

Patterns of ecological segregation among forest and woodland birds in south-eastern Australia

Richard H. LOYN[#]

Arthur Rylah Institute for Environmental Research Department of Natural Resources & Environment, PO Box 137 Heidelberg VIC 3084 Australia

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Abstract Much information has been gathered on birds of eucalypt forests and woodlands in south-eastern Australia. This was examined to assess some of the mechanisms of ecological segregation that may apply. A database was constructed of 209 species pairs (148 species from 48 genera). Most patterns resemble those reported overseas, with habitat and range featuring as major segregating mechanisms. Use of different strata and substrates was the dominant primary mechanism allowing use of identical space by congeners. Mechanisms such as specific food preferences, migration and choice of nest sites contributed but rarely as primary factors. One species pair appears to show no ecological segregation, despite co-existence in varying proportions over a large geographical range. Indiscriminate interspecific aggression is used by some species to maintain high levels of resources for themselves, in environments that can sustain such resources throughout the year. Communal breeding is a feature of those species. Implications for conservation are discussed.

Key words Birds, Co-existence, Ecological segregation, Eucalypts, Forests, Habitat

Two of the central questions that ecologists endeavour to address concern the number of species that can co-exist in a given habitat or area, and the mechanisms they have evolved to facilitate co-existence (Lack 1971). The questions are of theoretical interest in understanding adaptive radiation and the origin of species (Darwin 1859; Cody 1974; Quammen 1996). They are also of practical interest in our attempts to conserve species in areas of protected habitat that are typically diminished in area, isolated from other reserves and subject to a range of human pressures and threatening processes (May 1978; Diamond 1981; Tilman 1982). It is of special interest to examine these questions in Australia, where both the environment and the bird fauna have many unique features (Ford 1989).

When Lack (1971) presented his global analysis of ecological isolation in birds, much remained to be learned about the basic natural history and ecology of Australian forest birds. Since that time, great advances have been made by professional and amateur biologists, building on the pioneering studies such as

those by Keast (1957, 1968), Kikkawa (1968) and Kikkawa and Pearse (1969). Some studies have focused on ecology of particular species and groups (Ford 1985), while others have examined whole bird communities (Recher 1985). The amateur bird-watching community has grown and its energy has been harnessed to provide distributional data in two national Atlas projects (Blakers et al. 1984; Barrett et al. in prep.), the first attempted on a continental scale. Regional Atlases have been published using these and other data sets (e.g. Emison et al. 1987; Cooper & McAllan 1995). A temporal monitoring project (the Australian Bird Count) has been used with Atlas data to provide new insights on seasonal movements (Clarke et al. 1999; Griffioen 2001). Excellent ecological texts on birds have been published by Rowley (1974), Serventy and Whittell (1976), Keast et al. (1985) and Ford (1989). Data to help conserve threatened taxa have been compiled in an action plan (Garnett & Crowley 2000). Five volumes have been completed for a seven-volume Handbook of Birds of Australia, New Zealand and Antarctica (Marchant & Higgins 1990, 1993; Higgins & Davies 1996; Higgins 1999; Higgins et al. 2001).

Hence new information is available to re-examine

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[#] E-mail: Richard.Loyn@nre.vic.gov.au

patterns of co-existence in Australia. A comprehensive analysis should ideally await completion of the last two volumes of the Handbook, so this paper will focus mainly on aspects familiar to this author, relating to birds that inhabit the eucalypt forests and woodlands of south-eastern Australia, and some more open dry-land habitats in the same region.

This paper takes a mainly descriptive approach, in the belief that ecological understanding needs to be based on a holistic combination of detailed studies at particular sites, and more broad-scale work to put those studies in their proper context. Several authors have recognised the need for a broad-scale approach, to cater for the dynamics of bird communities in space and time (Wiens 1981; Catterall et al. 1997; Clarke et al. 1999); this has led some authors to question the concept of communities as functional units (MacNally 1995). Previous analyses of ecological segregation have focused mainly on detailed studies of small groups of species (Ford 1985, 1989) but such studies tend to be conducted in areas where those species are common, leading to inevitable biases (Clarke 1997). This paper attempts to redress the balance and complement previous work by drawing more on broad-scale surveys and experience than on localised studies of selected species.

SEGREGATION MECHANISMS

Lack (1971) identified three main mechanisms by which closely related species may reduce competition through ecological isolation (range, habitat and feeding or food). Subsequent authors have sub-divided this list in various ways, and have debated the extent to which such mechanisms may arise through co-evolution, coincidence or other mechanisms (e.g. Tilman 1982). Essentially, the mechanisms translate to hierarchical degrees of co-existence and depend upon the degrees to which closely related species have differentiated ecologically. If species are segregated by range, with no overlap, it may be because they have evolved in isolation and never come into secondary contact. This is a common situation with pairs of species inhabiting mainland south-eastern Australia and either Tasmania (separated by Bass Strait, 200 km, since the last Ice Age 10,000 years ago) or south-west Western Australia (separated more recently by arid desert, ~1400 km). Such pairs of species do not need to develop mechanisms for ecological segregation, and evolutionary divergence will occur in response to a range of environmental factors and com-

petitive pressures from non-congeners. If species show some overlap in range, and remain as distinct species, it is instructive to examine segregating mechanisms in the zone of overlap. This may help understand the ecology of the species and the capacity of a habitat to support a diversity of species, regardless of whether the mechanisms have arisen through co-evolution or coincidence.

Often it emerges that these species are segregated by habitat, with substantial overlap in range at the broad scale but little or none at the fine scale. Some habitats are occupied by one species, others by the other, within a mosaic of habitats not easily distinguished in coarse maps of species range. More commonly, there may be some habitats occupied solely by one or other species, and others where the species can be found together. If a particular habitat is potentially suitable for more than one species, random chance, conflict, predation and physical aggression may be involved in determining the occupant of each territory. This form of co-existence is qualitatively different from that where clearly identifiable habitats are selected by each species: it involves random or competitive segregation of horizontal space within a habitat, rather than segregation by differential choice of habitat.

A higher level of co-existence occurs where species actually occupy the same area, at the scale of the individual home range or territory, as mapped on the ground. Maps are two-dimensional and forests have three spatial dimensions and a temporal dimension, so scope remains for such species to reduce competition by using different parts of the forest space or using them at different times. This may involve segregation by foraging height or substrate, or selection of different nesting or roosting sites. Such co-existence contributes to alpha-diversity of a habitat, and may be driven by the capacity of the habitat to support such diversity. Segregation by nesting or roosting sites may only be important where safe and effective nesting or roosting sites are in limited supply. Temporal segregation usually involves seasonal changes in abundance, though use of resources at different times of day is also possible, as are fluctuations in habitat quality between years. The ultimate level of co-existence occurs where species are able to use the same space at the same time in any dimension. Theory postulates that such co-existence is only likely to occur when species take different foods, or differ from each other in major morphological features such as size (Lack 1971; Tilman 1982).

This hierarchy of mechanisms will be used as a framework for examining ecological segregation in forest birds of south-eastern Australia, with its main focus on the eucalypt forests and woodlands of Victoria and adjacent mainland states (South Australia and New South Wales).

STUDY AREA AND METHODS

1) Rainfall and climate

Australia covers a wide range of latitudes, from the tropical north to the temperate south. It is essentially a dry continent, with high rainfall occurring only in the tropical north (during the monsoonal summer wet season), along the east coast and the adjacent Great Dividing Range, in Tasmania and in the south-western corner of Western Australia (Fig. 1). In temperate regions of southern Australia, more rain falls in winter and spring than at other times. Most birds in south-eastern Australia breed in late winter, spring and early summer. Patterns of bird migration and breeding are closely linked to seasonal conditions for plant growth (Nix 1976). Rainfall generally increases with altitude in the Great Dividing Range, and drops rapidly on the inland slopes of that range.

2) Vegetation

Sclerophyllous open eucalypt forests dominate the natural vegetation over most of temperate Australia (Groves 1981). In the mainland state of Victoria, vegetation has been classified and mapped by Ecological Vegetation Class (EVC), based on floristic analysis of understorey and overstorey. This classification has been useful for modelling animal distributions (e.g. large owls, Loyn et al. 2001) but it is too detailed for use at a general descriptive level. A national classification of “bioregions” has been developed by Thackway and Cresswell (1995) using biological and climatic data, and is in use as a planning tool in Victoria through the State Biodiversity Strategy (Government of Victoria 1997). A simpler summary of habitats according to their use by birds was provided by Loyn (1985a), and is further summarised below.

A wide range of eucalypt species grow in the varied coastal and foothill forests, usually as mixed stands containing several species. Stringybark species dominate the ridges and slopes (with some other eucalypts such as Silvertop *E. sieberi*), and peppermints and smooth-barked gums are prominent in the gullies. A high diversity of understorey species may include wattles *Acacia* spp., various shrubs and tangles

of Forest Wire-grass *Tetrarrhena juncea*. Tall shrubs and tree-ferns grow prolifically in wet gullies. Heaths develop on poor or sandy soils, with little or no tree cover and dense understorey dominated by grass-trees or proteaceous plants such as *Banksia* spp. Patches of closed warm temperate rainforest (dominated by non-eucalypts such as Lilly-pilly *Acmena smithii*) occur in damp sheltered gullies where wild-fires are rare. At higher elevations, stands of tall open forest are typically dominated by a smaller number of tree species or a single species such as Mountain Ash *E. regnans*, Alpine Ash *E. delegatensis* or Shining Gum *E. nitens*, with understoreys resembling those of foothill gullies. The trees include the tallest flowering plants in the world, with Mountain Ash growing to over 100 m on occasion. At higher elevations again, multi-stemmed trees of Snow Gum *E. pauciflora* form a low subalpine woodland.

On the drier inland slopes of the Great Dividing Range, mixed foothills forests give way to box-ironbark forests at low elevation, where annual rainfall is between 400–700 mm. Typically these open forests include a range of box eucalypt species along with Red Stringybark *E. macrorhyncha* and either Red Ironbark *E. sideroxylon*, Mugga Ironbark *E. mugga* or Yellow Gum *E. leucoxylon*. Understoreys are usually open, with many herbs, grasses, orchids and scattered shrubs. In the floodplain of the River Murray, forests are dominated by River Red Gum *E. camaldulensis* with open grassy understoreys, relying on seasonal floods for their productivity.

On sandy soils in more arid country, extensive mixed stands of short multi-stemmed mallee eucalypts grow in a band from north-western Victoria and

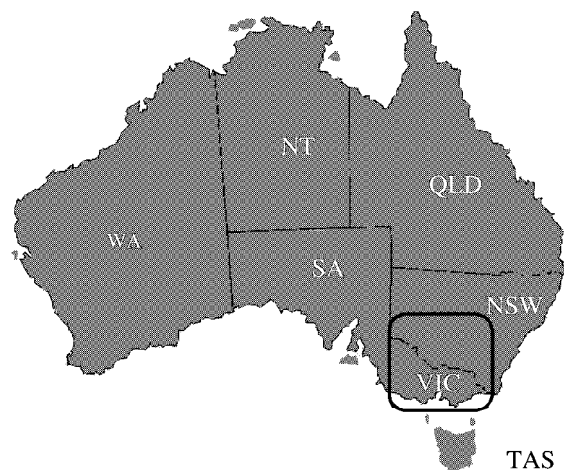


Fig. 1. Map of Australia, showing study region (circled).

south-western New South Wales through to Western Australia in the 300–400 mm annual rainfall zone. Stands of Black Box *E. largiflorens* often grow beside wetlands in these dry environments. Further inland, the vegetation is dominated by treeless chenopod shrublands or wattles such as Mulga *Acacia aneura*, with tall open woodland of River Red Gum growing along watercourses.

In this paper, all vegetation communities with trees are classed as forest or woodland. The discussion extends to include treeless vegetation (e.g. heathland, arid shrubland and cleared farmland), recognising the continuum that exists in the landscape as a result of rainfall gradients and human activities. Warm temperate rainforests occur northwards from eastern Victoria, and support a range of bird species that are not considered in this paper. Throughout south-eastern Australia, the low-lying forests in the 300–700 mm rainfall zone have been most subject to clearing, and forests are now heavily fragmented (Bennett et al. 1998). Forests at higher elevation in the Great Dividing Range are subject to a range of uses including logging, but largely remain as continuous forest. Many areas receive special protection as National or State Parks, or as Special Protection Zones or Special Management Zones within State Forest.

3) Bird fauna

Many Australian bird species are endemic to the Australasian region (Ford 1989; Schodde & Mason 1999). Molecular studies have shown that many major bird families have evolved in this region (which includes New Guinea and New Zealand), despite ecological and morphological similarities to families elsewhere in the world (Sibley & Alquist 1985). Waterbirds are not considered in this paper, although many of them depend heavily on seasonally inundated forests (or forests beside wetlands) for nesting and roosting sites.

4) Methods

This paper reviews some of the literature about ecology of forest birds, along with information based on personal experience. The aim is to document some interesting patterns of co-existence and competitive interactions among Australian forest and woodland birds, as a prelude to a possible more comprehensive analysis in future. The main focus is on pairs or groups of taxonomically similar species, and their means of co-existence or habitat segregation. Numerical analysis considered species pairs within genera

as currently defined by Christidis and Boles (1994) for non-passerines and Schodde and Mason (1999) for passerines.

In an attempt to quantify some of the ecological interactions for south-eastern Australian native land birds, all congeneric species were listed and grouped in pairs (1 pair for 2 species, 3 pairs for 3 species, up to 36 pairs for the maximum of 9 species). The analysis covered 48 genera, 148 species and 209 congeneric species pairs. The primary mechanism of ecological segregation was then identified for each species pair, along with any contributing mechanisms. Because differences in range or habitat can be identified for almost all species pairs, these were classified further to show the extent of overlap, on a scale from no overlap (separate ranges or completely distinct habitats within an overlapping range) to complete overlap where both species could always be found together. Segregation by range was recorded as the primary factor whenever there was no overlap in normal range. Segregation by foraging method, body size, type of food or stratum/substrate were scored whenever they appeared to be an important factor helping two species to share a habitat. However, just one mechanism was selected as the primary factor for each species. All factors would be expected to vary in detail between habitats as a secondary consequence of the different natures of each habitat (food availability, etc.) and such secondary differences were not scored. Comparisons were made between mean scores for species pairs with little or no overlap in range, and species pairs with substantial overlap in range.

RESULTS

1) Resource use by birds

Recher and Holmes (1985) compared the foraging methods used by Australian forest birds with those used by North American forest birds, and concluded that there were no substantial differences except where they related to special resources associated with Australian eucalypt forests. Two sets of special resources were identified. Firstly, many eucalypt forests produce copious flows of nectar and other carbohydrate exudates, both from the eucalypts themselves (via blossom and from insects and physical wounds) and from a wide range of understory species (via flowers). These are an essential part of the diet of many honeyeaters, lorikeets and certain other bird species (e.g. Ford & Paton 1977, 1982;

Paton 1980). This resource is more dominant in eucalypt forests than in temperate forests elsewhere in the world (Recher & Holmes 1985). Some eucalypts such as box and ironbark species are particularly attractive to honeyeaters, as are blossoms from mistletoes, correas and Proteaceous plants. Heathland floras often include a wide range of plants that produce copious nectar flows at all times of year. Secondly, many eucalypts shed some of their bark on an annual basis, leaving smooth trunks or branches. The decorticating deciduous bark and hanging bark ribbons provide a unique feeding substrate not found in other forests. This deciduous bark habit contrasts with the evergreen nature of the foliage. The habit is most prevalent among eucalypts of the sub-genus *Symphymyrtus*, including species known as gum or ash (which typically have smooth-barked trunks) and some of those known as box which typically have smooth upper branches. The relative importance of different resources for birds in eucalypt forests can be assessed from the proportions of various guilds in the bird fauna (Loyn 1985a; Keast 1985).

2) Interspecific territoriality

A special feature of some Australian forests and woodlands, is that they become dominated by one or more bird species that aggressively exclude other birds, leading almost to sole occupancy of space by the aggressive species (Dow 1977). Usually the aggressive species are honeyeaters, although other species may be associated with them (e.g. Grey Butcherbird *Cracticus torquatus* and babblers *Pomatostomus* spp.). The situation always occurs in lowland or foothill forests or in open woodlands with a climate that supports populations of the species concerned throughout the year. It never occurs in mountain forests or in forests that are unable to support high resident populations of birds, such as those of low fertility on steep sites (Loyn 1985a,b; Emison et al. 1987). The species concerned have complex communal breeding systems (Dow 1978; Ford 1989; Clarke 1995, 1997), though such systems are not confined to this group of species.

The habit is best developed in the honeyeater genus *Manorina*, and applies to varying degrees with all four species in the genus (Higgins et al. 2001). The four species occupy different habitats on a mesic-xeric gradient from broad foothill gullies (Bell Miner *Manorina melanophrys*) through open woodland or small patches of fragmented forests (Noisy Miner *M. melanocephala*), open or fragmented stands

of mallee eucalypts (Yellow-throated Miner *M. flavigula*) to interiors of extensive mature mallee (Black-eared Miner *M. melanotis*). Their habitats sometimes join but rarely overlap, except with Yellow-throated and Black-eared Miners where a hybrid zone has developed after extensive clearing of mallee: Black-eared Miners are now listed as critically endangered. Miners take a wide range of food mainly from eucalypts, including arthropods, nectar and lerps (the sweet waxy inanimate covers produced by nymphs of psyllid insects). Patches of forest occupied by Bell Miners and Noisy Miners often show signs of defoliation by insects (Loyn et al. 1983; Loyn 1987a,b; Low 1994; Stone 1996). Bell Miners are the most aggressive of the four species and Black-eared Miners the least (Higgins et al. 2001). Only the latter allow other psyllid-eating birds to nest within their territories (Starks 1987; McLaughlin 1990; R. Clarke pers. comm.), though specialist psyllid eaters such as Striated Pardalotes *Pardalotus striatus* often make forays into territories occupied by other species before being expelled.

The effects of the miners' aggressive behaviour have been demonstrated in translocation experiments where miners were removed from their habitat and released elsewhere (Loyn et al. 1983; Loyn 1987a, b; Clarke & Schedvin 1997; Grey et al. 1997, 1998; Catterall et al. 1998 and in press). As Bell Miners were removed, other birds invaded and quickly reduced the populations of psyllid insects to negligible levels (Loyn et al. 1983; Loyn 1987b), before dropping to low levels commensurate with the reduced food supply. The invading birds included common forest honeyeaters, treecreepers and insectivores, and two species of parrot that also consumed psyllids at a higher rate than the Bell Miners had done. This demonstrated the power of common birds to control insects and the necessity for Bell Miners to live in a group and aggressively exclude other birds. It also led to the concept of Bell Miners "farming" the psyllids (Loyn 1987b), using a range of mechanisms to conserve the psyllid resource. Poiani (1993) presented evidence that Bell Miners are no more selective in taking lerps (sugary inanimate covers) and leaving psyllid nymphs than are other birds, suggesting that one of three mechanisms proposed to account for the efficacy of "farming" may not have been valid. However, this did not affect the main conclusions or the farming analogy itself (Loyn 1995). When Noisy Miners were removed from small forest patches, similar influxes of other birds occurred,

showing that the small forest patches are capable of supporting more diverse faunas in the absence of Noisy Miners (Grey et al. 1997, 1998; Catterall et al. 1998 and in press).

The eucalypt canopy recovered from defoliation over subsequent months after Bell Miner removal (Loyn et al. 1983): this may be one of the few published examples of a second-order vegetation response after manipulating predation pressure on insects. Responses after Noisy Miner removal appear to be more complex, and await further analysis. An unexpected result of this study was that Grey Butcherbirds abandoned the habitats from which Noisy Miners had been removed, suggesting a synergistic relationship between these species (Grey et al. 1998; M. Grey pers. comm.). Grey Butcherbirds have also been observed associating with colonies of Yellow-throated and Black-eared Miners in the mallee (pers. obs.; E. Moysey pers. comm.). The butcherbirds may benefit from high levels of resources such as large insects sequestered by the miners, and this relationship deserves further study.

In conclusion, interspecific territorial aggression appears to be a necessary mechanism for maintaining high levels of food supply necessary to support high year-round populations of the aggressive species (and perhaps their symbiotic partners such as Grey Butcherbirds). The system develops in habitats of high potential productivity and low seasonal climatic variability, and it usually involves cooperative breeding as well as interspecific aggression. From the evidence above, the degree of aggression needed appears to vary from high in mesic environments (where potential competitors are numerous) to low in xeric environments (where potential competitors are sparsely distributed). The distribution of Noisy Miners and Yellow-throated Miners suggests that exclusive territories may be easier to defend in fragmented environments than in continuous forest. This idea is supported by the distribution of Noisy Miners in natural forests such as Barmah State Forest, a 25,000 ha forest of River Red Gum on the Murray River. In and near that forest, Noisy Miners were confined to isolated patches of forest on grassy flood-plains, and to strips of roadside vegetation outside the forest (Chesterfield et al. 1984).

Although the habit is most pronounced among miners, many honeyeaters defend territories against a range of bird species (Collins & Briffa 1982; McFarland 1986; Ford 1989; Higgins et al. 2001) and may have a similar effect in reducing bird diversity and in-

creasing local resources available for themselves (Traill et al. 1996). White-plumed Honeyeaters *Lichenostomus penicillatus* have become common in fragmented rural forests and urban environments, partly excluding other honeyeaters (Loyn 1985a). Extensive box-ironbark forests are often occupied by two dominant species (Fuscous Honeyeater *L. fuscus* and the larger Yellow-tufted Honeyeater *L. melanops*), co-existing with each other but attacking other honeyeaters and insectivores (MacNally & McGoldrick 1997; Silveira et al. 1997). Their territories may overlap with those of White-plumed Honeyeaters on the edge of River Red Gum stands, with dynamic competition for space at the ecotone. Such competition may have excluded Fuscous and Yellow-tufted Honeyeaters from Barmah Forest, where stands of Grey Box *E. microcarpa* and Yellow Box *E. melliodora* form less than 5% of the forest area, and the niche is occupied solely by White-plumed Honeyeaters (Chesterfield et al. 1984).

The dynamics of aggressive communal birds such as these have profound implications for conservation. Local removal of Bell Miners has been found necessary to establish new habitat for the endangered Helmeted Honeyeater *Lichenostomus melanops cassidix* (Pearce et al. 1995; Menkhorst et al. 1999; Garnett & Crowley 2000). Similar measures with Noisy Miners may be needed to help conserve the endangered Regent Honeyeater *Xanthomyza phrygia*. However, longer term solutions must be found that involve habitat protection and restoration for these species, reducing the edge effects that have favoured aggressive miners. One of the miners (Black-eared Miner *M. melanotis*) is itself endangered, and needs protective measures in its interior mallee habitat (Starks 1987; McLaughlin 1990; Garnett & Crowley 2000; Higgins et al. 2001).

3) Segregation mechanisms

Of the 209 pairs of species examined (Appendix 1), 25 had distinct ranges with no overlap or close encounters and a further 25 had separate ranges that abutted each other with little or no overlap (Table 1). In all of these 50 cases the habitats were also distinctly different, with just two pairs (bristlebirds *Dasyornis* spp. and fieldwrens *Calamanthus* spp.) occupying structurally similar habitat in separate ranges (Appendix 1). Of the remaining 159 species pairs, 101 were segregated by habitat as the primary mechanism, with varying degrees of overlap. Across the whole sample of 209 pairs, substantial differences in

Table 1. Numbers of species pairs showing various primary mechanisms for ecological segregation in mainland south-eastern Australia, (a) among species pairs with little or no overlap in local range (scored as 0 or 1 in Appendix 1); (b) among species pairs with substantial overlap in local range (scored as 2+), and (c) among all species.

Mechanism	(a) Species pairs with little or no overlap in local range	(b) Species pairs with substantial overlap in local range	All species
Range (and habitat)	32	1	33
Habitat	17	102	119
Stratum or substrate	1	36	37
Size	0	11	11
Food or foraging technique	0	3	3
Nest site	0	2	2
Complex or unclear	0	3	3
None (i.e. appear ecologically very similar)	0	1	1
Total	50	159	209

foraging behaviour were identified for eight pairs, in size for 39 pairs, in food for 29 pairs and in stratum or foraging substrate for 96 pairs, in ways that may have contributed to ecological segregation though not necessarily as primary factors (Appendix 1). Nest sites usually reflected the preferred habitats and foraging strata, but seven pairs showed major differences in nest site that may have contributed to ecological segregation. Twenty-six pairs showed habitat differences that varied seasonally and the subject of bird movements and migration is discussed further below. In terms of primary mechanisms, it was judged that habitat was the main factor for 119 pairs, stratum or substrate for 37 pairs, range for 33 pairs, size for 11 pairs, food or foraging behaviour for three pairs, and nest site for two pairs (Table 1 and Appendix 1). One pair (of woodswallows *Artamus* spp.) showed no ecological differences and three pairs of honeyeaters showed complex differences that were hard to classify.

4) Patterns of species occurrence and co-existence in relation to habitat

Habitat differences were generally related to occurrence in broad forest types such as those described in the introduction. For example, three congeneric honeyeaters of similar size (Fuscous, White-plumed and Yellow-plumed) are the dominant species in box-ironbark forest, riverine or fragmented forests and mallee, respectively (Keast 1968; Ford & Paton 1976; Loyn 1985a; Emison et al. 1987; Higgins et al. 2001). They can be seen together where these habitats inter-mingle, or when drought or major flowering events

induce birds to move and use new food sources, but their normal breeding habitats show little overlap.

For many insectivores, density of trees and shrubs appears to be a key variable affecting occurrence of particular species, and this in turn is related to local climate and hydrology. For example, Yellow-rumped Thornbills *Acanthiza chrysorrhoa* feed mainly from the ground in open woodland or sparse chenopod shrublands, and also venture into treeless grassland or cleared farmland. Buff-rumped Thornbills *A. reguloides* feed from open ground but among trees (where they also take food from the bark). The similar Slender-billed Thornbill *A. iredalei* inhabits treeless heaths and chenopod shrublands, rarely mixing with Buff-rumped Thornbills even when the habitats are adjacent. Chestnut-rumped Thornbills *A. uropygialis* behave like Buff-rumped Thornbills but inhabit arid areas with a drier, more open type of woodland (e.g. Black Box) and associated chenopod shrublands. The contrast between Yellow-rumped and Buff-rumped Thornbills is reflected in the winter range of Flame Robin *Petroica phoenicea* and Scarlet Robin *P. boodang* (see below under bird movements), and the two species are often seen in loose association with the respective thornbills.

Several genera contain species that replace each other along xeric-mesic gradients, often with two occupying extreme habitats and a third generalist overlapping broadly with both. The granivorous bronzewing pigeons are an example. Flock Bronzewings *Phaps histrionica* occur in sparsely treed arid and northern Australia (outside the region considered here for numerical analysis), overlapping in range

with Common Bronzewing *Phaps chalcoptera* but segregated by habitat, with the latter occurring among woodlands. Common Bronzewings have a wide continental range extending into open forests of the south-east, where they co-exist locally with Brush Bronzewing *Phaps elegans*. The latter is confined to southern Australia and occupies dense forest and coastal heath and dense stands of mallee. It is the sole species in some of these habitats with a dense tall shrub layer (e.g. tall wet forests of Mountain Ash *E. regnans*) (Loyn 1985a,b; Emison et al. 1987). However, in many forests and mallee both species can be found, selecting habitat according to the local density of shrub or eucalypt species. In areas of local food abundance (e.g. on recently logged coupes with abundant wattles *Acacia* spp.) both species can be seen feeding together along with a third ground-feeding pigeon, the Wonga Pigeon *Leucosarcia melanoleuca*. Breeding territories appear to be segregated by habitat at fine spatial scales, with little overlap. Similar patterns can be found among many insectivorous, nectarivorous and granivorous bird genera. Habitat selection appears to involve mutual choice rather than interspecific aggression in most cases other than honeyeaters (discussed above), with the robins *Petroica* spp. being a notable exception (see below under bird movements).

5) Patterns of species occurrence and co-existence in relation to stratum and substrate

Stratum or substrate was identified as a key primary or secondary (potential) segregating factor in more pairs of species with substantial range overlap (81/159=51%) than with little or no range overlap (15/50=30%) ($p < .01$) (Appendix 1). This suggests that it may be a common factor allowing similar congeners to occupy the same space. Stratum or substrate was identified as the primary segregating factor for 37 of the 209 species pairs (Table 1).

The trend was best developed in two species-rich families of birds (honeyeaters Meliphagidae and thornbills Acanthizidae), and may have contributed to the evolution and survival of so many species in these groups. Segregation in honeyeaters often involves differential use of resources such as nectar, honeydew, lerps and arthropods caught in aerial sallies or gleaned from leaves or bark, and these patterns have been well described (e.g. Keast 1968; Ford & Paton 1976, 1977, 1982; Collins & Briffa 1982; Paton 1980; Pyke 1983, 1985; Recher & Holmes 1985; Wykes 1985; McFarland 1986, 1988; Ford 1989;

Clarke & Clarke 1999; Higgins et al. 2001). For example, White-eared Honeyeaters *Lichenostomus leucotis* specialise at taking sap or honeydew from bark, and are common in environments such as Snow Gum woodlands and regrowth eucalypts where other honeyeaters are scarce (Wykes 1985; Loyn 1985a; Osborne & Green 1992). They co-exist with four or more congeners at intermediate levels of nectar resource, but are excluded from rich nectar sources by other honeyeaters. The number of species and diversity of foraging techniques allows for complex patterns of co-existence or exclusion at various spatial and temporal scales, and more detailed analysis of broad-scale patterns of abundance would be useful. Interspecific aggression also plays a major role in these species, with dominance hierarchies often excluding small species from the richest sources of nectar at a given time (Ford & Paton 1982; McFarland 1986; Ford 1989).

Thornbills are among the most common resident insectivores in many forests and woodlands where aggressive honeyeaters are unable to establish year-round exclusive territories (Loyn 1985a). Their foraging ecology has been studied by Recher et al. (1985), Recher and Holmes (1985) and Bell (1985). Three species co-exist in forests of the Great Dividing Range. Striated Thornbills *Acanthiza lineata* feed mainly in the eucalypt canopy and Brown Thornbills *A. pusilla* feed mainly among narrow-leaved shrubs, with Buff-rumped Thornbills feeding from bark and open ground in parts of the forest with sparse shrub layers. All three form mixed feeding flocks in winter, and their foraging niches expand when food is plentiful and contract when food is scarce (Bell 1985). The first two are so common that few areas of forest fail to support both species. In drier forest north or west of the Great Dividing Range a different set of species occupies similar niches, with Weebills *Smicrornis brevirostris* in the eucalypt canopy, Yellow Thornbills *A. nana* in narrow-leaved shrubs and either Buff-rumped, Yellow-rumped or Chestnut-rumped Thornbills feeding from the ground (depending on the stand density and aridity as discussed under Habitat). Some forests support both groups of thornbills, with segregation based firstly on fine-scale habitat and secondly on stratum (e.g. riverine and box-ironbark forests: Chesterfield et al. 1984; Traill et al. 1996; Silveira et al. 1997), but there is much overlap in some of these forests. Bill shapes have evolved to suit the respective lifestyles, with Striated Thornbills and Weebills having broad bills like pardalotes Pardalotidae, and

Brown Thornbills and Yellow Thornbills having fine bills for foraging among narrow-leaved shrubs.

6) Size, food and foraging technique

Size was identified as a partial segregating factor for 39 species pairs and the primary factor for ten of them. All of the latter were carnivores (hawks and owls) or nectarivores (lorikeets and honeyeaters). Some pairs of insectivores differed slightly in size but stratum or substrate was usually recognised as a more fundamental segregating mechanism in those cases. Many congeners take different foods (and use different foraging methods) as a result of their differences in size or preferences for particular substrates or strata. However, food preference was identified as a primary segregating mechanism for just two pairs. Little Wattlebirds *Anthochaera chrysoptera* show strong preferences for proteaceous flowers such as banksias *Banksia* spp., whereas Red Wattlebirds *A. carunculata* favour nectar from eucalypts (Paton & Ford 1977; McFarland 1986; Egan 1997; Higgins et al. 2001). They differ in size, often chase each other and sometimes feed together at abundant food sources, but the difference in food preference appears to be the most fundamental segregating mechanism. Glossy Black-Cockatoos *Calyptorhynchus lathami* are specialised for feeding on seeds of casuarinas *Alocasuarina* spp. whereas Yellow-tailed Black-Cockatoos *C. funereus* take a wide range of hard seeds and extract grubs from branches (Higgins 1999): again the difference in food preference appears to be fundamental. Foraging behaviour was identified as fundamental for just one pair: Grey Goshawks *Accipiter novaehollandiae* make more use of the “watch and pounce” hunting technique than do Brown Goshawks *A. fasciatus* (Olsen et al. 1990; Marchant & Higgins 1993). The two species also show substantial differences in diet, prey size and foraging habitat (Baker-Gabb 1984; Czechura 1985; Aumann 1988; Marchant & Higgins 1993) but the overlap in diet has been assessed as 50% (Olsen et al. 1990) and the differences may be driven by the difference in foraging behaviour.

7) Nest site

Each species has its own preferences for nest site, often related to preferred habitat or foraging stratum. Nest site was identified as the fundamental segregating mechanism for just two pairs. Spotted Pardalotes *Pardalotus punctatus* make their own tunnel nests in bare ground (Woinarski 1985), and use hollows in

trees only on an extremely local basis (S. Marchant pers. comm.). Striated Pardalotes *P. striatus* nest mainly in tree hollows, although they sometimes nest in loose groups in tunnels in sandy banks where such sites are available. The two species differ slightly in size and foraging methods, though both specialise at taking psyllid nymphs and lerps from eucalypt foliage (Woinarski 1985). Striated Pardalotes tend to favour smooth-barked eucalypts of the subgenus *Symphyomyrtus* (Loyn 1985a) and have a broader geographical range than Spotted Pardalotes. However, their ranges overlap extensively and they can often be found together, sometimes feeding simultaneously in the same trees (Woinarski 1985). Nest sites may limit both species, with Spotted Pardalotes needing patches of shrub-free open ground and Striated Pardalotes needing old trees with hollow spouts (Loyn 1998). These different needs may be of fundamental importance in allowing them to co-exist over broad areas of forest.

Nest sites also differed between the three swallows and martins, with Welcome Swallows *Hirundo neoxena* nesting on ledges (e.g. on open scars of old trees, and on houses and bridges), Fairy Martins *H. ariel* building bottle-shaped nests under overhangs or tunnelling into river-banks, and Tree Martins *H. nigricans* nesting mainly in hollow spouts of old trees. All species use buildings to various extents. The fundamental ecological segregation between Tree Martins and other species was identified as habitat, because Tree Martins nest mainly among trees and feed over forest and woodland (Blakers et al. 1984; Emison et al. 1987). However, it could be argued that this is a consequence of the preferred nest site. Welcome Swallows and Fairy Martins feed mainly in open country, where they are sometimes joined by non-breeding Tree Martins. The species differ somewhat in foraging method, with swallows swooping low over flat surfaces, and martins spending more time chasing insects high in the air. However, while breeding all three species are quite localised near suitable nesting sites. Hence it was concluded that the fundamental segregation between Welcome Swallows and Fairy Martins (and possibly between all three pairs) is based on nest site selection.

8) Complex patterns

Mechanisms of co-existence proved difficult to classify for three pairs of honeyeaters (Yellow-plumed Honeyeater *Lichenostomus ornatus* vs Purple-gaped Honeyeater *L. cratitius* and Grey-fronted

Honeyeater *L. plumulus*, and White-cheeked Honeyeater *Phylidonyris nigra* vs New Holland Honeyeater *Ph. novaehollandiae*), because of sparse information in the first cases and complexity in the third. Differences in habitat are likely to be the primary factor in the first cases, with Yellow-plumed Honeyeaters occupying dense stands of mallee eucalypts, Purple-gaped Honeyeaters reaching maximum density in mallee-heath or mallee-broombush and Grey-fronted Honeyeaters occupying a wide range of more arid habitats including sparse or young stands of mallee (Menkhorst & Davies 1983; Woinarski 1989; Higgins et al. 2001), but overlap is common, especially with Yellow-plumed and Purple-gaped Honeyeaters. White-cheeked Honeyeaters and New Holland Honeyeaters co-exist in heathlands of Western Australia and New South Wales (Blakers et al. 1984; Pyke 1985), but White-cheeked Honeyeaters are replaced by Crescent Honeyeaters *Phylidonyris pyrrhoptera* elsewhere in south-eastern Australia. New Holland Honeyeaters specialise at feeding from proteaceous flowers, and often dominate bird communities in heathlands where such flowers are abundant.

No evidence was found in this review for mechanisms such as predator-mediated co-existence (Sinclair 1995; Choquenot et al. 2001), though they may occur in some groups. Predation by native birds and introduced mammals may limit numbers of some Australian birds (Ford 1989), perhaps keeping them below levels where interspecific competition would arise. This could apply in particular to medium-sized ground-feeding birds such as bronzewings (discussed above).

One pair of species showed no ecological differences. White-browed Woodswallows *Artamus superciliosus* and Masked Woodswallows *A. personatus* often form mixed flocks and appear to be identical in their general ecology, travelling as highly mobile nomadic flocks and visiting rich food sources such as flowering eucalypts, concentrations of psyllids and lerps or swarms of plague locusts. They both inhabit a broad range across arid and semi-arid Australia, visiting less arid woodlands during times of drought. White-browed Woodswallows predominate in eastern Australia and Masked Woodswallows in western Australia but both species can be found to some extent throughout their range. No mechanism for ecological segregation is known.

9) Bird movements

In temperate parts of south-eastern Australia, many

bird species undertake regular migrations (Keast 1968; Nix 1976; Ford 1989; Clarke et al. 1999). Honeyeaters migrate by day and their visible migration has attracted much comment and detailed study (Hindwood 1956; Paton 1988; Munro & Wiltschko 1992; Munro et al. 1993; Munro & Munro 1998). Insectivorous birds also undertake highly predictable migrations, with a massive exodus of insectivores from wet forest in the Great Dividing Range for the winter and corresponding influxes in various parts of the country (Kikkawa & Pearse 1969; Recher et al. 1983; Loyn 1985a, b; Osborne & Green 1992; MacNally 1996; Catterall et al. 1997; Clarke et al. 1999). Some species are completely summer visitors to these forests (e.g. Satin Flycatcher *Myiagra cyanoleuca* and Rufous Fantail *Rhipidura rufifrons*) and others are completely summer visitors to wet forests (e.g. Grey Fantail *Rhipidura fuliginosa*) though some over-winter in dry forests. The commonest birds in these forests include resident insectivores (e.g. thornbills and treecreepers Climacteridae) and regular summer migrants such as Grey Fantail and Yellow-faced Honeyeater *Lichenostomus chrysops*. Yellow-faced Honeyeaters are largely insectivorous in summer, taking both insects and nectar from the eucalypt canopy, but switch to a more nectarivorous diet in their winter range. These regular patterns of migration provide opportunities for some species to share habitats by seasonal segregation. However, the reality is that movements track resources (Nix 1976) and the exodus of one species rarely provides opportunities for a related species to occupy vacated habitat. Just one example can be cited: Golden Whistlers *Pachycephala pectoralis* are winter visitors to lowland forests in the Murray-Darling Basin, and those same forests are occupied by Rufous Whistlers *P. rufiventris* in summer (Chesterfield et al. 1984; Loyn 1985a; Clarke et al. 1999).

A more common way in which migration allows species to share habitat, is that one species migrates and another does not: the two species share a habitat when resources are plentiful, and occupy separate habitats and ranges when resources are scarce. Golden Whistlers and Olive Whistlers *P. olivacea* share wet forest habitats in the breeding season, with further segregation by feeding stratum (Golden Whistlers foraging mainly among tall shrubs, and Olive Whistlers in the low shrub understorey). Golden Whistlers are common summer visitors to these forests whereas most Olive Whistlers remain over winter (Loyn 1985a, b). In some forest types

(e.g. foothill gullies containing Manna Gum *E. viminalis* and Narrow-leaf Peppermint *E. radiata*) Rufous Whistlers also occur as summer visitors, feeding in the eucalypt canopy. In those situations, all three species co-exist, segregated by foraging stratum. In the foothills, many Golden Whistlers may remain over winter, and their foraging extends into the eucalypt canopy when Rufous Whistlers have departed (Loyn 1985a). It is not known whether this behavioural change reflects the availability of food or the lack of competition from Rufous Whistlers.

The robins Petroicidae provide another example of this process. Scarlet Robins usually occupy dry forest habitats that can support resident pairs throughout the year, although they often need to expand their home range in winter (Robinson 1990, 1992). Flame Robins are regular migrants, totally vacating forest habitats in winter to congregate in farmland or open woodland. This habit allows them a greater choice of breeding habitat in the forests. Although they will compete aggressively with Scarlet Robins for territories in the foothills (Loyn 1980; Robinson 1992), the bulk of the population migrates to breed in wetter forest and at higher altitude (>800 m) where winter conditions would not support the resident species. Hence the migratory habit allows segregation by habitat, both in summer and winter, despite a large overlap where there is aggressive competition for space in the breeding season.

10) Interspecific associations

Many species form mixed-species flocks in winter and benefit in various ways such as early warning of predators and improved ability to find patchy resources (Bell 1985; Ford 1989). There may be more advantages in joining a mixed-species flock than a single-species flock, because ecological differences (as discussed above) will tend to reduce the total level of competition. There may also be direct benefits. Four examples can be cited from south-eastern Australian forests, based on well known but mainly anecdotal information. Firstly, Superb Lyrebirds *Menura novaehollandiae* forage by scratching vigorously at the forest floor, helping maintain understorey structure and regeneration (Ashton & Bassett 1997). In the process they displace more arthropods than they can catch or consume themselves. Lyrebirds are often followed by loose groups of other insectivores such as Eastern Yellow Robins *Eopsaltria australis*, White-browed Scrubwrens *Sericornis frontalis* and Pilotbirds *Pycnoptilus floccosus* that take advantage

of this revealed resource (Higgins et al. 2001). Secondly, many Grey Fantails migrate from foothill forests for the winter when flying insects are scarce, but those that remain spend substantial amounts of time following bark-foraging birds and catching winged insects displaced while those species forage behind loose bark. The main bark foragers concerned are White-throated Treecreepers *Cormobates leucophaea*, Red-browed Treecreepers *Climacteris erythrops*, Crested Shriketits *Falcunculus frontatus* and flocks of Varied Sittellas *Daphoenositta varia*. Both Grey Fantails and White-throated Treecreepers join mixed feeding flocks in winter (Bell 1985; Ford 1989). Thirdly, Willie Wagtails often concentrate their winter foraging round large mammals (kangaroos *Macropus* spp. or domestic stock), presumably benefiting from concentrations of insects near fresh warm dung. Fourthly, honeyeaters and other birds may congregate at fresh wounds in trees where marsupial possums or gliders (especially Yellow-bellied Gliders *Petaurus australis*) have made scars to extract exudates (Russell 1981; Loyn 1985b and unpublished; Chapman et al. 1999). These examples show how birds may benefit from the activities of unrelated birds and mammals in their environment.

DISCUSSION

The patterns of segregation revealed in this review resemble those described by Lack (1971) for continental avifaunas in various parts of the world. He identified habitat differences as much the commonest means of ecological isolation in continental passerines, and this is confirmed for the distinct group of birds inhabiting forests of south-eastern Australia. Differences of this sort allow multiple species to co-exist broadly in an area, but not to share habitats at the fine scale. Differences in foraging stratum or substrate were found to be important in allowing some species pairs to share the same habitat at the same time, increasing the diversity of those habitats. The species diversity of a given habitat is expected to be a function of its structural and floristic complexity, and those characteristics will set limits on the extent to which bird species can co-exist. Tilman (1982) presented a set of theoretical models for predicting outcomes of competitive exclusion and co-existence among organisms that may be useful in further interpretation of continental data on Australian birds.

The patterns identified differ in one respect from those described elsewhere, and that relates to the ag-

gressive honeyeater species that form interspecific territories (Dow 1977; Loyn et al. 1983; Loyn 1987a, b; Clarke 1995; Clarke & Schedvin 1997; Grey et al. 1997, 1998; Catterall et al. 1998 and in press). Ford (1989) discussed these species in relation to their communal breeding behaviour, and suggested that predator avoidance may have been a key driver for the evolution of communal breeding in these birds, many of which inhabit open and exposed woodland environments. A further reason is suggested by the experiments where Bell Miners were removed and other birds decimated their previously protected food supply: this showed that the level of resources needed to maintain the colony would not exist unless it was protected by an adequate number of birds within the group. Conversely, young birds would face great difficulties in establishing new territories without being part of a large enough group to maintain food supplies through territorial defence. A parallel situation has been reported for White-winged Choughs *Corcorax melanoleucos*, where young birds are encouraged to remain within the group (by kidnapping if necessary) in order to deter destructive attacks on the nest by other groups, in this case by conspecifics (Heinsohn 1987). Many factors contribute to evolution of communal breeding, but the ecological advantages (or necessities) of group living should be given due weight among them. Elsewhere in the world, various bird species appear to live as aggressive groups in temperate woodland habitats, and further work may show that communal defence of resources is an important factor in evolution of such systems.

This paper has focused mainly on ecological segregation between congeneric species, but the cases of interspecific aggression highlight the fact that competition occurs between all species, and can help determine the nature and health of the ecosystem. Woodland birds have declined in southern Australia (Robinson 1993; Barrett et al. 1994), and are vulnerable to competition from Noisy Miners in small grazed patches of forest (Loyn 1987a; Grey et al. 1997, 1998; Bennett 1999): active habitat management is needed to reverse such declines. A full analysis of competitive forces and the way they shape communities (Cody 1974; Kikkawa & Anderson 1984) must consider the full range of competing species. Species-based approaches will continue to be useful to conservation managers (e.g. Lambeck 1997; Loyn et al. 2001) but further understanding of ecological interactions will help progress to holistic ecosystem management.

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Ecological segregation in SE Australia

Appendix 1. Pairs of congeneric native bird species inhabiting forests, woodlands and shrublands of mainland south-eastern Australia (excluding species found mainly in warm temperate rainforest), showing the assessed primary mechanisms for ecological segregation along with other potentially important mechanisms, degree of overlap in total range (Australia) and local range (study region) and degree of habitat overlap in the study region.

Family	Species 1	Species 2	Primary segregation mechanisms ¹	Other potentially important segregating mechanisms ²	Overlap in total range ³	Overlap in local range ³	Habitat overlap ⁴
Phasianidae	<i>Coturnix pectoralis</i>	<i>C. ypsilophora</i>	h		2	2	1
	<i>Coturnix ypsilophora</i>	<i>C. chinensis</i>	h	sz	2	2	1
	<i>Coturnix pectoralis</i>	<i>C. chinensis</i>	h	sz	2	2	1
Accipitridae	<i>Accipiter fasciatus</i>	<i>A. novaehollandiae</i>	fg	fd	3	3	2
	<i>Accipiter novaehollandiae</i>	<i>A. cirrhocephalus</i>	sz	fg, fd	3	3	1
	<i>Accipiter fasciatus</i>	<i>A. cirrhocephalus</i>	sz	fg, fd	5	5	3
Columbidae	<i>Phaps chalcoptera</i>	<i>Ph. elegans</i>	h		3	3	3
Cacatuidae	<i>Calyptorhynchus banksii</i>	<i>C. lathami</i>	r	sz, fd	2	0	2
	<i>Calyptorhynchus banksii</i>	<i>C. funereus</i>	h		2	3	2
	<i>Calyptorhynchus lathami</i>	<i>C. funereus</i>	fd		3	3	3
Psittacidae	<i>Trichoglossus haematodus</i>	<i>T. chlorolepidotus</i>	sz	fd	3	3	4
	<i>Glossopsitta concinna</i>	<i>G. pusilla</i>	sz		4	4	3
	<i>Glossopsitta pusilla</i>	<i>G. porphyrocephala</i>	h		2	2	1
	<i>Glossopsitta concinna</i>	<i>G. porphyrocephala</i>	h		2	2	1
	<i>Polytelis swainsonii</i>	<i>P. anthopeplus</i>	r		0	0	2
	<i>Platyercus elegans</i>	<i>P. eximius</i>	h	s	2	2	1
	<i>Neophema chrysostoma</i>	<i>N. pulchella</i>	h	m	1	1	0
	<i>Neophema chrysostoma</i>	<i>N. chrysogaster</i>	h	m	2	2	1#
	<i>Neophema chrysostoma</i>	<i>N. splendida</i>	h	m	2	3	0#
	<i>Neophema chrysostoma</i>	<i>N. petrophila</i>	h	n, m	1	0	0#
	<i>Neophema chrysostoma</i>	<i>N. elegans</i>	h		2	2	1#
	<i>Neophema elegans</i>	<i>N. chrysogaster</i>	h	m	1	1	0#
	<i>Neophema elegans</i>	<i>N. splendida</i>	h	m	2	1	1
	<i>Neophema elegans</i>	<i>N. pulchella</i>	r		0	0	0
	<i>Neophema elegans</i>	<i>N. petrophila</i>	h	n, m	2	1	1#
	<i>Neophema petrophila</i>	<i>N. pulchella</i>	r		0	0	0
	<i>Neophema petrophila</i>	<i>N. splendida</i>	r		0	0	0
	<i>Neophema petrophila</i>	<i>N. chrysogaster</i>	h	n, m	1	0	1#
	<i>Neophema chrysogaster</i>	<i>N. pulchella</i>	r		0	0	0
	<i>Neophema chrysogaster</i>	<i>N. splendida</i>	r		0	0	0
<i>Neophema pulchella</i>	<i>N. splendida</i>	r		0	0	0	
Cuculidae	<i>Cacomantis variolosus</i>	<i>C. flabelliformis</i>	s		2	4	3
	<i>Chrysococcyx osculans</i>	<i>Ch. basalis</i>	s		4	3	4
	<i>Chrysococcyx basalis</i>	<i>Ch. lucidus</i>	h		3	3	2
	<i>Chrysococcyx osculans</i>	<i>Ch. lucidus</i>	h		2	2	2
Strigidae	<i>Ninox strenua</i>	<i>N. connivens</i>	sz	fg, fd	3	2	1
	<i>Ninox connivens</i>	<i>N. novaeseelandiae</i>	sz	fd	3	3	4
	<i>Ninox strenua</i>	<i>N. novaeseelandiae</i>	sz	fd	3	3	4
Tytonidae	<i>Tyto tenebricosa</i>	<i>T. novaehollandiae</i>	h	fd, fg	3	3	1
	<i>Tyto novaehollandiae</i>	<i>T. alba</i>	sz	fd	3	3	2
	<i>Tyto tenebricosa</i>	<i>T. alba</i>	h	sz, fd, s	3	3	0
Caprimulgidae	<i>Eurostopus mystacalis</i>	<i>E. argus</i>	h		1	1	1
Halcyonidae	<i>Todiramphus pyrrhopygia</i>	<i>T. sanctus</i>	h	sz	2	3	1
Climacteridae	<i>Climacteris affinis</i>	<i>C. erythrops</i>	r	fg, s	0	0	0
	<i>Climacteris erythrops</i>	<i>C. picumnus</i>	h	s	3	2	0
	<i>Climacteris affinis</i>	<i>C. picumnus</i>	s		2	3	2

Appendix 1. (Continued)

Family	Species 1	Species 2	Primary segregation mechanisms ¹	Other potentially important segregating mechanisms ²	Overlap in total range ³	Overlap in local range ³	Habitat overlap ⁴
Maluridae	<i>Malurus cyaneus</i>	<i>M. splendens</i>	h		1	1	0
	<i>Malurus cyaneus</i>	<i>M. leucopterus</i>	h		1	2	0
	<i>Malurus cyaneus</i>	<i>M. lamberti</i>	h		2	2	2
	<i>Malurus splendens</i>	<i>M. leucopterus</i>	h	s	3	2	1
	<i>Malurus splendens</i>	<i>M. lamberti</i>	s		2	3	3
	<i>Malurus</i>	<i>M. leucopterus</i>	h	s	2	3	1
	<i>Stipiturus malachurus</i>	<i>S. mallee</i>	r		0	0	0
Pardalotidae	<i>Pardalotus punctatus</i>	<i>P. striatus</i>	n	sz, s	3	3	1
Acanthizidae	<i>Dasyornis brachypterus</i>	<i>D. broadbenti</i>	r		0	0	3
	<i>Sericornis frontalis</i>	<i>S. magnirostris</i>	s		3	3	4
	<i>Hylacola pyrrhopygia</i>	<i>H. cauta</i>	h		1	1	0
	<i>Calamanthus fuliginosus</i>	<i>C. campestris</i>	r		0	0	1
	<i>Gerygone mouki</i>	<i>G. fusca</i>	r		0	0	0
	<i>Gerygone fusca</i>	<i>G. olivacea</i>	h		2	2	3
	<i>Gerygone olivacea</i>	<i>G. mouki</i>	h		2	2	0
	<i>Acanthiza pusilla</i>	<i>A. chrysorrhoa</i>	h	s	3	4	0
	<i>Acanthiza pusilla</i>	<i>A. iredalei</i>	h		1	1	1
	<i>Acanthiza pusilla</i>	<i>A. nana</i>	h		3	3	2
	<i>Acanthiza pusilla</i>	<i>A. apicalis</i>	r		1	1	2
	<i>Acanthiza pusilla</i>	<i>A. uropygialis</i>	s		2	2	2
	<i>Acanthiza pusilla</i>	<i>A. reguloides</i>	s		3	4	3
	<i>Acanthiza pusilla</i>	<i>A. lineata</i>	s		4	5	4
	<i>Acanthiza apicalis</i>	<i>A. iredalei</i>	h	s	4	3	1
	<i>Acanthiza apicalis</i>	<i>A. lineata</i>	r	s	1	1	0
	<i>Acanthiza apicalis</i>	<i>A. reguloides</i>	s		1	2	2
	<i>Acanthiza apicalis</i>	<i>A. chrysorrhoa</i>	s		3	3	2
	<i>Acanthiza apicalis</i>	<i>A. uropygialis</i>	s		4	4	3
	<i>Acanthiza uropygialis</i>	<i>A. iredalei</i>	h	s	3	3	1
	<i>Acanthiza uropygialis</i>	<i>A. reguloides</i>	h		2	2	2
	<i>Acanthiza uropygialis</i>	<i>A. chrysorrhoa</i>	h		3	3	1
	<i>Acanthiza uropygialis</i>	<i>A. lineata</i>	s		1	1	1
	<i>Acanthiza uropygialis</i>	<i>A. nana</i>	s		2	3	3
	<i>Acanthiza reguloides</i>	<i>A. iredalei</i>	h	s	1	3	0
	<i>Acanthiza reguloides</i>	<i>A. chrysorrhoa</i>	h		3	3	1
	<i>Acanthiza reguloides</i>	<i>A. nana</i>	s		4	4	3
	<i>Acanthiza reguloides</i>	<i>A. lineata</i>	s		4	4	4
	<i>Acanthiza iredalei</i>	<i>A. nana</i>	h	s	1	3	1
	<i>Acanthiza iredalei</i>	<i>A. lineata</i>	h	s	1	1	0
	<i>Acanthiza iredalei</i>	<i>A. chrysorrhoa</i>	h		3	3	1
	<i>Acanthiza chrysorrhoa</i>	<i>A. lineata</i>	h	s	3	3	0
	<i>Acanthiza chrysorrhoa</i>	<i>A. nana</i>	s		2	4	2
	<i>Acanthiza nana</i>	<i>A. lineata</i>	s		3	3	3
	Meliphagidae	<i>Anthochaera carunculata</i>	<i>A. chrysoptera</i>	fd	sz	3	3
<i>Philemon corniculatus</i>		<i>Ph. citreogularis</i>	sz		3	2	3
<i>Manorina melanophrys</i>		<i>M. melanocephala</i>	h	sz	3	2	0
<i>Manorina melanophrys</i>		<i>M. flavigula</i>	r	sz	0	0	0
<i>Manorina melanophrys</i>		<i>M. melanotis</i>	r	sz	0	0	0
<i>Manorina melanocephala</i>		<i>M. flavigula</i>	h		2	2	0
<i>Manorina melanocephala</i>		<i>M. melanotis</i>	h		3	2	0
<i>Manorina flavigula</i>	<i>M. melanotis</i>	h		3	3	2	

Ecological segregation in SE Australia

Appendix 1. (Continued)

Family	Species 1	Species 2	Primary segregation mechanisms ¹	Other potentially important segregating mechanisms ²	Overlap in total range ³	Overlap in local range ³	Habitat overlap ⁴
	<i>Lichenostomus chrysops</i>	<i>L. leucotis</i>	s	fd, m	2	3	3
	<i>Lichenostomus chrysops</i>	<i>L. melanops</i>	h	fd, s	3	3	1
	<i>Lichenostomus chrysops</i>	<i>L. virescens</i>	h	s	2	2	0
	<i>Lichenostomus chrysops</i>	<i>L. penicillatus</i>	h	s	2	2	1
	<i>Lichenostomus chrysops</i>	<i>L. cratitius</i>	r	s	1	1	0
	<i>Lichenostomus chrysops</i>	<i>L. ornatus</i>	r	s	1	1	0
	<i>Lichenostomus chrysops</i>	<i>L. plumulus</i>	r	s	1	0	0
	<i>Lichenostomus chrysops</i>	<i>L. fuscus</i>	h	s, m	5	3	1
	<i>Lichenostomus virescens</i>	<i>L. fuscus</i>	h	s	1	1	0
	<i>Lichenostomus virescens</i>	<i>L. leucotis</i>	h	s	2	2	0
	<i>Lichenostomus virescens</i>	<i>L. melanops</i>	h	s	2	2	0
	<i>Lichenostomus virescens</i>	<i>L. cratitius</i>	h	s	2	2	0
	<i>Lichenostomus virescens</i>	<i>L. penicillatus</i>	h	s	2	2	0
	<i>Lichenostomus virescens</i>	<i>L. ornatus</i>	h	s	3	3	1
	<i>Lichenostomus virescens</i>	<i>L. plumulus</i>	h	s	4	3	0
	<i>Lichenostomus leucotis</i>	<i>L. melanops</i>	h	fd, s	3	2	1
	<i>Lichenostomus leucotis</i>	<i>L. penicillatus</i>	s	sz, fd	2	2	1
	<i>Lichenostomus leucotis</i>	<i>L. ornatus</i>	s	sz, fd	3	3	2
	<i>Lichenostomus leucotis</i>	<i>L. fuscus</i>	s	sz, fd	3	2	1
	<i>Lichenostomus leucotis</i>	<i>L. plumulus</i>	s	sz, fd	2	3	1
	<i>Lichenostomus leucotis</i>	<i>L. cratitius</i>	s	sz, fd	3	3	1
	<i>Lichenostomus melanops</i>	<i>L. fuscus</i>	sz	s	4	4	4
	<i>Lichenostomus melanops</i>	<i>L. ornatus</i>	h	sz, s	1	1	0
	<i>Lichenostomus melanops</i>	<i>L. penicillatus</i>	h	sz, s	2	3	2
	<i>Lichenostomus melanops</i>	<i>L. plumulus</i>	r	sz, s	0	0	0
	<i>Lichenostomus melanops</i>	<i>L. cratitius</i>	r	sz, s	1	1	0
	<i>Lichenostomus cratitius</i>	<i>L. penicillatus</i>	h	s	2	3	0
	<i>Lichenostomus cratitius</i>	<i>L. fuscus</i>	r	s	1	1	0
	<i>Lichenostomus cratitius</i>	<i>L. plumulus</i>	h	s	2	3	3
	<i>Lichenostomus cratitius</i>	<i>L. ornatus</i>	?h	s	4	4	4
	<i>Lichenostomus ornatus</i>	<i>L. fuscus</i>	h		1	1	0
	<i>Lichenostomus ornatus</i>	<i>L. penicillatus</i>	h		2	2	0
	<i>Lichenostomus ornatus</i>	<i>L. plumulus</i>	?h	s	2	3	3
	<i>Lichenostomus plumulus</i>	<i>L. penicillatus</i>	h		2	2	0
	<i>Lichenostomus plumulus</i>	<i>L. fuscus</i>	r		1	0	0
	<i>Lichenostomus fuscus</i>	<i>L. penicillatus</i>	h	fd, s	2	3	1
	<i>Melithreptus gularis</i>	<i>M. brevirostris</i>	s	sz	2	3	3
	<i>Melithreptus brevirostris</i>	<i>M. lunatus</i>	s		2	3	3
	<i>Melithreptus lunatus</i>	<i>M. gularis</i>	s	sz, m	2	3	3
	<i>Phylidonyris pyrrhoptera</i>	<i>Ph. novaehollandiae</i>	h	fd, s	3	3	2
	<i>Phylidonyris pyrrhoptera</i>	<i>Ph. melanops</i>	h	fd, s	3	2	0
	<i>Phylidonyris pyrrhoptera</i>	<i>Ph. nigra</i>	r	fd, s	2	1	1
	<i>Phylidonyris pyrrhoptera</i>	<i>Ph. albifrons</i>	r		1	1	0
	<i>Phylidonyris novaehollandiae</i>	<i>Ph. melanops</i>	h	fd	3	3	1
	<i>Phylidonyris novaehollandiae</i>	<i>Ph. nigra</i>	c	s	2	2	3
	<i>Phylidonyris novaehollandiae</i>	<i>Ph. albifrons</i>	r		1	1	0
	<i>Phylidonyris nigra</i>	<i>Ph. melanops</i>	h	fd, s	2	2	1
	<i>Phylidonyris nigra</i>	<i>Ph. albifrons</i>	r	s	1	0	0
	<i>Phylidonyris albifrons</i>	<i>Ph. melanops</i>	h	fd, s	2	2	1
	<i>Ephthianura tricolor</i>	<i>E. albifrons</i>	h		2	3	3

Appendix 1. (Continued)

Family	Species 1	Species 2	Primary segregation mechanisms ¹	Other potentially important segregating mechanisms ²	Overlap in total range ³	Overlap in local range ³	Habitat overlap ⁴
Petroicidae	<i>Ephthianura tricolor</i>	<i>E. aurifrons</i>	h		4	4	3
	<i>Ephthianura aurifrons</i>	<i>E. albifrons</i>	h		2	3	4
	<i>Petroica boodang</i>	<i>P. phoenicea</i>	h	m	3	3	2\$
	<i>Petroica boodang</i>	<i>P. rosea</i>	h	s	2	3	1
	<i>Petroica boodang</i>	<i>P. goodenovii</i>	h		2	2	1
	<i>Petroica boodang</i>	<i>P. rodinogaster</i>	h		3	3	0
	<i>Petroica goodenovii</i>	<i>P. phoenicea</i>	h	m	2	2	0
	<i>Petroica goodenovii</i>	<i>P. rosea</i>	h	s	2	2	0
	<i>Petroica goodenovii</i>	<i>P. rodinogaster</i>	h		2	2	0
	<i>Petroica phoenicea</i>	<i>P. rodinogaster</i>	h	m	3	3	1
	<i>Petroica phoenicea</i>	<i>P. rosea</i>	h	s	2	3	1
Pomatostomidae	<i>Petroica rosea</i>	<i>P. rodinogaster</i>	s	m	2	4	3
	<i>Pomatostomus temporalis</i>	<i>P. superciliosus</i>	h		2	2	2
	<i>Pomatostomus superciliosus</i>	<i>P. ruficeps</i>	h		2	3	1
Cinclosomatidae	<i>Pomatostomus temporalis</i>	<i>P. ruficeps</i>	h	s	2	2	1
	<i>Psophodes olivaceus</i>	<i>P. nigrogularis</i>	r		0	0	0
Pachycephalidae	<i>Cinclosoma punctatum</i>	<i>C. castanotus</i>	r		0	0	0
	<i>Pachycephala olivacea</i>	<i>P. rufiventris</i>	s	m	2	3	2
	<i>Pachycephala olivacea</i>	<i>P. pectoralis</i>	s	m	3	3	3
	<i>Pachycephala olivacea</i>	<i>P. inornata</i>	h		0	0	0
	<i>Pachycephala olivacea</i>	<i>P. rufogularis</i>	r		0	0	0
	<i>Pachycephala rufogularis</i>	<i>P. inornata</i>	sz	fd	3	3	4
	<i>Pachycephala rufogularis</i>	<i>P. pectoralis</i>	s	sz	3	3	2
	<i>Pachycephala rufogularis</i>	<i>P. rufiventris</i>	s	sz	3	3	4
	<i>Pachycephala inornata</i>	<i>P. rufiventris</i>	s	m	3	3	4
	<i>Pachycephala inornata</i>	<i>P. pectoralis</i>	h		2	3	3
	<i>Pachycephala pectoralis</i>	<i>P. rufiventris</i>	s	m	2	3	2
Dicruridae	<i>Myiagra rubecula</i>	<i>M. cyanoleuca</i>	h		3	3	1
	<i>Myiagra cyanoleuca</i>	<i>M. inquieta</i>	s	sz, m	2	3	1
	<i>Myiagra rubecula</i>	<i>M. inquieta</i>	s	sz, m	2	2	2
	<i>Rhipidura rufifrons</i>	<i>M. fuliginosa</i>	s	m	3	3	4
	<i>Rhipidura fuliginosa</i>	<i>R. leucophrys</i>	h	s	3	3	1
Campephagidae	<i>Rhipidura rufifrons</i>	<i>R. leucophrys</i>	h	s	3	3	0
	<i>Coracina novaehollandiae</i>	<i>C. maxima</i>	h	s	3	3	3
	<i>Coracina novaehollandiae</i>	<i>C. papuensis</i>	h	sz	3	3	4
	<i>Coracina novaehollandiae</i>	<i>C. tenuirostris</i>	h	sz	3	3	3
	<i>Coracina papuensis</i>	<i>C. maxima</i>	h	s	2	1	1
	<i>Coracina papuensis</i>	<i>C. tenuirostris</i>	h		3	2	1
	<i>Coracina tenuirostris</i>	<i>C. maxima</i>	h	s	2	1	0
Artamidae	<i>Artamus leucorhynchus</i>	<i>A. cyanopterus</i>	h		2	3	1
	<i>Artamus leucorhynchus</i>	<i>A. personatus</i>	h		4	3	1
	<i>Artamus leucorhynchus</i>	<i>A. superciliosus</i>	h		4	3	1
	<i>Artamus leucorhynchus</i>	<i>A. cinereus</i>	h		4	4	0
	<i>Artamus personatus</i>	<i>A. cyanopterus</i>	h		3	4	2
	<i>Artamus personatus</i>	<i>A. cinereus</i>	h		5	3	1
	<i>Artamus personatus</i>	<i>A. superciliosus</i>	none!		5	5	5
	<i>Artamus superciliosus</i>	<i>A. cyanopterus</i>	h		3	4	2
	<i>Artamus superciliosus</i>	<i>A. cinereus</i>	h		5	3	1
	<i>Artamus cinereus</i>	<i>A. cyanopterus</i>	h	m	2	3	0
<i>Cracticus torquatus</i>	<i>C. nigrogularis</i>	h	sz	2	2	2	

Ecological segregation in SE Australia

Appendix 1. (Continued)

Family	Species 1	Species 2	Primary segregation mechanisms ¹	Other potentially important segregating mechanisms ²	Overlap in total range ³	Overlap in local range ³	Habitat overlap ⁴
Corvidae	<i>Strepera graculina</i>	<i>S. versicolor</i>	s	m	2	3	3
	<i>Corvus coronoides</i>	<i>C. tasmanicus</i>	h		2	2	1
	<i>Corvus coronoides</i>	<i>C. bennetti</i>	h		2	3	1
	<i>Corvus coronoides</i>	<i>C. mellori</i>	h		3	4	2
	<i>Corvus tasmanicus</i>	<i>C. mellori</i>	h		1	2	1
	<i>Corvus tasmanicus</i>	<i>C. bennetti</i>	r		0	0	0
	<i>Corvus mellori</i>	<i>C. bennetti</i>	r		2	2	1
Passeridae	<i>Taeniopygia guttata</i>	<i>T. bichenovii</i>	h		2	2	0
	<i>Stagonopleura guttata</i>	<i>S. bella</i>	h		2	2	0
Hirundinidae	<i>Hirundo neoxena</i>	<i>H. nigricans</i>	h	fg, s, m, n	2	4	2
	<i>Hirundo nigricans</i>	<i>H. ariel</i>	h	n	4	4	1
	<i>Hirundo ariel</i>	<i>H. neoxena</i>	n	fg, s, m	2	4	3
Sylviidae	<i>Cincloramphus mathewsi</i>	<i>C. cruralis</i>	h		4	4	0

¹ Ecological segregation mechanisms:

?=unsure; c=complex; fd=food; fg=foraging technique; h=habitat; m=migration; n=nest site; none!=none; r=range; s=stratum/substrate; sz=size. Range is given precedence to habitat as a primary mechanism, unless the two species occupy distinctly different habitats where their ranges join.

² Codes as above. Almost all species pairs show some differences in habitat and range, so these are not listed when considered only as secondary or potential mechanisms for ecological segregation. Degrees of overlap in range and habitat are described in the next three columns. The list of secondary mechanisms is not exhaustive.

³ Range overlap categories:

0=no contact; 1=ranges join, but little overlap; 2=substantial overlap; 3=range of one almost embraced by that of other, but latter covers much greater area; 4=ranges mostly overlapping, with range of one usually embraced by that of other; 5=ranges virtually identical.

⁴ Habitat overlap categories:

0=no overlap; 1=mainly separate habitats, but some overlap; 2=lots of separate habitat; substantial overlap too; 3=mainly overlapping but each species has separate habitats too; 4=one species has separate habitats but also completely overlaps habitat of the other species; 5=complete overlap. #=little or no overlap in breeding season, but may use similar habitats at other times. \$=less overlap in winter than in breeding season