

SPECIATION IN AUSTRALIAN BIRDS ADAPTED TO ARID HABITATS

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SUMMARY

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Several stages of speciation can now be identified in some birds occurring mainly in the mulga habitat of the arid parts of Australia. Speciation in birds adapted to the stony and *Triodia*-sandhill deserts has occurred more commonly than previously suspected. Only sedentary birds of the mulga and desert habitats have produced differentiated isolates. The Eyrean Barrier has played an important role in the production of species adapted to arid conditions from those adapted to mesic conditions and in the speciation of inhabitants of the mulga. Some isolates of desert species may have been formed during pluvial periods in the Pleistocene.

INTRODUCTION

Virtually all examples of speciation in Australia so far investigated have been among forms adapted to wet and semi-arid conditions (Keast 1961). Geographically such speciation has been caused by fragmentation and isolation of populations in climatically favourable refuges round the periphery of the continent and their subsequent genetic divergence. Opportunities for the break-up of continuously distributed species occurred repeatedly during the Pleistocene as the belts of humidity waxed and waned with the alternations of glacio-pluvial and arid interglacial periods (Gentili 1949; Keast 1961; Serventy 1971).

No such manner of geographical isolation and speciation has been proposed for birds adapted to arid and desert conditions. Thus, Keast (1961:414) stated that neither isolation nor speciation is to be found in birds of the mulga, saltbush and savanna-grassland because tracts of these are continuous or made continuous by interdigitation of the dry-country communities of vegetation. Brereton and Kikkawa (1963) claimed that in the arid inland no means of isolation and re-union exist; and that lack of structural diversity and productivity in inland areas allows little partitioning and sharing of habitat so that species would frequently become extinct through competition, if reunited. Hall (1970) suggested that a climatic phase that produced a shrinking of the desert environment in Australia would leave virtually one arid refuge and so would prevent opportunities for speciation. According to Serventy (1971), a reduction in the size of the arid environment would result in extermination instead of multiplication of species, and selective pressures on surviving forms would promote adaptability rather than specialization.

SPECIATION IN BIRDS OF THE MULGA

Keast (1961:460) stated that there were about twenty-four species confined to mulga (chiefly arid acacia-communities) and adjacent associations of vegetation in the arid part of Australia and that about fifty-nine species occurred mainly in savanna-grassland. Different stages of speciation can now be identified in forms occupying the mulga. In some, one branch (isolate or former isolate) of a speciating pair has undergone a shift in ecology, thus partly obscuring the fact that the habitat of the ancestral population included mulga. The geographical isolation in these inhabitants of the mulga has been caused by the Eyrean Barrier combined with Spencer Gulf. Presumably during extremely dry periods this barrier was more pronounced than it is now and split populations into western and eastern isolates. Kluge (1967) suggested that during Pleistocene pluvials the extremely large Lake Dieri, incorporating Lake Eyre, Lake Torrens and Lake Frome, also operated as a barrier between western and eastern populations of some arid species. This barrier has been further discussed by Serventy (1972), Ford and Parker (1973a) and Harrison (1973).

The following pairs of species and subspecies may have evolved because of the influence of the Eyrean Barrier:

WESTERN	EASTERN
<i>Psephotus varius</i>	<i>P. haematonotus</i>
<i>Psephotus h. haematogaster</i>	} <i>P.h. haematorrhous</i>
<i>P. h. narethae</i>	
<i>Pomatostomus superciliosus</i>	} <i>P. halli</i>
<i>Aphelocephala l. whitei</i>	} <i>A.l. leucopsis</i>
<i>A. l. castaneiventris</i>	
<i>Malurus splendens callainus</i>	<i>M.s. melanotus</i>
<i>Climacteris a. superciliosus</i>	<i>C.a. affinis</i>
<i>Psophodes occidentalis</i>	<i>P. cristatus</i>

Psophodes occidentalis and *P. cristatus* (Fig. 1a) provide a beautiful example of incipient speciation caused by the effect of the Eyrean Barrier (Ford and Parker 1973a), the eastern form *cristatus* having undergone a shift in habitat from arid acacia to low shrub-communities. *P. occidentalis* and *P. cristatus* have strikingly different songs but have few morphological differences. Eastern isolates of *Pomatostomus superciliosus* stock (Fig. 1b) have apparently twice been formed by the Eyrean Barrier, *P. ruficeps* evolving from the first and *P. halli* from the second. Since then, *superciliosus* has recrossed the Eyrean Barrier at its southern end and apparently outflanked the Simpson Desert in the north (Ford and Parker 1974). *P. superciliosus* occupies a range of habitats (like several other western forms) whereas the species that have budded from it are more specialized, *P. ruficeps* inhabiting open arid scrub and *P. halli* dense mulga-communities, particularly in stony terrain. Macdonald (1969) has drawn attention to subspeciation in *Climacteris affinis* (Fig. 1c).

Other pairs of which the western form has presumably moved east across the former barrier are *Psephotus varius* – *P. haematonotus* (Fig. 1d) and *P.h. haematogaster* – *P.h. haematorrhous* (Fig. 1e). Competition after re-contact may have accentuated changes in habitat adopted by each member of these pairs, because the western forms, *varius* and nominate *haematogaster*, favour arid acacia-habitats whereas the eastern, *haematonotus* and *haematorrhous*, inhabit respectively open eucalypt grasslands and associations of *Casuarina* – *Callitris* in semi-arid areas. *Neophema splendida* and *N. pulchella* provide another example of a pair that may have had an analogous evolutionary history, but *splendida* and *pulchella* occur in mainly eucalypt communities, not in acacia ones.

Acanthiza robustirostris (Fig. 1g) inhabits mulga; a population is apparently isolated east of the Eyrean Barrier in central western Queensland, which has not differentiated (Ford and Parker 1973b), but the stage is set for speciation. Storr (1973) has indicated that *Oreoica gutturalis*, a typical inhabitant of mulga, has an isolated population in eucalypt forest in inland eastern Queensland, which Mayr (1953) has indicated may be subspecifically distinct.

Three western members of pairs adapted to arid conditions have presumably been further split by a barrier consisting of the Nullarbor Plain and Great Victoria Desert. These are *Psephotus haematogaster*, *Aphelocephala leucopsis* (Fig. 1f) and *Malurus splendens* (Fig. 1m). *P. haematogaster* has the subspecies *narethae* and *haematogaster* roughly on the western and eastern sides of this barrier respectively; *A. leucopsis* has *castaneiventris* and *whitei*; and *M. splendens* has *splendens* and *callainus*.

Inhabitants of mulga and savanna-grassland with no isolated populations (at the undifferentiated, sub-specific or allospecific levels) are: *Turnix velox*, *Geopelia cuneata*, *Phaps histrionica*, *Nymphicus hollandicus*, *Neophema bourkii*, *Melopsittacus undulatus*, *Chrysococcyx osculans*, *Pteropodocys maxima*, *Artamus personatus*, *Artamus superciliosus*, *Ephthianura tricolor*, *Certhionyx niger*, *C. variegatus*, *Phylidonyris albifrons*, *Conopophila whitei* and *Acanthagenys rufogularis*. These species are nomadic, moving through most of the central regions of the continent. Presumably all except perhaps *Conopophila whitei* have been able to cross the geo-geographical barrier that allowed various degrees of speciation in sedentary forms like *Psophodes* spp, *Climacteris affinis* and *Pomatostomus* spp. Some partly migratory and sedentary species, for example *Petroica goodenovii*, *Acanthiza uropygialis* and *Pyrholaemus brunneus*, which extend from west to east across the arid region of the continent, however, have not produced isolates or differentiated former isolates; such species may be fairly recent colonists of inland eastern Australia from west of the Eyrean Barrier, or all evidence of past isolation between western and eastern populations of these species may have been obliterated by secondary contact.

SPECIATION IN BIRDS OF THE DESERTS

Species adapted to the stony (gibber) deserts and *Triodia*-sandhill country are usually considered to represent the only truly desert elements of the Australian avifauna (e.g. Keast 1961). Only *Amytornis* has been shown to be a genus in which speciation has occurred within the desert. Keast did not regard speciation as having occurred in desert forms of the genera *Cinclosoma*, *Stipiturus* and *Aphelocephala* but only *Eremiornis carteri* and *Ashbyia lovensis* of the characteristic desert passerines have not produced a morphologically distinct isolate or former isolate in the desert.

Cinclosoma cinnamomeum. This complex (Fig. 1h) probably consists of four distinct morphological forms (Ford 1974); *marginatum* in stony terrain overtopped with mulga in the mid-western part of the continent; *castaneothorax* in similar habitat in the inland parts of eastern Australia; nominate *cinnamomeum* in gibber country with light shrub-cover in the Lake Eyre basin; and *alisteri* in shrub steppe and limestone gibbers of the Nullarbor Plain. Two taxa, *alisteri* and *marginatum*, are probably isolated, whereas *cinnamomeum* and *castaneothorax* are in secondary contact in central western Queensland (Ford 1974).

Stipiturus ruficeps. This inhabitant (Fig. 1i) of *Triodia* has a morphologically distinct isolate, *mallee*,

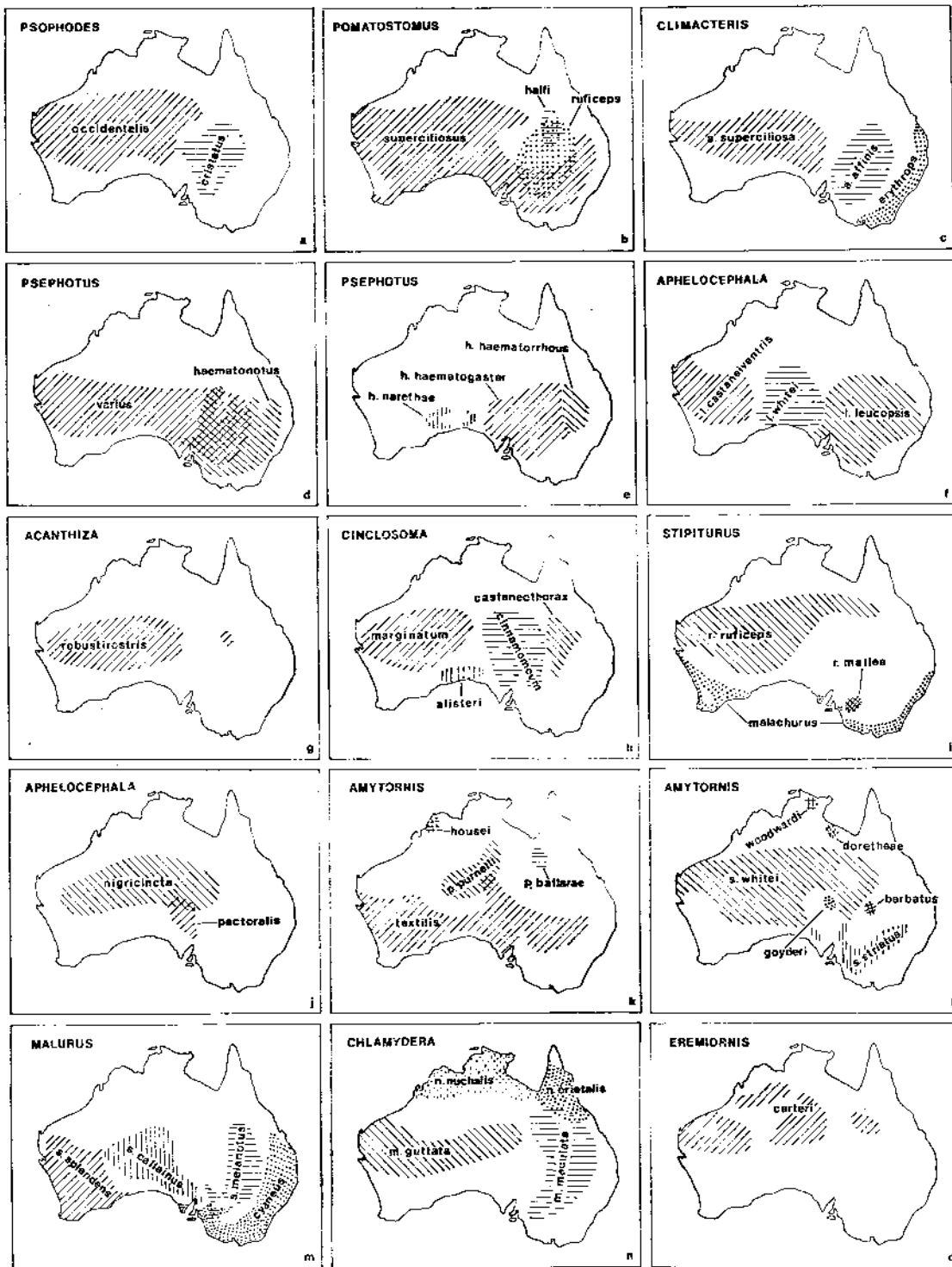


Figure 1. Maps of distributions of birds adapted to arid habitats, with some wet-country species.

in north-western Victoria and adjacent parts of South Australia, where its habitat is overtopped with mallee-eucalypts. Presumably the splitting of this species into two subspecies was caused by the Eyrean Barrier, but either a wet or dry period could have created the barrier. Keast (1961) did not include *S. ruficeps* in the group of actively speciating desert birds because he considered *mallee* to be a derivative of *S. malachurus*, a wet-country species, but Serventy (1953), Ford (1970a) and Ford and Parker (1974) considered *mallee* to be closely related to *ruficeps*.

Aphelocephala nigricincta - *A. pectoralis*. These species (Fig. 1j) are sympatric in the western part of the Lake Eyre basin. Both inhabit stony deserts but *nigricincta* also occurs in *Triodia*-clad dune-deserts. Their morphological similarity (both species have a breast-band though this is differently coloured, and they are rufous on the dorsum) suggests that they constitute a superspecies overlapping secondarily rather than that they are separate descendants of *A. leucopsis* stock. Presumably *pectoralis* evolved in the Lake Eyre region and *nigricincta* in the stony deserts of the mid-western part of the continent.

Amytornis textilis - *A. purnelli*. Parker (1972) has shown that *textilis* and *modestus* are conspecific and that *purnelli* is a separate species (pace Keast 1958a, 1961). They form a superspecies (Fig. 1k) overlapping secondarily in central Australia. Their habitats are quite different, *textilis* living mainly in country covered with saltbush, bluebush and cottonbush (with or without a stratum of trees), and *purnelli* inhabiting mountainous terrain clad with *Triodia*. *A. purnelli* has colonized north-western Queensland (area of Selwyn Range), where it has produced the slightly differentiated subspecies *ballarae* (Condon 1969; Carruthers *et al.* 1970), presumably by crossing the valley of the Georgina River (the northernmost part of the Eyrean Barrier) or by expanding eastwards across the Barkly Tableland when this area was more suitable. *A. housei*, in the rugged *Triodia*-clad mountainous region of north-western Kimberley, is possibly a member of the *textilis* species-group but the trend of increasing melanization in *A. striatus*, *A. dorotheae*, *A. woodwardi* and *A. housei* tends to suggest that *housei* is a member of the *striatus* group. An investigation of biochemical characters would help to elucidate its taxonomic position. The Hamersley Range provides a niche for a rock-inhabiting *Amytornis* but only *A. striatus* has been observed there (in *Triodia*).

Amytornis striatus - *A. goyderi* - *A. barbatus*. The parental form of this trio, *striatus*, (Fig. 1l) inhabits *Triodia* and other tall rank grasses growing in tufts and ranges widely through the arid parts of the continent. It probably has no subspecific isolates (Ford

and Parker 1974), but the intergradation between the subspecies *whitei* and *striatus* may be secondary. Probably a population of *striatus* was at one time isolated where *Stipiturus ruficeps mallee* now is. In the *striatus* species-group there are two species, *goyderi* and *barbatus*, in the centre of the continent and two, *dorotheae* and *woodwardi*, in *Triodia*-clad sandstone ranges in the north of the continent. Keast (1961) suggested that the northern species reached their present domains when *Triodia* extended much further north from the arid centre and replaced savanna-grassland. He (1958a) placed *goyderi* in the *textilis* group but it apparently belongs to the *striatus* group on morphological evidence (Parker 1972) and *barbatus* had not been discovered when he made his study. Both *goyderi* and *barbatus* have apparently undergone shifts in habitat, the former occurring in canegrass *Zygochloa paradoxa* on the northern edge of Lake Eyre (Morgan *et al.* 1961) and the latter in canegrass *Eragrostis australasica* and lignum *Meuhlenbeckia cunninghamii* in the overflow channels (Bulloorine) of the lower Bulloo River (Favaloro and McEvey 1968). Gentilli (1961) suggested that the main block of arid and semi-arid country occurred west of the central Australian highlands in Pleistocene glacio-pluvial periods. So, *goyderi* and *barbatus* were possibly formed during a pluvial period when *Triodia*-sandhill habitat and the distribution of *A. striatus* contracted to the central western part of the continent leaving behind small pockets in the Simpson Desert and the Bulloorine.

As with birds of the mulga, inhabitants of the stony and *Triodia*-sandhill deserts and desert steppe that have speciated are sedentary. Nomadic desert dwellers like *Polytelis alexandrae*, *Pezoporus occidentalis* and *Ephthianura aurifrons* have apparently been unable to produce isolated populations with the potential to speciate because any isolation has presumably been temporary.

Ashbyia lovensis is confined to the gibber plains of the Lake Eyre basin. Colonization of the Nullarbor Plain would possibly provide an opportunity for it to speciate but apparently it has been unable to cross the south-eastern arm of the Great Victoria Desert. *Eremiornis carteri* (Fig. 1o) is confined to the *Triodia*-habitat but only where it is tall and lush as in hilly and mountainous terrain where there are numerous small watercourses. *E. carteri* has undifferentiated isolates on several large islands off the coast of Western Australia (Mees 1961) and on the mainland (Ford and Parker 1974). The species is possibly partly nomadic because its numbers appear to increase in arid areas that have recently received cyclonic rains (N. Ives pers. comm.), which may explain why birds from north-western Australia, central Australia and north-western Queensland are

morphologically indistinguishable. Interestingly, the sedentary *Malurus leucopterus* has differentiated isolates on two islands (Barrow and Dirk Hartog) off the coast of Western Australia but shows little variation throughout its mainland range, the arid western and central parts of the continent.

PRODUCTION OF ARID FROM MESIC SPECIES

No one has proposed geographical pathways that could have allowed species adapted to arid conditions to form, though often such species have clearly been derived from wet-country ancestors. Some arid species like *Oreoica gutturalis*, *Eremiornis carteri*, *Nymphicus hollandicus* and *Melopsittacus undulatus* belong to monotypic genera and have no close relatives whereas others like *Polytelis alexandrae*, *Chrysococcyx osculans*, *Stipiturus ruficeps* and *Climacteris affinis* have allospecific relatives in humid or subhumid parts of the continent. Both the Eyrean Barrier combined with Spencer Gulf and the Nullarbor Plain combined with the Great Victoria and Gibson Deserts have probably been involved in the production of arid forms from southern wet-country (Bassian) ancestors. Pathways for adaptation to mulga and *Triodia*-habitats can be understood by analysing present-day patterns of distribution and speciation. Keast (1958b) has already outlined a possible pathway for the evolution of semi-arid (Eyrean) species inhabiting mallee from Bassian ones.

Pathway to mulga as indicated by the Malurus-cyaneus group.

Malurus splendens (Fig. 1m) is presumably an old western derivative of the wet-country form, *M. cyaneus*. Probably it became isolated in south-western Australia during an early Pleistocene arid interglacial when the Nullarbor Plain operated as a barrier. As with many other western members of east-west pairs (e.g. *Cinclosoma castanotum*, *Acanthiza apicalis*, *Gerygone fusca*, *Neositta chrysoptera pileata*, *Pardalotus striatus substriatus*, *Psophodes nigrogularis*, *Sericornis frontalis maculatus* and *Hylacola cauta*), *splendens* has become more gener-

alized in its adaptations and has expanded into a wider range of habitats than its eastern relative. Keast (1958b) and Ford (1971b) have suggested that this ecological versatility was promoted by the climate in south-western Australia (characterized by very wet winters and extremely dry hot summers), the reduction in competition arising from a depauperate fauna, the graduation of habitats from humid to dry rather than their demarcation, and the compression of the humidity refuge in the south-west during arid periods when selective forces would have induced adaptation to dry conditions. These adaptations together with climatic amelioration following divergence presumably allowed *splendens* to expand eastwards across the Nullarbor and Eyrean barriers. A subsequent return to arid conditions, which increased the severity of these barriers, split *splendens* into three populations, the eastern ones *callainus* and *melanotus* occupying mainly mulga. The subspecies *callainus* has become a member of the fauna of the arid zone and now ranges through the Gibson and Great Victoria Deserts and the deserts encircling the mountain ranges of central Australia. *Callainus* has become partly nomadic (Ford pers. obs.), whereas nominate *splendens* and possibly *melanotus* are sedentary.

Gerygone fusca, a western derivative of *G. olivacea* (Ford in prep.), has been similarly broken up into three populations (Fig. 2a) but these have diverged only slightly in morphology and ecology. The process has apparently proceeded further in *Barnardius zonarius* (Fig. 2b): for, in this the former central isolate *zonarius* is in secondary contact with *barnardi* (Cain 1955), once isolated in the eastern inland, and also with the former south-western isolate *semitorquatus*. In expanding westwards, *zonarius* probably displaced *semitorquatus* from dry habitats in the western parts of the continent.

Harrison (1972) suggested that *Malurus assimilis* evolved from an isolate in a humidity refuge centred in the Hamersley region of Western Australia. However, the similarity in the distributions of *M. assimilis* and the *M.-splendens* complex, and the pathway of

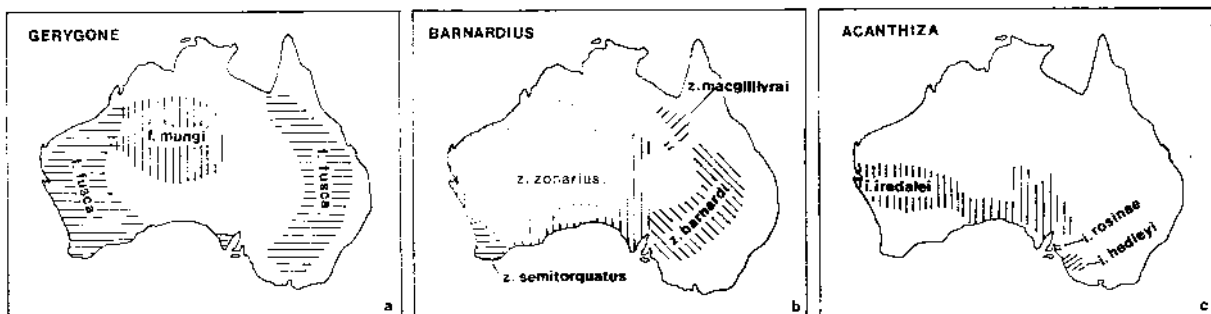


Figure 2. Maps of distributions of birds adapted to arid habitats.

speciation in *M. splendens*, suggest that *assimilis* may have evolved in the central east of the continent, perhaps in mulga and mallee communities in the area occupied by *M.s. melanotus*. Clearly the forms *M.d. dulcis*, *M.d. rogersi*, *M. amabilis*, *M. lamberti* and *M. elegans* originated in their present centres of distribution, but, as Harrison has suggested, *M. pulcherrimus* probably originated on Eyre Peninsula and has since invaded southern Western Australia, perhaps displacing *M. elegans* from drier habitats there. An analogous evolutionary sequence has been suggested to explain the origin of two subspecies of *Sericornis frontalis* in south-western Australia (Ford 1970b).

Pathway to mulga as indicated by Climacteris affinis.

C. affinis (Fig. 1c) is the arid-country representative of the *C. erythropus* superspecies (Keast 1957a). *C. erythropus* is confined to wet-sclerophyll eucalypt forest in south-eastern Australia, *C. affinis* occurs in mulga throughout central Australia and there is no semi-arid representative. Presumably *C. affinis* evolved from the parental *C. erythropus* in the western part of the continent during an arid phase. As in *Malurus splendens*, the precursor of *affinis* evolved marked versatility of habitat and presumably expanded from eucalypt into mulga communities, particularly as the climate improved during a subsequent pluvial. However, this or a later climatic improvement allowed wet-country and semi-arid birds of south-eastern Australia to re-invade the south-western part of the continent and *C. picumnus* stock arrived. Subsequently a population of this latter inhabitant of savanna-woodland became isolated in the south-west, evolved into *C. rufa* and presumably displaced *C. affinis* from eucalypt communities. *C. affinis* and *C. rufa* now appear to be ecologically exclusive (Serventy and Whittell 1948; Ford 1965, 1971a) but competition was possibly the final selective force that precipitated a species completely adapted to arid conditions.

Pathway to Triodia as indicated by the Stipiturus-malachurus superspecies.

The genus *Stipiturus* (Fig. 1i) consists of two allopatric species. *S. malachurus* inhabits sub-marshy heath in coastal south-eastern Australia, and sub-marshy and semi-arid heath in south-western Australia. *S. ruficeps* occurs in *Triodia* in the arid western and central parts of the continent, and in *Triodia*-mallee sandhill country in inland south-eastern Australia. Presumably *ruficeps* budded from a south-western ancestor because its distribution is essentially western. Possibly it originated in inland south-eastern Australia because *S. r. mallee* of this area forms a morphological and ecological link between *S. ruficeps* and *S. malachurus* (Keast 1957b); *mallee* has blue on the head like nominate *ruficeps* and dorsal streakings like *malachurus*. Presumably the ancestral form

was distributed right across the southern part of the continent but became divided into western and eastern isolates by increasing aridity across the Nullarbor Plain. Subsequently the western proto-*ruficeps* expanded inland and eastwards, and occupied dry habitats including associations of *Triodia* and low heath. During the pluvial that facilitated an expansion of proto-*ruficeps*, or perhaps a later wet phase, the south-western corner of the continent was re-invaded by parental *malachurus*. That the present-day south-western isolate of *malachurus* was able to occupy a diversity of habitats (i.e. semi-arid heath as well as wet-country heath) indicates that *ruficeps* had already undergone a complete displacement in its habitat requirements.

Pathway to arid habitats as indicated by Chlamydera maculata.

This species (Fig. 1n) is distributed from west of the Great Dividing Range to the mid-western part of the continent via the mountainous region of central Australia. There are two distinct taxa (here treated as subspecies but by some authors as species), which may be in secondary contact in the region of the Georgina River valley (see Ford and Parker 1974). The eastern *maculata* occurs mainly in riverine woodland, whereas the western *guttata* also occurs often in scrub thickets in mountain and break-away areas and its distribution is largely determined by *Ficus platypoda*, the fruit of which forms an important part of its diet (Serventy and Whittell 1948). Apparently *guttata* became adapted to drier habitats when it was geographically isolated in the arid western part of the continent. Presumably *C. nuchalis* of northern Australia and *C. maculata* were derived from the same stock; in fact they may be ranked as a superspecies. The ancestral form could have colonized north-western Australia (Pilbara region) or inland eastern and inland north-eastern Australia, and so given rise to *C. maculata*, because northern species demonstrate both patterns of distribution and speciation.

Serventy and Whittell (1948 : 44) and Kikkawa and Pearse (1969 : 836) have suggested that the Eyrean fauna is more closely related zoogeographically to the Bassian than to the Torresian wet-country fauna. This is borne out by the fact that more species adapted to dry conditions have southern wet-country rather than northern wet-country ancestors. Presumably the climatic vicissitudes of the Pleistocene favoured displacements in adaptations to arid habitats among southern birds.

It may seem that species of *Amytornis* had a northern origin because they are distributed only in the Eyrean and Torresian regions but Keast (1958a) suggested that *A. housei*, *A. woodwardi* and *A. dorothae* were derived from desert species. I agree with this because these northern species seem to be relics

of populations formerly widespread during an arid period. *Amytornis* is obviously an old Australian genus whose area of origin will probably remain obscure. Its relationships are discussed by Harrison (1969).

Malurus leucopterus of the arid and semi-arid parts of the continent is presumably a derivative of the stock that produced the New Guinean *M. alboscapulatus* or the Torresian *M. melanocephalus* because these three species are more closely related to each other than to any other species of *Malurus*. This group of species would be expected to have a Bassian representative if *leucopterus* had evolved by a southern pathway. *Eremiornis carteri* may have had a northern origin. Of all Australian birds, presumably *carteri* is most closely related to *Megalurus* (Ford and Parker 1974), which has a predominantly northern and extra-northern distribution except for one species *M. gramineus*. However Galbraith and Galbraith (1962 : 53) consider it to be more closely related to *Buettikoferella bivittata* of Timor and *Megalurulus marei* of New Caledonia.

Keast (1961) included *Geophaps plumifera* and *Emblema picta* in a group of species living in miscellaneous habitats, but their habitat (ranges and rocky gullies with *Triodia* and some surface water) might best be classified as arid. Certainly these species are mainly distributed in arid parts of the continent. The other three species of the genus *Emblema* are members of the southern wet-country fauna; so, *E. picta* may have had a southern origin, but *G. plumifera* is presumably of northern derivation because other members of this genus are Torresian. *Phaps histrionica* of the desert-grassland is also probably of northern origin though the other two species of *Phaps* are Eyrean-Bassian.

In the honeyeater genus *Meliphaga*, the species *cratitia*, *keartlandi*, *penicillata*, *ornata*, *plumula*, *fusca* and *flavescens* form a closely related group. Keast (1961 : 385) stated that current patterns of distribution indicate that *fusca* arose in the east, *flavescens* in the north (Kimberley — Northern Territory), and *ornata* and *cratitia* in the south of the continent. He did not comment on the evolution of the two arid-country representatives, *plumula* and *keartlandi*, which live mainly in low eucalypt-trees and mallees, nor on the evolution of *penicillata*, which inhabits riverine eucalypt-woodland in arid country and also in sub-humid south-eastern Australia. Possibly *plumula* and *keartlandi* evolved from southern ancestors as they are most closely related to *ornata* and *cratitia* respectively. *Kearlandi* may have arisen in the Hamersley or central highland region but where *plumula* arose is obscure.

WIDELY RANGING SPECIES

Several southern species with distributions extending well into the interior of the continent could have been split into western and eastern populations by the Eyrean Barrier during a past period of severe aridity or a pluvial period when Lake Dieri was full. Serventy and Whittell (1948 : 53) pointed out several dry-country (Eyrean) and widely distributed wet-country (Bassian) species with western and eastern subspecies on opposite sides of a line running north from Spencer Gulf but were unable to account for their separation. Recently Serventy (1972) invoked only Lake Dieri as possibly having caused the dichotomies and overlooked the possibility of very severe aridity as having the same effect. Presumably the Eyrean Barrier divided *Barnardius zonarius* into *B. z. zonarius* and *B. z. barnardi*, *Colluricincla harmonica* into *C. h. rufiventris* and *C. h. harmonica*, *Climacteris picumnus* into *C. [p.] rufa* and *C. [p.] picumnus*, *Chlamydera maculata* into *C. m. guttata* and *C. m. maculata*, and *Manorhina flavigula* into *M. [f.] flavigula* and *M. [f.] melanotis*.

In the past the Eyrean Barrier and Spencer Gulf apparently combined to cause several southern wet-country species to evolve into two species (or subspecies), a western one occupying both wet and dry habitats and an eastern one occupying essentially wet-country habitats. These west-east pairs (called Eyrean-Bassian pairs by Serventy and Whittell (1948 : 48)) include *Cinclosoma castanotum* — *C. punctatum*, *Acanthiza [p.] apicalis* — *A. [p.] pusilla*, *Gerygone fusca* — *G. olivacea*, *Neositta c. pileata* — *N. c. chrysoptera*, *Pardalotus striatus substriatus* — *P. s. striatus*, and *Strepera v. plumbea* — *S. v. versicolor*. Frequently the western form has crossed the former barrier and spread eastwards, sometimes to the western edge of the Great Dividing Range, giving the impression that the former barrier between these west-east pairs was this range (e.g. Serventy 1953). In these forms there is no example of the eastern member spreading westwards past the barrier into dry-country habitats, a fact illustrating the great ecological versatility of the western member. Apparently the humid-adapted eastern species were usually able to move westwards into the south-western part of the continent only when the Spencer Gulf and Nullarbor barriers broke down in pluvial periods.

Many species confined largely to the semi-arid parts of southern Australia have experienced breaks in their distribution in the region of Spencer Gulf, but it may be argued that the Gulf rather than the arid country to its north operated as the barrier. In birds of mallee (e.g. *Pachycephala gilberti*), heathland (e.g. *Hylacola* spp) and saltbush (e.g. *Acanthiza iredalei*, Fig. 2c), Spencer Gulf has apparently

been more important than the Nullarbor Plain in promoting subspeciation and speciation, because some vegetational communities in the Great Victoria Desert form a corridor north of the Nullarbor Plain between south-western Australia and Eyre Peninsula for many birds adapted to semi-arid conditions (Ford 1971a and c). Their separation by the southern edge of the Nullarbor Plain has also been less effective than that caused by Spencer Gulf. Some aspects of speciation in these birds will be discussed elsewhere.

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