowclough 1980b), an ephemeral existence of a hybrid zone is still tenable relative to geological time. The widths of hybrid zones in Australian birds appear to support the contention that the spread of alleles between hybridising taxa entails a fairly long time, for the widths are in accord with predictions

TABLE 2 Habitats of hybridising taxa in Australia.

| Habitats | Number of hybrid zones |
|-----------------------------|------------------------|
| Mangal | 4 |
| Mangal/woodland | 1 |
| Gallery forest and woodland | 7 |
| Eucalypt forest | 9 |
| Forest/woodland | 9 |
| Forest/mallee | 6 |
| Woodland | 40 |
| Savanna grassland | 5 |
| Woodland/mallee | 1 |
| Mulga | 2 |
| Mulga/steppe | 1 |
| Swamp grassland | 1 |
| Coastline littoral | 1 |
| Total | 87 |

based on cline theory. Therefore, ephemerality should not be interpreted as an instantaneous process.

Several hybrid zones apparently coincide with ecotonal belts, especially those on the inland margin of the Great Dividing Range and where mallee vegetation meets sclerophyll woodland/forest in south-eastern Australia. Generally, hybrid zones in western Victoria have been poorly sampled and the opportunity to investigate them in their undisturbed condition has been missed. Keast (1973) drew attention to the poor avian collections from the mallee areas of western New South Wales, Victoria and South Australia, especially along transects where this habitat is contiguous with forest formations. Ford (1974c) suggested that hybrids between the quail-thrushes *Cinlosoma cinnamomeum* and *C. castaneothorax* in the Beal Range, Queensland, were favoured in a bridging habitat between shrub steppe and mulga scrub, but this hybridisation may be an example of marginal overlap with occasional hybridisation (Ford 1983a). Hybrid zones between the dry inland and humid coastal pairs of the pardalote *Pardalotus striatus substriatus*—*P. s. ornatus* and *P. s. substriatus*—*P. s. melanocephalus*, the fairy-wrens *Malurus l. assimilis*—*M. l. lamberti*, the woodswallows *Artamus cinereus melanops*—*A. c. albiventris*, the magpies *Gymnorhina t. tibicen*—*G. t. leuconota*, and others, generally extend well beyond ecotonal belts. Curiously, no hybrid zone coincides with the extensive ecotonal formations lying along the mulga-eucalypt line in Western Australia, but perhaps they would only be expected if divergence were parapatric.

Shifts in the position but not in the widths of hybrid zones has been construed as evidence for the dynamic-equilibrium hypothesis (Moore & Buchanan 1985), for such hybrid zones tend to move by an imbalance in dispersal rates (population density) to a region of low density. Changes in hybrid zones in Australian birds have not been closely monitored and any changes that have occurred are associated with clearing and opening-up of habitats. Thus, in south-western Australia, phenotypes associated with the dry-country Ringneck *Barnardius z. zonarius* have spread into the range of the forest inhabitant *B. z. semitorquatus* as forests and woodlands have been replaced by farmlands since settlement by Europeans. In the south-eastern Australian mallee, the miner *Manorina (flavigula) melanotis* is being genetically overwhelmed by the open-country form *M. (f.) flavigula* (Schodde 1981; Joseph 1986). The hybrid interaction between the lapwings *Vanellus m. miles* and *V. m. novaehollandiae* and that between semispecific parrots *Platycercus adscitus palliceps* and *P. eximius splendidus* have broadened in the wake of clearing (Storr 1973).

Possibly the most interesting example of hybridisation in the Australian avifauna is that in the Varied Sittella *Daphoenositta chrysoptera* complex, which consists of five well-differentiated subspecies that have secondarily expanded from peripheral refugia (Mayr 1950; Keast 1961; Ford

1980a; Short *et al.* 1983a). A series of hybrid zones between contiguous forms meet in central Queensland where there is a complex swarm of hybrids (Ford 1980a, b; Fig. 2). Curiously, the characters of some subspecies are often a combination of its two contiguously nearest subspecies, a phenomenon suggestive of past cycles of junction and disjunction (Mayr 1950; Short *et al.* 1983a). Other examples of this phenomenon are found in *Cracticus torquatus latens*, which has a partial black bib as in southern-western population of *C. t. torquatus*; and *Platycercus eximius splendidus*, which has yellow on the mantle as in *P. adscitus palliceps*. Before the arid phase of 18 000–15 000 y BP, there was a pluvial phase across southern Australia during 30 000–40 000 y BP (Bowler *et al.* 1976; Bowler 1982) but apparently not in northern Australia (Rognon & Williams 1977; Galloway & Kemp 1984; Kershaw 1985; *pace* Bowler 1982). The last synchronous expansion of humid zones in northern and southern Australia was possibly 80 000–120 000 y BP. Despite these apparent cycles of geographical isolation of the various subspecies of *D. chrysoptera* and the pronounced morphological differentiation, their calls and behavioural mannerisms have remained remarkably alike.

Hybridisation between rejoined populations occurs when recognition signals have not significantly diverged. It is possible that some avian groups tolerate more divergence

TABLE 3 Hybrid zones in the Australian avifauna.

| Family | Hybrid zones | Breeding species |
|-------------------|--------------|------------------|
| Oystercatchers | 1 | 2 |
| Lapwings | 1 | 2 |
| Hérons | 1 | 16 |
| Falcons and Hawks | 1 | 24 |
| Pigeons | 3 | 21 |
| Parrots | 13 | 55 |
| Cuckoos | 4 | 13 |
| Owls | 0-4 | 8 |
| Frogmouths | 2-3 | 3 |
| Kingfishers | 3 | 10 |
| Campephagids | 2 | 7 |
| Pachycephalids | 9 | 34 |
| Monarchs | 1 | 12 |
| Pseudobabblers | 1-2 | 14 |
| Acanthizids | 6 | 36 |
| Malurids | 5 | 18 |
| Sittellas | 5 | 1 |
| Treecreepers | 1 | 6 |
| Pardalotes | 6 | 5 |
| Silvereyes | 2 | 3 |
| Honeyeaters | 3-4 | 69 |
| Estrildids | 2-3 | 21 |
| Orioles | 1 | 3 |
| Butcherbirds | 4 | 8 |
| Woodswallows | 1 | 6 |
| Bowerbirds | 1 | 10 |
| Total | 79-87 | 407 |

than others before recognition ceases. Table 3 summarises the incidence of hybrid zones in various groups. Most occur in parrots and passerines. Groups not included in the table do not have hybrid zones. Few hybrid zones occur in the honeyeaters despite the high number of species and geographical overlap or contact between related taxa. At the opposite extreme, there is only one sittella but it has five hybrid zones. Morphological differences between some allospecific honeyeaters are slight (e.g. *Lichenostomus fuscus* and *L. flavesceus*) and vocalisations are generally strongly different; in contrast morphological differences between hybridising subspecies in *Daphoenositta chrysop-tera* are strong and vocalisations are similar. Whether song (vocal signals) or plumage (visual signals) is generally a more critical factor in hybridisation cannot be ascertained from these data.

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References

- Ayala, F.J. (1975). Genetic differentiation during the speciation process. *Evol. Biol.* **8**, 1-75.
- Amadon, D. (1951). Taxonomic notes on the Australian butcher-birds (Family Cracticidae). *Am. Mus. Novit.* **1504**, 1-33.
- Ashby, E. (1922). The Dusky Miner (*Myzantha obscura*) Gould. *Emu* **21**, 252-256.
- Baird, R.F. (1984). The Pleistocene distribution of the Tasmanian Native-Hen *Gallinula mortierii mortierii*. *Emu* **84**, 19-123.
- Barrowclough, G.F. (1980a). Gene flow, effective population sizes, and genetic variance components in birds. *Evolution* **34**, 789-798.
- Barrowclough, G.F. (1980b). Genetic and phenotypic differentiation in a woodwarbler (Genus *Dendroica*) hybrid zone. *Auk* **97**, 655-668.
- Barrowclough, G.F. (1983). Biochemical studies of microevolutionary processes. In: *Perspectives in Ornithology* (eds A.H. Brush & G.A. Clark) pp. 223-261. Am. Ornith. Union, Cambridge, Mass.
- Barrowclough, G.F., & Shields, G.F. (1984). Karyotypic evolution and long-term effective population sizes of birds. *Auk* **101**, 99-102.
- Barton, N.H. (1980). The hybrid sink effect. *Heredity* **44**, 277-278.
- Barton, N.H. (1983). Multilocus clines. *Evolution* **47**, 454-471.
- Barton, N.H., & Hewitt, G.M. (1981). Hybrid zones and speciation. In: *Evolution and Speciation* (eds W.R. Atchley & D.S. Woodruff) pp. 109-145. Cambridge Univ. Press, Cambridge, London.
- Barton, N.H., & Hewitt, G.M. (1985). Analysis of hybrid zones. *Annu. Rev. Ecol. Syst.* **16**, 113-148.
- Beard, J.S. (1982). Late Pleistocene aridity and aeolian landforms in Western Australia. In: *Evolution of the Flora and Fauna of Australia* (eds W.R. Barker & P.J.M. Greenslade) pp. 101-106. Peacock Publs, Frewville, South Aust.
- Bigelow, R.S. (1965). Hybrid zones and reproductive isolation. *Evolution* **19**, 449-458.
- Black, A., & Ford, J. (1982). Magpies similar to the White-backed Magpie in inland Western Australia. *Corella* **6**, 114-118.
- Boehm, E.F. (1954). Status of the Yellow Rosella. *South Aust. Ornithol.* **21**, 28.
- Boles, W.E. (1979). Comments on *Sericornis beccarii* in southern Cape York Peninsula. *Sunbird* **10**, 70-72.
- Boles W.E. (1983). A taxonomic revision of the Brown Thornbill *Acanthiza pusilla* (Shaw) 1790 with description of a new subspecies. *Emu* **83**, 51-58.
- Bowler, J.M. (1976). Aridity in Australia: Age, origins and expression in aeolian landforms and sediments. *Earth-Sci. Rev.* **12**, 279-310.
- Bowler, J.M. (1982). Aridity in the late Tertiary and Quaternary of Australia. In: *Evolution of the Flora and Fauna of Arid Australia* (eds W.R. Barker & P.J.M. Greenslade) pp. 35-45. Peacock Publs, Frewville, South Aust.
- Bowler, J.M., Hope, G.S., Jennings, J.N., Singh, G. & Walker, D. (1976). Late Quaternary climates of Australia and New Guinea. *Quat. Res. (N.Y.)* **6**, 359-394.
- Brereton, J. le G. & Kikkawa, J. (1963). Diversity of avian species. *Aust. J. Sci.* **26**, 12-13.
- Brereton, J. le G. & Sourry, C. (1959). Some observations on the distributions and abundance of closely-related parrots of the New England District of New South Wales. *Emu* **59**, 93-100.
- Burton, T.C. & Martin, A.A. (1976). Analysis of hybridization between Black-backed and White-backed Magpies in south-eastern Australia. *Emu* **76**, 30-36.
- Bush, G.L. (1975). Modes of animal speciation. *Annu. Rev. Ecol. Syst.* **6**, 339-364.
- Bush, G.L. (1981). Stasipatric speciation and rapid evolution in animals. In: *Evolution and Speciation* (eds W.R. Atchley & D.S. Woodruff) pp. 201-218. Cambridge Univ. Press, Cambridge, London.
- Cain, A.J. (1955). A revision of *Trichoglossus haematodus* and of the Australian platycercine parrots. *Ibis* **97**, 432-479.
- Cain, A.J., & Currey, J.D. (1963). Area effects in *Cepaea*. *Phil. Trans. R. Soc. Lond., B. Biol. Sci.* **246**, 1-81.
- Cannon, C.E. (1983). Rosellas, *Platycercus* spp., and their hybrids in eastern Queensland-New South Wales border region. *Aust. Zool.* **21**, 175-184.
- Clarke, B. (1966). Evolution of morph-ratio clines. *Am. Nat.* **100**, 389-402.
- Condon, H.T. (1950). Variation in the Brown Hawk. *Emu* **50**, 152-174.
- Condon, H.T. (1954). Bird maps. *South Aust. Ornithol.* **21**, 40-44.
- Cooper, R.P. (1961). Field notes on the nesting of the Red-tipped Pardalote. *Emu* **61**, 1-6.
- Corbin, K.W. (1981). Genic heterozygosity in the White-crowned sparrow: a potential index to boundaries between subspecies. *Auk* **98**, 669-680.
- Corbin K.W., & Ferguson, A. (1979). Genic changes associated with establishment of sympatry in orioles of the genus *Icterus*. *Evolution* **53**, 624-633.
- Corbin K.W., & Sibley, C.G. (1977). Rapid evolution in the orioles of the genus *Icterus*. *Condor* **79**, 335-342.
- Courtney, J. (1986). Age-related colour changes and behaviour in the Northern Flunereal Black-cockatoo, *Calyptorhynchus f. funereus*. *Aust. Bird Watcher* **11**, 137-145.
- Crome, F.H.J. (1973). The relationship of the Helmeted and Yellow-tufted Honeyeaters. *Emu* **73**, 12-18.
- Crome, F.H.J., Carpenter, S.M. & Frith, H.J. (1980). Geographic variation and taxonomy of the Spinifex Pigeon, *Geophaps plumifera*. *Aust. J. Zool.* **28**, 135-150.
- Crow, J.F. & Kimura, K. (1970). *An Introduction to Population Genetics Theory*. Harper & Nelson, New York.

- Eddy, R.J. (1959). Heath-wrens in central Victoria. *Aust. Bird Watcher* **1**, 36-44.
- Endler, J.A. (1973). Gene flow and population divergence. *Science* **179**, 243-250.
- Endler, J.A. (1977). *Geographic Variation, Speciation and Clines*. Princeton Univ. Press, Princeton.
- Endler, J.A. (1982a). Problems in distinguishing historical from ecological factors in biogeography. *Am. Zool.* **2**, 441-452.
- Endler, J.A. (1982b). Pleistocene forest refuges: fact or fancy. In: *Biological Diversification in the Tropics*. (ed. G.T. Prance) pp. 641-657. Columbia Univ. Press, New York.
- Fairbridge, R.W. (1961). Eustatic changes in sea level. *Physics & Chemistry of Earth* **4**, 99-185.
- Fisher, D. (1970). *Geographic variation and evolution in the Australian Ringneck Parrot* (Barnardius). Ph.D. Thesis, Univ. Michigan, Michigan, U.S.A.
- Fjeldsa, J. (1983). Ecological character displacement and character release in grebes Podicipedidae. *Ibis* **125**, 463-481.
- Ford, H.A. (1981). A comment on the relationship between miners *Manorina* spp. in South Australia. *Emu* **81**, 247-250.
- Ford, J. (1966). Taxonomy and variation of the chestnut-shouldered wrens of Western Australia. *Emu* **66**, 47-57.
- Ford, J. (1970). Variation in the *Sericornis frontalis maculatus* subspecies group. *Emu* **70**, 168-172.
- Ford, J. (1971). Distribution, ecology and taxonomy of some Western Australian passerine birds. *Emu* **71**, 103-120.
- Ford, J. (1974a). Concepts of subspecies and hybrid zones and their applications in Australian ornithology. *Emu* **74**, 113-123.
- Ford, J. (1974b). Speciation in Australian birds adapted to arid habitats. *Emu* **74**, 161-168.
- Ford, J. (1974c). Taxonomic significance of some hybrid and aberrant-plumaged quail-thrushes. *Emu* **74**, 80-90.
- Ford, J. (1975a). Hybridization of Splendid and Turquoise Wrens. *Emu* **75**, 153-154.
- Ford, J. (1975b). Systematics and hybridization of figbirds *Sphecotheres*. *Emu* **75**, 163-171.
- Ford, J. (1977a). Conspecificity of the Black-throated and Fairy Warblers. *Emu* **77**, 75-79.
- Ford, J. (1977b). Area of origin of the Yellow Rosella. *Emu* **77**, 229-230.
- Ford, J. (1978a). Geographical isolation and morphological and habitat differentiation between birds of the Kimberley and Northern Territory. *Emu* **78**, 25-35.
- Ford, J. (1978b). Intergradation between the Varied and Mangrove Honeyeaters. *Emu* **78**, 71-74.
- Ford, J. (1978c). Subspeciation in the White-throated Warbler of Australia and New Guinea. *Emu* **78**, 90-92.
- Ford, J. (1978d). Hybridization between the white-vented and black-vented forms of the Black-faced Woodswallow. *Emu* **78**, 105-114.
- Ford, J. (1979a). Taxonomic status of some quail-thrushes. *Aust. Birds* **13**, 76-80.
- Ford, J. (1979b). Subspeciation, hybridization and relationships in the Little Shrike-thrush *Colluricincla megarhyncha* of Australia and New Guinea. *Emu* **79**, 195-210.
- Ford, J. (1980a). Hybridization between contiguous subspecies of the Varied Sittella. *Emu* **80**, 1-12.
- Ford, J. (1980b). Morphological and ecological divergence and convergence in isolated populations of the Red-tailed Black-Cockatoo. *Emu* **80**, 103-120.
- Ford, J. (1981). Geographical variation in *Cinclosoma castanotum* and its historical significance. *Emu* **81**, 185-192.
- Ford, J. (1982a). Hybridization and migration in Australian populations of the Little and Rufous-breasted Bronze-cuckoos. *Emu* **82**, 209-222.
- Ford, J. (1982b). Hybrid phenotypes in male Figbirds *Sphecotheres viridis* in Queensland. *Emu* **82**, 126-130.
- Ford, J. (1982c). Origin, evolution and speciation of birds specialized to mangroves in Australia. *Emu* **82**, 12-23.
- Ford, J. (1983a). Evolutionary and ecological relationships between quail-thrushes. *Emu* **83**, 152-172.
- Ford, J. (1983b). Taxonomic notes on some mangrove-inhabiting birds in Australasia. *Rec. West. Aust. Mus.* **10**, 381-415.
- Ford, J. (1985a). Secondary contact between subspecies of the White-browed Scrub-wren in eastern Australia. *Emu* **85**, 92-96.
- Ford, J. (1985b). Species limits and phylogenetic relationships in corellas of the *Cacatua pastinator* complex. *Emu* **85**, 163-180.
- Ford, J. (1986). Avian hybridization and allopatry in the region of the Einasleigh Uplands and Burdekin-Lynd Divide, north-eastern Queensland. *Emu* **86**, 87-110.
- Ford, J. & Parker, S.A. (1973). A second species of Wedgebill? *Emu* **73**, 113-118.
- Ford, J. & Parker, S.A. (1974). Distribution and taxonomy of some birds from south-western Queensland. *Emu* **74**, 177-194.
- Forshaw, J.M. (1981). *Australian Parrots*. Lansdowne, Melbourne.
- Futuyma, D.J. & Mayer, G.C. (1980). Non-allopatric speciation in animals. *Syst. Zool.* **29**, 254-271.
- Galbraith, I.C.J. (1956). Variation, relationships and evolution in the *Pachycephala pectoralis* superspecies (Aves, Muscicapidae). *Bull. Br. Mus. (nat. Hist.) Zool.* **4**, 133-222.
- Galbraith, I.C.J. (1969). The Papuan and Little Cuckoo-shrikes, *Coracina papuensis* and *robusta*, as races of a single species. *Emu* **69**, 9-29.
- Galbraith, I.C.J. (1974). Pachycephalidae. In: *Birds of the Harold Hall Australian Expeditions 1962-1970* (ed. B.P. Hall) pp. 244-265. Br. Mus. (nat. Hist.), London.
- Galloway, R.W. (1965). Late Quaternary climates in Australia. *J. Geol.* **73**, 603-618.
- Galloway, R.W. & Kemp, E.M. (1981). Late Cainozoic environments in Australia. In: *Ecological Biogeography of Australia* (ed. A. Keast) pp. 53-80. W. Junk, The Hague.
- Galloway, R.W. & Kemp, E.M. (1984). Late Cainozoic environments in Australia. In: *Vertebrate Zoogeography and Evolution in Australasia* (eds M. Archer & G. Clayton) pp. 83-95. Hesperian Press, Carlisle, W.A.
- Gentili, J. (1949). Foundations of Australian bird geography. *Emu* **49**, 85-129.
- Gill, F.B. (1973). Intra-island variation in the Mascarene White-eye *Zosterops borbonica*. *Am. Ornithol. Union Ornith. Monogr.* **12**.
- Gill, F.B., Stokes, F.J. & Stokes, C. (1973). Contact zones and hybridization in the Jamaican Hummingbird, *Trochilus polytmus* (L.). *Condor* **75**, 170-176.
- Grant, P.R. (1972). Convergent and divergent character displacement. *Biol. J. Linn. Soc.* **4**, 39-68.
- Grant, P.R. (1975). The classical case of character displacement. *Evol. Biol.* **8**, 237-337.
- Grosper, D.G. (1964). Pardalote hybrids. *Emu* **65**, 339-340.
- Hall, B.P. & Frith, C.B. (1974). Psittacidae. In: *Birds of the Harold Hall Australian Expeditions 1962-70*. (ed. B.P. Hall) pp. 97-118. Br. Mus. (nat. Hist.), London.
- Harper, A.A. & Lambert, D.M. (1983). The population genetics of reinforcing selection. *Genetica* **62**, 15-23.
- Harrison, C.J.O. (1970). The relationships of the Brown and Black-backed Treecreepers. *Emu* **70**, 9-11.
- Harrison, C.J.O. (1972). A re-examination of the chestnut-shouldered wren complex of Australia. *Bull. Br. Mus. (nat. Hist.) Zool.* **21**, 313-328.
- Harrison, C.J.O. (1974). Maluridae. In: *Birds of the Harold Hall Australian Expeditions 1962-1970* (ed. B.P. Hall) pp. 199-214. Br. Mus. (nat. Hist.), London.

- Hartert, E.J. (1927). Types of birds in the Tring Museum. *Novit. Zool.* **34**, 1-38.
- Hindwood, K. & Mayr, E. (1946). A revision of the stripe-crowned pardalotes. *Emu* **46**, 49-67.
- Hobbs, J.N. (1956). Yellow and Crimson Rosellas together at Tumut. *Emu* **56**, 212.
- Hobbs, J.N. (1958). Hybrid between Yellow and Crimson Rosella. *Emu* **58**, 418-419.
- Hope, J. (1984). The Australian Quaternary. In: *Vertebrate Zoogeography and Evolution in Australasia* (eds M. Archer & G. Clayton) pp. 69-81. Hesperian Press, Carlisle, W.A.
- Hughes, J.M. (1982). An explanation for the asymmetrical hybrid zone between White-backed and Black-backed Magpies. *Emu* **82**, 50-53.
- Immelmann, K. (1962). Besiedlungsgeschichte und bastardierung von *Lonchura castaneothorax* und *Lonchura flaviprymna* in Nordaustralien. *J. Ornithol.* **103**, 344-357.
- Immelmann, K. (1965). *Australian Finches in Bush and Aviary*. Angus & Robertson, Sydney.
- Jain, S.K. & Bradshaw, A.D. (1966). Evolutionary divergence among adjacent plant populations. *Heredity* **21**, 407-441.
- Jenning, J.N. (1975). Desert dunes and estuarine fill in the Fitzroy Estuary, north-western Australia. *Catena* **2**, 215-262.
- Jessup, R.W. (1968). Soil development in coastal South Australia in relation to glacio-eustatic changes of sea level. *Trans. 9th Int. Congr. Soil Sci.*, Adelaide, **4**, 641-649.
- Johnstone, R.E. (1981a). Notes on the distribution, ecology and taxonomy of the Partridge Pigeon (*Geophaps smithii*) and Spinifex Pigeon (*Geophaps plumifera*) in Western Australia. *Rec. West. Aust. Mus.* **9**, 49-64.
- Johnstone, R.E. (1981b). Notes on the distribution, ecology and taxonomy of the Red-crowned Pigeon and the Torres Strait Pigeon in Western Australia. *Rec. West. Aust. Mus.* **9**, 7-22.
- Johnstone, R.E. (1984). Intergradation between the Lemon-breasted Flycatcher and the Brown-tailed Flycatcher in Cambridge Gulf, Western Australia. *Rec. West. Aust. Mus.* **11**, 291-296.
- Jones, J. (1952). The Hattah Lakes Campout, October 1951. *Emu* **52**, 225-254.
- Joseph, L. (1986). The decline and present status of the Black-eared Miner in South Australia. *South Aust. Ornithol.* **30**, 5-13.
- Joseph, L. & Hope, R. (1984). Aspects of genetic relationships and variation in parrots of the Crimson Rosella *Platycercus elegans* complex. *Trans. R. Soc. South Aust.* **108**, 77-84.
- Keast, A. (1957a). Variation in the Australian whitefaces (Aves, genus *Aphelocephala*). *Proc. R. Soc. N.S.W.* 1955-56, 38-42.
- Keast, A. (1957b). Variation in the Australian kingfishers (Aves: Alcedinidae). *Rec. Aust. Mus.* **24**, 61-72.
- Keast, A. (1958a). Variation and speciation in the Australian Campephagidae (Passeres). *Aust. J. Zool.* **6**, 248-267.
- Keast, A. (1958b). Seasonal movements and geographic variation in the Australian Woodswallows (Artamidae). *Emu* **58**, 207-218.
- Keast, A. (1958c). Intraspecific variation in the Australian finches. *Emu* **58**, 219-246.
- Keast, A. (1958d). Variation and speciation in the Australian flycatchers. *Rec. Aust. Mus.* **24**, 73-108.
- Keast, A. (1961). Bird speciation on the Australian continent. *Bull. Mus. comp. Zool., Harv.* **123**, 305-495.
- Keast, A. (1973). The role of the museum in ornithology. *Emu* **73**, 242-247.
- Kershaw, A.P. (1981). Quaternary vegetation and environments. In: *Ecological Biogeography of Australia* (ed. A. Keast) pp. 83-101. W. Junk, The Hague.
- Kershaw, A.P. (1981). An extended Late Quaternary vegetation record from north-eastern Queensland and its implications for the seasonal tropics of Australia. *Proc. ecol. Soc. Aust.* **131**.
- Key, K.H.L. (1981). Species, parapatry and the morabine grasshoppers. *Syst. Zool.* **30**, 425-458.
- Lambert, D.M., Centner, M.R. & Paterson, H.E.H. (1984). Simulation of the conditions necessary for the evolution of species by reinforcement. *South Afr. J. Sci.* **80**, 308-311.
- Lande, R. (1979). Effective deme sizes during long-term evolution estimated from rates of chromosomal rearrangement. *Evolution* **33**, 234-251.
- Lande, R. (1980). Genetic variation and phenotypic evolution during allopatric speciation. *Am. Nat.* **116**, 463-479.
- Lendon, A.H. (1973). *Australian Parrots in Field and Aviary*. Angus & Robertson, Sydney.
- Littlejohn, M. (1981). Reproductive isolation: a critical review. In: *Evolution and Speciation* (eds W.R. Atchley & D.L. Woodruff) pp. 298-334. Cambridge Univ. Press, Cambridge.
- Lord, E.A.R. (1956). The birds of the Murphy's Creek district, southern Queensland. *Emu* **56**, 100-128.
- MacDonald, J.D. (1968). Speciation in the *Colluricincla harmonica* complex. *Emu* **67**, 215-223.
- MacDonald, J.D. (1968). Hybridization in *Pardalotus*. *Emu* **69**, 41-44.
- MacDonald, J.D. (1969b). Notes on the taxonomy of *Neositta*. *Emu* **69**, 169-174.
- McGill, A.R. (1970). *Australian Warblers*. Bird Observ. Club, Melbourne.
- Mack, G. (1934). A revision of the genus *Malurus*. *Mem. Nat. Mus. Victoria* **8**, 100-125.
- McKean, J.L. (1978). Some remarks on the taxonomy of Australasian oystercatchers, *Haematopus* spp. *Sunbird* **9**, 3-6.
- Mason, I.J. (1983). A new subspecies of Masked Owl *Tyto novaehollandiae* (Stephens) from southern New Guinea. *Bull. Brit. ornithol. Club* **103**, 123-128.
- Mason, I.J. & Schodde, R. (1980). Subspeciation in the Rufous Owl *Ninox rufa* (Gould). *Emu* **80**, 141-144.
- Mason, I.J., McKean, J.L. & Duszinski, M.L. (1984). Geographical variation in the Pheasant Coucal *Centropus phasianinus* (Latham) and a description of a new subspecies from Timor. *Emu* **84**, 1-15.
- May, R.M., Endler, J.A. & McMurtrie, R.E. (1975). Gene frequency clines in the presence of selection apposed by gene flow. *Am. Nat.* **109**, 659-676.
- Mayr, E. (1950). Taxonomic notes on the genus *Neositta*. *Emu* **49**, 282-291.
- Mayr, E. (1954). Notes on Australian whistlers (Aves, *Pachycephala*). *Am. Mus. Novit.* **1653**, 1-22.
- Mayr, E. (1963). *Animal Species and Evolution*. Harvard Univ. Press, Cambridge, Mass.
- Mayr, E. & Jennings, K. (1952). Geographic variation and plumages in Australian bowerbirds (Ptilonorhynchidae). *Am. Mus. Novit.* **(1602)**, 1-18.
- Mayr, E. & Serventy, D.L. (1938). A review of the genus *Acanthiza* Vigors & Horsfield. *Emu* **38**, 245-292.
- Mees, G.F. (1961). An annotated catalogue of a collection of bird skins from West Pilbara, Western Australia. *J. R. Soc. West. Aust.* **44**, 97-143.
- Mees, G.F. (1964a). Geographical variation and distribution of some birds from Western Australia. *J. R. Soc. West. Aust.* **47**, 91-96.
- Mees, G.F. (1964b). A revision of the Australian owls (Strigidae and Tytonidae). *Zool. Verh. (Leiden)* **65**, 1-62.
- Mees, G.F. (1965). The status of *Pardalotus ornatus* Temminck. *Emu* **65**, 97-102.
- Mees, G.F. (1969). A systematic review of the Indo-Australian Zosteropidae (Part III). *Zool. Verh. (Leiden)* **102**, 1-390.

- Meise, W. (1975). Natürliche bastardpopulationen und speziationsprobleme bei vogeln. *Abh. Verh. naturwiss. Ver. Hamb.* **18-19**, 187-254.
- Milne, M.V. (1936). Overlapping of certain Victorian birds. *Emu* **36**, 130-132.
- Moore, J.A. (1957). An embryologist's view of the species concept. In: *The Species Problem*. (ed. E. Mayr) pp. 325-338. AAAS, Washington, D.C.
- Moore, W.S. (1977). An evaluation of narrow hybrid zones in vertebrates. *Quart. Rev. Biol.* **52**, 263-277.
- Moore, W.S. & Buchanan, D.B. (1985). Stability of the northern flicker hybrid zone in historical times: implications for adaptive speciation theory. *Evolution* **39**, 135-151.
- Nagylaki, T. (1965). Conditions for existence of clines. *Genetics* **80**, 595-615.
- Nelson, E.C. (1981). Phytogeography of southern Australia. In: *Ecological Biogeography of Australia* (ed. A. Keast) pp. 733-759, W. Junk, The Hague.
- Nix, H. & Kalma, J.D. (1972). Climate as a dominant control in the biogeography of northern Australia and New Guinea. In: *Bridge and Barrier. The Natural and Cultural History of Torres Strait* (ed. D. Walker) pp. 61-91. Aust. Nat. Univ., Canberra.
- Parker, S.A. (1970). Critical notes on the status of some Northern Territory birds. *South Aust. Ornithol.* **25**, 115-125.
- Parker, S.A. & Eckert, H.J. (1983). Remarks on the taxonomy of the genus *Calamanthus* (Field-wrens). *South Aust. Ornithol.* **29**, 65-71.
- Parker, S.A. & Reid, N.C.H. (1983). Birds [of south-eastern South Australia]. In: *Natural History of the South East*, pp. 135-150. R. Soc. South Aust., Adelaide.
- Parsons, R.F. (1969). Distribution and palaeogeography of two mallee species of *Eucalyptus* in southern Australia. *Aust. J. Bot.* **17**, 323-330.
- Parsons, R.F. (1970). Mallee vegetation of the southern Nullarbor and Roe Plains, Australia. *Trans. R. Soc. South Aust.* **94**, 227-242.
- Paterson, H.E.H. (1978). More evidence against speciation by reinforcement. *South Afr. J. Sci.* **74**, 369-371.
- Paterson, H.E.H. (1981). The continuing search for the unknown and unknowable: a critique of contemporary ideas on speciation. *South Afr. J. Sci.* **77**, 113-119.
- Paterson, H.E.H. (1982). Perspective on speciation by reinforcement. *South Afr. J. Sci.* **78**, 53-57.
- Pizzey, G. (1980). *A Field Guide to the Birds of Australia*. Collins, Sydney.
- Pratt, H.D. (1980). Intra-island variation in the Elepaio on the island of Hawaii. *Condor* **82**, 449-458.
- Reid, N., Paton, J.B. & Paton, D.C. (1977). Critical range limits of the Turquoise and Black-backed Wrens in S.A. *South Aust. Ornithol.* **27**, 216-221.
- Remington, C.L. (1968). Suture zones of hybrid interaction between recently joined biotas. *Evol. Biol.* **2**, 321-428.
- Rising, J.D. (1983). The progress of oriole hybridization in Kansas. *Auk* **100**, 885-897.
- Rognon, P. & Williams, M.A. (1977). Late Quaternary climatic changes in Australia and North Africa. A preliminary interpretation. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **21**, 285-327.
- Rohwer, S.A. (1972). A multivariate assessment of interbreeding between the meadowlarks, *Sturnella*. *Syst. Zool.* **23**, 313-338.
- Rowley, I. (1970). The genus *Corvus* (Aves: Corvidae) in Australia. *CSIRO Wildl. Res.* **15**, 27-71.
- Ryan, J.V. (1979). Nearly forty years with *Hylacola* spp. *Aust. Bird Watcher* **8**, 42-47.
- Sage, R.D. & Selander, R.K. (1979). Hybridization between species of the *Rana pipiens* complex in central Texas. *Evolution* **33**, 1069-1088.
- Salomonsen, F. (1961). Notes on flowerpeckers (Aves, Dicaeidae): the superspecies *Pardalotus striatus*. *Am. Mus. Novit.* **2068**, 1-31.
- Saunders, D.A. (1979). Distribution and taxonomy of the white-tailed and yellow-tailed black-cockatoos *Calyptorhynchus* spp. *Emu* **79**, 215-227.
- Schluter, D., Price, T.D. & Grant, P.R. (1985). Ecological character displacement in Darwin's Finches. *Science* **227**, 1056-1058.
- Schodde, R. (1975). *Interim List of Australian Songbirds: Passerines*. RAOU, Melbourne.
- Schodde, R. (1981). Bird communities of the Australian mallee: composition, derivation, distribution, structure and seasonal cycles. In: *Mediterranean-Type Shrublands* (eds F. di Castri, D.W. Goddall & R.L. Specht) pp. 387-415. Elsevier, Netherlands.
- Schodde, R. (1982a). Origin, adaptation and evolution of birds in arid Australia. In: *Evolution of the Flora and Fauna of Arid Australia* (eds W.R. Baker & P.J.M. Greenslade) pp. 191-224. Peacock Pubs, Frewville, South Aust.
- Schodde, R. (1982b). *The Fairy Wrens: A Monograph of the Maluridae*. Lansdowne, Melbourne.
- Schodde, R. & Mason, I.J. (1975). A new subspecies of *Colluricincla megarhyncha* from the Northern Territory. *Emu* **75**, 109-114.
- Schodde, R. & Mason, I.J. (1976). Infra-specific variation in *Alcedo azurea* Latham (Alcedinidae). *Emu* **76**, 161-166.
- Schodde, R. & Mason, I.J. (1980). *Nocturnal Birds of Australia*. Lansdowne, Melbourne.
- Schodde, R., Mason, I.J., Dudzinski, M.L. & McKean, J.L. (1980). Variation in the Striated Heron *Butorides striatus* in Australasia. *Emu* **80**, 203-212.
- Schodde, R., Smith, J.T., Mason, I.J. & Weatherly, R.C. (1979). Relationships and speciation in the Australian corellas (Psittacidae). *Bull. Brit. Ornithol. Club.* **99**, 128-137.
- Schuchmann, K.L. (1978). Allopatrische artbildung bei der kolibri-gattung *Trochilus*. *Ardea* **66**, 156-172.
- Schueler, F.W. & Rising, J.D. (1976). Phenetic evidence for natural hybridization. *Syst. Zool.* **25**, 283-289.
- Selander, R. (1971). Systematics and speciation in birds. In: *Avian Biology*, Vol 1 (eds D.S. Farner & J.R. King) pp. 57-147. Academic Press, New York.
- Serventy, D.L. (1951). The evolution of the chestnut-shouldered wrens (*Malurus*). *Emu* **51**, 113-120.
- Serventy, D.L. (1951). Some speciation problems in Australian birds. *Emu* **53**, 131-145.
- Serventy, D.L. (1972). Causal ornithogeography in Australia. *Proc. Int. Ornithol. Congr.* **15**, 574-585.
- Serventy, D.L. & Whittell, H.M. (1976). *The Birds of Western Australia*. 5th ed. Univ. West. Australia, Perth.
- Short, L.L. (1969). Taxonomic aspects of avian hybridization. *Auk* **86**, 84-105.
- Short, L.L. (1972). Hybridization, taxonomy and avian evolution. *Ann. Mo. Bot. Gard.* **59**, 447-453.
- Short, L.L., Schodde, R. & Horne, J.F.M. (1983a). Five-way hybridization of Varied Sittellas *Daphoenositta chrysoptera* (Aves: Neositidae) in central Queensland. *Aust. J. Zool.* **31**, 449-516.
- Short, L.L., Schodde, R. & Horne, J.F.M. (1983b). Hybridization of 'White-headed' and 'Orange-winged' Varied Sittellas, *Daphoenositta chrysoptera leucocephala* and *D. c. chrysoptera* (Aves: Neositidae) in eastern Australia. *Aust. J. Zool.* **31**, 517-531.
- Short, L.L., Schodde, R. & Horne, J.F.M. (1983c). Vocal behaviour, morphology and hybridization of Australian Spotted and

- Yellow-rumped Pardalotes (Aves: *Pardalotus*). *Am. Mus. Novit.* **2756**, 1-15.
- Shields, G.F. (1982). Comparative avian cytogenetics: a review. *Condor* **84**, 45-58.
- Sibley, C.G. (1957). The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. *Condor* **59**, 166-191.
- Sibley, C.G. (1961). Hybridization and isolating mechanisms. In: *Vertebrate Speciation* (ed. W.F. Blair) pp. 69-88. Texas Univ. Press, Austin.
- Singh, G. (1981). Environmental upheaval: The vegetation of Australia during the Quaternary. In: *The History of the Australian Vegetation* (ed. J.M.B. Smith) pp. 90-108. McGraw-Hill, Sydney.
- Slatkin, M. (1973). Gene flow and selection in a cline. *Genetics* **75**, 733-756.
- Slatkin, M. (1975). Gene flow and selection in a two locus cline. *Genetics* **81**, 787-802.
- Slatkin, M. (1980). Ecological character displacement. *Ecology* **61**, 163-177.
- Slatkin, M. (1981). Fixation probabilities and fixation times in a subdivided population. *Evolution* **35**, 477-488.
- Strenseth, N.C. & Maynard Smith, J. (1984). Coevolution in ecosystems: Red Queen or stasis? *Evolution* **38**, 870-880.
- Storr, G.M. (1973). List of Queensland birds. *Spec. Publ. West. Aust. Mus.* **5**, 1-177.
- Storr, G.M. (1977). Birds of the Northern Territory. *Spec. Publ. West. Aust. Mus.* **7**, 1-130.
- Storr, G.M. (1980). Birds of the Kimberley Division, Western Australia. *Spec. Publ. West. Aust. Mus.* **11**, 1-117.
- Storr, G.M. (1984). Revised list of Queensland birds. *Rec. West. Aust. Mus. Suppl.* **19**, 1-189.
- Storr, G.M. (1985a). Birds of the Gascoyne Region, Western Australia. *Rec. West. Aust. Mus. Suppl.* **21**, 1-66.
- Storr, G.M. (1985b). Birds of the mid-eastern interior of Western Australia. *Rec. West. Aust. Mus. Suppl.* **22**, 1-45.
- Templeton, A.R. (1980). Modes of speciation and inferences based on genetic distances. *Evolution* **34**, 719-729.
- Templeton, A.R. (1981). Mechanisms of speciation: a population genetic approach. *Annu. Rev. Ecol. Syst.* **12**, 23-48.
- Thorpe, R.S. (1984). Primary and secondary transition zones in speciation and population differentiation: a phylogenetic analysis of range expansion. *Evolution* **38**, 233-243.
- Van Tets, G.F., D'Andria, A.H. & Slater, E. (1967). Nesting, distribution and nomenclature of Australasian vanelline plovers. *Emu* **67**, 85-93.
- Warham, J. (1960). The Spur-winged Plover in North Queensland. *Emu* **60**, 61-63.
- Watt, W.B. (1972). Intragenic recombination as a source of population genetic variability. *Am. Nat.* **106**, 737-753.
- Weatherly, R., Baker-Gabb, D.J. & Mooney, N.J. (1985). Juvenile plumage and plumage variation in the Brown Falcon *Falco berigora*. *Emu* **85**, 257-260.
- White, M.J.D. (1978). *Modes of Speciation*. Freeman, San Francisco.
- Woinarski, J.C.Z. (1984). Interbreeding of the Spotted and Yellow-rumped Pardalote *Pardalotus punctatus* and *P. xanthopygus*. *Emu* **84**, 80-86.
- Woinarski, J.C.Z., Dorwood, D.F. & Cullen, J.M. (1983). Variation in the *Pardalotus striatus* complex in south-eastern Australia. *Emu* **83**, 82-93.
- Woodroffe, D.S., Thom, B.J. & Chappell, J. (1985). Development of widespread mangroves swamps in mid-Holocene times in northern Australia. *Nature* **317**, 711-713.
- Woodruff, D.S. (1973). Natural hybridization and hybrid zones. *Syst. Zool.* **22**, 213-218.
- Wright, S. (1978). *Evolution and Genetics of Populations: Variability within and among Natural Populations*. Chicago Univ. Press, Chicago, Ill.
- Wunderle, J.M. (1981). An analysis of a morph ratio cline in the Bananaquit *Coeereba flaveola* on Grenada, West Indies. *Evolution* **35**, 333-334.
- Wyrwoll, K.H. (1979). Late Quaternary climates of Western Australia: evidence and mechanisms. *J. R. Soc. West. Aust.* **62**, 129-142.

Appendix

Summary of hybrid zones and parapatric contact zones between subspecies and allospecies of Australian birds

Butorides striatus Striated (Mangrove) Heron.

The pale *stagnatilis* (with its rufous and greyish substrate-ecotypes) of north-western mangrove-clad coastlines and the dark *macrorhynchus* of eastern coasts meet along the southern shores of the Gulf of Carpentaria (Schodde *et al.* 1980). Both subspecies decrease in size clinally northward but *macrorhynchus* is consistently isolatitudinally larger. That the contact between these subspecies is secondary is presumed because they would have been isolated by the Torres Strait land bridge when sea-levels were lower.

Falco berigora Brown Falcon.

Weatherly *et al.* (1985) showed progressive paling following each moult until achievement of fully adult plumage so subspecific boundaries based on colouration are suspect (*pace* Condon 1950). Nevertheless, there is a steep change in size across the Great Dividing Range from the eastern coastal *berigora* to the inland and western *occidentalis-centralia* population-group. Whether the small-sized south-western *occidentalis* intergrades sharply with *centralia* is doubtful.

Alectura lathami Australian Brush-turkey.

The red-and-yellow wattled *lathami* of the humid, north-eastern Queensland uplands is altitudinally replaced by the purple- and white-wattled *purpureicollis* north of Cooktown (Storr 1984; Ford 1986).

Turnix varia and *olivei* Painted & Buff-breasted Button-quail.

On proceeding northward in eastern Australia *varia* becomes progressively restricted to uplands. On the lowlands northward of Cooktown it is parapatrically replaced by the allospecies *olivei* (Storr 1984; Ford 1986).

Haematopus fuliginosus Sooty Oystercatcher.

H. f. fuliginosus of southern coasts and the stout-billed, fleshy eye-ringed *H. f. ophthalmicus* of northern coasts intergrade between Shark Bay and Point Cloates (Hartert 1927; McKean 1978; Storr 1985a). Though *fuliginosus* now has a discontinuous distribution along the west coast, it was probably continuous when sea-levels were lower and rocky limestone shores exposed. Their breeding ranges do not meet on the eastern coast (Storr 1984).

Vanellus miles Masked (Spur-winged) Lapwing.

A broad variable hybrid zone extends inland from the coast

between Townsville and Bowen, intermediates having varying amounts of black on the nape and sides of the breast (van Tets *et al.* 1967; Warham 1960; Pizzey 1980). The northern *miles* differs from the south-eastern *novaehollandiae* in being white rather than black on the nape, shoulders and sides of breast. In captivity *miles* and *novaehollandiae* interbreed freely, produce fertile offspring and respond to each other's calls (van Tets *et al.* 1967).

Ptilinopus regina Rose-crowned Fruit-Dove.

P. r. regina of humid coastal eastern Australia is much redder on the crown and undersurface than *P. r. ewingii* of coastal north-western Australia. Remnant isolates of intermediate colouration (Johnstone 1981b), possibly of hybrid origin, occur on the Sir Edward Pellew Islands and along the Edward River, western Cape York Peninsula. The two subspecies might have come into contact along the margins of the Gulf of Carpentaria during the pluvial phase of about 8000 BP (Ford 1979b).

Petrophassa scripta Squatter Pigeon.

The red orbital-skinned *peninsulae* of Cape York Peninsula intergrades with the bluish orbital-skinned *scripta* of eastern Queensland along the southern slopes of the Einasleigh Uplands and Burdekin-Lynd Divide and through the Burdekin Barrier (Ford 1986).

Petrophassa plumifera Spinifex Pigeon.

The isolated, pale rufous-bellied *mungi* in south-west Kimberley ranges is intermediate between the dark rufous-bellied, red-eyed *ferruginea* of the Pilbara-Gascoyne and the white-bellied, white pectoral-banded, yellow-eyed *proxima* (= *plumifera*) in the eastern Kimberley and adjacent Northern Territory: for it is paler dorsally and ventrally than *ferruginea*, approaching *plumifera* in dorsal colouration and has variably intermediate (including orange) coloured irides. Crome *et al.* (1980) produced aviary hybrids between *ferruginea* and *plumifera* resembling *mungi*. Johnstone (1981a) claims *mungi* is a primary intergrade but this view is difficult to reconcile with its present isolation from *ferruginea* by the Great Sandy Desert and from *plumifera* by 90 km of non-rangeland plains. It has all the credentials of a hybrid population.

Calyptrorhynchus magnificus Red-tailed Black-Cockatoo.

The two large-billed, long-winged subspecies, north-eastern *magnificus* and north-western *macrorhynchus* intergrade in the Capentarian lowlands (Ford 1980b). Besides differences in colouration of the tail band (orange in *macrorhynchus* and red in *magnificus*), they differ in certain aspects of size.

Calyptrorhynchus funereus Yellow-tailed Black-Cockatoo.

An intergrade population in central Victoria may connect the small *xanthonotus* of southern South Australia-eastern Victoria with the large *funereus* of coastal New South Wales and south-eastern Queensland (Saunders 1979), although Courtney (1986) suggests these taxa have speciated. Tasmania is populated by *xanthonotus*.

Calyptrorhynchus baudinii White-tailed Black-Cockatoo.

In south-western Australia, the breeding ranges of *baudinii* and *C. f. latirostris*, a white-tailed form of the eastern Yellow-tailed species, have almost abutting breeding ranges but overlap in the non-breeding season (Saunders 1979). *C. f. latirostris* appears to be the secondary invader unless the divergence between *latirostris* and *baudinii* occurred *in situ*, which seems unlikely.

Cacatua roseicapilla Galah.

Hall & Frith (1974) indicated that the near-isolated mid-western subspecies *assimilis* has a disjunct population in south-western Kimberley in contact with, and presumably intergrading

with, the small, pallid Kimberley-Arnhem Land variant, *kuhli*. However, a long series from western Kimberley collected in 1986 consisted entirely of *kuhli*. The richly coloured eastern form, nominate *roseicapilla*, presumably also now intergrades with the north-western *kuhli* in the region of the Barkly Tableland.

Cacatua sanguinea Little Corella.

C. s. westralensis and *C. s. gymnopsis* have recently expanded southward and secondarily contacted the Western Long-billed Corella *C. pastinator* and Eastern Long-billed Corella *C. tenuirostris* respectively without significant hybridisation (Schodde *et al.* 1979; Ford 1985b). A hybrid zone between the diminutive *C. s. normantoni* of western Cape York Peninsula and *C. s. gymnopsis* of inland eastern Australia presumably occurs south of the lower Norman River, and another between nominate *sanguinea* of north-western Australia (Kimberley-Arnhem Land) and the smaller, more reddish-lore central-eastern *gymnopsis* in the region of latitude 16°S about the Barkly Tableland (Ford 1985b).

Cacatua galerita Sulphur-crested Cockatoo.

The white periophthalmic *galerita* of coastal-eastern Australia and the blue periophthalmic *fitzroyi* of the north-west apparently intergrade along the lower Nicholson River (Forshaw 1981).

Platycercus flaveolus Yellow Rosella.

Hybrids and interspecific pairs with the Crimson Rosella *P. elegans elegans* have been reported from the headwaters of the Murray (Hobbs 1956, 1958) at the extreme eastern limit of the riparian *flaveolus*. Lendon (1973) remarked that *P. elegans adelaidae* of the Mt. Lofty Range follows the Marne River down to the Murray where it meets *P. flaveolus* without any hybridisation but allozyme data and specimens indicate there is a gene flow via the Marne connection (Joseph & Hope 1984; Joseph pers. comm.). Boehm's (1954) report of a sparse intergrade population resembling *flaveolus* in the mallee west of the north-west bend of the Murray also suggests some introgression.

Platycercus elegans Crimson Rosella.

The extremes of this complex, the crimson-plumaged *P. e. elegans* of coastal south-eastern Australia and the yellowish-plumaged *P. e. subadelaidae* of the Flinders Range are connected by a clinal series of subspecies consisting of *P. e. melanoptera* on Kangaroo Island, *P. e. 'fleurieuensis'* on Fleurieu Peninsula and *P. e. adelaidae* in the Mt. Lofty Range but there are range disjunctions between *elegans* and *'fleurieuensis'* (across the Coorong), between *melanoptera* and *'fleurieuensis'* (Backstairs Passage) and possibly between *adelaidae* and *subadelaidae* (the Burra-Spalding tussock-grassland plain) (Serventy 1953; Condon 1954; Cain 1955; Lendon 1973; Forshaw 1981). Ford (1977b) gives an explanation of the origin of this sequence. Evidence in support of a hybrid origin for *adelaidae* is provided by Forshaw (1981) who states that it is indistinguishable from *elegans* x *flaveolus* hybrids produced in aviaries. Joseph & Hope (1984) are concerned that *subadelaidae* might have become isolated from *adelaidae* following habitat destruction through agricultural activities but how it became isolated is irrelevant, because it also has apparently been introgressed by *elegans* genes.

Platycercus eximius Eastern Rosella.

The northern subspecies *splendidus* has certain characters (a greenish-blue rump and golden-yellow margins to the back feathers) connecting it with the southern subspecies *palliceps* of *P. adscius* with which it is altitudinally parapatric, if not partly sympatric, in south-eastern Queensland and extreme north-eastern New South Wales. In this region *palliceps* largely avoids highlands whereas *splendidus* is largely confined to them. Hybridisation between *splendidus* and *palliceps* is probably more frequent than

present evidence (Brereton & Sourry 1959; Forshaw 1981; Cannon 1983) indicates. Using the nomenclature of Short (1969), their interaction forms a zone of overlap and hybridisation, and of Woodruff (1973), a localised sympatric hybrid zone. Past gene flow is suggested by their common set of characters.

Platycercus adscitus Pale-headed Rosella.

A hybrid zone between the yellow-breasted, pale yellow-backed *adscitus* of Cape York Peninsula and the blue-breasted, golden-yellow-backed *palliceps* of eastern Queensland extends from the central ridge of the Einasleigh Uplands and Burdekin-Lynd Divide northwards to the Mitchell River, which lies within the Normanby Barrier (Ford 1986).

Barnardius barnardi Mallee Ringneck.

The semispecies *zonarius* and *barnardi* are connected by a widely distributed hybrid population in the Lake Torrens basin and Flinders Range (Fisher 1970) and the population of *barnardi* in the Flinders Range ('whitei') owes its peculiar characteristics to introgression of *zonarius* genes (Cain 1955; Hall & Frith 1974; Forshaw 1981).

Barnardius zonarius Port Lincoln Ringneck.

The south-western forest form, *semitorquatus*, with its all-green belly and prominent red frons, intergrades sharply with the smaller, inland and arid-country form *zonarius*, with its broad yellow-breast-band and vestigial red frons, on the eastern margins of the sclerophyll forest of jarrah-marri-karri (Fisher 1970; Serventy & Whittell 1976; Forshaw 1981). Following widespread land clearing, *zonarius* genes have now introgressed *semitorquatus* on the Swan coastal plain (Fisher 1970). In the region of the Murchison River, *zonarius* intergrades with the distinctively pallid, lemon-yellow bellied *occidentalis* of the Pilbara-Gascoyne region (Cain 1955; Fisher 1970; Forshaw 1981) but intergradation is possibly primary (Fisher 1970).

Northiella (= *Psephotus*) *haematogaster* Blue Bonnet Parrot.

A broad zone of intergradation between the red-shouldered, red-vented *haematorrhous* and the olive-shouldered, yellow-vented *haematogaster* occurs from the Warrego River, Queensland, to beyond the Barwon and Castlereagh Rivers, New South Wales (Ford 1974b; Forshaw 1981). The red-vented subspecies is confined to the interior of southern Queensland and inland north-eastern New South Wales.

Cuculus variolosus Brush Cuckoo.

Intergradation between the small, yellowish northern *dumetorum* and dark, southern *variolosus* apparently occurs in the Burdekin lowland (Mason *et al.* 1984).

Centropus phasianinus Pheasant Coucal.

In the region of the Burdekin lowlands there is a steep, abrupt step in the south-north clinal decrease in size of appendages (wing, tail and bill) where eastern *phasianinus* adjoins northern *melanurus* (Mason *et al.* 1984).

Chrysococcyx minutillus Little Bronze-Cuckoo.

A hybrid swarm known as *russatus* on Cape York Peninsula is interposed between the western *minutillus* and the coastal-eastern *barnardi*, the steepest changes to the less rufescent *minutillus* and *barnardi* occurring on the mid-west coast of Cape York Peninsula and in the Burdekin lowlands (Ford 1982a).

Ninox rufa Rufous Owl.

Mason & Schodde (1980) suggest the small, pale form (*meesi*) on Cape York Peninsula might intergrade north of Cooktown with the large, dark form (*queenslandica*) of coastal central-eastern

Queensland.

Ninox novaeseelandiae Southern Boobook.

The extremely dark *lurida* of the rainforests of north-eastern Queensland (Mt. Amos to Mt. Spec) is hemmed in by the paler, pan-continental *boobook* (*cf.* Mees 1964b) but they might be isolated (Storr 1973, 1984). Whether there is any steep zone of intergradation in Australia cannot be ascertained from the various descriptive analyses of geographic variation (see Mees 1964b; Schodde & Mason 1980).

Ninox connivens Barking Owl.

An abrupt change in size and colour across the Normanby Barrier occurs between the small, pale *peninsularis* of Cape York Peninsula and *connivens* of eastern coastal Australia (Schodde & Mason 1980; Ford 1986) but they might be isolated.

Tyto novaehollandiae Masked Owl.

A pronounced change in size between the small *galei* of Cape York Peninsula and *novaehollandiae* apparently occurs across the Normanby Barrier (Mason 1983; Ford 1986).

Podargus strigoides Tawny Frogmouth.

A steep zone of intergradation in size and colouration occurs across the Great Dividing Range between the large, dark south-eastern *strigoides* and smaller, paler, western *brachypterus*, and another between *strigoides-brachypterus* and the small, silvery-grey northern *phalaenoides* (Ford 1986).

Ceyx (= *Alcedo*) *azurea* Azure Kingfisher.

Schodde & Mason (1976) demonstrated a sharp decrease in size and a distinct change in ventral colour across the Normanby Barrier between the rufous-brown-breasted *ruficollaris* of Cape York Peninsula and cinnamon-brown-breasted *azurea* of eastern-coastal Australia. However, in the large series of specimens from eastern Australia in the collection of the American Museum of Natural History, I was unable to confirm their conclusion.

Dacelo novaeguineae (= *gigas*) Laughing Kookaburra.

Keast (1957b) indicated *minor* of Cape York Peninsula was isolated but Ford (1986) demonstrated a steep zone of intergradation in size between this short-winged subspecies and the eastern and south-eastern *novaeguineae*.

Dacelo leachii Blue-winged Kookaburra.

The distinctive white-headed *cliftoni* of the Pilbara-Gascoyne hybridises with the streaked-crowned *leachii* in the extreme south-west Kimberley (Keast 1957b), indicating a formerly continuous distribution across the Canning Barrier.

Coracina papuensis White-bellied Cuckoo-shrike.

A step in the north-south cline of increase in wing length occurs across the Burdekin Barrier at about 20°S (Galbraith 1969).

Coracina novaehollandiae Black-faced Cuckoo-shrike.

There is a rather sharp zone of intergradation through the Murchison between the pale-backed *subpallida* of the Pilbara-Gascoyne and the south-western population of *novaehollandiae* (Mees 1964a; Ford unpubl.).

Microeca flavigaster Lemon-bellied Flycatcher.

The population in the Cambridge Gulf mangrove forests is variably intermediate in colouration and size between the yellow-bellied *flavigaster* of the Northern Territory and lipochromeless *tormenti* of the Kimberley mangrove fringe (Johnstone 1984).

Microeca leucophaea Jacky Winter.

Western *assimilis* has recontacted the more white-tailed *leucophaea* where mallee approaches sclerophyll woodlands in south-eastern Australia along the eastern side of the Mt. Lofty Range and in north-western Victoria (Keast 1958d; Ford & Parker unpubl.) but evidence of hybridisation is meagre. Intergradation between the small, pale *pallida* of northern Australia and eastern *leucophaea* is apparently fairly sharp along the eastern edge of the Carpentarian Barrier (Ford unpubl.).

Pachycephala pectoralis Golden Whistler.

There are apparently two hybrid zones, one between western *fuliginosa* and south-eastern *pectoralis* and another between *pectoralis* and coastal eastern *ashbyi* (Ford unpubl.). Buff-bellied and vented *fuliginosa* intergrades with pale grey-bellied and vented *pectoralis* in the Victorian mallee, and introgression is evident in the western-most segment of *pectoralis* (= 'youngi') on the basis of it having grey not olive on the base of the tail. Yellow-vented *ashbyi* meets pale-vented *pectoralis* in the sclerophyll forests of mid-coastal New South Wales (Mayr 1954; Galbraith 1956;). The form 'youngi' might have also been affected by gene flow from *glauca* when Tasmania was connected to Victoria during the last glaciation.

Pachycephala melanura Mangrove Golden Whistler.

Males of *spinothraupis* and *melanura* are generally similar in colouration but females are strikingly different: *spinothraupis* is yellow on the breast, abdomen and under tail-coverts and *melanura* is yellow only on the under tail-coverts. Between Port Warrender and Napier Broome Bay, Kimberley, females have varying amounts of ventral yellow (Ford 1978a, 1982c, 1983b).

Myiagra rubecula Leaden Flycatcher.

Presumably a sharp intergrade zone occurs in the McPherson Range area between the pale-lored *rubecula* of southern-eastern and dark-lored *yorki* of northern eastern Australia (Keast 1958d).

Colluricincla megarrhyncha Little Shrike-thrush.

There is a minor hybrid zone between eastern-coastal *rufogaster* and north-eastern 'parvissima' and a major, discontinuous hybrid zone between *parvula* and the *rufogaster*-group (Ford 1979b). The hybrid zone between *rufogaster* and 'parvissima' is a sharp step superimposed on a south-north cline of decreasing size and lies within the Burdekin Barrier. Black-billed, grey-brown plumaged *parvula* of the Kimberley-Northern Territory coastal areas and brown-billed, rufous-plumaged *rufogaster*-group have produced an exactly intermediate hybrid population on the lower Roper (Ford 1979b) and an isolated, long-billed population (*aelptes*) at the mouth of the McArthur (Schodde & Mason 1975) which owes its intermediacy to past introgressive hybridisation and possibly to drift. Evidence suggests *parvula* and *rufogaster*-group came into contact (Ford 1979b, 1982c) when mangrove forests were more extensively distributed across northern Australia about 7000 y ago (Woodroffe *et al.* 1985).

Colluricincla harmonica Grey Shrike-thrush.

This almost pan-Australian species has a major hybrid zone between the south-western *rufiventris* and south-eastern *harmonica* (Ford & Parker 1973) but whether a hybrid zone or clinal intergradation occurs between *harmonica* and northern *brunnea* has not been determined (*cf.* Macdonald 1968). Grey-mantled, cinnamon-vented *rufiventris* and sepia-mantled, grey-vented *harmonica* hybridise along a line running north of Spencer Gulf through the south-west Queensland (Ford & Parker 1974). The extremely pallid *anda* of the Lake Eyre basin deserts might have been once isolated from *harmonica* by the Grey Range Divide (Ford unpubl.) but no geographical isolation is now evident. There might be some intrusion of *rufiventris* genes into *brunnea* in the south-eastern

fringe of the Kimberley (Galbraith 1974; Ford pers. obs.).

Spophodes cristatus and *occidentalis* Wedgebills.

These recently evolved allospecies lie on more or less opposite sides of the Eyrean Barrier (Ford & Parker 1973). The contact boundary runs between Oodnadatta and Charlotte Waters. These forms differ strikingly in song but slightly in colouration, *cristatus* being streaked on the breast.

Cinclosoma cinnamomeum Cinnamon Quail-thrush.

A zone of contact and some hybridisation occurs between *C. cinnamomeum* of the Lake Torrens-Lake Eyre-Lake Frome basins and *C. castaneothorax* Chestnut-breasted Quail-thrush of inland New South Wales-Queensland where sparsely vegetated gibber plains adjoin mulga-clad dissected sub-plateaus and escarpments (Ford 1974c, 1983a). Hybrids have been collected in the Beal Range, Queensland.

Pomatostomus temporalis Grey-crowned Babbler.

Variation in this species has not been analysed quantitatively in order to determine any steep zones of intergradation indicative of secondary contact despite the distinct differences between extreme forms (*temporalis* and *rubeculus*). Storr (1977) considered variation was only clinal but there might be a step across the Carpentarian plain.

Malurus splendens Splendid Fairy-wren.

A variable intermediate population in the mulga scrubs of the south Gibson Desert lies between the western, violet-plumaged *splendens* and the central, black-backed, turquoise-plumaged *callainus* (Ford 1975a). The possibility of some gene-flow between *callainus* and the inland south-eastern black-backed *melanotis*, as indicated by some intermediacy in 'whitei', the segment of *melanotis* on the south-western side of the Flinders Range, has been hypothesised (Reid *et al.* 1977) but since rejected (Reid pers. comm.). With the equivocal evidence that certain tones of colouration in the population in the Flinders Range might be due to either gene flow or Gloger clinal influences, Schodde (1982b) suggested this population was a hybrid one but minor ecotypic clines in *callainus* and *melanotis* have apparently combined to confuse the relationship between these isolated forms.

Malurus lamberti Variegated Fairy-wren.

Two or three hybrid zones occur in this species: between Kimberley *rogersi* and centralian *assimilis* in the south Kimberley and Victoria River region (Ford 1979a); between coastal-eastern *lamberti* and *assimilis* across the Great Dividing Range (Mack 1934; Harrison 1972; Schodde 1982b); and between Arnhem Land *dulcis* and centralian *assimilis* along the Roper (Harrison 1972; Schodde 1982). Ford (1979a) reported an intergrade series between the bluish-backed females of *rogersi* and the grey-brown plumaged *assimilis*. Harrison (1972) considered a faint bluish-grey bloom on the back and deeper blue on the tails of some specimens from the lower Roper as indicating intergradation between white-lored *dulcis*, with its bluish females and chestnut-lored *assimilis*. A broad zone of intergradation between Goondiwindi, Wide Bay, Rockhampton and Emerald connects violet-mantled, pale-blue-headed *assimilis* with the royal-blue-mantled, dark-blue-headed *lamberti*. Intergradation between *amabilis* of Cape York Peninsula with its white-lored, black-billed females and brown-billed *assimilis*, based on one abnormal specimen from Normanton (Harrison 1972, 1974), is weak evidence (Schodde 1982b). In south-western Australia and on Eyre Peninsula, other forms of the *lamberti*-complex meet or overlap (*elegans-pulcherrimus* and *pulcherrimus-assimilis*) without interbreeding (Serventy 1951; Ford 1966). *M. pulcherrimus* and *M. lamberti assimilis* overlap extensively in south-western Australia, especially along the western coastal plain (Ford

1966), but they may be parapatric on Eyre Peninsula.

Malurus elegans and *pulcherrimus* Red-winged and Blue-breasted Fairy-wrens.

These allospecies are in parapatric contact on the inland margin of the Jarrah-Marri forested area of south-western Australia (Ford 1966).

Malurus melanocephalus Red-backed Fairy-wren.

A variable hybrid zone connects the red-backed, northern *cruentatus* with the orange-backed, long-tailed eastern *melanocephalus*. Schodde (1982b) hypothesised that *cruentatus* and *melanocephalus* were formerly isolated by the Burdekin Barrier but the axis of the hybrid zone coincides with the spine of the Burdekin-Lynd Divide and Einasleigh Uplands and may be another example of these once cold uplands splitting lowland populations (Ford 1986; unpubl.).

Sericornis beccarii and *magnirostris* Tropical and Large-billed Scrubwrens.

Northern *S. beccarii* and southern *S. magnirostris* adjoin around Cooktown (McGill 1970; Boles 1979) but might be altitudinally isolated, for *beccarii* is in gallery forest and lowland rainforest and *magnirostris* in vine scrubs and rainforest on ranges (Storr 1984).

Sericornis frontalis White-browed Scrubwren.

Black-faced, buff-bellied *laevigaster* of coastal eastern Queensland and brown-faced, streak-throated, olive-bellied *frontalis* of coastal south-eastern Australia intergrade sharply round the McPherson Range (Ford 1985a). Though *rosinae* of the Mt. Lofty Range is usually considered part of the *frontalis*-group, Condon's (1954) remark that it serves as a link between this and the *maculatus*-group emphasises its morphological intermediacy. Contact between *rosinae* and rufous-flanked *osculans* of the mangrove-clad shores of St Vincent Gulf was presumably continuous before denudation of the Adelaide plain. The nature of the contact between the yellow-bellied *maculatus* and whitish-bellied *mellori-balstoni* in south-western Australia is uncertain (Ford 1970).

Sericornis cautilus and *pyrrhopygius* Shy and Chestnut-rumped Hylacolas.

S. cautilus and *S. pyrrhopygius* have almost contiguous ranges but remain steadfastly in different habitats near Bendigo, Victoria (Eddy 1959; Ryan 1979), where *cautilus* favours whipstick mallee and *pyrrhopygius* favours understorey heath of ironbark forest.

Sericornis fuliginosus Calamanthus.

Parker & Eckert (1983) argued for the olive-yellow-backed, south-eastern *fuliginosus* and the rufescent, grey and olive-grey backed forms (inland and western *campestris-montanellus* group) as being separate species on the basis of presumed past secondary contact on the 90-Mile Plain and supposed character-displacement in *winiam*, which has a shallower bill than all other forms. The bill of *fuliginosus* is generally straight and wedge-shaped and that of others, slender and curved. However, morphological shifts resulting from interspecific competition have been very difficult to prove or demonstrate (Grants 1972, 1975; Slatkin 1980; but see Fjeldsa 1983; Schluter *et al.* 1985).

Gerygone palpebrosa Fairy (Black-throated) Gerygone.

A series of intermediate populations across the Burdekin-Lynd Divide connect blackish-throated *personata* of Cape York Peninsula with pale-throated *flavida* of coastal eastern Queensland (Ford 1977a) but intergradation might be primary or secondary.

Gerygone olivacea White-throated Gerygone.

Eastern *olivacea* with, and northern *rogersi* without, a white base

to the tail apparently meet and hybridise along the lower Leichhardt, Carpentarian lowlands (Ford 1978c).

Acanthiza pusilla Brown Thornbill.

The coastal-eastern semispecies *A. pusilla* and western *A. apicalis*, Inland Thornbill, apparently have contiguous ranges on the inland foothills of the Great Dividing Range and eastern side of the Mt. Lofty Range without hybridising (Mayr & Serventy 1938) but an intermediate population occurs throughout the 90-Mile Plain of south-eastern South Australia and contiguous Victoria (Boles 1983). Inland *apicalis* has reduced dorsal lipochrome, whitish terminal crescents on the frons, more white rectricial tipping, a rufous rump and a broad black subterminal band on the tail whereas coastal *pusilla* has a somewhat dull olive concolorous dorsum, buff subterminal and black terminal crescents on the frons and a narrow black subterminal band on the tail. The tail-cocking habit of *apicalis* is also usually distinctive.

Aphelocephala leucopsis Southern Whiteface.

A disjunct, variable hybrid population in mulga-clad terrain lies geographically between the western chestnut-flanked *castaneiventris* and central, buff-flanked *whitei* (Storr 1985b). The eastern, pale-flanked *leucopsis* and *whitei* meet and intergrade to the west of the Flinders Range and north of Eyre Peninsula (Keast 1957a).

Daphoenositta chrysoptera Varied Sittella.

Five hybrid zones connect the various peripherally pan-Australian subspecies (Mayr 1950; Ford 1980a) and a penta-hybrid swarm exists in Central Queensland (Ford 1980a; Short *et al.* 1983a). The subspecies are *pileata* (south-western), *leucoptera* (north-western), *striata* (north-eastern), *leucocephala* (central-coastal eastern) and *chrysoptera* (south-eastern). The hybrid zones *pileata* x *leucoptera* (Parker 1970), *pileata* x *chrysoptera* (Ford 1980a), *chrysoptera* x *leucocephala* (Ford 1980a; Short *et al.* 1983b) and *leucocephala* x *striata* (Ford 1980a) are broad, whereas the zone between *striata* and *leucoptera* is quite narrow (Macdonald 1969b; Short *et al.* 1983a). Though there is a complex combination of hybrid phenotypes in central Queensland, an individual from the hybrid swarm cannot be unequivocally assigned penta-hybrid status on the basis of morphological criteria alone because a combination of character states of any four subspecies including *leucocephala* can be used to assemble the fifth subspecies.

Climacteris picumnus Brown Treecreeper.

Blackish *melanota* of Cape York Peninsula and brownish *picumnus* of eastern Australia hybridise in a relatively narrow zone across the Burdekin-Lynd Divide and Einasleigh Uplands (Harrison 1970, 1974; Ford 1986).

Manorina flavigula Yellow-throated Miner.

This species consists of two dark subspecies, *obscura* in the south-west and *melanotis* in the south-east and a paler-rumped subspecies *flavigula* in northern and arid areas. Gradation in the inland south-west is fairly smooth (Serventy 1953; Serventy & Whittell 1976; pace Ashby 1922) except where *flavigula* has only recently made contact with *obscura* in the lower south-east of Western Australia (pers. obs.). In south-eastern Australia, hybridisation between *flavigula* and *melanotis* was detected only recently (H. Ford 1981), but the remarks of Jones (1952) may be reinterpreted as indicating these forms and therefore intermediates have co-occurred in the same nesting colonies at Hattah Lakes, north-western Victoria for a considerable period. Widespread clearing of mallee in the Murray region has allowed *flavigula* to penetrate deeply into the range of *melanotis* to such an extent that genetic swamping is now widespread (Schodde 1981; Joseph 1986). The original zone of contact or steep intergradation was

apparently along the Murray from north-western Victoria to where it turns south in South Australia. Note: though *melanotis* is currently treated as a species in RAOU official lists (Schodde 1975), it appears to have species recognition signals not unlike those of *flavigula* as demonstrated by the extensive interbreeding between them.

Lichenostomus versicolor and *fasciocularis* Varied and Mangrove Honeyeaters.

The mangrove inhabitants *versicolor* of north-eastern coast and *fasciocularis* of eastern coasts intergrade steeply in colouration near Townsville (Ford 1978b).

Lichenostomus leucotis White-eared Honeyeater.

The small, western *novaenoriae* intergrades with the large, coastal-eastern *leucotis* on the eastern edge of the 90-Mile Plain (Ford 1971). This hybrid zone probably extends into New South Wales but has not been localised.

Lichenostomus melanops Yellow-tufted Honeyeater.

No integral segment of the ring series of subspecies *meltoni*, *melanops*, *gippslandicus* and *cassidix* in south-eastern Australia apparently originated by hybridisation because each form is fairly uniform rather than variable (Crome 1973). Ring contact between *cassidix* and *meltoni* is probably only occasional and arises from vagrant *meltoni* wandering coastally southward across cleared parts of the Great Dividing Range north of Melbourne.

Lichenostomus fuscus and *flavescens* Fuscous and Yellow-tinted Honeyeaters.

These allopecies replace each other along the northern edge of the Einasleigh Uplands and Burdekin-Lynd Divide (Ford 1986).

Lichenostomus penicillatus White-plumed Honeyeater.

Whether the extraordinary geographical variation in this species involved past splitting and rejoining of populations has not been determined. Large, dark greenish birds in southern Victoria-Mt. Lofty Range (*mellori*) give way to slightly paler ones in inland south-eastern Australia (*penicillatus*) and smaller, more yellowish birds in inland Australia west to the Kimberley and Pilbara (*leilavalensis*) and finally to slightly darker birds in coastal western Australia (*carteri*) (Condon 1954; pers. obs.). This variation could be ascribed to ecotypic adaptation arising from Gloger and Bergmann effects but for the fact that this species must have been fragmented during the last glacial aridity. A zone of secondary intergradation, since blurred by strong gene exchange, might have occurred near the contact between the magpies *tibicen* and *leuconota*.

Melithreptus gularis Black-chinned Honeyeater.

A pronounced change in facial-skin colour occurs along the northern side of the Einasleigh Uplands and Burdekin-Lynd Divide between the south-eastern *gularis* and northern *laetior*. Though *gularis* becomes progressively more yellowish dorsally in the northern half of its range and so approaches *laetior* in plumage colour, its facial skin remains aqua-blue whereas that of *laetior* is yellow-green (Ford 1986).

Pardalotus punctatus and *xanthopygus* Spotted and Yellow-rumped Pardalotes.

Contact zones between these semispecies lie in south-western and south-eastern Australia where sclerophyll forests and mallee woodlands abut. The forest form *punctatus* mainly differs from *xanthopygus* in having a buffy suffusion on the abdomen and on the dorsal pale-spots, and a chestnut-buff rather than yellow-rump. Milne's (1936) remark that they intergrade near Bendigo was confirmed by Woinarski (1984) who found five mixed pairs in a

group of seven nesting pairs and a number of intermediate immatures in this area. Hybrids have also been collected in lower south-eastern South Australia (Parker & Reid 1983), western Victoria (Short *et al.* 1983), 90-Mile Plain (Short *et al.* 1983c) and the Mt. Lofty Range (Parker, pers. comm.; Short *et al.* 1983c). In south-western Australia some intermediates have been collected, but there appears to be no hybrid zone (Ford unpubl.). Hybridisation in eastern Australia may have been facilitated by widespread clearing of forests and mallee because an enclave of *xanthopygus*, apparently untainted by the locally widespread *punctatus*, formerly occurred near Adelaide (Storr pers. comm.). Ford (1971b) suggested *punctatus* and *xanthopygus* arose in the south-east and south-west respectively and then expanded west and east but the new evidence on their interaction suggests another possibility: a continuous *punctatus*-like ancestor became split into three isolates, the south-western and south-eastern remaining as *punctatus* under stabilising selection induced by similar climatic regimes, and the central isolate (in the Mt. Lofty-Eyre Peninsula refugium of arid times) evolving into *xanthopygus* (Ford unpubl.).

Pardalotus striatus Striated Pardalote.

Three di-hybrid zones and a tri-hybrid zone occur in eastern Australia. Two subspecies of the black-crowned group, the northern yellow-rumped *uropygialis* and the coastal eastern Queensland, cinnamon-chestnut-rumped *melanocephalus* have hybridised and produced a variably intermediate swarm on the base of Cape York Peninsula (Salomonsen 1961; Ford 1986). Two subspecies of the striped-crowned group, the south-eastern *ornatus* and western *substriatus*, differing mainly in the amount of white edging on the primaries, freely interbreed and hybridise along the western margins of the Great Dividing Range (Cooper 1961; Woinarski *et al.* 1983). Black-crowned *melanocephalus* and stripe-crowned *substriatus* hybridise more or less along the Great Dividing Range in south-eastern Queensland between Charleville and Emu Vale (Lord 1956; Salomonsen 1961; Macdonald 1969a). Various hybrid combinations of *melanocephalus*, *ornatus* and *substriatus* occur where their ranges meet around the Queensland-New South Wales border (Grosper 1964; Macdonald 1969a; Storr 1984); hybrids and pairings between *melanocephalus* and *ornatus* are certainly known from Chinchilla, Emu Vale and Grafton. Salomonsen (1961) proposed a hybrid origin for *ornatus* but this was dismissed by Hindwood & Mayr (1946) and Mees (1965).

Zosterops lateralis Silvereye.

There are three zones of intergradation in this southern and eastern coastal species (Mees 1969). On the eastern side of the Great Australian Bight, the western yellow-throated, uniformly green-backed *gouldi* hybridises narrowly with the grey-throated, grey-backed *halmaturina* of South Australia. Along a zone running northward just east of Melbourne, *halmaturina* intergrades broadly with the yellow-throated *familiaris* (= *westernensis*) of eastern Australia. The north-eastern Queensland subspecies *ramsayi* is generally smaller and more yellow on the under-tail coverts than *familiaris* and smoothly intergrades with it in the region of Mackay (Mees 1969), so intergradation is presumably primary (Storr 1973).

Emblema temporalis Red-browed Firetail.

In the vicinity of Cooktown, the grey-naped, white-throated *minus* of the Cape York Peninsula lowlands is altitudinally replaced on uplands by the generally darker plumaged *temporalis* of coastal south-eastern Australia (Storr 1984; Ford 1986). The nominate form becomes slightly more pallid in north-eastern Queensland (Keast 1958c) but the major change in the species is at the southern end of the Normanby Barrier.

Poephila bichenovii Double-barred Finch

Variable hybrid populations between the north-western, white-rumped *annulosa* and the north-eastern, black-rumped *bichenovii* occur at Borroloola, McArthur River, and Alexandria, Barkly Tableland (Keast 1958c).

Poephila cincta Black-throated Finch.

A hybrid population, straddling the Burdekin-Lynd Divide and Einasleigh Uplands, and consisting of birds with variable amounts of black and white on the rump, links the black-rumped *atropygialis* of Cape York Peninsula and white-rumped *cincta* of coastal-eastern Queensland (Keast 1958c; Ford 1986).

Poephila acuticauda and *cincta* Long-tailed and Black-throated Finches.

Long-tailed, white-rumped *P. acuticauda* extends across tropical northern Australia east to the middle Leichhardt while the short-tailed, black-rumped *P. c. atropygialis* extends west to the lower Leichhardt (Storr 1984; Ford 1986), so they probably meet.

Poephila acuticauda Long-tailed Finch.

Harrison (1974) implies that intergradation between yellow-billed *acuticauda* of the Kimberley and red-billed *hecki* of the Northern Territory is fairly steep whereas Immelmann (1965) believes it is gradual in this woodland-savanna species.

Lonchura flaviprymna and *castaneothorax* Yellow-rumped and Chestnut-breasted Mannikins.

Immelmann (1962) suggests that the interaction between these forms in the Ord and Victoria River valleys may be secondary overlap with hybridisation over a wide area. Storr (1980) points out that *castaneothorax* invaded the Ord valley this century.

Sphecotheres viridis Figbird.

A variable hybrid population in the coastal Burdekin lowlands connects the yellow-throated *flaviventris* of northern Queensland with the grey-throated *vieilloti* of coastal eastern Australia (Ford 1982b). The hybrid zone is some 370 km deep. Hybrid phenotypes, which include white-throated types, suggest that two diallelic loci code the differences in throat colouration (Ford 1982b).

Chlamydera nuchalis Great Bowerbird.

Geographic variation in this species is essentially clinal except for a pronounced step between north-eastern, more variegated *orientalis* and north-western, more uniformly coloured *nuchalis* between the Flinders and Leichhardt Rivers (Mayr & Jennings 1952).

Artamus cinereus Black-faced Woodswallow.

The white-vented *albibentris* of eastern and northern Queensland and the black-vented *melanops* of western and arid Australia hybridise along a line from the head of the Gulf of Carpentaria

down the inland side of the Great Dividing Range to the Darling Downs. Birds in the hybrid zone have various amounts of black and white on the vent and undertail coverts (Ford 1978d).

Strepera versicolor Grey Currawong.

The south-eastern *versicolor* and former Mt. Lofty isolate *melanoptera* are connected by a variably hybrid population in western Victoria and adjacent part of South Australia (Amadon 1951; J. Dell pers. comm.). Grey-plumaged *versicolor* has a large white wing-speculum, blackish *melanoptera* has no white patch and hybrids have intermediate characteristics.

Strepera graculina Pied Currawong.

The large-billed *magnirostris* of Cape York Peninsula is abruptly replaced by *graculina* on the uplands of north-eastern Queensland (Ford 1986).

Cracticus nigrogularis Pied Butcherbird.

Large-sized *nigrogularis* extends narrowly from the Pilbara along the pindan margin of the Eighty-Mile Beach to the south-west Kimberley where it intergrades with the small, northern *picata* (Mees 1964a).

Gymnorhina tibicen Australian Magpie.

A hybrid zone occurs between northern, black-backed *tibicen* and south-eastern, white-backed *leuconota* from south-eastern New South Wales, through central Victoria to east of the Mt. Lofty Range and across northern Eyre Peninsula (Burton & Martin 1976; Condon 1954) and another between *tibicen* and south-western *dorsalis* through the Murchison region (Ford, unpubl.). Hughes (1982) suggested the difference between *tibicen* and *leuconota* was based essentially on two diallelic unlinked loci, *tibicen* being homozygous white, *leuconota* homozygous black, and alleles coding for black dominant over white and cumulative in expression. Genetic differences between *tibicen* and *dorsalis* are not so simply explained because male *dorsalis* is white- and female *dorsalis* broadly black-backed and some female hybrids are like *leuconota* (Black & Ford 1982).

Corvus coronoides Australian Raven.

Rowley (1970) stated that Eyre Peninsula birds are like south-western ones in size and generally smaller than eastern. He also suggested the size difference between eastern and western *coronoides* had possibly evolved by character displacement in the eastern population through competitive interactions with sympatric *C. mellori*. An alternative explanation is that the western (*perplexus*) and eastern populations underwent divergence while isolated by the Eyrean Barrier during the last glaciation. The intermediate size of South Australian birds suggest, therefore, that there might be a steep step in size between *perplexus* and nominate *coronoides* in eastern South Australia.