
**Riparian and Upslope Influences on the Regional
Avifauna of the Semi-Arid Mulga Lands of South
West Queensland.**

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Abstract

Riparian areas have been widely recognised by wildlife biologists as a critically important and functionally dominant component of terrestrial landscapes. This viewpoint has its genesis in high concentrations of species and individuals across a wide range of environments and strong interactions between riparian areas and the surrounding landscape. Despite major concerns regarding conservation management in the Australian arid zone, few studies have specifically examined the importance of riparian areas to the terrestrial bird fauna of arid and semi-arid Australia.

This research aimed to examine the role of riparian areas in sustaining regional assemblages of terrestrial birds within the Australian arid zone. More specifically I asked: (1) How do riparian and upslope arid zone bird assemblages differ and to what extent are they interrelated? (2) Do these inter-relationships vary temporally with season, rainfall and year? (3) To what extent does surface water influence riparian and upslope bird assemblages?

This study was carried out in semi-arid Mulga Lands bioregion of south west Queensland (c. 181000 km²) where bird densities, species richness and composition were compared among 124 sites which were distributed throughout the bioregion and surveyed over two seasons (summer, winter) and two years (1997, 1998). El Niño-related drought conditions prevailed over both seasons during 1997 but not 1998. Monthly rainfall was not dependent on either season or year. The extent to which the availability of surface water in these areas also influences terrestrial birds was investigated by comparing bird

abundance, diversity and species composition at riparian and upslope sites, with and without permanent water. Upslope sites with permanent water were modelled using artesian bore drains.

Overall bird densities were twice as high in riparian areas as upslope habitats but about 20% more species were found in upslope habitats. The estimation of species richness in circumstances where there are major differences in abundance emerged as an important issue for riparian-upslope comparisons. Riparian areas were also characterised by higher levels of species dominance and similarity in species composition than upslope areas. Riparian-preferring species accounted for 68% of total bird abundance and many were common in the surrounding landscape. Similarly, many upslope-preferring species were common in riparian areas. The number of species shared between riparian and upslope areas was maximised at riparian sites with permanent water, implying that these areas were of near-universal advantage. These results suggested that riparian habitats of the Mulga Lands exert a fundamental influence on the entire terrestrial avifauna and are therefore important centres of avian biodiversity.

Despite high levels of climatic variation but only slight seasonal differences in mean rainfall and plant growth response, I observed a strong summer increase in species richness (overall and among many functional groups) but not in overall abundance. Fewer individuals and species were observed during the drought conditions of 1997. About half of the species (21 of 41) that could be individually categorised showed seasonal or inter-annual differences in occurrence, suggesting extensive inter-bioregional movements. Riparian usage was generally higher during periods of low monthly rainfall, but it was complicated by riparian interactions. Insectivores that forage mainly in the upper stratum,

and seed-eaters such as pigeons, parrots and cockatoos, made greater use of riparian areas as rainfall declined, whereas the number of low-feeding insectivore species increased in riparian areas with increasing rainfall. Overall riparian usage was also higher during drought, but not necessarily summer. Species composition was strongly influenced by season, year and rainfall, and there were strong species composition linkages between riparian and upslope bird communities. These results support the proposition that riparian areas have an important if not crucial role in sustaining bird populations, not only during prolonged drought as refuge habitat, but also over much smaller time scales.

Birds also responded strongly to the presence of surface water. The relative strength of the effects of riparian status and water availability were similar for most species and functional groups, although where differences were detected all favoured the effect of riparian status. Most species and functional groups showed specialised preferences for specific combinations of riparian status and water availability rather than generalised responses to either or both. Most displayed a dominant preference for riparian or upslope habitats and preferentially sought to meet their need for water within these areas. Because of the specialised responses, the presence of permanent water could only partially explain differences in bird assemblages between riparian and upslope sites. A significant role for higher productivity and/or structural complexity in riparian areas was suggested by strong associations between riparian status and vegetation structure that were only weakly related to the presence of surface water. Small insectivorous passerines, many of which are already uncommon or declining in other bioregions, appear most vulnerable to the planned closure of bore drains.

This study suggests that, as far as the Mulga Land birds are concerned, the bird communities of riparian and upslope components of the landscape are functionally interrelated. This is despite strong structural and floristic differences in habitat, and the fact that many bird species show distinct preferences for one habitat or the other. Almost all terrestrial species were found in both the riparian and upslope habitats, although their use appeared to be strongly related to spatial and temporal variations in resource availability. As most birds are capable fliers, and changes in relative abundance were rapid, these patterns are likely to more strongly reflect movement between habitats (and in some cases, bioregions), than differences in recruitment and mortality. In fluctuating and unpredictable environments the ability to move between habitats may be an important adaptive strategy to dampen spatial and temporal variations in resources and facilitate species persistence. The overall picture is one of a shared and responsive avifauna.

As many of the specific responses observed in this study appeared to be a predictable outcome of spatial variations in productive potential and temporal variations in resource availability, a conceptual model was proposed to explain spatio-temporal variations in terrestrial bird community organization in the Australian arid zone. The model establishes a graphical response domain, defined by a spatial axis that represents long-term cumulative outcomes of prevailing spatial and temporal productive processes (e.g. spatial variation in nutrient status, soil moisture and vegetation biomass) and a temporal axis that represents short-term availability of productive resources (e.g. rainfall). Within this domain, individual response surfaces were proposed to predict relative site-based differences in overall bird abundance, dominance, species richness, and inter-habitat movement. In addition to responses at average levels of resource availability, the

response domain was also used to consider how birds might vary their use of the landscape under two extremes of environmental variability, drought and production pulses after extensive rainfall. The model may also predict assemblage differences in other biomes.

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Statement of Originality

This work has not previously been submitted for a degree or diploma in any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

Mark B. Kingston

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1.0 General Introduction

1.1 Riparian zones and their importance

The word *riparian* is derived from the Latin *riparius*, land adjacent to a body of water (Naiman and Décamps, 1997; Voller, 1998). Stream ecologists have long recognised the importance of stream-side vegetation to the structure and function of stream ecosystems (e.g. Cummins, 1974). In this ecological context, *riparian* takes on a broader meaning, referring to the ecological interface (ecotone) between terrestrial and aquatic systems (Gregory *et al.*, 1991; Bunn, 1993). Although precise definitions vary (Voller, 1998; Wenger, 1999; National Research Council, 2002), the mutual influence of aquatic and terrestrial ecosystems is a recurrent theme in the ecological literature (National Research Council, 2002). In this thesis the terms riparian area, riparian zone, and riparian habitat are used synonymously. The term *upslope* refers to the non-riparian portion of the terrestrial landscape.

Riparian habitats have a number of features that set them apart from other types of ecotone. Rather than reflecting a simple discontinuity, the processes that create riparian habitats are highly directional. Fluvial processes ensure that water, sediment, nutrients and organic materials are all channelled into, and moved along valley floors (Gregory *et al.*, 1991). These materials are concentrated in riparian areas often resulting in high soil moisture, nutrient rich soils and lush vegetation growth (Brinson *et al.*, 1981). Subject to flood disturbances, the effects of which may vary greatly in magnitude, time and space, riparian areas are also thought to be unusually dynamic parts of the landscape (Gregory

et al., 1991; Naiman and Décamps, 1997). Riparian ecotones are uniquely linear and dendritic, providing lateral and longitudinal linkages to most types of habitat in the landscape (Brinson *et al.*, 1981). Furthermore, at one scale, riparian areas are ecotones between the terrestrial and aquatic, and at a finer scale they represent a distinct habitat with separate riparian-upslope and riparian-aquatic ecotones (Malanson, 1993).

Terrestrial faunas are influenced both by the riparian habitat itself (including aquatic elements) and by environmental gradients arising from the nature of the riparian-upslope interface (Brinson *et al.*, 1981; Kelsey and West, 1998; Price and McLennon, 2001). Many studies have shown that that riparian zones support a disproportionately high component of total terrestrial biodiversity (see reviews of Thomas *et al.*, 1979a; Brinson *et al.*, 1981; Knopf, 1988a; Knutson and Naef, 1997; Kelsey and West, 1998; National Research Council, 2002). It has also been suggested that riparian habitats are important to the functioning of the adjacent ecological systems (Szaro and Jakle, 1985; Risser, 1990; Gregory *et al.*, 1991; Naiman *et al.*, 1993). Naiman *et al.* (1993, 1997) claimed that riparian habitats are the most diverse, dynamic and complex terrestrial habitats on Earth. Knopf (1988a; after Wilson, 1979) characterised the riparian zone as the *aorta of an ecosystem*. Hunt (1985) claimed that these areas are among the most productive and valuable ecosystems on Earth.

However, riparian habitats occupy a small proportion of the terrestrial landscape (less than 1% in some landscapes; Hewitt, 1990), are highly valued by human populations, and thus represent areas of maximum potential conflict between users and the needs of wildlife (Thomas *et al.*, 1979a). Disruption of riparian-upslope habitat complexes may occur as a result of many activities including forestry, agriculture, grazing, urbanisation,

mining and recreation. The extents of such impacts are not well documented (Montgomery, 1996) but, in some U.S. states, more than 80% of riparian habitats have been destroyed (Hewitt 1990; Montgomery, 1996).

Most research on the role of riparian habitats for terrestrial wildlife focuses on birds and originates in North America (Catterall, 1993; Wilson and Imhof, 1998). Despite an appalling record of species extinction and decline since European colonisation (Woinarski and Fisher, 2003; Smyth and James, 2004) and a unique flora and fauna (Stafford Smith and Morton, 1990; James *et al.*, 1995), there have been very few quantitative studies that have compared the avifauna of Australian riparian habitats to adjacent parts of the landscape.

1.2 Riparian Influences on Terrestrial Wildlife

1.2.1 Riparian Habitat Features

A number of features of riparian habitats themselves contribute to high wildlife densities and diversity. However, many of the properties of riparian habitats are interrelated and species commonly respond to more than one (Naiman and Décamps, 1997).

Productivity, food, water and microclimate

High riparian primary production is realised through the combination of fertile alluvial soils, the ready availability of surface and sub-surface water, and sunlight (Cummins,

1993; Brinson *et al.*, 1981; Peterjohn and Correll, 1984; National Research Council, 2002). Although most riparian zones are more productive than nearby upslope sites (Brinson *et al.*, 1981; Malanson, 1993; Naiman and Décamps, 1997), they may have low productivity if they are poorly drained (Price and McLennon, 2001) or constantly exposed to flood disturbance or inundation (Brinson *et al.*, 1981).

Whether or not these conditions translate into correspondingly high levels of secondary production is not known, however a large number of studies from many taxonomic groups and bioregional settings show higher abundances in riparian habitats. Brinson *et al.* (1981) listed nine studies from a range of locations in the US that compared bird densities between riparian and upslope habitats. All favoured riparian habitats, many at densities more than twice that found in adjacent habitats. Similar patterns are apparent in the Australian bird literature (e.g. Recher *et al.*, 1991; Bentley and Catterall, 1997; MacNally *et al.*, 2000; Woinarski and Ash, 2002). Examples from other taxa include: Cross (1985, small mammals), Warren and Hurst (1982, small mammals), Mc Elfresh *et al.* (1980, small mammals), Dickson (1989, small mammals); Brode and Bury (1984; amphibians and reptiles); and Parson (1981; invertebrates). Significantly, for most of these studies, the riparian habitats supported taller or denser vegetation than the surrounding landscape. Where riparian and upslope habitats are more similar, differences in bird (McGarigal and McComb, 1992; Croonquist and Brooks, 1993), reptile and amphibian (Degraaf and Rudis, 1990; McComb *et al.*, 1993a, 1993b) and small mammal (McComb *et al.*, 1993a, 1993b; Cross, 1985; Doyle, 1990) densities appear less obvious, or more closely reflect other parameters such as compositional and structural differences in habitat (Kelsey and West, 1998).

The effects of elevated riparian productivity are also suggested by positive faunal associations with soil moisture (birds, Smith, 1977, Douglas *et al.*, 1992; small mammals, Armstrong, 1977, Miller and Getz, 1977) and the production of food resources (birds, Rosenberg *et al.*, 1982; Strong and Bock, 1990; Gates and Griffin, 1991; Aumann, 2001; small mammals, Doyle, 1990). Food resources in riparian habitats may also be enhanced by “aquatic” insects, many of which have adult stages that emerge from rivers and streams and move into adjacent riparian habitats (Lynch and Catterall, 1999; Lynch *et al.*, 2002). In some cases essential food resources may only be available in the riparian zone. The production of fleshy fruits, for instance is typically associated with mesic conditions and has been linked to high densities of frugivorous birds (Price, 2004) and flying foxes (*Pteropus* spp; Palmer and Woinarski, 1999) in northern Australia. Throughout Australia, koala (*Phascolarctos cinereus*) feed exclusively on a limited number of eucalypt (and related species) species, many of which prefer moist fertile soils (Strahan, 1983) that are common in riparian areas (e.g. forest red-gum *Eucalyptus tereticornis*, tallowwood *E. microcorys*, swamp mahogany *E. robusta*). In the more arid parts of the continent, koala feed-species such as river red-gum (*E. camaldulensis*) are essentially restricted to floodplain habitats.

The riparian and adjacent aquatic environments provide wildlife with water to drink, feed, rest, and reproduce (Thomas *et al.*, 1979a; Malanson, 1993; Klapproth and Johnson, 2000). Many amphibians and macroinvertebrates need water to reproduce and are consequently confined to riparian habitats (Klapproth and Johnson, 2000). Surface water is also the preferred feeding substrate of many waterbirds and kingfishers (Brinson *et al.*, 1981). In arid landscapes, surface water may only be available along watercourses and many species including most large mammals cannot survive without drinking water

(Landsberg *et al.*, 1999; Kelsey and West, 1998). Many birds, especially seed-eaters, do not obtain sufficient moisture from their food, and are rarely found far from drinking water (Fisher *et al.*, 1972; Dawson, 1976; Schodde, 1982). Holstein (1984) attributed high avian abundance (and diversity) to the presence of water and nutrients present in the riparian zone but absent from the adjacent drought stressed vegetation. Studies in the Australian arid zone (Landsberg *et al.*, 1999; Harrington, 2002) show that the provision of artificial water increased biomass production among native birds, large native mammals (such as kangaroos), feral herbivores and predators. Similar patterns occur elsewhere (see Harrington, 2002).

The influence of vegetation and proximity to water may also moderate microclimate, making riparian areas more habitable to some species (Thomas *et al.*, 1979a). Riparian vegetation reduces the effects of wind, intercepts solar radiation and transpires moisture from groundwater thus moderating temperature, humidity and soil moisture relations (Malanson, 1993). As a result, riparian habitats are thought to be especially important for species sensitive to desiccation (e.g. amphibians; Dupuis *et al.*, 1995) or those seeking refuge from harsher conditions elsewhere (Lynch and Catterall, 1999). For example, Best and Stauffer (1980) found that the nesting success of birds was lower in exposed open areas than in more sheltered riparian sites. Doyle (1990) observed lower and more stable temperatures in riparian areas and suggested that this could reduce energy expenditure, and thus partially explain high densities of small mammals in riparian areas.

Riparian productivity is also frequently linked to wildlife (and plant) diversity, however this connection is less well established than the association with abundance

(Waide *et al.*, 1999; Mittelbach *et al.*, 2001). A number of theories that attempt to explain local variations in species diversity recognise that productive capacity influences diversity but also incorporate other moderating factors such as spatial heterogeneity (Tilman, 1982), biotic feedbacks (Menge and Sutherland, 1987) and disturbance (Huston, 1979, 1994).

Structural and floristic complexity

Compared to adjacent upslope areas riparian zones are known to contain high floristic and structural plant species diversity (Gregory *et al.* 1991; Meave *et al.* 1991; Naiman and Décamps, 1997). This diversity provides a complex range of niches for wildlife allowing many different species to live in the same place by partitioning the environment (MacArthur, 1958; Bull and Skovlin, 1982).

Particular wildlife species often have specialised autecological requirements which are satisfied in the riparian zone. For example, among birds these include nesting and perching sites (Glinski and Ohmart, 1983; Fiedler and Starkey, 1986), preferences for specific floristic associations (Strong and Bock, 1990; Woinarski *et al.*, 2000), or even individual species of tree (Stapanian, 1982). Furthermore, there is widespread agreement that a complex vegetation structure provides resources that can be simultaneously utilised by many species (Stamp, 1978; Stauffer and Best, 1980; Gutzwiller and Anderson, 1987; Strong and Bock, 1990; Mills *et al.*, 1991; Douglas *et al.*, 1992). Conversely, when riparian habitats are impoverished by grazing, wildlife densities and species richness generally decline (Knopf *et al.*, 1988b; Taylor, 1986; Taylor and Littlefield, 1986; Powell *et al.*, 2000; Jansen and Robertson, 2001;

Woinarski and Ash, 2002). Ground cover density in riparian areas appears particularly important to small mammals and amphibians (Cross, 1985; Doyle, 1990; Kelsey and West, 1998; Woinarski and Ash, 2002).

Many kinds of wildlife make use of standing (Thomas *et al.*, 1979b) and fallen woody debris (Maser *et al.*, 1979), which is often abundant in riparian areas (Brinson *et al.*, 1981; Knutson and Kaef, 1997). In Australia, tree hollows provide essential habitat for many species of birds (e.g. parrots, cockatoos, owls; Gibbons and Lindenmayer, 2002) and arboreal mammals (e.g. bats, possums, gliders; Jarman, 1986). Standing dead trees are also commonly used for perching, roosting or nesting by waterbirds, raptors, kingfishers and aerial insectivores. In many arid regions, trees (hence dead trees and tree-hollows) are restricted to riparian areas. Fallen woody debris provides cover and reproductive sites for many ground-dwelling species including: small and medium-sized mammals (e.g. antechinus, bandicoots, wallabies, canines) and rodents such as the partially aquatic water rat (*Hydromys chrysogaster*); monotremes such as the echidna (*Tachyglossus aculeatus*); in addition to reptiles, amphibians and invertebrates (see MacNally, 2001; MacNally *et al.*, 2001).

Habitat heterogeneity and edge influences

Habitat heterogeneity is variation between habitats. It is a common feature of riparian zones, caused by various scales of fluvial disturbance, which vary both longitudinally downstream and laterally across the floodplain (Gregory *et al.*, 1991). Regular and episodic disturbances contribute to local variations in topography, hydrology and soils and it is common to find specific vegetation communities associated with differing

substrates (e.g. deposits of sand, soil, gravel and organic materials, rock outcrops, springs, soaks and wetlands; Klapproth and Johnson, 2000) and in different stages of succession (Gregory *et al.*, 1991; Malanson, 1993; Naiman *et al.*, 1998). In a study of the riparian vegetation of the Murray River, Margules *et al.*, (1990) catalogued 767 species of vascular plant from 20 structural classes and 37 separate floristic communities. Claims of exceptional plant diversity in riparian areas are largely attributed to this mosaic of habitat patches (Naiman *et al.*, 1993; Naiman and Décamps, 1997; Pollock *et al.*, 1998).

The influence of habitat heterogeneity on wildlife is well established (Anderson, 1978; Fox, 1983; Rosenzweig, 1995) but in riparian areas quantitative associations have been limited to a number of bird studies. Specific influences on riparian bird communities have been inferred from associations with elevation and stream size (Knopf, 1985; Finch, 1989, 1991; Lock and Naiman, 1998; Woinarski *et al.*, 2000); successional sequences (Kessler and Kogut, 1985; Roche, 1989; Kelsey and West, 1998) and biogeographical parameters such as patch size, shape, isolation and width (Stauffer and Best, 1980; Dobkin and Wilcox, 1986; Gutzwiller and Anderson, 1987; Smith and Schaefer, 1992; Croonquist and Brooks, 1993; Spackman and Hughes, 1995; Bentley and Catterall, 1997; Kilgo *et al.*, 1998; Saab, 1999; Miller *et al.*, 2003).

Further contributions to habitat heterogeneity arise from the ecotonal transitions between different riparian habitats and between riparian habitats and adjacent aquatic or upslope environments. Such transitions may be discrete (edges) or gradual and often promote unique combinations of resources (Yahner, 1988), which spawn novel edge-mediated species interactions (see Fagan *et al.*, 1999). Examples include: high abundances of bird

resources such as fruits and insects (Kroodsmas, 1984); dense cover for both predators and prey; and contextual features such as conspicuous perches, nesting, roosting and foraging habitat (Gates and Griffin, 1991). Indeed, due to the linear arrangement of riparian habitats in the landscape, extensive edge influences are characteristic of riparian ecosystems (Thomas *et al.*, 1979a; Naiman and Décamps, 1997). In Australia, species such as the platypus (*Ornithorhynchus anatinus*), water rat, bats, macroinvertebrates and many birds make extensive use of the riparian habitats and the adjacent aquatic environment.

Migration and dispersal corridors

The linear arrangement of riparian habitats has led to the idea that riparian areas function as dispersal and migration corridors for birds and other species (Thomas *et al.*, 1979a; Noss, 1983; Brinson *et al.*, 1981; Foreman and Godron, 1986). Although many studies show that wildlife use riparian (see above) and other linear habitats (Saunders and Hobbs, 1991; Bennett, 1999; MacDonald, 2003), few have demonstrated migration or dispersal along riparian areas (Naiman and Décamps, 1997). Nonetheless, there is some evidence that riparian habitats are favoured by migratory landbirds. In south east Queensland, Bentley and Catterall (1997) observed high densities of winter migrants in riparian areas in both forested and highly fragmented matrices. In the arid south west of North America, densities of insectivorous migratory birds more than 10 times that of upslope sites have been reported (Stevens *et al.*, 1977; Hehnke and Stone, 1979). Significantly, however, Skagen *et al.* (1998) found that small fertile and isolated oases in the same region also supported high numbers of migratory insectivores, suggesting that

many migratory species use riparian areas as stopover sites rather than migratory pathways.

There is also evidence for smaller-scale movement within riparian habitats. Knopf (1985) for example found that riparian bird communities were more similar to each other than among upslope habitats within a northern Colorado catchment. Finch (1989, 1991) made similar findings in Wyoming but attributed their observations to elevation-related differences in habitat complexity. Wauer (1977) suggested that some birds move altitudinally along riparian corridors between different seasons. Riparian woodlands that extend between high and low elevations may be similarly important for seasonal movements of some large mammals such as elk and deer (Thomas *et al.*, 1979a). In a manipulative experiment, Machtans, *et al.* (1996) examined bird movements in riparian buffer strips before and after harvesting of an adjacent forest in Alberta, Canada. They found that juvenile birds used the riparian corridors for dispersal, however the number of adults decreased immediately after harvest, negating any inferred riparian movement. It seems the adult response was complicated by extensive “off-territory” explorations (i.e. riparian-upslope linkages, see below) which were disrupted by the clearing.

1.2.2 Riparian-Upslope Gradients

Although riparian habitats commonly have unique combinations of attributes which are attractive to wildlife, their importance may ultimately depend on the nature of the gradient that distinguishes them from the rest of the landscape. Riparian-upslope gradients vary spatially, temporally and at different scales of resolution (Gregory *et al.*, 1991; Malanson, 1993; Naiman and Décamps, 1997). Many of the studies showing that

riparian zones sustain higher levels of wildlife abundance and diversity than adjoining habitats have been conducted in settings with steep riparian-upslope habitat gradients. For example in arid North America, Knopf (1985) noted that 82% of all bird species breeding in northern Colorado occur in riparian areas. Szaro and Jakle (1985) reported bird densities 3-4 times higher in a riparian island than in the surrounding central Arizonan desert uplands. Johnson and Haight (1985) recorded bird population densities and species diversity 5-10 times that of the adjacent desert habitat. Saab (1999) found that the landscape context (composition and structure of the habitat matrix) influenced riparian birds more than macrohabitat (e.g. riparian patch size) and microhabitat features (e.g. canopy cover). Comparatively high numbers of birds and species are also commonly found in riparian areas which are embedded in agricultural and urbanised matrices (Emmerich and Vohs, 1982; Strong and Bock, 1990; Croonquist and Brooks, 1993; Smith and Schaefer, 1992; Bentley and Catterall, 1997; Miller *et al.*, 2003), however, total bird densities are often influenced by a few abundant cosmopolitan species that thrive in human-modified areas. Examples of the use of riparian areas at different times of the year (Stevens *et al.*, 1977; Hehnke and Stone, 1979; Wiebe and Martin, 1998) suggest that species also respond to temporal variations in the strength of the riparian-upslope gradient. Greater use of riparian areas might also be expected during drought when extreme gradients in water (and food) availability exist between riparian and upslope areas.

In areas, or at times, where the riparian-upslope habitat gradient is less extreme wildlife appear to respond to more subtle variations in habitat conditions. McGarigal and McComb (1992) compared bird communities between riparian and upslope areas within moist and mixed coniferous forests in Oregon and found that upslope areas supported

higher avian abundances and species richness than the associated riparian zones. They explained their observations partially in terms of favourable aspects of vegetation structure, such as snags and large conifers away from the riparian zone, but noted a number of fundamental differences between their study sites and those of arid environments: 1) in arid areas water may only be available in the riparian zone; 2) transpiration gradients are likely to be much more dramatic between arid zone riparian and non-riparian areas, imposing severe energetic costs; and 3) unlike coniferous forests, riparian vegetation in arid areas may be structurally more complex when compared to adjacent non-riparian areas. In a similar forest in south eastern Alaska, Kessler and Kogut (1985) found that riparian areas supported greater avian abundance and species richness than non-riparian areas of the same successional stage. Their explanation for this was that old growth (upslope) forests do not support a complex understorey. Croonquist and Brooks (1993; north east USA) found that bird abundance and diversity remained relatively constant throughout their moist forested reference catchment. Stauffer and Best (1980) assessed avifaunal differences between riparian and non-riparian woodland in Iowa, and also found little difference in species richness, but that the riparian areas supported higher bird densities.

Together these studies suggest that if important habitat features (or combinations thereof) are present in both the riparian and upslope components of the landscape, the value of the riparian habitat is diminished. Conversely, where riparian habitats contain important attributes and adjacent upslope areas do not their value is enhanced. Indeed it seems almost tautological; that the more similar that the riparian and adjacent upslope habitats are, the more similar the fauna should be.

1.3 Riparian-upslope linkages

Although there is a clear geomorphological pathway to suggest that upslope areas influence the form and function of riparian habitats (see Section 1.1 above), claims that riparian habitats influence the functioning of adjacent terrestrial ecosystems are commonly also made (Szaro and Jackle, 1985; Risser, 1990; Gregory *et al.*, 1991; Naiman *et al.*, 1993; Knopf and Samson, 1994) but rarely tested. This is surprising given the high degree of habitat overlap commonly observed between riparian and upslope fauna assemblages in relatively natural contexts. Even in arid zones, across extreme riparian-upslope gradients, most species of bird appear to occur, if only occasionally, in both parts of the landscape (see Szaro and Jackle, 1985). Indeed on a global basis, Buckton and Ormerod (2002) found only 60 riparian “specialist” bird species (none of which occur in Australia). Although allocation to such categories is largely a matter of definition, these observations suggest that while riparian habitats are commonly utilised by many birds (and other fauna), the vast majority of species also use other types of habitat, presumably moving into and out of riparian areas as necessary. Knopf and Samson (1994) point out that most wildlife studies have focussed on the riparian zone itself, or the differences between riparian and upslope habitats, and consequently underestimate the linkages between them.

Several approaches have been used to describe the extent to which species are apparently dependent on riparian habitats. These include: assessments of the generality of habitat use (Stauffer and Best, 1980; Finch, 1989); allocation to response guilds based on habitat occupancy (Cronquist and Brooks, 1991, 1993); and various autecological approaches (Johnson *et al.*, 1977; Collier, 1994; Kelsey and West, 1998; Buckton and Ormerod,

2002). Dependencies, however, are complicated and may involve one or more of the riparian features discussed previously (nest sites, cover, roosting, migratory stopovers, foraging opportunities, water availability etc.), and occur diurnally, seasonally or for some species, irregularly, as refuge habitat during adversity such as drought or fire (Catterall, 1993). Kelsey and West (1998) regarded taxa as riparian “obligates” as those likely to disappear with the loss of riparian habitat from a drainage basin. Although it is overly simplistic to conceptualise riparian dependency as a binary state (rather than a continuum), this definition nonetheless acknowledges that species may be critically dependent on riparian resources even if rarely observed in riparian areas. Such linkages may be particularly important in arid and other harsh environments, where there are strong and fluctuating riparian-upslope gradients in essential resources such as water.

1.4 The Australian arid zone

Australia’s arid lands are a dominant geographic feature of the continent, occurring where rainfall is insufficient to support the production of agricultural crops (Stanley, 1982; Morton, 1986). Wilson and Graetz, (1979) estimated that the arid zone occupies about 69% (5.3 million km²; other estimates vary slightly) of the continent, one of the largest arid regions in the world (Northcote and Wright, 1982). This area is essentially bound by annual rainfall of about 250 mm in the inland and south, but extends to the 675 mm isohyet in the east and north, where plant growth remains restricted by rainfall seasonality and reliability. Compared to other hot and dry regions, such as the North American deserts, where much of the riparian research has originated, there are a number of physical differences in the Australian arid zone that, in combination, set it apart, and in turn structure a unique flora and fauna (Stafford Smith and Morton, 1990).

Lack of rainfall is a defining feature of arid zones across the globe, however rainfall in arid Australia is also characterised by unusually high temporal and spatial variability (Gentili, 1971; Stafford Smith and Morton, 1990). Rain-producing mechanisms affecting the arid zone include: monsoonal influences in the north; summer rain depressions from tropical cyclones, which sometimes penetrate into the arid interior to cause major rainfall events including flooding; and less extensive rainfall from temperate fronts during winter in the south (Body, 1982). A bias toward summer rainfall over much of the arid zone is counteracted by increased evaporation during the hotter months, with the consequence that plant growth is only moderately seasonal (Nix, 1982). Superimposed on these influences is the El Niño Southern Oscillation (ENSO) phenomenon, which greatly increases rainfall variability and is a major cause of extended drought (Nicholls and Kariko, 1993; Bureau of Meteorology, 1997). Climate change scenarios for arid Australia indicate that rainfall variability and unpredictability will increase (Hughes, 2003).

The ENSO phenomenon is also thought to be largely responsible for characteristic periods of widespread rain, highly variable river flows and flooding that occur in the Australian arid zone (Young, 2001). Such events structure the landscape by transferring organic matter, sediment and nutrients to alluvial floodplains and floodouts, reworking microtopography and recharging water tables, surface and sub-surface flows, and storages (Pickup, 1988; Ludwig *et al.*, 1997). Stafford Smith and Morton (1990) proposed that these processes contribute to greater water availability for growth than would be expected from a similar mean rainfall, and thus partially explain the ability of the Australian arid zone to sustain a high biomass of long-lived plant species. About

80% of the Australian arid zone is vegetated, dominated by five broadly-defined plant communities: *Acacia* shrubland (33%, mulga); hummock grassland (31%, spinifex); tussock grasslands (9%, mitchell grass); chenopod shrublands (8%, saltbush) and *Eucalyptus* shrubland (8%, mallee; Morton, 1986; see also Williams, 1982).

Stafford Smith and Morton (1990) also proposed another major physical difference in Australia's arid zone; an ancient, flat, infertile but well-sorted landscape. Although soils of arid Australia are infertile compared to other regions of similar aridity (Williams and Raupach, 1983), the flatness of the landscape promotes complex runoff/runon patterns which enhance soil productive capacity by concentrating sediment, nutrients and water at different spatial scales (Stafford Smith and Morton, 1990). At the finer scales, differences in productive capacity occur because perennial vegetation is able to persist during drought and intercept runoff when it rains. This increases nutrient status and soil moisture under the vegetation and results in a mosaic of vegetated groves and intergroves (Ludwig *et al.*, 1997). At the scale of the broader landscape, productive resources are further concentrated in permanent and ephemeral lakes, runon areas (such as dune swales and floodouts), and along river channels and their floodplains (James *et al.*, 1995). These areas are the most productive, provide the best opportunities for sustained plant growth, and in the case of riparian habitats, are commonly populated by a wide range of plants including large trees (Stafford Smith and Morton, 1990).

Other consequences of these physical influences on arid zone flora may include: (1) limits to herbivory, promotion of sclerophylly, the absence of deciduous leaves, and inhibition of microbial breakdown caused by poor fertility; (2) promotion of fire, by the presence of a high standing crop of perennial plants in a dry environment, and its role in

maintaining plant diversity and nutrient cycling and; (3) production pulses driven by irregular rainfall (Stafford Smith and Morton, 1990). Together these factors produce a diverse and highly-patterned landscape mosaic reflecting interrelated gradients in fertility and water availability (Stafford Smith and Morton, 1990).

Physical factors affecting Australian arid zone plant communities may also partially explain differences in the composition of Australian arid zone fauna. Again these are usefully described in terms of a functional continuum that extend from dry and infertile erosional parts of the landscape to depositional areas such as riparian zones where nutrients concentrate and water is more readily available. Stafford Smith and Morton (1990) proposed that although perennial plants occupy much of the Australian arid zone, infertile soils across most of the landscape render them poor forage, focusing limited herbivory onto the irregular growth of ephemerals. Consequently, they suggested that Australian arid lands support comparatively few mammals, and large amounts of biomass go to a high diversity of ants (which can buffer unfavourable conditions by surviving on seeds stored in their galleries; Morton, 1986), and directly into the detritivorous pathway, which is dominated by termites. High numbers of termites and ants may, in turn, support small predators with low metabolic rates such as spiders, lizards and other reptiles. In contrast, continuous production in much more limited areas such as riparian zones, may provide a focus for native mammalian and invertebrate herbivores and many groups of birds, as well as introduced mammals (rabbits, livestock etc.; see also Griffin and Friedel, 1984; Morton, 1990; Stafford Smith and Morton, 1990). Stafford Smith and Morton (1990) also predict that diversities of avian insectivores, nectar feeders, seed eaters, predators and scavengers should all be

higher in riparian areas than on the less fertile upslope *Acacia* shrublands (mulga), a result generally consistent with the North American studies.

In recent years research into ecological functioning in arid Australia has been propelled by some profound and disturbing declines in biodiversity, presumed to be a consequence of pastoralism and other anthropogenic sources of change (James *et al.*, 1995). Since European settlement, 20 arid zone mammals have become extinct and a further six have been confined to captive or wild populations on offshore islands (Woinarski and Fisher, 2003). This represents one third of the arid zone mammal fauna (James *et al.*, 1995) and is widely recognised as one of the world's most dramatic losses of biodiversity in historic times (Woinarski and Fisher, 2003). Morton (1990) hypothesised that many of these extinctions were a consequence of their dependence on small fertile areas (riparian or run-on areas), the nature of which were altered by high populations of introduced herbivores and predators. Nix (1993) proposed similar arguments to explain less dramatic, but nonetheless, broad-scale declines in some arid and semi-arid avifauna (e.g. see Reid and Fleming, 1992, Smith and Smith, 1994, Reid, 1999, Woinarski and Catterall, 2004).

There is strong evidence of significant recent human impacts on the arid zone biota arising from (or coincident with) the advent of pastoralism (Smyth and James, 2004). These impacts include various combinations of: overgrazing (Freudenberger *et al.*, 1997; Pringle and Landsberg, 2004) by domestic (sheep, cattle, horses, goats, donkeys, camels), native (macropods and some rodents) and feral herbivores (mice, rats, rabbits, pigs, goats; Edwards *et al.*, 2004); vegetation clearing in attempts to establish pasture (Glaznig, 1995; Wilson, 1997); predation by introduced cats, rats, foxes, pigs and dogs

(Morton, 1990; Edwards *et al.*, 2004); invasions of exotic plants (Grice, 2004) and inappropriate fire regimes (in some areas the absence of fire has led to the conversion of vast areas of productive grasslands to unpalatable shrubland; Hodgkinson and Harrington, 1985; Witt *et al.*, 2000).

Many of these changes have been facilitated by the provision of “artificial” water derived from unconfined and artesian aquifers (James *et al.*, 1999). Prior to European settlement, water was often extremely scarce in the arid zone (James *et al.*, 1999) but watering points are now so numerous that they are rarely more than 10 km apart (Landsberg and Gillieson, 1999). Since water is a key to biological activity in the arid zone, it is doubtful if pastoralism, and many of the coincident species introductions, could have persisted without it (James *et al.*, 1999). The extensive provision of artificial water has also had profound influences on the distribution and abundance of native species and assemblages including birds (James *et al.*, 1999; Harrington, 2002). Potential interactions between the provision of artificial water and riparian-upslope relationships have not yet been addressed. James *et al.* (1995) emphasised that knowledge and understanding of the processes responsible for spatial and temporal patterning of native biota is essential if further human impacts in the arid zone are to be avoided and conservation outcomes improved.

1.5 Study aims and approach

1.5.1 Aims, scope and approach

This study is focussed on understanding how fauna assemblages relate to riparian and upslope components of the landscape, with reference to terrestrial birds. Relative to other groups, birds are conspicuous and common in the landscape and are thus easily sampled (Mac Nally *et al.*, 2004). Their relatively high diversity and wide range of life history strategies permits testing of a wide range of hypotheses. They are also highly mobile, and although this may limit their utility as general indicators (Mac Nally *et al.*, 2004), their mobility permits rapid responses to environmental change, an important quality in dynamic and unpredictable environments (James *et al.*, 1995). Furthermore, birds are the most commonly studied riparian fauna (Catterall, 1993), a fact that facilitates cross-study comparisons.

The principal aim of this thesis is to examine the role of riparian areas in sustaining regional assemblages of terrestrial birds within the Australian arid zone. To do this it is necessary to understand how birds use the riparian and upslope components of the landscape. Characteristics of this region, such as the moderate seasonal influences, the presence of long-lived perennial vegetation in both riparian and upslope habitats, highly variable patterns of rainfall and river flow, and the availability of surface water away from the riparian zone present significant opportunities to examine riparian-upslope linkages among terrestrial birds.

More specifically this thesis asks:

1. How do riparian and upslope arid zone bird assemblages differ and to what extent are they interrelated?
2. Do these inter-relationships vary temporally with season, rainfall and year?
3. To what extent does surface water influence riparian and upslope bird assemblages?

The study focussed on the semi-arid Mulga Lands of south west Queensland (Thackway and Cresswell, 1995). Although similar in ecology and biota to other parts of the Australian arid zone, which are dominated by *Acacia* shrublands, physical and climatic conditions in the Mulga Lands at the time of the study presented a number of unique opportunities to address the questions above. The study spanned an abrupt discontinuity in El Niño-related drought and more mesic conditions. Mulga Land vegetation systems contain a range of woodland and shrubland upslope habitats; riparian areas are dominated by large trees and occur with and without permanent water; bore drains from the artesian aquifers provide permanent water in a non-riparian context; and plant growth in the region is uniquely aseasonal (Nix, 1976).

The study is based on an empirical analysis of bird observations from a large number of sites located within different landscape zones, and with differing access to water, distributed across the entire bioregion, and surveyed repeatedly during two years and two seasons. Statistical models are used to derive response groups based on spatial and

temporal differences in relative density, prevalence, richness and species composition. The results are used to infer inter-habitat and inter-bioregional spatial and temporal patterns of occupancy, overlap and linkage.

1.5.2 Thesis outline

In Chapter 2, an overview is provided of the study area, including physical conditions, climatic influences, patterns of vegetation, details of study sites, and sampling procedures. These features are common methodological components that underpin many of the analyses contained in the following chapters. Although many of the statistical analyses used in this thesis are similar between chapters, there are many subtle differences. Consequently, these are detailed separately in each of the Chapters 3, 4 and 5. Notwithstanding this, where statistical procedures are identical reference is made to their first mention in Chapter 3.

Chapter 3 investigates the broad spatial patterns of riparian and upslope occupancy, and inter-habitat overlap among the terrestrial avifauna of the Mulga Lands. This involved establishing whether or not riparian areas supported a richer or more abundant avifauna and the extent to which riparian and upslope bird assemblages were distinctive and influenced each other. Implications for conservation and management arising from proposed expansion of agricultural activities are also discussed.

Chapter 4 examines broad temporal patterns by considering the relative influence of season, localised rainfall, and inter-annual climatic variation on riparian and upslope bird

assemblages. The results presented in this chapter test the ideas that species track rainfall, and/or use riparian habitats to compensate for seasonal or irregular fluctuations in their resource base such as those caused by drought.

The observation that riparian areas contain surface water but that upslope areas do not is a frequent generalisation that has led to the hypothesis that species are common in riparian areas because of the presence of water (Thomas, 1979a; Szaro and Jackle, 1985; McGarigal and McComb, 1992). In Chapter 5, this idea is tested by comparing bird responses to riparian and upslope habitats with and without permanent water. The relative importance of riparian-upslope differences in vegetation structure is also evaluated, and implications for the avifaunal use of artificial water are discussed.

Chapter 6 synthesises information from the preceding chapters to describe the overall patterns of riparian and upslope usage. This chapter also considers (1) a number of methodological issues that affect riparian-upslope biodiversity comparisons, and (2) causal mechanisms that may underlie riparian-upslope bird community patterning and linkages in the Mulga Lands and elsewhere.

Details of a preliminary analysis of some of the work undertaken for this thesis (Kingston *et al.*, 2002) are presented in Appendix 1.

2.0 Study Area, Sites and Sampling Procedures

2.1 Study area

Data for the study were collected between July 1997 and January 1999 from 124 sites distributed throughout the Mulga Lands biogeographic region (Thackway and Cresswell, 1995) of south west Queensland (Fig. 2.1). The study area covers about 181000 km² and contains major portions of the Maranoa/Balonne, Warrego, Paroo, and Bulloo River catchments, and the townships of St. George, Charleville, Cunnamulla and Quilpie.

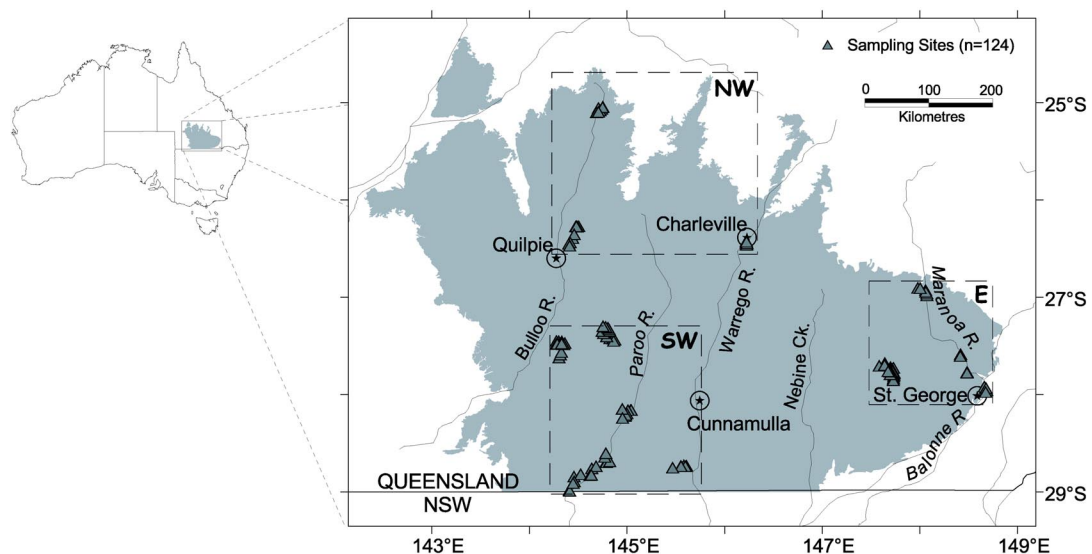


Figure 2.1 Map of Mulga Lands study area showing sampling sites, major rivers and towns. NW, SW, E indicate geographic regions used in analyses.

Mulga *Acacia aneura* occurs widely as a dominant canopy species throughout the study area; its distribution closely related to extensive areas of weathered Tertiary

land surfaces supporting loamy, sandy or gravelly red earths (Neldner, 1984; Wilson, 1999). Vegetation structure ranges from forest and woodland in the less arid eastern parts of the region, to shrublands in the west. The riparian component of the landscape is much more limited in extent, and occurs on alluvial clays of Quaternary origin as forest or woodland formations throughout the region (Neldner, 1984; Wilson, 1999). Artesian bore drains, many of which were established in the late nineteenth century to provide water for livestock (Noble and Tongway, 1983), are common in the landscape and flow over open earth channels, often for tens of kilometres.

2.2 Study sites

Birds were counted (see Section 2.4 for sampling procedures) during each of four sampling periods (Winter 1997, 11 July 1997 to 12 August 1997; Summer 1997/8, 15 November 1997 to 4 February 1998; Winter 1998, 3 July 1998 to 27 August 1998; Summer 1998/9, 23 November 1998 to 20 December 1998).

The 124 study sites comprised 19 to 28 replicates within each of the following site types: (1) riparian sites with permanent water (RW, $n = 22$, Plate 2.1); (2) riparian sites with ephemeral water (RD, $n = 20$ except Winter 1998 where $n = 19$, Plate 2.2); (3) upslope sites in close proximity to riparian areas (UC, $n = 22$ except Winter 1998 where $n = 21$, Plate 2.3); (4) upslope sites distant from riparian areas (or other water; UD; $n = 26$ for Winter 1997 and Summer 1997/8, $n = 27$ for Winter 1998, $n = 28$ for Summer 1998/9; Plate 2.3) and; (5) upslope areas with permanent water (artesian bore drains, UW, $n = 18$, Plate 2.4). Thus, Riparian sites consisted of the RW and RD site

types and the Upslope sites comprised the UC, UD and UW site types. To ensure that any observed riparian effects were not simply related to the availability of water, site types were also grouped, in some analyses, based on their proximity to permanent water. Watered sites were defined by the RW and UW site types and Dryland sites by the RD, UC and UD site types. Since the distributional limits of numerous birds species occur within the bioregion, sites were also grouped geographically (see Fig. 2.1). A full list of sites and their locations is presented in Appendix 2.

Riparian sites were selected from areas within the readily defined forested vegetation community associated with major permanent or ephemeral rivers or creeks. Riparian vegetation was typically dominated by large trees to 18 m; in particular river red gum *Eucalyptus camaldulensis*, coolibah *E. coolibah*, and/or yapunyah *E. ochrophloia*. Riparian sites with permanent water (RW) were typically woodland to open-forest formations often with well-developed mid and lower strata, whereas sites associated with ephemeral drainage lines (RD) were generally more open (e.g. open-woodland) and with poorer understorey development. Upslope sites were located at least 200 m away from riparian areas. These sites sampled a wide range of structural formations (open-forest to shrubland) associated with mulga *A. aneura* and/or poplar box *E. populnea* dominated vegetation communities. Upslope close sites (UC) were between 200 m and 500 m from a riparian area, while distant and bore drain sites (UD and UW respectively) were at least 2 km (often much more) from riparian areas or other known sources of permanent water. With the exception of Riparian and Upslope close sites (which may have been separated by a minimum of 200 m), sites were placed no closer than 2 km from each other. Subject to these constraints and accessibility, sites were distributed randomly within each location (see Appendix 2). To ensure that the

sampling represented the bioregion as a whole, locations were distributed widely across the study area. Grasslands, clay pans and cleared pasture were avoided for all site types.



Plate 2.1 Typical permanent water riparian site (site type = RW).



Plate 2.2 Typical ephemeral riparian site (site type = RD).



Plate 2.3 Typical upslope site (site type = UC or UD).



Plate 2.4 Typical artesian bore drain representing upslope sites with permanent water (site type = UW).

2.3 Climatic influences

The climate of the area is semi-arid, 60% to 70% of the annual average rainfall of between 270 mm and 570 mm occurring during the summer months (October to March; Neldner, 1984). Annual evaporation rates (*c.* 2000 mm) greatly exceed rainfall, and periods of drought are common. Severe droughts of more than six months duration occur at intervals of less than ten years while seasonal droughts occur every few years (Neldner, 1984). Average monthly temperatures exceed 35°C (maximum) during summer and fall below 5°C (minimum) during winter (Neldner, 1984).

To assess climatic influences I obtained historical records (Bureau of Meteorology, 1999) for localised monthly rainfall and the Southern Oscillation Index (SOI), from the closest weather recording station to each site (Appendix 3). If sampling took place in the latter part of any month then the localised monthly rainfall variable MON_RAIN used the rainfall figures for that month otherwise data from the previous month was used. The same procedure was used to assign monthly SOI values (SOI_AVE) to the bird observations.

For the period of the study, rainfall was well below average during winter 1997, well above during summer 1997/8 and into winter 1998, and about average during summer 1998/9 (Fig. 2.2). Although, rainfall was typically sporadic throughout, sustained falls were experienced between November 1997 and February 1998. The study period also straddled the transition between El Niño and La Nina phases of the SOI. The strongly negative SOI values of 1997 coincided with extensive drought conditions. Fortuitously, over the study period, monthly rainfall was essentially uncorrelated with both season and year ($R^2 = 0.05$ and 0.01 respectively; based on $n = 165$ monthly rainfall observations from various locations within the bioregion; Bureau of Meteorology, 1999), making it possible to separate short term rainfall effects from the seasonal and inter-annual influences.

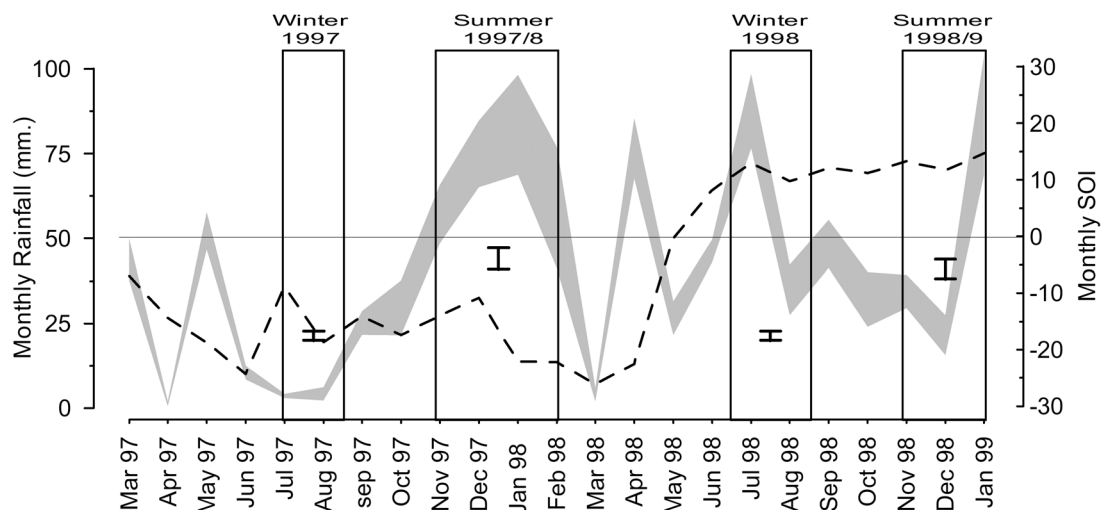


Figure 2.2 Variation in localised monthly rainfall and the Southern Oscillation Index (SOI) over the study period. Shaded areas indicate average monthly rainfall from sampling localities throughout the study area. Dashed line indicates monthly values of the SOI. Outlined regions show the duration of each sampling period. Error bars indicate long-term (> 30 yr.) monthly average rainfall (± 1 SE) for each sampling period.

2.4 Sampling procedures

At each site, measurements were obtained of bird species abundance, using standardised area counts. Three circular sub-plots (25 m radius, *c.* 0.2 ha) were evenly spaced along a 300 m long by 50 m wide site. Each site was visited on two separate mornings by an observer who spent 10 min at each sub-plot, recording the species and number of individuals of all birds seen (i.e. for each sampling period, total time spent per site was: 10 min X 3 sub-plots X 2 days or 60 min). Sites were sampled alongside and parallel to the drainage channel if located within 500 m of the channel. Sites distant from the drainage channel were not aligned in any particular direction. Data collection took place between 0.5 h and 3.5 h after sunrise, and rainy or very windy days were avoided. Almost all of the 124 sites surveyed were used repeatedly over the four sampling periods and sampled twice during each ($n = 865$ site-visits).

In addition to the bird surveys, detailed information was also collected on vegetation structure, floristics, and the presence of specific habitat features at each site and sampling period. In particular, I visually estimated the average percentage vegetation cover within defined relative height groups and the average height of the upper stratum, in order to account for differences in vegetation structure between riparian and upslope areas. Relative height groups were defined as follows: Ground/Lower stratum (lower 20% height band relative to the height of the upper stratum), Mid stratum (next 40%), Upper stratum (remaining 40%) and Emergent stratum (< 5% cover above Upper stratum).

3.0 Use of Riparian and Upslope Habitats by Mulga Land Birds

3.1 Introduction

As the interface between the terrestrial and aquatic, riparian areas have been widely recognised by wildlife biologists as a critically important and functionally dominant component of terrestrial landscapes (Knopf *et al.*, 1988; Catterall, 1993; Malanson, 1993; Knopf and Samson, 1994; Naiman and Décamps, 1997). This viewpoint has its genesis in high concentrations of species and individuals across a wide range of environments (see reviews by Knopf and Samson, 1994; Naiman and Décamps, 1997) and strong interactions among riparian and other components of the landscape (Stevens *et al.*, 1977; Szaro and Jakle, 1985; Knopf, 1985). However, riparian areas are also vulnerable to disturbance (Naiman *et al.*, 1993; Jansen and Robertson, 2001), occupy a small proportion of the landscape (Knopf *et al.*, 1988; Hewitt, 1990; Gregory *et al.*, 1991) and are among the most highly productive landscapes exploited by humans. Most research into the ecological roles of riparian areas has been carried out in the northern hemisphere, especially North America, where arid and semi-arid riparian systems have been identified as particularly important to migratory and resident bird populations (Knopf *et al.*, 1988; Knopf and Samson, 1994). Despite major concerns regarding conservation management in the Australian arid zone (Morton, 1990; Woinarski and Braithwaite, 1990; James *et al.*, 1995; Woinarski and Fisher, 2003), few studies have specifically examined the importance of riparian areas to the terrestrial bird fauna of arid and semi-arid Australia.

North American research suggests that riparian habitats typically support greater avian diversity and/or abundance than adjacent upslope areas. For example, Knopf *et al.* (1988) reported that 82% of all species annually breeding in northern Colorado occurred in riparian areas, and that insectivorous neotropical migrants used riparian areas as breeding habitat at rates greatly exceeding (up to 14 times) that of the surrounding habitat. Similarly, Szaro and Jakle (1985) recorded bird densities three to four times higher in a riparian island than in the surrounding central Arizonan desert uplands. In semi-arid Australia, Kingston *et al.* (2002; Appendix 1) reported riparian bird densities up to 3.8 times those in adjacent upslope areas, with 29% more species. In seasonally arid monsoonal northern Australia, Woinarski *et al.* (2000) found 36% more species and 45% more individuals within riparian areas than in matched non-riparian areas. Even in more mesic regions of Australia, higher riparian abundances and diversity appear to prevail (e.g. temperate eucalypt woodland, central Victoria, Mac Nally *et al.* 2000; subtropical eucalypt forests, south east Queensland, Bentley & Catterall 1997, Catterall *et al.* 2001; temperate eucalypt forests, south east New South Wales, Recher *et al.* 1991.).

Knopf and Samson (1994) argued that riparian and adjacent upslope areas are not independent, and that these sorts of statistics have resulted in a disproportionate conservation focus toward riparian areas themselves. They suggested that management, which is focused only on riparian areas is likely to disadvantage a significant proportion of species, and that a landscape scale management perspective is required to maintain the character and integrity of regional avifaunas. The idea that riparian areas are important to the functioning of the adjacent ecological systems is frequently advocated (Gregory *et al.*, 1991; Bunn, 1993; Knopf and Samson, 1994;

Naiman and Décamps, 1997) but empirical studies showing such interrelationships among terrestrial fauna are uncommon. Szaro and Jakle (1985) found asymmetric contributions between habitats; the commonest species found in riparian areas comprised between 7% and 33% of the birds found in the adjacent desert, yet birds characteristic of desert habitats contributed only 1% to 2% of those found in the riparian area. Johnson *et al.* (1977) reported that 51% of all bird species were completely dependent on riparian vegetation in the south west United States, and Thomas *et al.* (1979) claimed that 288 of 363 (79%) species of terrestrial fauna found in the Blue Mountains of Oregon and Washington were at least partially dependent on riparian habitats. In Australia, Woinarski *et al.* (2000) found that nectarivores were more prevalent in riparian habitats when nectar production declined in the non-riparian landscape (but see French *et al.* 2003). Kingston *et al.* (2002; Appendix 1) suggested that temporal fluctuations in the strength of the riparian/upslope relationship were due to shifts in habitat preference brought about by seasonal and climatic variation. Indeed, climatic unpredictability is a dominant feature governing the abundance and distribution of biota in arid and semi-arid areas of Australia (Barker and Greenslade, 1982). Moreover, it has been widely proposed that localised fluctuations in resources are minimised at sites (such as riparian areas) where there is higher soil fertility and moisture (James *et al.* 1995). For highly mobile animals such as birds, this spatial and temporal patterning should promote significant inter-habitat exchange.

In this chapter, I investigate patterns of riparian occupancy and inter-habitat overlap among terrestrial birds of the semi-arid Mulga Lands of south west Queensland, Australia. Specifically, I ask the following questions. (1) Do riparian habitats support richer or more abundant avifaunas than adjacent upslope areas? (2) To what extent do

riparian and upslope habitats support distinctive species assemblages? (3) How much do the riparian and upslope bird assemblages influence each other? (4) What are the conservation and management issues that arise from the observed patterns of inter-habitat overlap?

3.2 Methods

3.2.1 Analysis

3.2.1.1 Bird abundance and diversity

Generalised Linear Models (GLM; *sensu* McCullagh and Nelder, 1983) were used to compare differences between Riparian and Upslope values of the following aspects of the bird assemblage: (1) occurrence of individual common species; (2) abundance within selected groups (all species, foraging guilds, taxonomic groups, uncommon species) and; (3) species richness within selected groups (as above). Occurrence was defined as a binary variable indicating the presence (or absence) of each species irrespective of the number of individuals (abundance) recorded. Analyses of the variation in the occurrence of individual species thus assumed a binomial distribution, and the Logit link function was used (i.e. logistic regression). Poisson regression (Poisson distribution, Log link) was used to model the other response variables. Generalized Estimating Equation modelling (GEE; Liang and Zeger, 1986), based on initial GLM parameter estimates, was used to account for possible correlations among repeated site-visits and sampling periods. GLM and associated GEE analyses were carried out using PROC GENMOD within SAS (SAS Institute Inc. 1999). The statistical models included the main design variable: SITETYPE (RD, RW, UC, UD,

UW; see Chapter 2) and a number of covariates known from preliminary analyses to account for significant variation in the data; SEASON (Summer, Winter), YEAR (1997, 1998), REGION (East, South-west, North-west; see Fig 1), MON_RAIN (localised monthly rainfall; Bureau of Meteorology, 1999), SITETYPE*SEASON, SITETYPE*YEAR and SITETYPE*MON_RAIN. The specific effects of these covariates and potential water availability influences are addressed in Chapters 4 and 5. The GLM analyses were carried out at the following sampling resolutions: the sub-plot level ($n = 2544$; 10 min samples) for the occurrence of individual species; the site-visit level ($n = 865$; 30 min samples) for the abundance of selected groups and; the site-sampling period level ($n = 433$; 60 min samples) for species richness estimates.

For sample-based data sets, differences in abundance between treatments may result in misleading comparisons of species richness (Gotelli and Colwell, 2001). Therefore, to compare treatments while directly controlling for abundance, rarefaction was conducted prior to the analysis of all species richness responses. This was achieved by randomly selecting equal numbers of individuals from each sample and recalculating the mean species richness over $n = 100$ iterations. For each sample, I chose a number of individuals from each sample equal to $S + 1$, (where S is the number of species in the most species-rich sample) based on Tipper (1979). Comparisons of species richness are also affected by different patterns of relative abundance between treatments (Denslow, 1995; Gotelli and Colwell, 2001). Relative abundance distributions determine the shape of the randomised species accumulation curve (rarefaction curve) with steeper curves resulting from more even samples (Gotelli and Graves, 1996). Because species accumulation and rarefaction curves are non-linear, tending to an asymptote, comparisons of species richness across treatments may vary with number of

individuals accumulated. I use the term “sub-asymptotic species richness” to refer to an estimate (or comparison) of the number of species for a given number of individuals, where the number of individuals remains below the species richness asymptote. In extreme cases such curves may cross leading to changes in the rank order of estimated sub-asymptotic richness among treatments (Gotelli and Colwell, 2001). To ensure that my sub-asymptotic species richness comparisons had general application across a wide range of sampling scales I also compared rarefaction curves for both Riparian and Upslope samples re-scaled to equal numbers of individuals (computed using *EstimateS*; Colwell, 2000). A first-order jackknife estimator of species richness was used to compare asymptotic values (see Colwell and Coddington, 1994).

All “fly over” observations and non-terrestrial bird species were excluded from analysis. Allocations of species to foraging guilds were derived from the author’s unpublished data together with information from Blakers *et al.* (1984), Pizzey and Knight (1997), and Schodde and Tiedemann (1986). Mutually exclusive foraging guild membership was based on dominant foraging strategy and diet (Appendix 4). Species found at fewer than 20 sub-plots were considered “Uncommon” and were not individually analysed (Appendix 4). The Australian raven (*Corvus coronoides*) and little crow (*C. mellori*; both of which occur in the study area) were not reliably differentiated in the field and observations for these two species were regarded as “Corvus Sp.” With this exception, species taxonomy follows Christidis and Boles (1994). Common and scientific names for all terrestrial birds species observed during this study are listed in Appendix 4.

Individual species and groups of species were classified into riparian response groups (*riparian*, *upslope*, *indifferent*) based on the results of the statistical models. Allocation to each group was based on a rule-set associated with a number of “generalised” and “specialised” contrasts involving linear combinations of the variable SITETYPE (ESTIMATE statement, PROC GENMOD within SAS; SAS Institute Inc. 1999; Table 3.1). I report parameter estimates (as count ratios for Poission regressions and odds ratios for the logistic regressions i.e. $e^{\text{Parameter estimate}}$) associated with the contrast(s) that defined the response group. Species or groups were considered *indifferent* if a *riparian* or *upslope* response was not determined and the variance associated with the generalised riparian contrast (i.e. $H_0: \mu(\text{RW}, \text{RD}) = \mu(\text{UW}, \text{UC}, \text{UD})$) was similar to those with a significant effect. Such determinations were made if the scaled confidence interval associated with the relevant parameter estimate (i.e. $((e^{\text{Est_hi}}/(1+e^{\text{Est_hi}})) - (e^{\text{Est_low}}/(1+e^{\text{Est_low}})))$ where Est_hi and Est_low are the upper and lower 95% confidence limits for the parameter estimate respectively) was less than a threshold defined as the mean plus one standard deviation of the same statistic across all species (or groups) exhibiting a significant effect. Thresholds for species richness (sub-asymptotic) and abundance within selected groups, and for the occurrence of individual species, were calculated separately, although the species group thresholds for each response variable were calculated collectively on the basis of all groups showing a significant effect (i.e. foraging guilds, taxonomic groups, uncommon species, all species). Thus, a species classified as *riparian indifferent* (RipInd, Table 3.1) occurred at similar abundances in Riparian (RW, RD) and Upslope treatments (UW, UC, UD). All other responses were regarded as *not determined*. Within this latter category, no distinction was made between those exhibiting naturally high variation and those with insufficient data.

Table 3.1 Generalised linear modelling contrast criteria used to determine riparian response groups (Rip, Riparian; Ups, Upslope; Ind, Indifferent). Site types in parentheses in the response group column indicate the dominant influence of the site type specified. These specialised responses are derived from the results of the contrasts indicated. Remaining responses are generalised, derived from the results of the generalised contrast of overall riparian status (i.e. $H_0: \mu(RW, RD) = \mu(UW, UC, UD)$). Probability values used to test the hypotheses were $P \leq 0.1$ for the occurrence of individual species and $P \leq 0.05$ for species groups.

Criterion number	Contrast criteria	Riparian response group
1	$H_1: \mu(RW) > \mu(UW, UC, UD)$ and $H_1: \mu(RW) > \mu(RD)$	Rip(RW)
2	$H_1: \mu(RD) > \mu(UW, UC, UD)$ and $H_1: \mu(RW) < \mu(RD)$	Rip(RD)
3	$H_1: \mu(RW, RD) > \mu(UW, UC, UD)$ and not 1 or 2 above	Rip
4	$H_1: \mu(UW) > \mu(RW, RD)$ and $H_1: \mu(UW) > \mu(UC, UD)$	Ups(UW)
5	$H_1: \mu(UC, UD) > \mu(RW, RD)$ and $H_1: \mu(UW) < \mu(UC, UD)$	Ups(UCUD)
6	$H_1: \mu(UW, UC, UD) > \mu(RW, RD)$ and not 4 or 5 above	Ups
7	$H_0: \mu(RW, RD) = \mu(UW, UC, UD)$ and not 1,2,4 or 5 above and where variance is below a specified threshold (i.e. <i>Indifferent</i> , see text for details)	RipInd

To detect broad trends in riparian occurrence, sub-asymptotic species richness and total abundance with distance from riparian areas, all GLM analyses were repeated with the explanatory variable SITETYPE replaced with a variable RIPDIST representing sites classified on an ordinal scale (Riparian = 1, Upslope close = 2, Upslope distant = 4). For these analyses, species (or groups) were regarded as *increasers* if the RIPDIST term was negative and significant ($P < 0.05$). *Decreasers* were similarly defined by a positive and significant ($P < 0.05$) RIPDIST parameter estimate.

3.2.1.2 Bird community composition

Bird communities were ordinated using partial Detrended Correspondence Analysis (pDCA; program CANOCO v4.0, ter Braak and Smilauer, 1998). This eigenanalysis-based procedure allows both species and samples to be ordinated simultaneously, with adjustment for covariates. DCA assumes a unimodal species response and the axes give a quantitative measure of species turnover (beta diversity; ter Braak and

Smilauer, 1998). Sites that differ by four or more SD (Standard Deviation) units normally have no species in common (ter Braak and Prentice, 1988).

The species by sample data matrix for these analyses was resolved to the site-sampling period level. That is, abundances for individual species over three sub-plots and two visits were summed to give the species abundances at each of 433 unique site and sampling period combinations (samples). All samples and species were included, however since it was likely that rare species were inadequately represented these were “downweighted” according to the routine used by CANOCO. This resulted in 428 active samples and 119 active species. Detrending was accomplished by the use of 26 segments. A variable RIPSTAT, representing the generalised difference in riparian status ($H_0: \mu(RW, RD) = \mu(UW, UC, UD)$) was specified as the “environmental variable” while the following variables were nominated as “covariates”: REGION, MONRAIN, SEASONYR (Winter 1997, Summer 1997/8, Winter 1998, Summer 1998/9) and PERMWATER ($H_0: \mu(RW, UW) = \mu(RD, UC, UD)$). All analyses were carried out on raw abundances. Given the limited range and distribution of abundances, algebraic transformations were not considered necessary or biologically relevant. The results of the ordinations were displayed as a biplot (see Jongman *et al.*, 1995) to show the configuration of Riparian and Upslope samples (after controlling for the covariates) in relation to all species for which a response group determination had been made in the univariate analyses.

Partial Canonical Correspondence Analysis (pCCA; program CANOCO v4.0; ter Braak and Smilauer, 1998) and associated Monte Carlo permutation tests were used to determine whether species composition differed between Riparian and Upslope

samples after controlling for covariates. Due to the temporal stratification of the experimental design, samples were permuted at random within each season.

3.2.1.3 Relative contributions

Two approaches were used to investigate the relative contributions of *riparian* species to Upslope areas and *vice versa*. The first was based on two-way tabulation of the abundance of each response group within Riparian (n = 164) and Upslope (n = 266) samples. The relative contributions of *riparian* species to Upslope samples and *vice versa* were compared by testing the difference between the proportions using a Z statistic (Rao, 1998) based on equal numbers of randomly selected Riparian and Upslope samples (n = 164).

The second approach involved a GLM comparison (Normal distribution; Identity link) of the species tolerance values (derived from the pDCA) among *riparian* and *upslope* response groups. Species tolerance is a measure of the variance associated with the locations of species in ordination space (often interpreted as niche width; ter Braak and Smilauer, 1998). I used the root mean squared standard deviation across four ordination axes (RMSTOL, as calculated by CANOCO) as a summary of each species' overall tolerance. Species with high tolerance values are found over a wide range of samples and possibly environmental conditions, whereas species with low tolerances are confined to samples with similar species compositions. Thus, these comparisons may also indicate whether species typical of riparian habitats are more or less cosmopolitan than species more commonly observed in upslope habitats.

3.3 Results

3.3.1 Bird abundance and diversity

3.3.1.1 Occurrence of individual species

Over the four sampling periods, 7694 observations were made of 13559 individuals from 119 species (Appendix 4). Using the logistic regression models, response group determinations or significant riparian distance trends were obtained for 37 species (Table 3.2). Among the 36 species for which a response group determination was made, 23 were significantly ($P < 0.1$) more likely to be found in Riparian areas. This represents a significant departure from even proportions in each category ($\chi^2 = 20.3$, $P < 0.001$) and the number of species exhibiting a *riparian* response was significantly greater than the number of species exhibiting an *upslope* response (23 of 36 *riparian* vs 14 of 36 *upslope*; $Z = 1.86$, $P = 0.03$). Only one species, the crested pigeon, showed no apparent preference for Riparian or Upslope habitats.

With the exception of the galah, willie wagtail and corvids (which showed odds ratios of 1.8, 1.9 and 1.8 respectively; Table 3.2) all species exhibiting a *riparian* response were more than twice as likely to occur in Riparian areas (i.e. odds > 2.0). The highly abundant white-plumed honeyeater was at least 15 times more likely to occur in Riparian sites (lower 95% CI). All species that showed an *upslope* response were more than twice as likely to occur within that habitat. Species such as chestnut-rumped thornbill and singing honeyeater were more than 10 times more likely to occur in Upslope areas. Species in this response group were also generally characterised by relatively high variances, indicating patchy patterns of occurrence.

Specialised responses, indicating the dominant influence of individual site types, were found in about half (19 of 35 species, Table 3.2) of the species showing a *riparian* or *upslope* response

Table 3.2 Riparian response for the occurrence of individual bird species: results of generalised linear modelling for those species with response group determinations and/or significant riparian distance trends. Occurrences are the number of times the species was observed at Riparian (n=989, 10 min samples) and Upslope (n=1555, 10 min samples) sub-plots. Riparian fidelity is the mean percentage of all observations from Riparian sites. Odds presented are in favour of the effect indicated (R, Riparian; U, Upslope), values in parentheses indicate 95% confidence interval. Significance levels: ^ $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Site types in parentheses in the Response group column indicate responses defined by a specialised contrast (see text). Blanks in the response group and distance trend columns indicate species considered as "not determined" for that criterion.

Bird species (Abbreviation)	Occurrences			Riparian odds	Response group	Distance trend
	Riparian	Upslope	Riparian fidelity (%)			
White-plumed Honeyeater (WPHE)	612	231	80.6	24.3*** (15.7- 37.5)R	Riparian(RW)	Increaser
Noisy Miner (NOMI)	87	21	86.7	12.4*** (5.7- 27.1)R	Riparian(RD)	Increaser
Little Friarbird (LIFB)	118	50	78.8	10.5*** (5.5- 20.0)R	Riparian(RW)	Increaser
Sacred Kingfisher (SAKF)	72	22	83.7	6.8*** (3.6- 12.9)R	Riparian(RW)	
Brown Treecreeper (BRTC)	83	36	78.4	6.1*** (3.5- 10.7)R	Riparian(RW)	Increaser
Peaceful Dove (PEDO)	27	8	84.1	5.7*** (2.5- 12.9)R	Riparian(RW)	Increaser
Yellow-throated Miner (YTMI)	195	163	65.3	5.0*** (2.8- 8.9)R	Riparian(RD)	
Fairy Martin (FMAR)	24	1	97.4	4.7** (1.8- 12.3)R	Riparian(RW)	Increaser
Whistling Kite (WHKI)	22	2	94.5	4.5*** (2.1- 9.7)R	Riparian(RW)	Increaser
Grey Shrike-thrush (GSTH)	91	48	74.9	3.7*** (2.3- 5.9)R	Riparian	Increaser
White-winged Chough (CHOU)	14	4	84.6	3.7* (1.2- 10.9)R	Riparian(RD)	
Laughing Kookaburra (LAKO)	37	9	86.6	3.5*** (1.7- 7.1)R	Riparian	
Mulga Parrot (MUPA)	18	24	54.1	2.9* (1.1- 7.5)R	Riparian(RD)	
Magpie-lark (MALA)	68	47	69.5	2.7*** (1.6- 4.4)R	Riparian	Increaser
Australian Ringneck (AURN)	124	88	68.9	2.6*** (1.6- 4.0)R	Riparian	Increaser
Red-winged Parrot (RWPA)	60	43	68.7	2.5*** (1.5- 4.2)R	Riparian	
Black-faced Cuckoo-shrike (BFCS)	46	30	70.7	2.5*** (1.4- 4.2)R	Riparian	
Restless Flycatcher (REFC)	33	14	78.8	2.4* (1.1- 5.2)R	Riparian	
Little Corella (LITC)	18	6	82.5	2.1^ (0.9- 4.8)R	Riparian	
Apostlebird (APOS)	33	54	49.0	2.0^ (1.0- 4.1)R	Riparian(RD)	Increaser
Willie Wagtail (WIWA)	127	111	64.3	1.9*** (1.4- 2.7)R	Riparian	
Galah (GALA)	72	67	62.8	1.8* (1.1- 3.0)R	Riparian	Increaser
Corvus Sp. (CORV)	37	40	59.3	1.8* (1.0- 3.2)R	Riparian	
Crested Pigeon (CRPI)	35	68	44.7	1.0 (0.6- 1.7)U	Indifferent	
Crested Bellbird (BELL)	7	33	25.0	1.5 (0.7- 3.5)U		Decreaser
Common Bronzewing (COBW)	28	55	44.5	2.1* (1.1- 4.0)U	Upslope(UW)	
Spiny-cheeked Honeyeater (SPHE)	127	204	49.5	2.3*** (1.4- 3.9)U	Upslope(UW)	
Striped Honeyeater (STHE)	1	37	4.1	2.7* (1.1- 6.6)U	Upslope	
Rufous Whistler (RUWH)	27	107	28.4	3.4*** (1.5- 7.8)U	Upslope	Decreaser
Mistletoebird (MIST)	1	32	4.7	4.0** (1.5- 10.4)U	Upslope	
Jacky Winter (JAWI)	1	54	2.8	4.4** (1.7- 11.4)U	Upslope	Decreaser
Splendid Fairy-wren (SPFW)	0	31	0.0	4.6** (1.7- 12.5)U	Upslope(UW)	
Red-capped Robin (RCRO)	2	48	6.1	4.8*** (2.0- 11.5)U	Upslope(UW)	
Weebill (WEEB)	27	164	20.6	8.4*** (4.2- 16.6)U	Upslope(UW)	
Double-barred Finch (DBFI)	4	35	15.2	9.5*** (3.1- 28.9)U	Upslope(UW)	
Singing Honeyeater (SIHE)	7	83	11.7	13.3*** (4.7- 37.9)U	Upslope(UW)	Decreaser
Chestnut-rumped Thornbill (CRTB)	2	140	2.2	14.0*** (6.7- 29.6)U	Upslope	Decreaser

Among the 17 species that showed a statistically significant riparian distance trend, 12 exhibited an increased occurrence toward Riparian areas, while five decreased (Table 3.2). All of the *increasers* also showed a *riparian* response, and all but one of the *decreasers* (crested bellbird) were included in the *upslope* response group. In total, 23 of 37 species showed either a *riparian* response or an *increasing* riparian distance trend, while 13 species either *decreased* or were classified as *upslope*.

3.3.1.2 Abundance of species groups

Unambiguous *riparian* responses in abundance were observed among larger carnivores, nectar feeders and aerial insectivores (Table 3.3). Together these groups accounted for about 25% of species but only 10% of all individuals. The modelling suggests that about three times as many larger carnivores were observed at close range (fly-over observations were excluded) in Riparian compared with Upslope areas (Riparian/upslope ratio = 3.1, Table 3.3). This group included raptors (Accipitridae), Corvids (*Corvus* spp.), and kingfishers (Halcyonidae), all of which showed a *riparian* response. On average, Riparian areas contained four times more nectar feeding birds. This group, which included noisy and little friarbirds and blue faced honeyeater, in addition to some of the less common smaller honeyeaters (e.g. black, brown and pied honeyeaters) accounted for only 3% of all individuals. Aerial insectivores were dominated by woodswallows (*Artamus* spp.), the fairy martin and rainbow bee-eater and were between 3.7 and 15.3 (95% CI, Table 3.3) times more abundant in Riparian areas.

Riparian abundance responses were also observed among seed eaters and low insectivores, however the results were strongly influenced by dominant taxa (Table 3.3). The response of most of the 23 seed eating species was divided among several families: parrots (Psittacidae, 8 spp., *riparian*), cockatoos (Cacatuidae, 5 spp., *not determined*), doves and pigeons (Columbidae, 4 spp., *indifferent*), and finches (Passeridae, 3 spp., *upslope*). The analysis suggests that on average approximately twice as many parrots were observed in Riparian compared with Upslope areas. The finches, on the other hand, showed a strong affinity with Upslope sites. The *indifferent* response of the four species comprising the Columbidae family in this study is a reflection of the contrasting responses of the two dominant species; crested pigeon and common bronzewing (Table 3.2). Among the 35 low insectivores, a number of individual species exhibited a *riparian* response (brown treecreeper, white-browed treecreeper, apostlebird, white-winged chough, magpie-lark, restless flycatcher, willie wagtail; Table 3.2), while several groups were much more abundant in Upslope areas; fairy wrens (Maluridae), thornbills (*Acanthiza* spp.), robins (Petroicidae) and babblers (Pomatostomidae).

Numbers of high insectivores were more than three times greater in Riparian areas. Even after excluding the white-plumed honeyeater, which accounted for about half of all individuals in this group, more than twice as many high insectivores were observed in Riparian habitats (Table 3.3). High densities of white-plumed honeyeaters appeared to account for the specialised responses favouring RW site types; without their influence high insectivores were most abundant at riparian areas without permanent water (RD site types). Species with a fruit-dominated diet were classified in the *upslope* category. This group was confined to a limited number of species (most

Table 3.3 Riparian response for bird abundance and sub-asymptotic species richness of selected species groups: results of generalised linear modelling. Abundance analyses are based on mean number of individuals at each site-visit (i.e. n=865, 30 min samples). Sub-asymptotic species richness estimates are based on site-sampling periods (n=433, 60 min samples) calculated after rarefaction using the number of samples and individuals indicated (see text for details). Count ratios presented are in favour of the effect indicated (R, Riparian; U, Upslope), values in parentheses indicate 95% confidence interval. Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Site types in parentheses in the Response group columns indicate specialised responses defined by a specialised contrast (see text). Blanks in the response group columns indicate species considered as "not determined" for that criterion.

Species grouping	No. of species	% of total abundance	No. of site-visits present	Abundance		Species richness		
				Count ratio	Response group	Post-rarefaction site-sampling periods (individuals sampled)	Count ratio	Response group
Larger Carnivores (all)	16	3.3	261	3.1*** (2.3 - 4.1)R	Rip	29 (5)	1.6*** (1.3 - 1.9)R	Rip(RD)
Raptors (Accipitridae)	6	0.4	38	5.2*** (2.7 - 10.1)R	Rip(RW)	22 (3)		
Corvids (Corvidae)	2	0.9	75	2.1*** (1.2 - 3.7)R	Rip	31 (3)		
Kingfishers (Halcyonidae)	3	1.3	121	8.6*** (4.9 - 15.3)R	Rip(RW)	35 (3)	1.2** (1.2 - 1.3)U	Ups(UW)
Nectar Feeders	7	3.0	187	4.0*** (2.3 - 6.9)R	Rip(RW)	57 (3)	1.0 (0.9 - 1.1)U	RipInd
Aerial Insectivores	7	3.5	107	7.5*** (3.7 - 15.3)R	Rip(RW)	35 (4)	1.2*** (1.1 - 1.3)U	Ups(UCUD)
Seed Eaters (all)	23	18.0	481	1.4* (1.1 - 1.7)R	Rip	80 (9)	1.5*** (1.2 - 1.7)R	Rip(RD)
Parrots (Psittacidae)	8	7.0	278	1.9*** (1.4 - 2.6)R	Rip	76 (5)	1.3*** (1.2 - 1.5)R	Rip
Cockatoos (Cacatuidae)	5	5.9	158			65 (4)	1.1 (0.9 - 1.3)R	RipInd
Doves and Pigeons (Columbidae)	4	3.5	192	1.2 (0.8 - 1.8)R	RipInd	35 (4)	1.4*** (1.2 - 1.7)R	Rip(RW)
Finches (Passeridae)	3	1.2	49	19.8*** (8.2 - 47.4)U	Ups(UW)	36 (3)		
Low Insectivores	35	22.3	649	1.1 (0.9 - 1.4)U	RipInd	70 (13)	2.7*** (1.9 - 3.7)U	Ups
Fairy-wrens (Maluridae)	3	1.4	65	3.7* (1.1 - 12.8)U	Ups	35 (3)	1.0 (0.9 - 1.1)R	RipInd
Thornbills (<i>Acanthiza</i> spp.)	4	3.8	156	27.1*** (13.0 - 56.6)U	Ups	53 (5)	1.3*** (1.2 - 1.4)U	Ups
Robins (Petroicidae)	4	1.4	119	8.6*** (4.1 - 18.0)U	Ups	30 (3)	1.2*** (1.1 - 1.2)U	Ups
Babblers (Pomatostomidae)	4	1.5	55	4.5*** (1.6 - 12.5)U	Ups	47 (3)		
High Insectivores (all)	26	47.7	763	3.3*** (2.8 - 3.9)R	Rip(RW)	245 (9)	1.5*** (1.3 - 1.6)U	Ups
Excluding white-plumed honeyeater	25	23.6	672	2.4** (1.9 - 3.0)R	Rip(RD)	148 (8)	1.6*** (1.4 - 1.9)U	Ups
Fruit Eaters	4	0.8	84	2.7** (1.4 - 5.2)U	Ups	22 (3)		
Uncommon Species	57	4.8	205	1.9* (1.2 - 3.2)U	Ups(UW)	47 (5)	1.3** (1.1 - 1.5)U	Ups
Species Richness	119	98.6	840	not applicable		258 (21)	1.2*** (1.1 - 1.3)U	Ups
Total Abundance (all)	138^	100.0	863	2.1*** (1.8 - 2.3)R	Rip(RW)		not applicable	
Excluding white-plumed honeyeater	137^	75.9	840	1.5*** (1.0 - 1.2)R	Rip(RD)		not applicable	

^ includes 19 taxa not identified to species level

common were spotted bowerbird and mistletoebird) and together accounted for less than 1% of all individuals recorded. Uncommon species were about twice as abundant in Upslope habitats.

The high proportion of total abundance accounted for by *riparian* responses of specific foraging groups is also reflected in the analysis of total abundance (Table 3.3). Overall abundance of terrestrial birds was more than twice as high in Riparian areas with permanent water (RW site types) as Upslope areas, although this was strongly influenced by the highly abundant white-plumed honeyeater which dominated RW habitats. Without its influence, abundance was highest in RD (not RW) site types and about 50% more birds were found there than in Upslope areas.

Notwithstanding differences in absolute abundance, patterns of relative abundance also varied among Riparian and Upslope samples. While all upslope site types were characterised by relatively even distributions, RW site types were strongly dominated by the white-plumed honeyeater and RD site types by both the white plumed honeyeater and the yellow-throated miner (Fig. 3.1). Although the rank order of species dominance often varied between site types many of the most dominant species were dominant in both Riparian and Upslope samples. Seven species (white-plumed honeyeater, yellow-throated miner, spiny-cheeked honeyeater, Australian ringneck, apostlebird, galah and willie wagtail) were among the ten most dominant species in both situations. The white-plumed honeyeater was the most dominant species in both Riparian and Upslope samples (not shown).

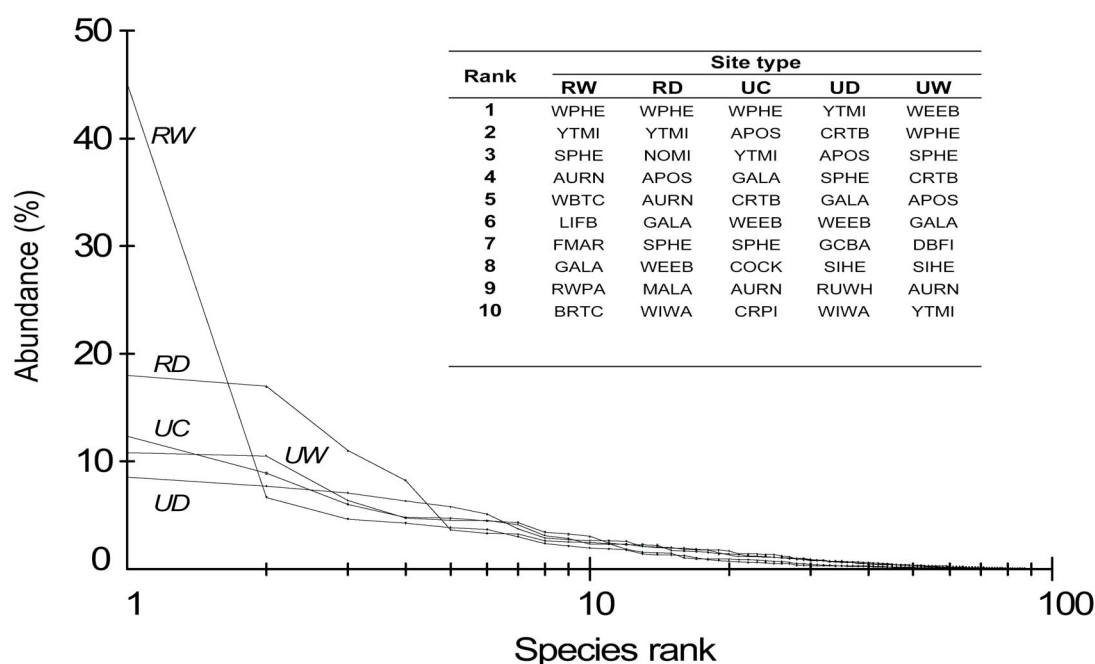


Figure 3.1 Species dominance plots for each site type. The inset identifies the ten most abundant species for each site type in order of decreasing dominance. Species abbreviations are detailed in Table 3.2 except the following: WBTC, white-browed treecreeper; COCK, cockatiel; GCBA, grey-crowned babbler.

3.3.1.3 Species group richness

Statistically significant differences in sub-asymptotic species richness were also detected, and some were in marked contrast to their abundance responses (Table 3.3). Unlike total abundance, which favoured Riparian sites, overall sub-asymptotic species richness was approximately 20% higher in Upslope areas. Comparison of the riparian and upslope rarefaction curves, neither of which appeared to have reached a clear asymptote (Fig. 3.2), suggests that Upslope areas were favoured across the full range of possible sampling scales. The asymptotic estimates of species richness suggest an upslope/riparian ratio of 1.2 (126 species from Upslope habitats and 104 Riparian; Fig. 3.2), which was the same as the sub-asymptotic estimate (Table 3.3). Sub-

asymptotic richness within both the high and low insectivore foraging groups also strongly favoured Upslope habitats; approximately 50% more high insectivores and nearly three times as many low insectivore species were recorded from Upslope sites (Table 3.3). The number of uncommon species was also highest at Upslope sites. In contrast, more species of seed eaters and larger carnivores were recorded in Riparian areas, a result consistent with their abundance response. Interestingly, aerial insectivores were much more abundant in Riparian areas but more speciose in Upslope areas. Nectar feeders showed a similar though less acute response.

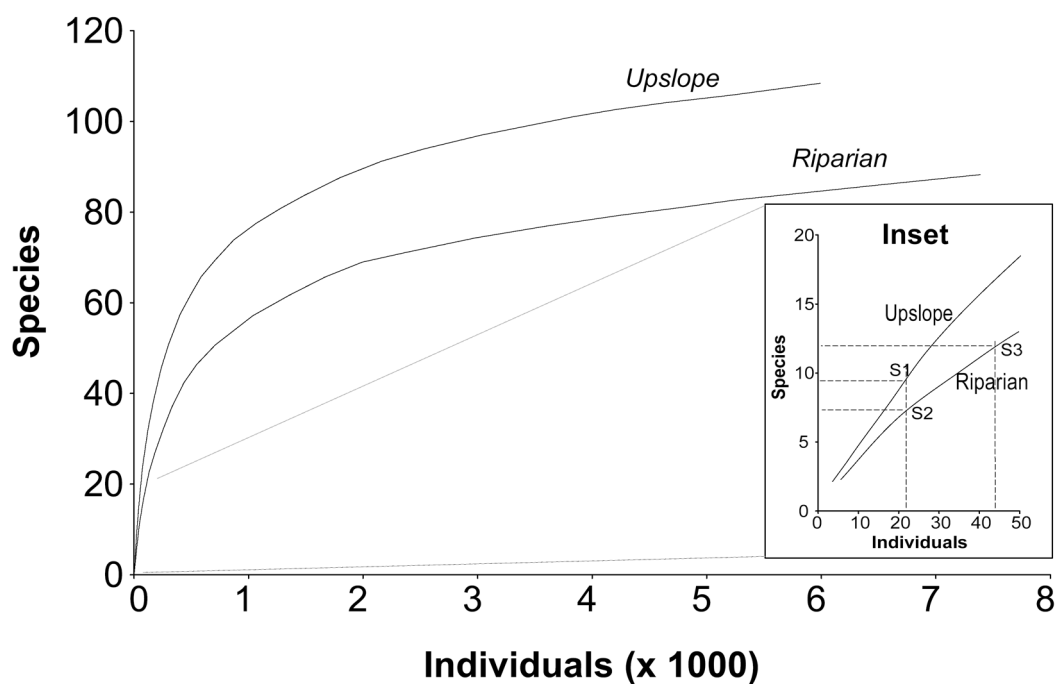


Figure 3.2 Rarefaction curves for Riparian and Upslope samples re-scaled to equal numbers of individuals. Inset shows detail at the sampling scale used for overall sub-asymptotic species richness (21 individuals; Table 3.3). S1 and S2 indicate the mean number of species observed at this sampling scale. S3 indicates the number of species estimated for the Riparian samples without adjustment for differences in Riparian and Upslope bird density (i.e. without rarefaction). Asymptotic estimates: Upslope = 126 species; Riparian = 104 species.

3.3.2 Bird community composition

There was a high degree of overlap in species composition between Riparian and Upslope samples (Fig. 3.3). Approximately 95% of all samples were within 4.0 SD of each other suggesting complete species turnover only at the extremes. Of the 36 species for which a response group determination was made, only the splendid fairy-wren was found exclusively in one habitat (Upslope, Table 3.2). Moreover, at least 15% of all occurrences for 19 of 23 *riparian* species were derived from Upslope areas (Riparian fidelity, Table 3.2). Among *upslope* species, the overlap was less obvious, however 6 of 12 species had more than 10% of their occurrences in Riparian habitats. Nevertheless, the results of the pCCA Monte Carlo permutation tests indicated that the riparian effect (Riparian vs Upslope) accounted for a small but significant separation of the samples after controlling for covariates (2.51% of overall variation; $P < 0.01$). This separation is reflected in the first pDCA axis; both *riparian* species and Riparian samples are more apparent to the left while *upslope* species and to a lesser extent Upslope samples are more apparent to the right (Fig. 3.3).

The ordination (Fig. 3.3) also shows Upslope samples are widely dispersed in the ordination space indicating high between-sample diversity, and full species turnover among the least similar sites. Further examination of Upslope sub-groupings (i.e. UC, UD, UW site types ; not shown) and possible locational influences (i.e. groups of sites within geographic regions; Fig. 2.1) failed to reveal any additional structure. In contrast, Riparian samples, particularly those associated with permanent water (RW site type), were tightly clustered, indicating a high similarity in species composition

among these samples. The location of this group toward the centre of the ordination further indicates: 1) the presence of species from the outer sectors of the ordination and/or; 2) a dominance of ubiquitous species in the Riparian samples. To investigate if this was mainly due to the latter, I repeated the ordinations firstly by omitting the white-plumed honeyeater (which accounted for approximately one-quarter of all observations) and secondly by transforming the abundances (Log (sample abundance

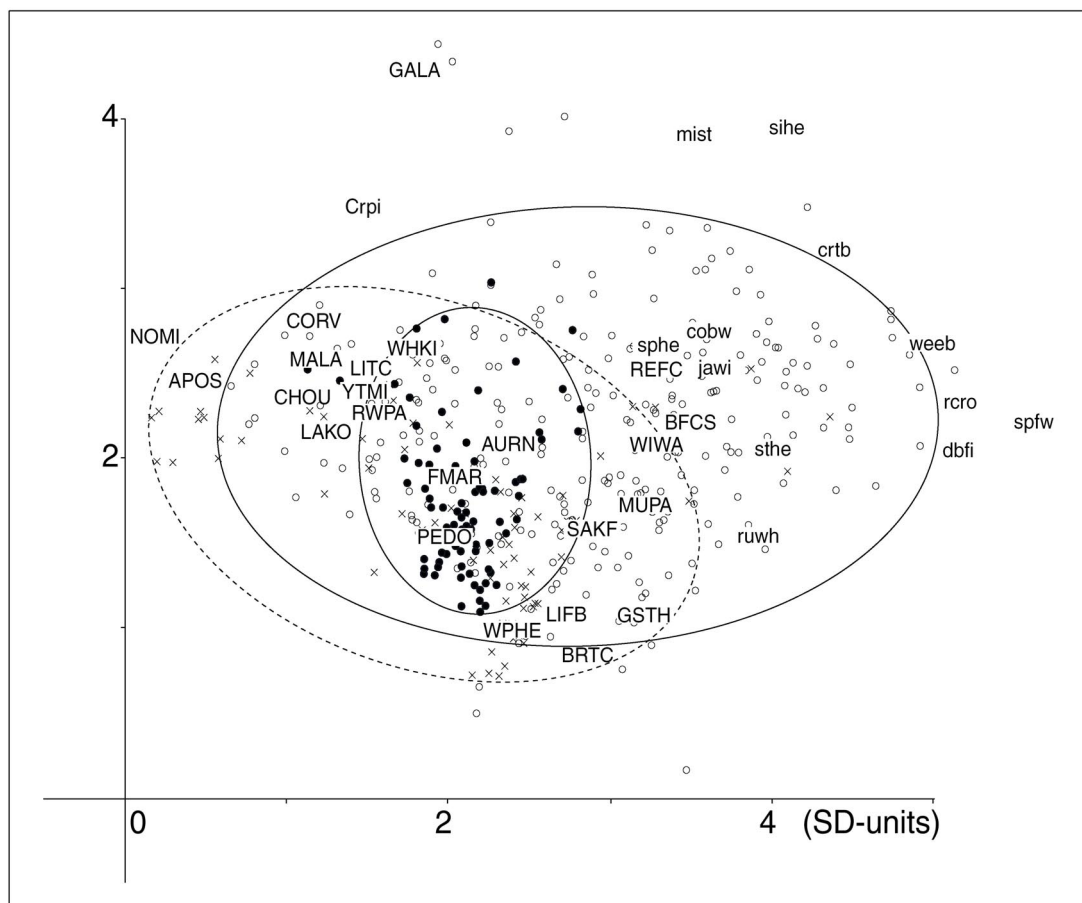


Figure 3.3 Ordination of Riparian and Upslope samples by bird species composition from partial Detrended Correspondence Analysis (pDCA). Points represent site-sampling periods ($n = 428$, 60 min samples); open circles = Upslope samples ($n = 264$); black closed circles = Riparian samples with permanent water ($n = 87$); crosses = Riparian samples without permanent water ($n = 77$). Inner solid line encloses 95% of Riparian samples with permanent water; outer solid line encloses 95% of Upslope samples; dashed line encloses 95% of Riparian samples without permanent water. Species shown are those for which a response group determination was made (see text for details); upper case = *riparian* species, lower case = *upslope* species, title case = *indifferent* species. Species abbreviations are detailed in Table 3.2.

+ 1)) to moderate the influence of the species dominance characteristic of riparian areas (Fig. 3.1). The results of both ordinations (not shown) were substantially the same; RW samples were tightly clustered and Upslope samples were widely dispersed. However, when the white-plumed honeyeater was excluded the RW cluster moved to the left, suggesting a relatively strong influence of this species on the composition of both Riparian and Upslope samples.

The first pDCA axis appears to reflect a broad gradient of canopy cover, decreasing from left to right. As noted, many of the RD site types were woodland and open woodland formations, most RW site types were woodland or open forest, and many of the Upslope sites closed shrublands. Larger-bodied bird species are more frequent on the left and smaller species on the right of the ordination.

3.3.3 Relative contributions

Although Riparian and Upslope samples shared many species, the relative contributions were asymmetric. A greater proportion of individuals of *upslope* species were recorded from Riparian areas (30.2%) than was the case for *riparian* species in Upslope areas (20.7%; $Z = 7.72$, $P < 0.001$; Fig. 3.4). However, as a group, *riparian* species (9.7 birds/sample) made a higher overall contribution to Upslope samples than the *upslope* species themselves (6.9 birds/sample; $Z = 8.96$, $P < 0.001$). The 23 *riparian* species accounted for 68.4% of all birds counted.

The pattern of clustering of samples in the ordination (Fig. 3.3) is also reflected in the comparisons of species tolerance among response groups (Fig. 3.5). *Upslope* species

were characterised by broader distributions than *riparian* species (GLM $\chi^2 = 10.83$, $df=33$, $P < 0.001$).

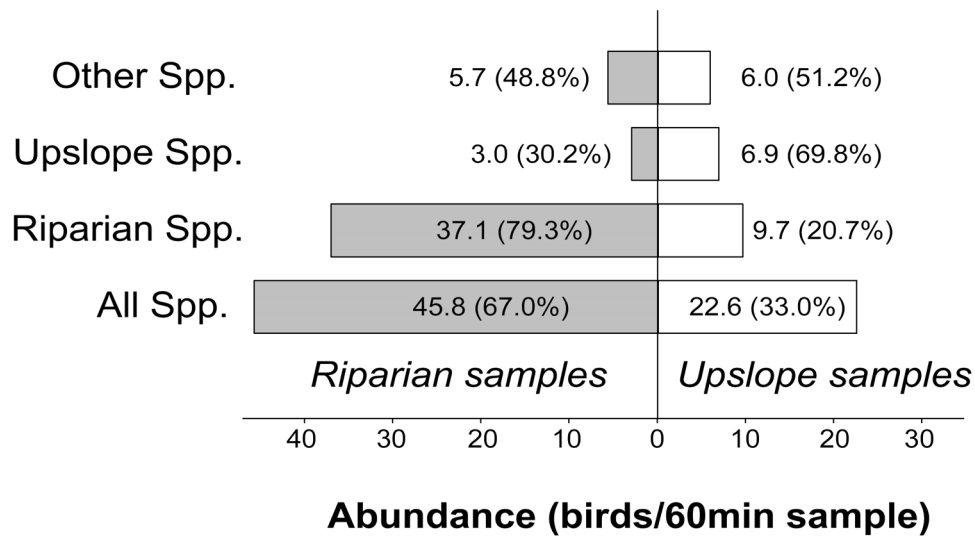


Figure 3.4 Absolute and relative contributions of response groups to the abundance of birds in Riparian ($n = 164$) and Upslope ($n = 266$) samples. Abundance is the mean number of birds per 60 min sample. Percentages are relative to the total abundance in each response group.

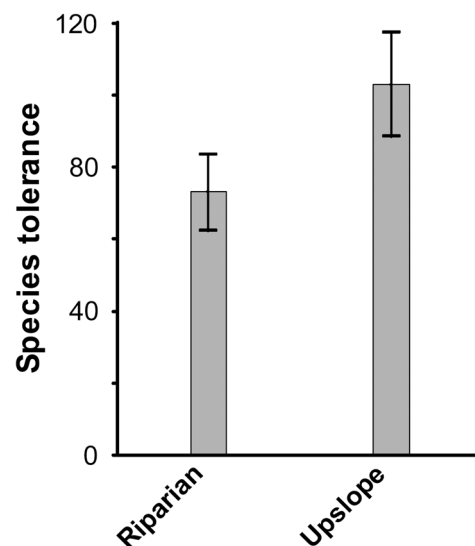


Figure 3.5 Differences in species tolerance among response groups. Species tolerance is a measure of the heterogeneity in site usage calculated in standard deviation units from the ordination analyses. Species of Upslope habitats ($n = 12$) exhibited significantly ($P < 0.05$) broader distributions than the *riparian* ($n = 23$) response group (see text for details). Error bars are 95% confidence limits.

3.4 Discussion

3.4.1 Riparian-upslope differences in bird occurrence, abundance and richness

High overall abundance combined with unambiguous Riparian preferences for a disproportionately large number of individual species suggest that riparian areas provide important resources for a significant component of the terrestrial avifauna. The fact that riparian-preferring species come from a wide range of foraging guilds and taxonomic groups further suggests that these resources are diverse and/or of ubiquitous advantage. About one third of species for which a determination was made (12 of 36; Table 3.2) showed a strong preference for upslope habitats. Most (10 species) of these were small insectivores, a response likely to reflect the low and dense foliage that was more prevalent in the mulga vegetation of many Upslope sites. Indeed Upslope abundances were higher only among some low insectivores (fairy-wrens, thornbills, robins and babbler), fruit eaters and finches (which together accounted for about 10% of all observations; Table 3.3) and the uncommon species group. In contrast, Riparian habitats supported greater numbers of larger carnivores, nectar feeders, aerial insectivores, high insectivores and seed eaters (although some taxa within the latter showed other patterns). The strong overall riparian effect in relation to species occurrence and abundance is consistent with the overwhelming body of existing literature for studies from semi-arid regions in North America (see McCarigal and McComb, 1992 for discussion on this issue and overviews by Knopf *et al.*, 1988; Hewitt, 1990; Catterall, 1993; Knopf and Samson, 1994). The pattern is also similar to the results of a number of other Australian studies that compared

riparian and upslope habitats in relatively natural areas across a range of biogeographical contexts (Table 3.4).

Table 3.4 Comparison of bird total abundance and species richness ratios between riparian and upslope habitats (short-term measurements at local sites) for the present study and several other Australian studies.

Study	Biogeographical context	Sampling scale	Riparian/upslope ratio		
			Total abundance	Species "richness"*	Sub-asymptotic / Asymptotic species richness
Recher <i>et al.</i> (1991)	Temperate dry and wet eucalypt forests, south east New South Wales; sub-regional scale (c. 1500 sq km)	120 min over 0.5 ha	1.68	1.32	? / ?
Chan (1995)#	Subtropical eucalypt open woodland, western New England Tablelands, New South Wales; sub-regional scale?	120-150 min over 0.2 ha	-	1.17	? / ?
Bentley & Catterall (1997)	Subtropical eucalypt forests, south east Queensland; sub-regional scale (c. 3000 sq km)	45 min over 0.3 ha	1.86	1.83	? / ?
Mac Nally <i>et al.</i> (2000)	Temperate eucalypt woodland, central Victoria; local scale (c. 500 sq km)	? min over 2 ha	1.86	1.36	? / ?
Woinarski <i>et al.</i> (2000)	Tropical savanna, Northern Territory; bioregional scale (c. 540000 sq km)	50 min over ? ha	1.36	1.45	? / ?
Catterall <i>et al.</i> (2001)	Subtropical eucalypt forests, south east Queensland; local scale (c. 4 sq km)	240-320min over 0.4 ha	1.77	1.36	? / ?
Kingston <i>et al.</i> (2002)	Semi arid Mulga Lands, south west Queensland; bioregional scale (c. 181000 sq km)	60 min over 0.2 ha	2.38	1.29	? / ?
Woinarski and Ash (2002)	Tropical savanna, north east Queensland; sub-regional scale (c. 2300 sq km)	8 "instantaneous" surveys over 1.0 ha	2.32	1.88	? / ?
Present study	Semi arid Mulga Lands, south west Queensland; bioregional scale (c. 181000 sq km)	30 min over 0.2 ha	2.10	—	0.83 / 0.83

* Estimates in this column are all calculated from "richness" values reported by these studies. All are based on counts of the number of species in equal area-time units without adjustment for differences in the number of individuals sampled (abundance). Gotelli and Colwell (2001) claimed that such comparisons are comparisons of species density rather than species richness.

Chan (1995) referred only the "number of species" but his comparisons were not explicitly adjusted for differences in the number of individuals at each treatment.

The results for both asymptotic and sub-asymptotic species richness, however, appear to differ from the commonly reported findings of higher riparian diversity both in Australia (Table 3.4) and elsewhere. This difference is the consequence of using rarefaction to remove the effect of greater bird densities in riparian sites, which was not done in any of the other studies listed in Table 3.4. I report higher riparian sub-asymptotic species richness only within a small number of selected groups; the larger

carnivores and two of the seed eating taxa, the parrots (Psittacidae) and the doves and pigeons (Columbidae). Most significantly, overall species richness (asymptotic and sub-asymptotic) was approximately 20% higher in Upslope habitats (compared to Riparian habitats), assisted by strong upslope responses within the low and high insectivores which together accounted for nearly three quarters of all observations and half of all species (Table 3.3). Indeed, there were 2.7 times as many species of low insectivore in Upslope habitats and more the 50% more high insectivores, even in the presence of the white-plumed honeyeater, which dominated the RW site types.

Bird diversity comparisons are commonly standardised on the basis of sampling effort (e.g. equal area-time units) rather than similar numbers of individuals collected or observed. Therefore, such comparisons are actually comparisons of *species density* (the number of species per unit area) rather than *species richness* (Gotelli and Colwell, 2001). Species density (in this context) is strongly influenced by absolute abundance (Gotelli and Colwell, 2001). Since total abundance in riparian areas is usually substantially greater than in upslope areas (Table 3.4 and references cited previously), it is not clear whether comparisons of species density between riparian and upslope sites reflect underlying differences in species richness or simply differences in abundance. The difference in the conclusions which follow is illustrated in Fig. 3.2. I estimated that there were about twice as many individuals in Riparian areas (count ratio = 2.1; Table 3.3) but about 20% less species (i.e. Riparian/Upslope ratio = 1/1.2 for samples of 21 individuals; Table 3.3). Had I used species density I would have obtained a Riparian/Upslope ratio of 1.22, implying that species richness was about 20% higher in riparian areas. Although it is possible that such discrepancies could be due to differences in relative rather than absolute abundance

(Gotelli and Colwell, 2001), this could only occur if the Riparian and Upslope rarefaction curves crossed. This was not the case and the differences consistently favoured Upslope habitats across all sampling scales. Thus in this case, species density reflected the higher absolute riparian abundances but provided very little insight into differences in species richness.

A further problem with riparian/upslope comparisons of diversity is that they are rarely based on long-term observations. Although the asymptotic and sub-asymptotic comparisons of species richness gave identical ratios, these comparisons were based on a single two-year snapshot. Given the extremely strong linkages between the riparian and upslope components of the landscape (see below) and great potential for temporal fluctuation in resource availability in the region (Barker and Greenslade, 1982; James *et al.*, 1995) it appears likely that the riparian and upslope rarefaction curves might converge or even cross, over more realistic temporal scales (e.g. decades). While the latter possibility might support the commonly articulated generalisation that riparian areas are more diverse than adjacent habitats, the causal mechanisms are likely to involve considerable inter-habitat exchange and are clearly at odds with the view (see Knopf and Samson, 1994) that these parts of the landscape can be regarded as separate ecological entities.

3.4.2 Riparian-upslope linkages

Numerous observations from the present study show a high degree of habitat overlap which suggest localised movements among particular groups of birds: 1) very few species were found exclusively in one habitat or another; 2) many species exhibited

increasing or decreasing occurrence with riparian distance; 3) many of the species that were dominant in Riparian areas were also dominant in Upslope areas and; 4) a large proportion of species and groups, including those with a clear preference for one habitat or another, occurred regularly in both the Riparian and Upslope sites. The simple observation of overlapping species assemblages does not necessarily imply interdependency. Such patterns could result from unimodal, linear, or even disjunct species responses to an environmental gradient represented by differences in riparian and upslope conditions, rather than movement between them. However, in that case, a distinct separation of Riparian and Upslope samples in the pDCA ordinations would be expected, due to the preference of different species for either end of the gradient. Instead, Riparian sites with permanent water were concentrated toward the centre of the ordination with other types of site much more widely dispersed around them. Indeed, this pattern was evident despite the fact that no attempt was made to control for the obvious structural and floristic differences in the riparian and upslope habitats. Considering a large proportion of upslope-preferring birds were observed in riparian habitats (30.2%, Fig. 3.4), these results imply that some riparian areas are of universal, or near universal, advantage to the entire terrestrial avifauna.

This view is also supported by the behaviour of Upslope-preferring species. For this group habitat fidelity appeared high (Table 3.3) suggesting highly specific resource needs, yet these same species had high tolerances (Fig. 3.5) suggesting a relatively broad or heterogeneous resource base. There are at least two possible reasons for this. First, in upslope habitats where concentrations of resources are likely to be low and temporally unstable, multiple resource requirements may not be satisfied simultaneously leading to highly variable individual and species responses, and hence

greater variation in species composition. Indeed, the absence of locational structure in the widely dispersed Upslope samples suggests a high turnover of species even within restricted localities. The second reason is methodological, and arises because species' responses were defined on the basis of the proportion of time (observations) that a given species was in a particular habitat without regard for differences in time required to obtain essential resources. If an essential resource such as water was only available in riparian habitats, then species that spend almost all of their time foraging in upslope areas would need to access riparian areas only briefly. Hence, such species would be classified as "upslope" despite being critically dependent on riparian resources.

Indeed, landscape-scale gradients in resource availability may provide a significant incentive for inter-habitat movement. Numerous reviews have highlighted the proposition that water in arid, semi arid and seasonally arid regions is a limiting resource uniquely associated with riparian habitats (Johnson *et al.*, 1977; Thomas *et al.*, 1979; Naiman and Décamps, 1997). Water was clearly an influential factor for some species in this study and may have contributed to the significant habitat overlap through localised movements. Raptors, kingfishers, nectar feeders, aerial insectivores and many individual species were most abundant in riparian areas with permanent water. Other species such as the double-barred finch, weebill and singing honeyeater (among others) and the more uncommon species showed a strong Upslope response, which was largely due to a high numbers of observations from bore drain sites (UW; Tables 3.2 and 3.3). Since granivores are considered to be most dependent on surface drinking water in the Australian arid zone (Fisher *et al.*, 1972; Dawson, 1976; Schodde, 1982) it was paradoxical that the seedeaters as a group showed no obvious

preference for either Riparian or Upslope habitats with permanent water (Table 3.3). However, their observed response is consistent with localised movements that reflected both their need for water and their need for seed resources, which may have been generally more available in the upslope habitats. It is also likely that because riparian habitats are areas of concentrated resources (Gregory *et al.*, 1991; James *et al.*, 1995) I would have recorded them at higher density in these areas even though they could have spent most of their time foraging at lower average densities in upslope areas. Furthermore, many in this group (e.g. the parrots and cockatoos) are hollow-nesting species and at least within the more arid areas of the bioregion, tree hollows were essentially confined to riparian habitats. Similar arguments could apply to species that perch in emergent trees and stags (e.g. raptors, corvids, kingfishers, and the aerial insectivores), which were also observed to be more prevalent in Riparian areas. Riparian-preferring species may make opportunistic movements to upslope areas in search of resources that are either not available or costly to obtain in the riparian zone, while the less abundant species of upslope areas utilise riparian areas for the purpose of securing essential resources.

Szaro and Jakle (1985) reported asymmetric interdependencies among riparian and adjacent habitats in terms of a lower overall contribution of upslope birds to riparian habitats (< 2%) compared to the proportion of riparian birds they found in upslope areas (up to 33%). My results are similar; 6.6% (3.0/45.8, Fig 3.4) of total riparian abundance came from upslope species, but riparian species were responsible for 42.9% (9.7/22.6, Fig 3.4) of upslope abundance. However, considering the major differences in density between riparian and upslope habitats such results are not surprising and provide only limited insight into the role each landscape component

may have for particular groups of birds. In this respect, the observations that about 30% of upslope species abundance came from riparian habitats and about 20% of riparian species abundance came from upslope habitats (Fig. 3.4) appear more relevant. Indeed, for groups that are essentially defined because of their habitat fidelity, the overlap is striking and clearly highlights the extent of the landscape interactions.

3.4.3 Management and conservation

In this study, the riparian bird assemblage was characterised by high abundances and levels of species dominance but relatively low alpha and beta diversity. Conversely, abundance in the upslope assemblage was lower but more evenly distributed and species richness was higher both within and between sites. There was also evidence for very strong riparian/upslope linkages, indicating that the ecological interface (at least in the case of Mulga Land birds) is much fuzzier and more permeable than that implied by the clear physical boundary evident in the vegetation. Resources available exclusively or dominantly in one habitat component or the other appear to be potentially available to the entire bird community although differences in responses among individual taxa clearly indicate variation in access. This implies that major changes in land (or water) management which affect one component are likely to precipitate changes in the other because they disrupt prevailing riparian/upslope relationships. Management therefore, needs to explicitly recognise that although individual species may utilise these components of the landscape in very different ways, they are in fact intimately related. These conclusions agree with Knopf and

Samson (1994); ensuring the integrity of the riparian/upslope complex should feature prominently in approaches to reserve selection and land management.

Despite extensive land degradation (Wilson, 1999), the Mulga Lands region has experienced continuing pressure for greater agricultural development (see Wilson, 1997; Kingsford, 1999). One form of development is the clearing or thinning of upslope woodland and shrubland habitats to increase grazing capacity. In general, my results would predict this would favour birds of more open country (principally the larger bushbirds and their allies) over the smaller and often less common sedentary insectivores, which were more closely associated with the denser habitats. It could be argued that the small insectivores would maintain populations by shifting their dominant focus to riparian habitats since they already access these areas for some purposes. However, many of the larger species likely to benefit from upslope clearing (such as the yellow-throated miner, laughing kookaburra, corvids, white-winged chough, Australian magpie, magpie-lark) also dominate riparian areas and are likely to be competitively superior in these areas. Furthermore, the dominance of the highly aggressive white-plumed honeyeater in many riparian areas may limit access by small upslope species to insect food resources. Therefore, the small-bodied insectivores of the Mulga Lands seem likely to follow the widespread trend for the decline in woodland birds observed in adjacent and more agriculturally developed bioregions (Reid and Fleming, 1992; Smith and Smith, 1994, Reid, 1999; Seddon *et al.*, 2003; Woinarski and Catterall, 2004).

Indeed, it is notable that many of the small insectivores remain relatively common in the Mulga Lands yet are in serious decline elsewhere (e.g. white-browed treecreeper,

brown treecreeper, chestnut-rumped thornbill, jacky winter, red-capped robin, hooded robin, grey-crowned babbler, crested bellbird, rufous whistler, restless flycatcher, white-browed woodswallow; Reid, 1999). More optimistically, landscape changes that result in more extensive grassy habitats are likely to benefit granivorous species, many of which have also become rare (Reid and Fleming, 1992; Smith and Smith, 1994, Reid, 1999) and some of the raptors which hunt live prey over open ground. However, unlike the small insectivores, most of these species are relatively large, capable of flying long distances and for reasons outlined previously were generally common in riparian areas.

The findings also foreshadow possible problems for some species arising from the ongoing closure of free-flowing bore drains throughout the arid zone (Murray, 2002). A number of common and many of the rarer species clearly favoured upslope habitats in association with artificial water (Ups(UW) response, Tables 3.2 and 3.3). The bore drains provided upslope species with convenient access to surface water. Since riparian zones are likely to provide the only other reliable source of surface water once the bores are capped, we need to ask whether these birds will be able to shift their focus and at what cost. As upslope species were relatively common in riparian areas, individuals living close to a source of riparian water may be unaffected (although see potential for competitive interactions above). However, many of the areas serviced by bore drains are large distances (tens of km) from riparian areas with reliable water. Since the territories of many small insectivores of the region appear to be confined to a few hectares or more (Schodde and Tidemann, 1986; Blakers *et al.*, 1984), it is doubtful that birds resident in these more distant locations could adequately access water within their normal home ranges. While artificial water may

still be potentially available in the form of stock troughs, these systems are likely to be physically unsuitable and may be regularly turned off to manage grazing pressure. Although it can be argued that the advent of artificial water has allowed the populations of some species to increase beyond their normal limits (James *et al.* 1999) I do not subscribe to the view that removing the resource will result in the restoration of a “natural balance”. Vast changes to the Mulga Lands ecosystems have taken place since European settlement (Hodgkinson and Harrington, 1985; Witt and Beeton, 1995; Wilson, 1997; James *et al.*, 1999; Witt *et al.* 2000) and in the context of the widespread decline of many small passerines any management action that may contribute to this merits more thorough investigation.

Riparian habitats are restricted to small proportion of the landscape (Knopf *et al.*, 1988; Hewitt, 1990). Based on 2001 vegetation mapping (Accad *et al.*, 2003) I estimate that habitats directly associated with active drainage lines occupy about 8% of the Mulga Lands landscape. In the xeric western regions of the United States, Knopf *et al.* (1988) claim that the proportion of extant riparian vegetation is even lower at one percent. If the effective functioning of upslope habitats depends on healthy riparian areas, this suggests that the loss or degradation of very small areas of riparian habitat may have disproportionate impacts on the entire bird community. In such circumstances riparian habitats could be regarded as keystone habitats; the landscape equivalent of keystone species (Paine, 1969). Furthermore, in the Mulga Lands, riparian habitats appeared to be the common feature that linked the composition of disparate, or temporally dynamic, upslope assemblages. Although species richness was typically lower in the riparian samples, these habitats may be critical centres of biodiversity for terrestrial birds of the Mulga Lands.

4.0 The Influence of Season, Rainfall and Inter-annual Variability on Riparian and Upslope Bird Assemblages of the Mulga Lands

4.1 Introduction

In arid and semi arid landscapes the spatial and temporal mix of water and nutrients limits primary productivity, and these factors are dominant influences on the distribution and abundance of terrestrial biota (James *et al.*, 1995). Several recent studies have found that many fauna, including birds, are present in higher concentrations in parts of the landscape where both water and nutrients accumulate (Reid *et al.*, 1993; Naiman and Décamps, 1997; Kingston *et al.*, 2002, Appendix 1; Chapter 3). Superimposed on these spatial patterns are temporal fluctuations that determine when resources are available. These include not only regular seasonal influences such as high daytime temperatures and evaporation rates during summer, which make acute energetic demands on arid zone biota (Dawson, 1976; Schodde, 1982), but also less predictable fluctuations in rainfall that often lead to drought. To be successful, species need to be able to tolerate, or avoid, hard times and, to exploit resources when they occur. Although these are key issues for conservation planning in the Australian arid zone (James *et al.*, 1995), few studies have specifically investigated the influence of temporal variations in climate on regional fauna assemblages, and how they relate to spatial patterns across the landscape.

Unlike other vertebrate groups, almost all birds are capable fliers, and this gives them the potential to both track favourable resources and avoid stressful situations. The

expression of this mobility takes many forms; some species undergo regular seasonal migrations; some appear to be nomadic, turning up whenever conditions are favourable, while others are essentially sedentary (Schodde, 1982; Chan, 2001; Griffioen and Clarke, 2002). Even among the sedentary species, most are highly mobile and capable of daily movements between different types of habitat, thereby maximising the resources available. In addition, many arid zone birds cope with harsh and uncertain conditions by utilising a wide range of other behavioural and physiological adaptations such as opportunistic, precocious and cooperative breeding (Davies, 1976; Rowley, 1976; Schodde, 1982); and adaptations to conserve water, or to exploit it (Dawson, 1976; Astheimer and Buttemer, 2002).

In the Australian arid zone, climatic conditions at any point in time are a highly uncertain function of global, seasonal and local-scale meteorological influences (Bureau of Meteorology, 1997). Due to its limiting influence on arid zone ecosystem processes (Noy-Meir, 1973), rainfall is an obvious climatic element likely to influence bird species and assemblages. However, the distinction is rarely made between its direct physiological influence on rehydration and cooling, and its indirect influence through the stimulation of plant growth. Rainfall that stimulates primary production may be expected to have more ubiquitous and long-lasting benefits for birds, and other animals, than the simple provision of moisture in an otherwise depauperate environment. Not all rainfall stimulates plant growth, and it is only above certain thresholds of quantity and frequency that production pulses occur (Ludwig *et al.*, 1997). Even substantial falls may not stimulate much growth if they occur in mid summer when evaporation rates are extreme (Hodgkinson and Freudemberger, 1997). The relationship between rainfall and bird response is further complicated by lag times. Models of arid zone plant growth

response (Nix, 1976; Hodgkinson and Freudenberger, 1997) predict that growth rates for evergreen shrubs and trees (and to a lesser extent perennial grasses) will increase to a maximum over subsequent months then gradually decline in the absence of sufficient follow-up rainfall. Nonetheless, localised and sporadic rainfall is often the only source of surface water over much of the landscape, and the ability to track it may be crucial for some species.

With the exception of the seasonally arid wet/dry tropics, most of inland Australia experiences only slight seasonal differences in rainfall, and these averages are typically overwhelmed by high levels of variation between years (Nix, 1982). The strongest source of rainfall variation is associated with El Niño Southern Oscillation (ENSO) phenomena (Bureau of Meteorology, 1997). Most of the widespread and severe droughts affecting northern and eastern Australia have been linked with El Niño events (Nicholls and Kariko, 1993; Stone *et al.*, 1996; Bureau of Meteorology, 1997), and there is also mounting evidence of ENSO related influences on terrestrial fauna including birds (Jaksic and Lazo, 1999; Sillett *et al.*, 2000; Jaksic, 2001; Nott *et al.*, 2002). In these circumstances, it seems unlikely that arid zone birds should respond strongly to seasonal cues.

Riparian areas are one component of the landscape where both water and nutrients accumulate and many studies have reported higher concentrations of terrestrial fauna, including birds, in these habitats than in adjacent habitats (see reviews by Knopf *et al.*, 1988; Catterall, 1993; Naiman and Décamps, 1997). Indeed, the differences often appear most pronounced in studies from more arid biomes (e.g. Szaro and Jakle 1985; Johnson and Haight, 1985), including the Mulga Lands (Kingston, *et al.*, 2002,

Appendix 1; Chapter 3). Notwithstanding the differences, a strong overlap in riparian and upslope bird assemblages also observed in Chapter 3 that was attributed to localised movements between these components of the landscape. Although no studies I am aware of have specifically studied the effects of drought on riparian utilisation, it seems likely that birds may concentrate more in riparian areas during drought. Similarly, riparian areas may also be favoured by locally-resident species when rainfall is low, or over hot summer periods.

In this chapter, I examine the relative influence of season, rainfall and inter-annual variation on the regional bird assemblage of the semi-arid Mulga Lands of south west Queensland, Australia. The study was conducted over two years and spanned an abrupt discontinuity between drought and mesic conditions which were closely aligned to values of the ENSO index. I ask (1) to what extent do Mulga land bird assemblages vary between summer and winter? (2) What is the extent of inter-annual variation? (3) Is there any evidence that species track rainfall events? (4) How do these patterns relate to riparian usage? In particular, I test the proposition that riparian areas are utilised more frequently by both migrant and resident species, during the dry and hot summer season, and during El Niño drought. Since many other regions of the Australian arid zone share similar climatic influences and habitat conditions with the Mulga Lands, the results are likely to be also more broadly relevant.

4.2 Methods

4.2.1 Statistical Analysis

4.2.1.1 Bird abundance and diversity

Generalised Linear Models (GLM; *sensu* McCullagh and Nelder, 1983) were used to simultaneously assess seasonal and other effects on the following bird response variables: (1) occurrence of individual common species; (2) abundance within selected groups (all species, resource guilds, relative height groups, uncommon species) and; (3) sub-asymptotic species richness within selected groups (as above). Occurrence was defined as a binary variable indicating the presence (or absence) of each species irrespective of the number of individuals (abundance) recorded. Analysis of the variation in the occurrence of individual species thus assumed a binomial distribution, and the Logit link function was used (i.e. logistic regression). Poisson regression (Poisson distribution, Log link) was used to model the other response variables. Generalized Estimating Equation modelling (GEE; Liang and Zeger, 1986) based on initial GLM parameter estimates was used to account for possible correlations among sub-plots and site-visits. GLM and associated GEE analyses were carried out using PROC GENMOD within SAS (SAS Institute Inc. 1999).

Poisson regression models (abundance and sub-asymptotic species richness within selected groups) included the following explanatory variables: SEASON (Summer, Winter), MON_RAIN, YEAR (1997, 1998), RIP_STAT (Riparian, Upslope); and covariates, PERMWATER (Non-Permanent, Permanent), REGION (East, South-west, North-west; see Fig. 2.1), RIP_STAT*SEASON, RIP_STAT*YEAR,

RIP_STAT*MON_RAIN, PERMWATER*SEASON and RIP_STAT*PERMWATER. For the Logistic regression models (occurrence of individual species), the best subsets of these same variables were derived by stepwise selection (PROC LOGISTIC; SAS Institute Inc. 1999) with the forced inclusion of SEASON, RIP_STAT and PERMWATER only. The GLM analyses were carried out at the following sampling resolutions: the sub-plot level (n = 2544; 10 min samples) for the occurrence of individual species; the site-visit level (n = 865; 30 min samples) for the abundance of selected groups and; the site-sampling period level (n = 433; 60 min samples) for sub-asymptotic species richness estimates.

For sample-based data sets, differences in abundance between treatments may result in misleading comparisons of species richness (Gotelli and Colwell, 2001). Therefore, to compare treatments while directly controlling for abundance, rarefaction was conducted prior to the analysis of all species richness responses. Details of the rarefaction procedure are contained in Chapter 3.

All “fly over” observations and non-terrestrial bird species were excluded from analysis. The Australian raven (*Corvus coronoides*) and little crow (*C. mellori*; both of which occur in the study area) were not reliably differentiated in the field and observations for these two species were regarded as “Corvus Sp.” With this exception, species taxonomy follows Christidis and Boles (1994). Allocations of species to resource guilds were taken from Reid and Hobbs (1996). Species were also grouped based on their observed abundance in the specific relative height groups (Ground/Lower, Mid and Upper strata) described previously. Species primarily observed in the Emergent stratum were classified but not analysed due to the previous

exclusion of all “fly over” observations. Species not classified into a stratigraphic group were all found at fewer than 20 sub-plots and were thus considered “Uncommon spp.”. Due to the numeric dominance of the white-plumed honeyeater and its potential to overwhelm species group responses (see Chapter 3), the GLM analyses were carried out on the relevant groups with and without the inclusion of this species. Membership of resource guilds, relative height and uncommon species groups is shown in Appendix 4.

Individual species and groups of species were allocated to seasonal, inter-annual, rainfall and riparian response groups based on the contribution of specific variables (SEASON, YEAR, MON_RAIN and RIP_STAT respectively) to the statistical models. In the case of seasonal responses, species (or groups) were considered to exhibit a *summer* or *winter* response if the response variable was significantly higher ($P \leq 0.05$) during Summer or Winter respectively. I report parameter estimates (as count ratios for Poisson regressions and odds ratios for the logistic regressions i.e. $e^{\text{Parameter estimate}}$) associated with the effect that defined the response group. Species or groups were considered *indifferent* if the seasonal effect was not significant ($P > 0.05$) and their variance was similar to those with a significant effect. The procedure used to determine *indifferent* species or groups are detailed in Chapter 3. No attempt was made to determine *indifferent* responses to localised monthly rainfall.

Three approaches were used to examine riparian influences on the temporal variation. First, significant interactions were identified between riparian status (RIP_STAT) and each of the temporal factors; SEASON, YEAR, and MON_RAIN in the GLM analyses. Second, I tested whether abundance and sub-asymptotic species richness within the

temporal response groups (e.g. *summer* as defined above) varied with riparian status. In this case the GLM models were repeated using the abundance or sub-asymptotic species richness of each derived temporal response group as the dependent variable. Third, at the scale of the entire study, chi squared exact tests of association (PROC FREQ; SAS Institute Inc., 1999) were applied to two way contingency tables of the number of species within response group combinations (e.g. seasonal and riparian groups). Where non-significant associations ($P > 0.05$) were found I further explored the likely trends by relaxing the P value criterion used to determine response group membership and repeated the tests of association. This latter procedure increased the number of species classified into a specific response group cross-tabulation at the expense of membership certainty.

4.2.1.2 Bird community composition

Bird communities were ordinated using partial Canonical Correspondence Analysis (pCCA; program CANOCO v4.0, ter Braak and Smilauer, 1998). This eigenanalysis-based procedure allows both species and samples to be ordinated simultaneously, with adjustment for covariates. CCA partitions explained variation rather than overall variation and assumes a unimodal species response (Jongman *et al.*, 1995).

The species by sample data matrix for these analyses was resolved to the site-sampling period level. That is, abundances for individual species over three sub-plots and two visits were pooled to yield the species abundances at each of 433 unique site and sampling period combinations (samples). All 119 species were included. All analyses were carried out on raw abundances. Since my primary interest was in the

influence of the temporal factors on species composition I specified, SEASON, MON_RAIN and YEAR as “environmental variables”. Variables representing riparian status, presence of permanent water, geographical region, height of the vegetation in the upper stratum, and percentage cover for each of the upper, mid and lower strata were included as covariates. Monte Carlo permutation tests (program CANOCO v4.0; ter Braak and Smilauer, 1998) were used to determine the relative influence and significance of the design variables (SEASON, MON_RAIN, YEAR) on species composition after controlling for covariates. Due to the riparian stratification of the experimental design, samples were permuted at random within Riparian and Upslope samples. The results of the ordination were displayed as a biplot (see Jongman *et al.*, 1995) to show the configuration of samples (after controlling for the covariates) in relation to the environmental variables and bird species.

4.3 Results

4.3.1 Bird abundance and diversity

4.3.1.1 Seasonal variation

Over the four sampling periods, 7694 observations were made of 13520 individuals from 119 species (Appendix 4).

Among the 28 species for which a seasonal response group determination was made, fourteen were significantly ($P < 0.05$) more likely to be found in one season or another (Table 4.1). Four species (weebill, white-plumed honeyeater, crested bellbird and hooded robin) were most frequently observed during Winter. The remaining ten exhibited an apparent preference for Summer. Fourteen species were present in sufficient numbers to be analysed but appeared *indifferent* to seasonal influences, at least during the period of the study.

High levels of seasonal fidelity were uncommon. Only the rainbow bee-eater and dollarbird were observed exclusively during one season (Summer) although the sacred kingfisher approached these levels with more than 90% of its observations from Summer. Other species that showed a significant *summer* or *winter* response were, in general, much less faithful to their favoured season. All were at least 50% (odds ratio = 1.5; Table 4.1) more likely to be recorded in one season or another.

Statistically significant differences in overall seasonal abundance were not detected ($P > 0.05$), however between 15 and 30% (95% CI, Table 4.2) more species were

Table 4.1 Seasonal response for the occurrence of individual bird species: results of generalised linear modelling. Occurrences shown represent the number of times the species was observed at Summer (n=1288, 10 min samples) and Winter (n=1258, 10 min samples) sub-plots. Summer fidelity is shown as the mean percentage of all observations from Summer samples. Odds presented in favour of season indicated (S, Summer; W, Winter). Values in parentheses indicate 95% confidence interval. Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. # indicates significant riparian status by season interaction ($P < 0.05$). Response groups: Rip, Riparian; Ups, Upslope; Win, Winter; Sum, Summer; Ind, Indifferent; ND, Not determined.

Bird species	Occurrence			Seasonal odds	Response Group	
	Summer	Winter	Summer fidelity (%)		Season	Riparian
Rainbow Bee-eater	58	0	100.0	5.99*** (3.03-11.84)S	Sum	Ind
Sacred Kingfisher	86	8	91.3	5.52*** (3.12-9.78)S	Sum	Rip
Restless Flycatcher	39	8	82.6	3.21*** (1.61-6.38)S	Sum	Rip
Little Friarbird	119	49	70.3	2.77*** (1.73-4.44)S	Sum	Rip
Dollarbird	23	0	100.0	2.49* (1.16-5.32)S	Sum	ND
Noisy Friarbird	27	7	79.0	2.31* (1.15-4.67)S	Sum	ND
Rufous Whistler	93	41	68.9	2.23*** (1.45-3.43)S	Sum	Ups
Laughing Kookaburra	33	13	71.3	1.89* (1.03-3.47)S	Sum	Rip
Willie Wagtail	152	87	63.1	1.82*** (1.32-2.50)S	Sum	Rip
Black-faced Cuckoo-shrike	49	27	63.9	1.76* (1.07-2.89)S	Sum	Rip
Crested Pigeon	64	39	61.6	1.55 (0.96-2.52)S	Ind	Ind
Grey Shrike-thrush	83	56	59.1	1.43 (0.96-2.13)S	Ind	Rip
Common Bronzewing	47	36	56.0	1.28 (0.80-2.04)S	Ind	Ind
Galah	75	64	53.4	1.17 (0.76-1.78)S	Ind	Rip
Australian Ringneck	100	112	46.6	1.12 (0.78-1.61)S	Ind	Rip
Magpie-lark	60	55	51.6	1.05 (0.67-1.66)S	Ind	Rip
Red-winged Parrot	51	52	48.9	1.02 (0.66-1.59)W	Ind	Rip
Apostlebird	47	40	53.4	1.09 (0.64-1.87)W#	Ind	ND
Corvus Sp.	38	39	48.8	1.11 (0.70-1.77)W	Ind	Rip
Spiny-cheeked Honeyeater	134	197	39.9	1.12 (0.78-1.60)W	Ind	Ups
Chestnut-rumped Thornbill	67	75	46.6	1.18 (0.78-1.80)W	Ind	Ups
Jacky Winter	24	31	43.1	1.23 (0.73-2.09)W	Ind	Ups
Brown Treecreeper	53	66	44.0	1.27 (0.80-2.01)W	Ind	Rip
Yellow-throated Miner	159	199	43.8	1.37 (0.94-1.98)W	Ind	Rip
White-plumed Honeyeater	380	463	44.5	1.56** (1.13-2.16)W	Win	Rip
Weebill	68	123	35.1	1.98** (1.32-2.97)W	Win	Ups
Crested Bellbird	12	28	29.5	2.11* (1.11-3.99)W	Win	ND
Hooded Robin	7	22	23.7	2.15* (1.05-4.43)W	Win	Ups

observed during Summer. A number of groups showed seasonal differences in abundance (Table 4.2). These include the Aerial Insectivores (7 spp., 4% of individuals), Larger Bushbirds (11 spp., 5% of individuals), Pigeons, Parrots and Cockatoos (16 spp., 15% of individuals) all of which were more abundant in Summer, and the Honeyeaters (17 spp., 44% of individuals; although this was strongly influenced by the white-plumed honeyeater) and Nomads (12 spp., 3% of

Table 4.2 Seasonal response for bird abundance and sub-asymptotic species richness within species groups: results of generalised linear modelling. Abundance analyses are based on mean number of individuals at each site-visit (n = 865, 30 min samples). Sub-asymptotic species richness estimates are based on site-sampling periods (n = 433, 60 min samples) calculated after rarefaction using the number of samples and individuals indicated (see text for details). Species richness groups with fewer than 4 species were not analysed. Response groups: Rip, Riparian; Ups, Upslope; Win, Winter; Sum, Summer; Ind, Indifferent; ND, Not determined. Count ratios presented are in favour of the effect indicated (S, summer; W, Winter; R, Riparian; U, Upslope), values in parentheses indicate 95% confidence interval. Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. # indicates significant riparian status by season interaction ($P < 0.05$).

Species grouping	No. of species	% of total abundance	No. of site-visits present	Abundance			Sub-asymptotic species richness			
				Count ratio	Seasonal response group	Riparian response group	Post-rarefaction site-sampling periods (individuals sampled)	Count ratio	Seasonal response group	Riparian response group
Resource guilds										
Aerial Insectivore	7	4.1	268	3.35*** (2.09- 5.37)S	Sum	Rip	46 (4)	1.30** (1.07- 1.59)S	Sum	ND
Larger Bushbird	11	4.6	302	1.70** (1.23- 2.34)S	Sum	Rip	35 (6)	1.14 (0.88- 1.46)S#	ND	ND
Raptor	10	0.4	42	1.36 (0.70- 2.64)S	ND	Rip		ND	ND	ND
Pigeons, Parrots & Cockatoos	16	15.6	446	1.50** (1.14- 1.97)S	Sum	Rip	85 (8)	1.05 (0.91- 1.22)W	Ind	Rip
Ground Generalist	6	5.4	93	1.58 (0.63- 3.98)W	ND	ND	60 (3)	1.02 (0.91- 1.16)S	Ind	Ind
Bushbird Insectivore	37	20.1	642	1.08 (0.90- 1.28)S	Ind	Ups	70 (12)	1.09 (0.83- 1.43)W	ND	Ups
Honeyeaters, Flowerpeckers etc.	17	44	697	1.25* (1.05- 1.49)W	Win	Rip	224 (8)	1.14** (1.04- 1.25)S	Sum	Ups
Excluding white-plumed honeyeater	16	20.9	564	1.06 (0.84- 1.33)W	Ind	Rip	142 (7)	1.07 (0.93- 1.23)S#	Ind	Ups
Finch	3	1.2	49	1.53 (0.44- 5.27)W	ND	Ups		ND	ND	ND
Nomad	12	3.2	97	3.23** (1.43- 7.27)W	Win	ND	33 (4)	1.06 (0.74- 1.54)W	ND	ND
Relative height groups										
Upper Strata	41	76.9	823	1.00 (0.88- 1.14)W	Ind	Rip	215 (18)	1.27*** (1.17- 1.37)S	Sum	Ups
Excluding white-plumed honeyeater	40	53.8	803	1.16 (0.99- 1.36)S	Ind	Rip	158 (17)	1.17** (1.06- 1.30)S	Sum	Ind
Mid Strata	11	10.2	477	1.19 (0.97- 1.46)S	Ind	Ups	51 (8)	1.14 (0.89- 1.46)S	ND	Ups
Ground/Lower	5	3.1	178	1.01 (0.65- 1.58)S	Ind	Ups	42 (4)	1.22* (1.05- 1.42)W	Win	Ind
Uncommon Species	58	4.8	206	1.06 (0.66- 1.71)S	ND	ND	47 (5)	1.30 (0.91- 1.88)W	ND	Ind
Species Richness	119	98.6	840	not applicable			258 (21)	1.23*** (1.15- 1.31)S	Sum	Ups
Excluding white-plumed honeyeater	118	75.4	837	not applicable			193 (21)	1.18*** (1.08- 1.28)S	Sum	Ups
Total Abundance	138^	100	863	1.00 (0.90- 1.12)W	Ind	Rip		not applicable		
Excluding white-plumed honeyeater	137^	76.9	862	1.11 (0.97- 1.27)W	Ind	Rip		not applicable		

^ includes 19 taxa not identified to species level

individuals) which were more abundant in Winter. Within individual groups, *summer* responses for sub-asymptotic species richness were recorded only within the Aerial Insectivores, Honeyeaters (due mainly to the white-plumed honeyeater) and species most prevalent in the Upper stratum (41 spp., 77% of individuals). A significant *winter* sub-asymptotic species richness response was observed only within the Ground/Lower relative height group (5 spp., 3% of individuals). Ground Generalists (6 spp., 5% of individuals) and the Pigeons, Parrots and Cockatoos showed similar numbers of species in both seasons. The remaining groups all exhibited substantial variation, although the Uncommon species showed a near-significant trend ($P = 0.15$, not shown) favouring higher sub-asymptotic richness during Winter.

4.3.1.2 Inter-annual variation

Seven individual species, only one of which exhibited a significant *summer* or *winter* seasonal response (crested bellbird), showed significant inter-annual variation (Table 4.3). Six of these were most prevalent during 1998 while only the Australian magpie was observed more frequently during 1997. Seventeen species were observed at similar frequencies in both years.

Inter-annual variation favouring 1998 was also evident within species groups (Table 4.4). On average, there were about 14% more birds in 1998. Major contributions to this were made by the Pigeons, Parrots and Cockatoos, Bushbird Insectivores (37 spp., 20% of individuals), Upper stratum species, and many of the honeyeaters. Aerial Insectivores and the Larger Bushbirds were present in similar numbers in both years.

Table 4.3 Inter-annual response for the occurrence of individual bird species: results of generalised linear modelling. Occurrences shown represent the number of times the species was observed at 1997 (n = 1258, 10 min samples) and 1998 (n = 1288, 10 min samples) sub-plots. 1997 fidelity is shown as the mean percentage of all observations from 1997 samples. Odds presented in favour of year indicated (97, 1997; 98, 1998). Values in parentheses indicate 95% confidence interval. Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. No significant riparian status by year interactions ($P < 0.05$) were detected. Response groups: Rip, Riparian; Ups, Upslope; 97, 1997; 98, 1998; Ind, Indifferent; ND, Not determined

Bird species	Occurrence			Inter-annual odds	Response Group	
	1997	1998	1997 fidelity (%)		Inter-annual	Riparian
Australian Magpie	40	16	71.9	2.39**(1.30-4.40)97	97	ND
Jacky Winter	36	19	66.0	1.65(0.96-2.82)97	Ind	Ups
Sacred Kingfisher	54	40	58.0	1.35(0.85-2.14)97	Ind	Rip
Spiny-cheeked Honeyeater	179	152	54.7	1.36(0.93-1.98)97#	Ind	Ups
Black-faced Cuckoo-shrike	41	35	54.5	1.13(0.69-1.83)97#	Ind	Rip
Willie Wagtail	128	111	54.1	1.21(0.90-1.64)97	Ind	Rip
Weebill	96	95	50.9	1.03(0.68-1.55)97	Ind	Ups
Brown Treecreeper	60	59	51.0	1.00(0.63-1.58)98	Ind	Rip
White-plumed Honeyeater	418	425	50.2	1.01(0.73-1.39)98	Ind	Rip
Crested Pigeon	51	52	50.1	1.02(0.63-1.63)98	Ind	Ind
Apostlebird	43	44	50.0	1.00(0.60-1.69)98	Ind	ND
Common Bronzewing	38	45	46.4	1.11(0.70-1.76)98	Ind	Ind
Rufous Whistler	60	74	45.4	1.17(0.77-1.79)98	Ind	Ups
Yellow-throated Miner	154	204	43.6	1.38(0.95-1.99)98	Ind	Rip
Grey Shrike-thrush	56	83	40.9	1.44(0.97-2.13)98	Ind	Rip
Corvus Sp.	31	46	40.8	1.36(0.85-2.98)#	Ind	Rip
Chestnut-rumped Thornbill	57	85	40.7	1.47(0.97-2.22)98	Ind	Ups
Little Friarbird	67	101	40.4	1.46(0.94-2.27)98	Ind	Rip
Australian Ringneck	86	126	41.1	1.52*(1.06-2.18)98#	98	Rip
Galah	52	87	38.0	1.67*(1.08-2.59)98	98	Rip
Magpie-lark	43	72	37.9	1.67*(1.05-2.65)98	98	Rip
Red-winged Parrot	38	65	37.4	1.68*(1.08-2.61)98	98	Rip
Crested Bellbird	6	34	15.3	2.99**(1.53-5.84)98	98	ND
Rufous Songlark	3	19	13.9	2.17*(1.03-4.57)98	98	ND

Overall sub-asymptotic species richness was also similar between years although near-significant ($P = 0.11$, not shown) in favour of 1998. Without the influence of the white-plumed honeyeater, which was abundant in both years (Table 4.3), approximately 10% more species were observed in the 1998 samples. Sub-asymptotic species richness within the Upper stratum, Honeyeater, Nomad, and Uncommon species groups was also significantly ($P < 0.05$) higher in 1998. Although the

abundance of the Pigeons, Parrots and Cockatoos was about 40% higher in 1998, the sub-asymptotic number of species was similar in both years.

4.3.1.3 Rainfall response

Three species exhibited a significant ($P < 0.05$) response to monthly rainfall (fairy martin, Australian ringneck, spiny-cheeked honeyeater; Table 4.5). All were observed less frequently with increasing rainfall.

Influenced most strongly by the Aerial Insectivores, Pigeons, Parrots and Cockatoos, Honeyeaters, Nomads and Upper stratum species, higher overall abundances were also observed with decreasing monthly rainfall (Table 4.5). This pattern, however, was not evident in the sub-asymptotic species richness response. No evidence was found to suggest that overall sub-asymptotic species richness was influenced by monthly rainfall, although there were some significant ($P < 0.05$) responses within selected groups. Aerial Insectivores showed a negative correlation while both the Bushbird Insectivore and Larger Bushbird groups appeared to be more species rich when and where monthly rainfall was higher.

4.3.1.4 Riparian influences

The apostlebird was the only species to exhibit a significant interaction between riparian status and season (Table 4.1). Examination of the interactions (not shown) indicate that this species was significantly ($P < 0.05$) more likely to occur in Riparian areas during Winter and Upslope areas during Summer. No species groups exhibited a

significant riparian by seasonal interaction for abundance, however the Larger Bushbirds and the Honeyeaters without the white-plumed honeyeater both showed significant sub-asymptotic species richness interactions (Table 4.2). Both of these groups exhibited a strong divergence in their Riparian/Upslope response during Winter (Fig. 4.1). The Larger Bushbirds were most speciose in Riparian areas during Winter while greater numbers of Honeyeater species (other than the white-plumed honeyeater) were observed in Upslope sites in this season.

Species from both *summer* and *winter* response groups were more abundant in Riparian areas (Table 4.6), however the *winter* response group consisted of only four species that showed different riparian preferences. The white-plumed honeyeater was more prevalent in Riparian areas whereas the weebill and hooded robin were both more frequently observed in Upslope areas (Table 4.1). The strong riparian response of the *summer* species also extended to sub-asymptotic species richness; about 50% more *summer* species were observed in Riparian areas. Higher Riparian abundances were also observed for species likely to be seasonal migrants (*summer* or *winter* response) and those likely to be year round residents (seasonally *indifferent*), however this pattern was not reflected in sub-asymptotic species richness. Similar numbers of species from these groups were found in both Riparian and Upslope areas.

Tests of independence among the 24 species for which both a seasonal and riparian response had been determined failed to reveal an overall deviation from mutual independence either for the full three by three table ($P = 0.61$, not shown) or for the

Table 4.4 Inter-annual response for bird abundance and sub-asymptotic species richness within species groups: results of generalised linear modelling. Abundance analyses are based on mean number of individuals at each site-visit (n = 865, 30 min samples). Sub-asymptotic species richness estimates are based on site-sampling periods (n = 433, 60 min samples) calculated after rarefaction using the number of samples and individuals indicated (see text for details). Species richness groups with fewer than 4 species were not analysed. Response groups: Rip, Riparian; Ups, Upslope; 97, 1997; 98, 1998; Ind, Indifferent; ND, Not determined. Count ratios presented are in favour of the effect indicated (97, 1997; 98, 1998; R, Riparian; U, Upslope), values in parentheses indicate 95% confidence interval. Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. # indicates significant riparian status by year interaction ($P < 0.05$).

Species grouping	No. of species	% of total abundance	No. of site-visits present	Abundance			Sub-asymptotic species richness			
				Count ratio	Inter-annual response group	Riparian response group	Post-rarefaction site-sampling periods (individuals sampled)	Count ratio	Inter-annual response group	Riparian response group
Resource guilds										
Aerial Insectivore	7	4.1	268	1.09 (0.78- 1.51)97	Ind	Rip	46 (4)	1.01 (0.85- 1.21)98	ND	ND
Larger Bushbird	11	4.6	302	1.07 (0.81- 1.42)98#	Ind	Rip	35 (6)	1.02 (0.80- 1.29)98	ND	ND
Raptor	10	0.4	42	1.34 (0.71- 2.52)98	ND	Rip		ND	ND	ND
Pigeons, Parrots & Cockatoos	16	15.6	446	1.42**(1.09- 1.86)98#	98	Rip	85 (8)	1.10 (0.95- 1.27)98	Ind	Rip
Ground Generalist	6	5.4	93	1.31 (0.73- 2.35)97	ND	ND	60 (3)	1.00 (0.92- 1.10)98	Ind	Ind
Bushbird Insectivore	37	20.1	642	1.24*(1.04- 1.48)98	98	Ups	70 (12)	1.06 (0.79- 1.43)98	ND	Ups
Honeyeaters, Flowerpeckers etc.	17	44	697	1.14 (0.96- 1.35)98#	Ind	Rip	224 (8)	1.10*(1.01- 1.20)98#	98	Ups
Excluding white-plumed honeyeater	16	20.9	564	1.22*(1.00- 1.49)98	98	Rip	142 (7)	1.09 (0.97- 1.23)98#	Ind	Ups
Finch	3	1.2	49	1.27 (0.42- 3.89)98	ND	Ups		ND	ND	ND
Nomad	12	3.2	97	1.91 (0.76- 4.79)98#	ND	ND	33 (4)	1.35*** (1.15- 1.58)98	98	ND
Relative height groups										
Upper Stratum	41	76.9	823	1.16*(1.03- 1.31)98#	98	Rip	215 (18)	1.09*(1.01- 1.18)98#	98	Ups
Excluding white-plumed honeyeater	40	53.8	803	1.21** (1.05- 1.41)98#	98	Rip	158 (17)	1.11*(1.01- 1.23)98	98	Ind
Mid Stratum	11	10.2	477	1.11 (0.91- 1.35)98	Ind	Ups	51 (8)	1.12 (0.91- 1.39)98#	ND	Ups
Ground/Lower Stratum	5	3.1	178	1.26 (0.85- 1.87)97	Ind	Ups	42 (4)	1.11 (0.94- 1.32)98#	ND	Ind
Uncommon Species	58	4.8	206	1.41 (0.89- 2.22)98	ND	ND	47 (5)	1.27*(1.02- 1.59)98	98	Ind
Species Richness	120	98.6	840	not applicable			258 (21)	1.05 (0.99- 1.13)98#	Ind	Ups
Excluding white-plumed honeyeater	118	75.4	837	not applicable			193 (21)	1.10*(1.01- 1.19)98	98	Ups
Total Abundance	138^	100	863	1.14*(1.03- 1.27)98#	98	Rip		not applicable		
Excluding white-plumed honeyeater	137^	76.9	862	1.18*(1.04- 1.33)98#	98	Rip		not applicable		

^ includes 19 taxa not identified to species level

Table 4.5 Localised response to increased monthly rainfall for the occurrence of individual species, bird abundance and sub-asymptotic species richness within species groups: results of generalised linear modelling. Occurrence of individual species based on sub-plots (n = 2544, 10 min samples). Abundance analyses are based on mean number of individuals at each site-visit (n = 865, 30 min samples). Sub-asymptotic species richness estimates are based on site-sampling periods (n = 433, 60 min samples) calculated after rarefaction using the number of samples and individuals indicated (see text for details). Species richness groups with fewer than 4 species were not analysed. Response groups: Rip, Riparian; Ups, Upslope; Neg, Negative; Pos, Positive; Ind, Indifferent; ND, Not determined. # indicates significant riparian status by rainfall interaction ($P < 0.05$).

Species grouping	No. of species	% of total abundance	No. of site-visits present	Occurrence/ Abundance				Sub-asymptotic species richness					
				Estimate (SE)	<i>P</i>	Rainfall response group	Riparian response group	Post-rarefaction site-sampling periods (individuals sampled)	Estimate (SE)	<i>P</i>	Rainfall response group	Riparian response group	
Individual species													
Fairy Martin		1.1	22	-0.019 (0.008)	0.0146	Neg	Rip		not applicable				
Australian Ringneck		3.5	167	-0.019 (0.006)	0.0031	Neg	Rip		not applicable				
Spiny-cheeked Honeyeater		4.7	243	-0.027 (0.006)	<.0001	Neg#	Ups		not applicable				
Crested Pigeon		2.1	93	-0.006 (0.008)	0.4205	#	Ind		not applicable				
Resource guilds													
Aerial Insectivore	7	4.1	268	-0.018 (0.007)	0.012	Neg#	Rip	46 (4)	-0.005 (0.002)	0.0225	Neg#	ND	
Larger Bushbird	11	4.6	302	-0.003 (0.004)	0.3752		Rip	35 (6)	0.008 (0.002)	0.0004	Pos	ND	
Raptor	10	0.4	42	-0.001 (0.007)	0.8844		Rip		ND			ND	
Pigeons, Parrots & Cockatoos	16	15.6	446	-0.017 (0.004)	<.0001	Neg#	Rip	85 (8)	-0.000 (0.002)	0.9735		Rip	
Ground Generalist	6	5.4	93	-0.011 (0.009)	0.2263		ND	60 (3)	-0.000 (0.001)	0.7954		Ind	
Bushbird Insectivore	37	20.1	642	0.002 (0.002)	0.3483		Ups	70 (12)	0.019 (0.005)	<.0001	Pos#	Ups	
Honeyeaters, Flowerpeckers etc.	17	44	697	-0.004 (0.002)	0.0209	Neg	Rip	224 (8)	-0.001 (0.001)	0.1502		Ups	
Excluding white-plumed honeyeater	16	20.9	564	-0.007 (0.003)	0.0206	Neg	Rip	142 (7)	-0.001 (0.002)	0.5231		Ups	
Finch	3	1.2	49	-0.005 (0.013)	0.7082		Ups		ND			ND	
Nomad	12	3.2	97	-0.023 (0.008)	0.0037	Neg	ND	33 (4)	0.000 (0.002)	0.9882		ND	
Relative height groups													
Upper Strata	41	76.9	823	-0.007 (0.002)	<.0001	Neg#	Rip	215 (18)	-0.000 (0.001)	0.5689		Ups	
Excluding white-plumed honeyeater	40	53.8	803	-0.010 (0.002)	<.0001	Neg#	Rip	158 (17)	0.000 (0.001)	0.7647		Ind	
Mid Strata	11	10.2	477	-0.002 (0.003)	0.413		Ups	51 (8)	0.007 (0.004)	0.0583		Ups	
Ground/Lower	5	3.1	178	0.002 (0.006)	0.6946		Ups	42 (4)	0.007 (0.003)	0.0148	Pos	Ind	
Uncommon Species	58	4.8	206	0.004 (0.005)	0.3862		ND	47 (5)	0.008 (0.004)	0.0806		Ind	
Species Richness													
Species Richness	120	98.6	840		not applicable			258 (21)	-0.000 (0.001)	0.9583		Ups	
Excluding white-plumed honeyeater	118	75.4	837		not applicable			193 (21)	0.001 (0.001)	0.181		Ups	
Total Abundance	138^	100	863	-0.007 (0.002)	<.0001	Neg#	Rip		not applicable				
Excluding white-plumed honeyeater	137^	76.9	862	-0.009 (0.002)	<.0001	Neg#	Rip		not applicable				

^ includes 19 taxa not identified to species level

Table 4.6 Riparian response for bird abundance and sub-asymptotic species richness within seasonal, inter-annual, and localised monthly rainfall species response groups: results of generalised linear modelling. Abundance analyses are based on mean number of individuals at each site-visit (n = 865, 30 min samples). Sub-asymptotic species richness estimates are based on site-sampling periods (n = 433, 60 min samples) calculated after rarefaction using the number of samples and individuals indicated (see text for details). Species richness groups with fewer than 4 species were not analysed. Response groups: Rip, Riparian; Ups, Upslope; Ind, Indifferent; ND, Not determined. Count ratios presented are in favour of the effect indicated (R, Riparian; U, Upslope), values in parentheses indicate 95% confidence interval. Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Species grouping	No. of species	% of total abundance	No. of site-visits present	Abundance		Sub-asymptotic species richness		
				Count ratio	Response group	Post-rarefaction site-sampling periods (individuals sampled)	Count ratio	Response group
Seasonal								
Summer	10	9.06	463	1.87*** (1.49- 2.35)R	Rip	49 (8)	1.54*** (1.27- 1.87)R	Rip
Indifferent	14	38.05	705	1.56*** (1.26- 1.92)R	Rip	165 (11)	1.01 (0.92- 1.11)U	Ind
Winter	4	27.12	523	3.24*** (2.60- 4.03)R	Rip	200 (5)	1.33*** (1.22- 1.46)U	Ups
Summer or Winter	14	36.17	662	2.69*** (2.26- 3.21)R	Rip	181 (10)	1.00 (0.88- 1.14)R	Ind
Inter-annual								
1997	1	0.52	54	1.33 (0.60- 2.95)R	ND			
Indifferent	17	61.26	797	2.22*** (1.93- 2.55)R	Rip	276 (11)	1.12** (1.04- 1.20)U	Ups
1998	6	10.69	380	1.82** (1.27- 2.61)R	Rip	107 (5)	1.14* (1.01- 1.28)R	Rip
Monthly rainfall								
Negative	3	9.23	359	1.57* (1.10- 2.25)R	Rip			

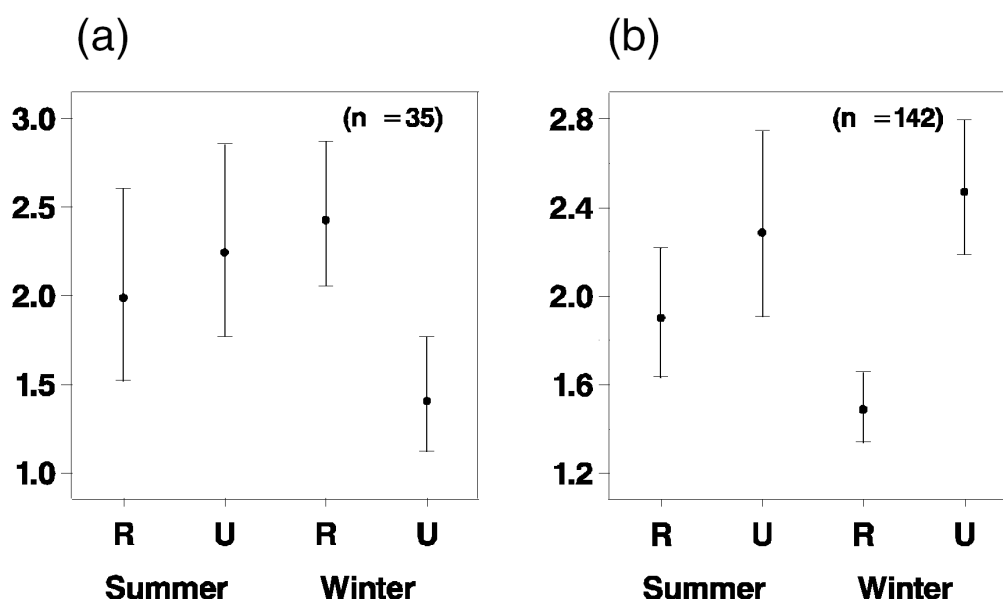


Figure 4.1 Interactions between riparian and seasonal effects on sub-asymptotic bird species richness. (a) Larger Bushbirds; (b) Honeyeaters, Flowerpeckers etc. (excluding the white-plumed honeyeater). Estimates are based site-sampling periods ($n = 433$, 60 min samples) calculated after rarefaction using the number of samples and individuals indicated in Table 4.2. Error bars are 95% confidence limits.

two by two subset of 16 species showing non-indifferent response ($P = 0.18$). Using a $P < 0.2$ significance level criterion (instead of $P < 0.05$) to determine response group membership more species were classified (38, 19 of which showed a non-*indifferent* response) but again this did not reveal any significant ($P > 0.05$) departure from mutual independence.

Significant inter-annual by riparian interactions were detected only among four individual species (spiny-cheeked honeyeater, black-faced cuckoo-shrike, *Corvus* sp., Australian ringneck; Table 4.3) but were found within numerous species groups (Table 4.4, Fig. 4.2). Significant interactions within the abovementioned individual species and abundance groups (Fig. 4.2 a-f) were all characterised by strong Riparian-

Upslope divergence during 1997. For most, Upslope abundances appeared depressed during that year. In contrast, most of the species richness groups with significant interactions (Fig. 4.2 g-k) showed strongest Riparian/Upslope divergence in 1998 in favour of the Riparian sites. The only exception to this was for the 11 species of Mid stratum species which showed strongest divergence during 1997.

Species more prevalent in 1998 and those apparently indifferent to inter-annual variation were both nearly twice as abundant in Riparian areas, but showed differing

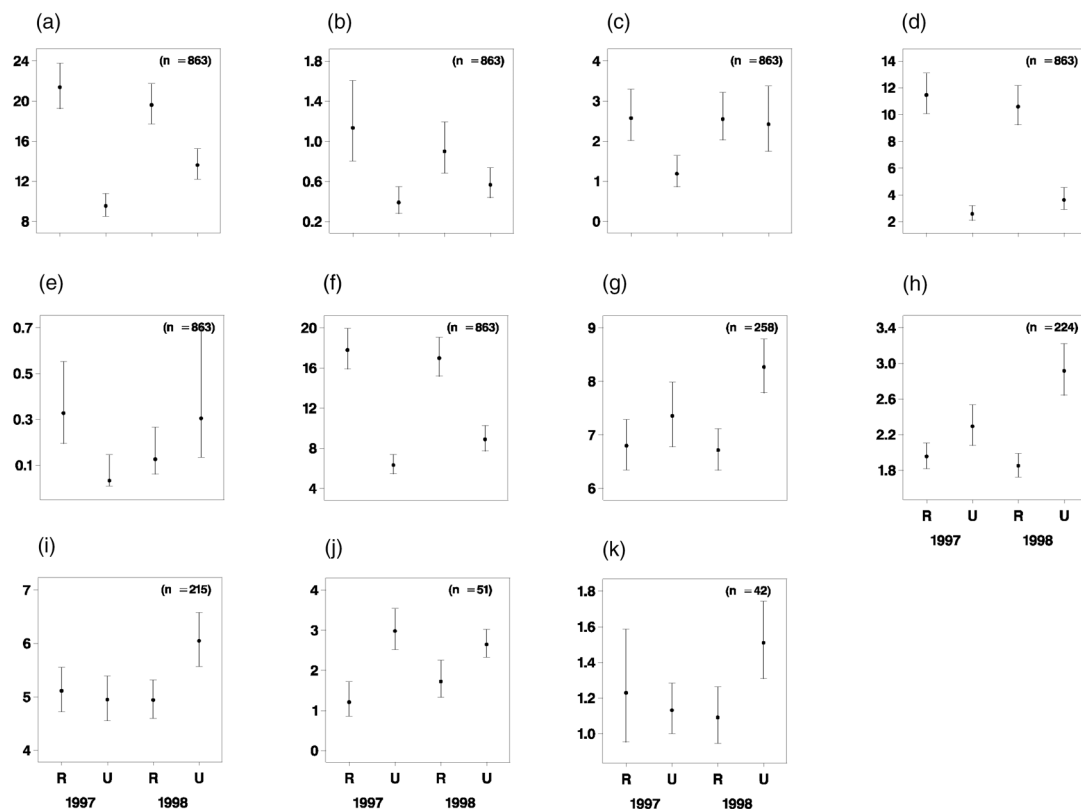


Figure 4.2 Interactions between riparian and inter-annual effects on abundance and sub-asymptotic bird species richness. (a) Total abundance; (b) abundance of Larger Bushbirds; (c) abundance of Pigeons, Parrots & Cockatoos; (d) abundance of Honeyeaters, Flowerpeckers etc.; (e) abundance of Nomads; (f) abundance of Upper stratum species; (g) Overall species richness; (h) species richness of Honeyeaters, Flowerpeckers etc; (i) species richness of Upper stratum species; (j) species richness of Upper Stratum species; (k) species richness of Mid stratum species; (l) species richness of Ground stratum species. Abundance estimates are based on site-visits ($n = 865$, 30 min samples). Sub-asymptotic species richness estimates are based site-sampling periods ($n = 433$, 60 min samples) calculated after rarefaction using the number of samples and individuals indicated in Table 4.4. Error bars are 95% confidence limits.

sub-asymptotic species richness responses (Table 4.6). *Indifferent* species were richest in Upslope areas while *1998* species were richest in Riparian areas. Examination of the associations among species showing both a riparian and inter-annual response showed no evidence to suggest that *riparian* species were disproportionately represented in either year ($P > 0.05$, not shown).

Significant riparian interactions with localised monthly rainfall were detected for only two species, the spiny-cheeked honeyeater and crested pigeon (Table 4.5). Both

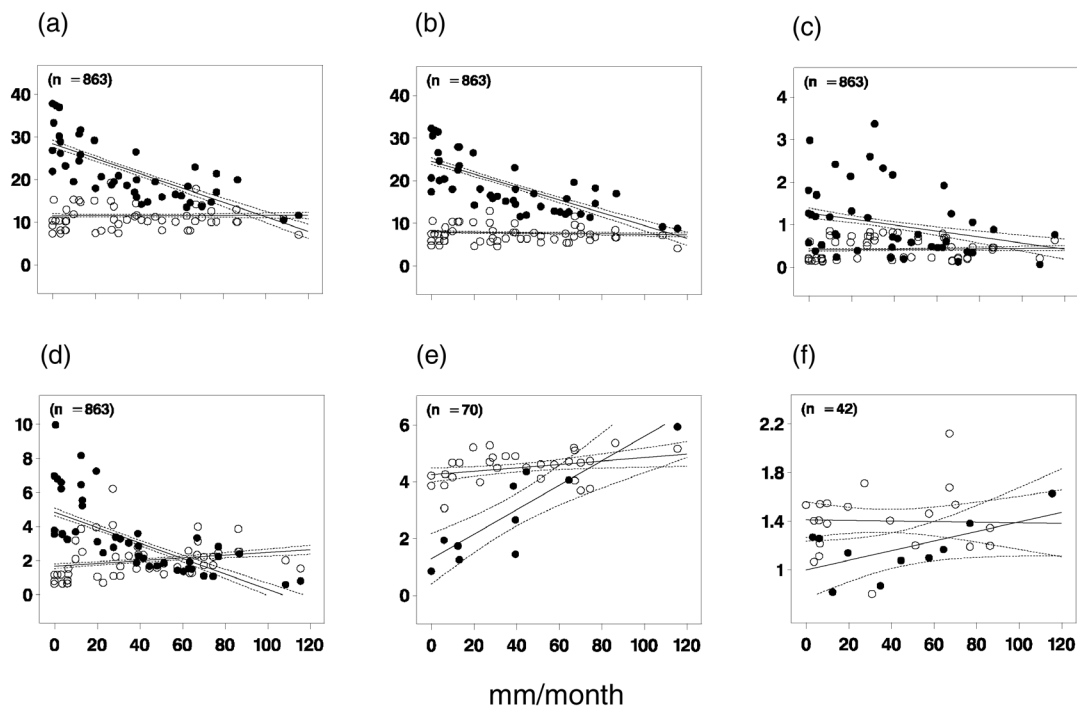
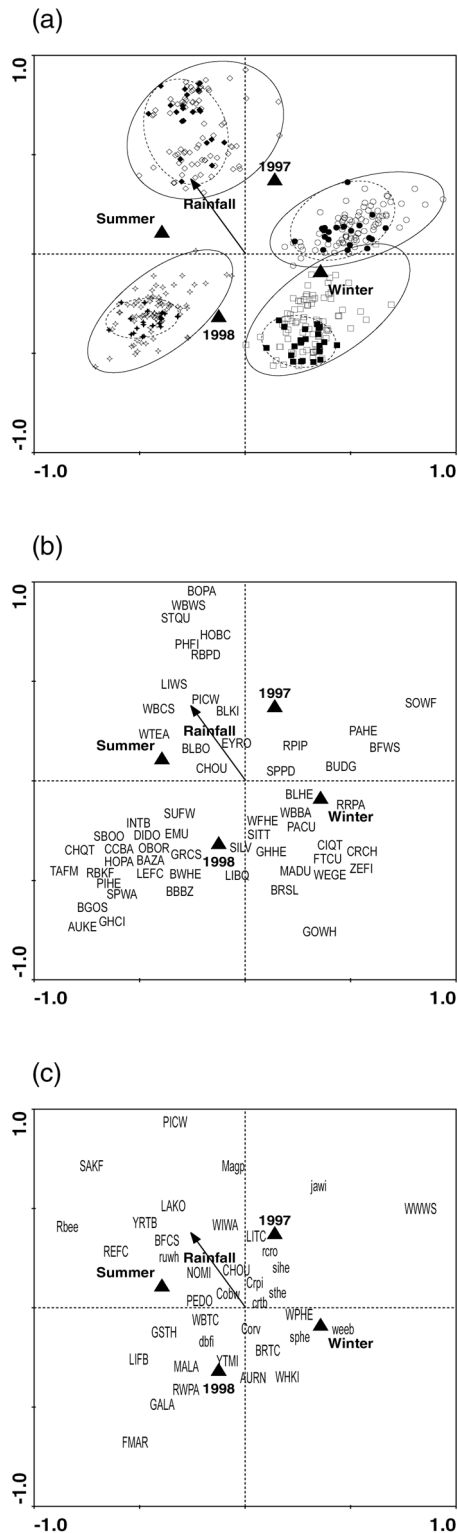


Figure 4.3 Interactions between riparian status and localised monthly rainfall effects on bird abundance and sub-asymptotic species richness. (a) Total abundance; (b) abundance of Upper stratum species (c) abundance of Aerial Insectivores; (d) abundance of Pigeons, Parrots & Cockatoos; (e) species richness of Bushbird Insectivores; (f) species richness of Ground/Lower stratum species. Points are estimates of the mean Riparian (black dots) and Upslope (open circles) values for differing localised monthly rainfall samples. Lines show a fitted linear predictor (solid line) with 95% confidence limits on the mean predicted values (dashed lines). Abundance estimates are based on site-visits ($n = 865$, 30 min samples). Sub-asymptotic species richness estimates are based site-sampling periods ($n = 433$, 60 min samples) calculated after rarefaction using the number of samples and individuals indicated in Table 4.5.

species were significantly ($P < 0.05$) more likely to be observed in Riparian areas during periods of low rainfall, although the crested pigeon was also more likely to be present in Upslope areas during high rainfall. Notwithstanding, numerous interactions were observed within species groups (Fig. 4.3). In all cases, the interaction was primarily due to variation in the Riparian rather than Upslope samples. The groups dominated by insectivores from the upper stratum (Upper stratum species with and without the white-plumed honeyeater, total abundance, Aerial Insectivores; Fig. 4.3 a-c) and the seed-eating Pigeons, Parrots and Cockatoos (Fig. 4.3d) were all more abundant in Riparian areas during lower rainfall. Insectivores from the lower stratum (Bushbird Insectivores, Fig. 4.3e; Ground Stratum species, Fig. 4.3f; the near significant Mid stratum species, Table 4.5) showed the reverse trend expressed as greater numbers of species in the Riparian areas with increasing rainfall. Taken as a group, the three species showing a negative response to localised monthly rainfall were about 60% more abundant in Riparian areas (Table 4.6).

4.3.2 Bird community composition

There was a clear separation of sampling periods in ordination space (Fig 4.4a), reflecting the strong temporal influence on species composition. Monte Carlo permutation tests indicated that the environmental variables of SEASON, YEAR and MON_RAIN together accounted for a statistically significant proportion of overall variation (1.3%, $P = 0.002$). Although small, this variation represents 17.2% of that explained (i.e. environmental variables and co-variables). Individually all environmental variables were significant at $P < 0.05$; SEASON accounted for 8.1% (F



= 2.78, $P = 0.002$), YEAR for 5.0% ($F = 1.8$, $P = 0.002$) and monthly rainfall for 4.1% ($F = 1.47$, $P = 0.012$) of explained variation.

Apart from the clear temporal separation of samples the ordination also indicates that species composition was more similar between the two Winter samples than between the Summer samples. This appears largely due to the influence of the rarer species. A number of Uncommon species were associated with increasing monthly rainfall, however most species in this group, were present in 1998 but not in 1997 (Fig. 4.4b). To check this interpretation I repeated the ordinations after “downweighting” Rare species according to the routine used by CANOCO. The resulting ordination (not shown) showed the sampling periods arranged in a much more symmetrical configuration.

Figure 4.4 Ordination biplots based on partial canonical correspondence analysis (pCCA) showing variation in bird species composition with respect to season, year and localised monthly rainfall. (a) Samples. Points represent site-sampling periods ($n = 428$, 60 min samples). Solid ellipses enclose samples from each sampling period; clockwise from upper right quadrant, Winter 1997, Winter 1998, Summer 1998/9, Summer 1997/8. Riparian samples with permanent water indicated by solid symbols enclosed by dashed ellipses. (b) Uncommon species. (c) *Riparian* (upper case), *upslope* (lower case) and *indifferent* species (title case). P values for environmental variables: Season (Summer, Winter), $P = 0.002$; Year (1997, 1998), $P = 0.002$; Rainfall, $P = 0.012$. Species abbreviations detailed in Appendix 4.

For each sampling period Riparian sites with permanent water are tightly clustered within a more dispersed constellation of Upslope and ephemeral Riparian sites. This pattern prevailed with and without the inclusion of riparian status as a covariate, indicating that differences in species composition between these groups were characterised by their differing patterns of variability, rather than differences in their weighted averages. The observation that the Riparian clusters were smaller in 1998 than 1997 (Fig. 4.4a) further suggests that the Riparian and Upslope assemblages overlapped more in 1997. Given the ordination pattern, it is not surprising that there was a high degree of overlap among *riparian*, *upslope* and riparian *indifferent* species response groups (Fig. 4.4c). Notwithstanding, most *riparian* species appear more closely associated with the Summer than Winter samples.

4.4 Discussion

4.4.1 Temporal patterns

From 30 species for which some form of large-scale temporal response (seasonal, inter-annual) was determined, 19 species showed a directional (non-*indifferent*) change. While the results reflect only a single bioregion over a limited time period, and some of the temporal variations may have been due to rapid turnover in recruitment and mortality, it is likely that a large proportion of the changes were due to inter-bioregional movements. Schodde (1982) estimated that about half of the landbird species of the Australian arid zone are widely mobile, somewhat greater than estimates by Chan (2001; 36%) and Griffioen and Clarke (2002; 37%). Since the surveys were conducted throughout the entire bioregion, and almost all of the species whose temporal responses were determined, were common and conspicuous, these results suggest that inter-bioregional movements among terrestrial birds of the Mulga Lands are extensive.

The magnitude of species turnover, however, was typically modest; very few of the more common species were observed exclusively in any particular temporal circumstance. Thus, with the notable exceptions of certain species such as the rainbow bee-eater, dollarbird and sacred kingfisher most of those exhibiting a directional preference appear to be partial seasonal migrants or partially nomadic. These observations are consistent with Chan (2001) who reasoned that partial migration is a behavioural response to climatic variability. Most of the seasonal responses observed among individual species were consistent with movement patterns inferred from

recent analyses of bird atlas data (Griffioen and Clarke, 2002), and other sources (e.g. Blakers *et al.*, 1984; Schodde and Tidemann, 1986; Reid and Fleming, 1992; Pizzey and Knight, 1998). For example, all ten *summer* species (Table 4.1) were identified as undertaking large-scale movements and all 14 *indifferent* species were regarded as sedentary by Griffioen and Clarke (2002).

In addition to those species showing a seasonal preference, the data suggest nomadic behaviour by a separate suite of seven species that were observed more frequently in one year or another (Table 4.3). Interestingly, all except the rufous songlark were described as sedentary by Griffioen and Clarke (2002) yet their observed inter-annual differences suggested inter-bioregional movements. Although this apparent inconsistency may simply reflect idiosyncratic responses to extreme conditions experienced during this study, it nonetheless highlights a more substantive issue; the importance of non-seasonal movements in areas such as the Mulga Lands. Indeed, many of the species showing an *indifferent* temporal response, or a directional response to localised monthly rainfall, may in fact have been locally nomadic.

A conspicuous feature of this study was the dominance of the *summer* response among individual species and the extent to which overall sub-asymptotic species richness was higher in that season (about 15-30%, Table 4.2). This was unexpected given that: (1) most of the difficulties of arid zone survival are likely to be accentuated during summer when daytime temperatures are often extreme and evaporation greatly exceeds precipitation; (2) the analyses specifically controlled for potentially confounding influences such as the presence of permanent water, localised rainfall, and inter-annual influences that may be associated with longer term

prevailing conditions and; (3) the Mulga Lands of south west Queensland is uniquely aseasonal with respect to plant growth response (Nix 1976). There are a number of explanations for this. First, most of the *summer* species are at least partial aerial insectivores and their prevalence during summer may reflect higher abundances of flying insects during the warmer months. Although this hypothesis has not to my knowledge been tested in the Mulga Lands, there is evidence of summer increases in insectivorous birds and their insect prey from elsewhere (Pyke, 1985; Robinson, 1992; Osborne and Green, 1992). The proposition is also consistent with the Summer sub-asymptotic species richness response observed within other groups that feed exclusively or substantially on flying insects (Aerial Insectivores, Upper stratum species, Honeyeaters; Table 4.2). Indeed, it is revealing that the other major insectivorous group, the Bushbird Insectivores, which mainly feed from solid substrates closer to the ground (see Recher and Davis, 1997; Morris and Wooller, 2001), failed to show a similar pattern.

Second, the strong summer response could also have been caused extrinsically, from the movement of birds into the bioregion as a response to seasonal shifts in climate or resources in neighbouring bioregions. Indeed, it was on the basis of alternating seasonal variations in plant growth and temperature known to occur in the north and south of the continent that Nix (1976) predicted a dominant north-south migration axis over much of eastern Australia with overwintering areas in the north. This prediction also appears to be supported by the more recent empirical analysis of Griffioen and Clarke (2002) which suggests that all long distance movement patterns that affect the Mulga Lands conform to this trend. If correct, these patterns suggest stronger seasonal linkages with areas to the north than the south. Notwithstanding the

well known summer visitors from northern Australia (e.g. sacred kingfisher, dollarbird, rainbow bee-eater), there may also be finer scale seasonal influences that underlie these continental generalisations. In particular, relatively strong gradients in the timing of seasonal pulses in plant growth (see Nix, 1976) appear to favour summer movements toward the Mulga Lands from north east, east and possibly the south east.

The strength of the inter-annual effects favouring the 1998 surveys is more easily explained. This inter-annual variation was strongly correlated with alternate phases of the southern oscillation index; SOI was strongly negative (El Niño phase) during 1997 surveys and positive for the 1998 surveys (Fig. 2.2). Since rainfall was not correlated with SOI over the study period, the simple conclusion that species were responding directly to increased rainfall is clearly not sufficient to explain the observed variation between years. However, the explanation that birds were responding indirectly to rainfall with a lag time of several months is consistent with the idea that production pulses follow rainfall but only over certain thresholds (Hodgkinson and Freudenberger, 1997). The possibility that the observed inter-annual response was in fact a reflection of the difference in prevailing conditions between 1997 and 1998 is also supported by the presence of riparian interactions (see below) and additional analysis (not shown), indicating strong divergence in the seasonal response for both species richness (sub-asymptotic) and total abundance in 1997 compared with 1998. Moreover, it provides an explanation for why the Summer species compositions appeared less similar than the Winter samples from different years. Physiological stresses on both birds and their habitats are likely to be more acutely experienced during summer than winter, with the consequence that species composition is more

sensitive at this time to variations in prevailing conditions. In 1998, there were clear differences in occurrence of common species, and also higher numbers of Uncommon species (Table 4.4). This is likely to be due to reproductive or migratory responses to favourable conditions triggered by sustained rainfall during late 1997.

Significant responses to localised monthly rainfall were observed among a limited number of individual species. Although these responses are likely to represent idiosyncratic aspects of their ecology, it is notable that (after accounting for other effects) none were recorded more frequently after local rainfall (Table 4.5). Negative responses to rainfall were also common within species groups including overall abundance but were complicated by numerous riparian interactions (see below).

4.4.2 Riparian influences

Patterns of use of riparian habitats interacted in several ways with the effects of temporal factors (season, rainfall and inter-annual variation). First, the inter-annual responses for total abundance and sub-asymptotic species richness (overall and for most groups) was typically complicated by both higher numbers of birds and species present in Riparian compared with Upslope areas during drought conditions (1997), and high variability in the response of Upslope samples between years (Fig. 4.2). This is consistent with the prediction that species and individuals that remained locally throughout the drought could compensate for the adverse conditions by spending more time in riparian areas. The preference for riparian areas occurred both among species likely to be residents (seasonally *indifferent*) and most of those likely to be migrants (*summer* or *winter*, 1998 response; Table 4.6), however stronger responses

were seen among the latter. This suggests an important role for riparian areas in the maintenance of both resident and migratory or nomadic populations in the region.

As predicted, overall riparian usage was strongest when and where local monthly rainfall was low. The most obvious explanation for this is that localised rainfall, even if it does not immediately promote plant production, allows many species to temporarily refocus their activities in upslope areas far from waterways. Conversely, when surface water is difficult to find, birds must visit riparian areas to drink. Since moisture content of seed forage is generally low and many graminivorous species need to actively drink to rehydrate (Fisher *et al.*, 1972; Dawson, 1976; Schodde, 1982), it is not surprising that a dramatic expression of this was seen within the seed-eating Pigeons, Parrots and Cockatoos group.

Less expected, however, were the contrasting patterns displayed by the high and low insectivores (Fig. 4.3b, 4.3c vs Fig. 4.3e, 4.3f). The high insectivore groups displayed the expected response of increased riparian usage with declining rainfall, however the low insectivores appeared to make greater use of riparian areas during periods of higher rainfall when surface water would be available in their “preferred” habitat. This suggests that their attraction to riparian areas was driven by conditions other than water availability. It also raises the possibility that many of these species are prevented from utilising riparian areas at other times by competitive interactions from high insectivores, such as the white-plumed honeyeater and yellow-throated miner, which usually dominate riparian habitats.

Although the use of Upslope habitats appeared relatively insensitive to variations in rainfall (Fig. 4.3), this was not unexpected given that riparian habitats occupy only about 8% of the Mulga Lands (Chapter 3). Under these circumstances even substantial movements into upslope habitats would result in very modest increases in bird density. This phenomenon may also at least partially account for the dearth of significant riparian interactions with season, year or monthly rainfall for individual species.

Another anomaly was the lack of interactions between riparian and seasonal factors that would suggest enhanced use of Riparian areas during Summer. In fact, the apostlebird (the only individual species to show a significant interaction), the Larger Bushbirds, and Honeyeaters (without the white-plumed honeyeater) all showed trends in other directions (Fig. 4.1). Thus, it appears that after accounting for localised rainfall and prevailing conditions (the inter-annual response) any residual seasonal interactions such as high daytime temperatures were of minor consequence, at least over the study period. However, riparian habitats still appeared to be generally favoured by many response groups (Table 4.6), but without evidence of behavioural or opportunistic switching between riparian and upslope habitats in response to summer (seasonal) conditions.

Riparian status also had profound influence on species composition. Overall species composition was influenced by all temporal variables but within these constraints the relationship between Riparian and Upslope samples remained relatively static. Irrespective of the temporal status of the bird community, Riparian samples (particularly those with permanent water) were tightly clustered at the centre of the

constellation (Fig 4.4a.). This pattern indicates that both riparian and upslope communities were affected in similar ways but perhaps more importantly reflects strong linkages between these two components of the landscape (see also Chapter 3). Because almost all species divided their time in some way between riparian and upslope habitats, the temporal destinies of the bird communities were linked. If this were not so, the temporal trajectories of the Riparian and Upslope communities would follow different paths. Indeed, one might predict that because the bird communities of riparian areas are more insulated from the long and short term effects of rainfall deficit, we might see Riparian samples toward the centre of the ordination space, with Upslope communities in temporal orbit around them. This was not the case, simply because of the strength of the riparian/upslope linkages.

Moreover, the relative size and location of the clusters reflected predictable variation in both the similarity of the bird communities between sampling periods and the degree of riparian/upslope overlap within individual sampling periods. Given that Summer 1997/8 occurred at the end of a prolonged drought, the effects of which had been relieved by Summer 1998/9, and that the physiological difficulties of drought would be most acute during the summer months, it is not surprising that the Summer samples were most affected by differences between years. Similarly, the drought conditions during 1997 are likely to be responsible for the higher degree of overlap between Riparian and Upslope samples of that year. Interestingly, this overlap was most apparent during Summer 1997/8 which as noted, occurred at the end of an extended drought. Although the region remained affected by drought during this period, good rains were experienced toward the end of the surveys in this year (Fig. 2.2). I suspect that this rainfall precipitated the extensive inter-habitat movements

implied by the ordination and strong interactions between riparian status and monthly rainfall discussed previously.

4.4.3 Conclusions

This study provides useful insights into the spatio-temporal patterning of arid zone bird communities. Analysis of total abundance and sub-asymptotic species richness (overall and among most groups) and species composition consistently suggested that riparian areas were most important during drought (1997) and between rainfall events, but not necessarily during summer. Thus, avifaunal changes in riparian use appeared to partially compensate for adverse and unpredictable temporal circumstances such as drought. Apart from helping to sustain populations through difficult periods, such behaviour should also maximise the use of temporally unstable resources from the rest of the landscape. Given the small proportion of the landscape occupied by riparian habitats (Knopf, 1988; Hewitt, 1990; Gregory *et al.*, 1991), their vulnerability to disturbance (Naiman *et al.*, 1993) and potential degradation from human exploitation (Sattler, 1993), such areas could act as the weak link that holds regional bird (and perhaps other faunal) assemblages together. This is likely to be particularly so in drought-prone environments such as the Australian arid zone.

Although such behaviour can be seen as an adaptation to climatic variability, it was nonetheless insufficient to fully counteract significant seasonal and inter-annual influences, which suggest extensive inter-bioregional movements. High numbers of species and individuals present in 1998 appeared to be related to my sampling either side of a sharp gradient in the SOI. Although this can be seen as a simple reflection of

favourable conditions in that year, it highlights (1) the ability of the bird community to respond to irregular (non-seasonal) climatic variation, such as the ENSO, and (2) the potential importance of these phenomena to terrestrial fauna.

More significantly, climate change predictions for much of arid and semi-arid Australia suggest greater climatic variability and unpredictability (see Hughes, 2003). In this context, I would expect greater non-seasonal turnover of birds and an increasing reliance on riparian habitats.

5.0 Relative Influences of Riparian Status and Water Availability on Terrestrial Birds of the Mulga Lands

5.1 Introduction

In arid and semi arid landscapes the availability of water and nutrients are dominant influences on the distribution and abundance of terrestrial biota (James *et al.*, 1995). Both water and nutrients accumulate in riparian zones, and many studies have reported higher concentrations of terrestrial fauna in these areas than in adjacent habitats (Knopf *et al.*, 1988; Naiman and Décamps, 1997; Kingston *et al.*, 2002, Appendix 1; Chapter 3). Furthermore, the differences often appear most pronounced in studies from more arid biomes (e.g. Szaro and Jakle 1985; Johnson and Haight, 1985), especially during drought (Chapter 4) and least pronounced in studies from more mesic areas (McGarigal and McComb, 1992). Faunal communities in arid zones also respond strongly to the availability of water (Davies, 1972; Fisher, *et al.*, 1972; James *et al.*, 1999). However, no studies have attempted to compare the relative influence of riparian status and water availability on faunal assemblages.

Two factors make it difficult to address this question in field studies. First, there are a number of direct and indirect influences of water availability on riparian function. Water (and the materials it transports) may stimulate the growth of riparian vegetation, which in turn provides resources for terrestrial fauna (Gregory *et al.*, 1991; Catterall, 1993). Alternatively, fauna may concentrate in riparian areas because there is greater access to surface water. Second, it is difficult to find situations that allow the effects of

surface water availability to be separated from other riparian influences. Riparian areas are typically associated with water while upslope habitats are not. For useful comparisons, we also need riparian habitats that do not generally support surface water and upslope habitats that do.

The Mulga Lands of south west Queensland provide a suitable testing ground to address this issue. In this semi-arid region, riparian habitats are present both with and without permanent water. In general, sites of the latter type are structurally and floristically similar to those with permanent water but due to minor variations in local geomorphology only carry water during extended rainfall or flood. The region also supports upslope habitats with permanent water in the form of bore drains. These drains originate from artesian bores, many of which were drilled in the late nineteenth century to provide water for introduced livestock (Noble and Tongway, 1983), and flow over open earth channels often for tens of kilometres. The vegetation bordering bore drains is structurally and floristically similar to the upslope habitats through which they flow, but the drains provide a permanent source of water in a linear spatial configuration, similar to that provided by natural watercourses. The Mulga Lands are typical of many of the *Acacia*-dominated shrubland landscapes that occupy much of arid and semi-arid Australia. Most of these areas are used as rangelands and are heavily grazed by sheep and cattle. The viability of this pastoral industry is highly dependent on permanent riparian waterholes (lakes are commonly ephemeral and saline) and sources of artificial water such as artesian bores. Artificial watering points are rarely more than 10 km apart and few areas remain beyond the reach of large domestic, feral, and native animals (James *et al.*, 1999).

As well as providing insights into the relative influence of surface water on riparian and upslope fauna, determining the ecological roles of bore drains may also have implications for land and water management in arid and semi-arid regions. For example, current government policy is to close bore drains in favour of livestock watering troughs (Murray, 2002) and this may have consequences for native biodiversity, including the regional avifauna. Work by Landsberg *et al.* (1999) found that many bird species increased or decreased in abundance with distance from artificial sources of water, and that in the Queensland Mulga Lands many more species were present close to artificial water than away from it. In Chapter 3 it was observed that birds found most frequently in upslope habitats (principally small insectivorous passerines) appeared to prefer bore drain habitats, presumably as a source of water. These findings raise some important questions. For example, what will happen to the species that appear to prefer bore drain habitats in the face of their closure and a landscape-wide reduction in artificial water resources? Will they retreat to riparian areas, make greater use of upslope areas or simply decline in abundance? Are small insectivorous passerines most vulnerable to such changes in the landscape?

In this chapter, I first compare the relative influence of surface water availability and riparian status on the abundance, diversity and species composition of the Mulga Lands bird assemblage of south west Queensland, Australia. Second, I consider some of the likely consequences for the regional avifauna that may arise from the closure of artesian bore drains.

5.2 Methods

5.2.1 Statistical Analysis

5.2.1.1 Bird abundance and diversity

Generalised Linear Models (GLM; *sensu* McCullagh and Nelder, 1983) were used to simultaneously assess the effects of riparian status and surface water availability on the following aspects of the bird assemblage: (1) abundance of individual common species; (2) abundance within selected groups (all species, resource guilds, uncommon species) and; (3) sub-asymptotic species richness within selected groups (as above). A Poisson error distribution and Log link function was used to model the response variables. GLM analyses of abundance and species richness were carried out at the site-visit ($n = 865$; 30 min samples) and site-sampling period levels ($n = 433$; 60 min samples) respectively. Generalized Estimating Equation modelling (GEE; Liang and Zeger, 1986), based on initial GLM parameter estimates, was used to account for possible correlations among repeated site-visits and sampling periods. GLM and associated GEE analyses were carried out using PROC GENMOD within SAS (SAS Institute Inc., 1999). The statistical models included the main design variable: SITETYPE (RD, RW, UC, UD, UW) and a number of covariates that were known from previous work (see Chapters 3 and 4) to account for significant variation in my data; SEASON (Summer, Winter), YEAR (1997, 1998), REGION (East, South-west, North-west; see Fig. 2.1), MON_RAIN (localised monthly rainfall), SITETYPE*SEASON, SITETYPE*YEAR and SITETYPE*MON_RAIN.

For sample-based data sets, differences in abundance between treatments may result in misleading comparisons of species richness (Gotelli and Colwell, 2001). Therefore, to

compare treatments while directly controlling for abundance, rarefaction was conducted prior to the analysis of all species richness responses. Details of the rarefaction procedure are contained in Chapter 3.

All “fly over” observations and non-terrestrial bird species were excluded from analysis. The Australian raven (*Corvus coronoides*) and little crow (*C. mellori*; both of which occur in the study area) were not reliably differentiated in the field and observations for these two species were regarded as “Corvus Sp.” With this exception, species taxonomy follows Christidis and Boles (1994). Allocations of species to resource guilds were taken from Reid and Hobbs (1996). Species found at fewer than 20 sub-plots were considered “Uncommon spp.”. Due to the numeric dominance of the white-plumed honeyeater and its potential to overwhelm species group responses (see Chapter 3), the GLM analyses were carried out on the relevant groups with and without the inclusion of this species. Membership of resource guilds and the Uncommon species group is shown in Appendix 4.

Individual species and groups of species were allocated to riparian status and surface water availability response groups based on the results of the statistical models. Allocation to each group was based on a rule-set associated with a number of “generalised” and “specialised” contrasts involving linear combinations of the variable SITETYPE (ESTIMATE statement, PROC GENMOD within SAS; SAS Institute Inc., 1999; Table 5.1). I report parameter estimates as count ratios (i.e. $e^{\text{Parameter estimate}}$) associated with the contrast(s) that defined the response group. Species or groups were considered *indifferent* to riparian status if a *riparian* or *upslope* response was not determined and the variance associated with the generalised riparian contrast (i.e. H_0 :

$\mu(\text{RW}, \text{RD}) = \mu(\text{UW}, \text{UC}, \text{UD}))$ was similar to those with a significant effect. The procedure used to determine *indifferent* species or groups are detailed in Chapter 3.

Table 5.1 Generalised linear modelling contrast criteria used to determine riparian and water availability response groups (Rip, Riparian; Ups, Upslope; Wat, Watered; Dry, Dryland; Ind, Indifferent). Site types in parentheses in the response group column indicate the dominant influence of the site type specified. These specialised responses are derived from the results of the contrasts indicated. Remaining responses are generalised, derived from the results of the generalised contrast of overall riparian status (i.e. $H_0: \mu(\text{RW}, \text{RD}) = \mu(\text{UW}, \text{UC}, \text{UD}))$ or water availability (i.e. $H_0: \mu(\text{RW}, \text{UW}) = \mu(\text{RD}, \text{UC}, \text{UD}))$). The probability value used to test the hypotheses was $P \leq 0.05$.

Criterion number	Contrast criteria	Response group
1	$H_1: \mu(\text{RW}) > \mu(\text{UW}, \text{UC}, \text{UD})$ and $H_1: \mu(\text{RW}) > \mu(\text{RD})$	Rip(RW)
2	$H_1: \mu(\text{RD}) > \mu(\text{UW}, \text{UC}, \text{UD})$ and $H_1: \mu(\text{RW}) < \mu(\text{RD})$	Rip(RD)
3	$H_1: \mu(\text{RW}, \text{RD}) > \mu(\text{UW}, \text{UC}, \text{UD})$ and not 1 or 2 above	Rip
4	$H_1: \mu(\text{UW}) > \mu(\text{RW}, \text{RD})$ and $H_1: \mu(\text{UW}) > \mu(\text{UC}, \text{UD})$	Ups(UW)
5	$H_1: \mu(\text{UC}, \text{UD}) > \mu(\text{RW}, \text{RD})$ and $H_1: \mu(\text{UW}) < \mu(\text{UC}, \text{UD})$	Ups(UC,UD)
6	$H_1: \mu(\text{UW}, \text{UC}, \text{UD}) > \mu(\text{RW}, \text{RD})$ and not 4 or 5 above	Ups
7	$H_0: \mu(\text{RW}, \text{RD}) = \mu(\text{UW}, \text{UC}, \text{UD})$ and not 1,2,4 or 5 above and where variance is below a specified threshold (i.e. <i>Indifferent</i> , see text for details)	RipInd
8	$H_1: \mu(\text{RW}) > \mu(\text{RD}, \text{UC}, \text{UD})$ and $H_1: \mu(\text{RW}) > \mu(\text{UW})$	Wat(RW)
9	$H_1: \mu(\text{UW}) > \mu(\text{RW}, \text{UC}, \text{UD})$ and $H_1: \mu(\text{RW}) < \mu(\text{UW})$	Wat(UW)
10	$H_1: \mu(\text{RW}, \text{UW}) > \mu(\text{RD}, \text{UC}, \text{UD})$ and not 8 or 9 above	Wat
11	$H_1: \mu(\text{RD}) > \mu(\text{RW}, \text{UW})$ and $H_1: \mu(\text{RD}) > \mu(\text{UC}, \text{UD})$	Dry(RD)
12	$H_1: \mu(\text{UC}, \text{UD}) > \mu(\text{UW}, \text{RD})$ and $H_1: \mu(\text{RD}) < \mu(\text{UC}, \text{UD})$	Dry(UC,UD)
13	$H_1: \mu(\text{RD}, \text{UC}, \text{UD}) > \mu(\text{RW}, \text{UW})$ and not 11 or 12 above	Dry
14	$H_0: \mu(\text{RD}, \text{UC}, \text{UD}) = \mu(\text{RW}, \text{UW})$ and not 8,9,11 or 12 above and where variance is below a specified threshold (i.e. <i>Indifferent</i> , see text for details)	WatInd

To determine if there were significant differences ($P \leq 0.05$) in the magnitude of the riparian and surface water availability effects I obtained the regular parameter estimates, P values and confidence intervals from the linear combination formed from the difference in the two respective dominant contrasts (i.e. difference ratio).

Chi squared exact tests of association (PROC FREQ; SAS Institute Inc., 1999) were used to examine two way contingency tables created to investigate possible

associations of species' frequencies between riparian and surface water availability response groups at the scale of the entire study.

5.2.1.2 Bird community composition

Bird communities were ordinated using partial Canonical Correspondence Analysis (pCCA; program CANOCO v4.0, Ter Braak and Smilauer, 1998). This eigenanalysis-based procedure allows both species and samples to be ordinated simultaneously, with adjustment for covariates. CCA partitions explained variation rather than overall variation and assumes a unimodal species response (Ter Braak and Smilauer, 1998).

The species by sample data matrix for these analyses was resolved to the site-sampling period level (i.e. samples consisted of the pooled abundances for individual species over three sub-plots and two site-visits per sampling period). All 119 species were included, however for clarity UC sites were omitted from these analyses leaving 343 samples. All analyses were carried out on untransformed abundances. Given the limited range and distribution of abundances, algebraic transformations were not considered necessary or biologically relevant. Since my primary interest was in the relative influence of riparian status (RIPARIAN; RW,RD vs UW,UD) and surface water availability (WATER; RW,UW vs RD,UD) on species composition I specified these as “environmental variables”. The following variables were included as covariates; REGION, MON_RAIN, SEASON and YEAR. Monte Carlo permutation tests (program CANOCO v4.0; Ter Braak and Smilauer, 1998) were used to determine the relative influence and significance of the design variables (RIPARIAN and WATER) on species composition after controlling for covariates. Due to the

temporal stratification of the experimental design, samples were permuted at random within the four sampling periods. Variables representing height of the upper vegetation stratum (UPPER_HT), and percentage cover for each of the upper, mid and lower strata (UPPER_COV, MID_COV, LOW_COV respectively) were included passively to illustrate their relationship with the effects of riparian status and surface water availability. The results of the ordination were displayed as a biplot (see Jongman *et al.*, 1995) to show the configuration of samples and species in relation to the design and passive variables. The statistical significance of the species composition relationships between the “environmental” and passive variables was assessed by regressing the sample scores for the first ordination axis derived from two separate ordinations (one consisting of the variable RIPARIAN and the covariates above, the other consisting of variable WATER and the covariates above) on each of the passive variables (UPPER_HT, UPPER_COV, MID_COV, LOW_COV).

To illustrate possible shifts in the bird assemblage arising from bore drain closures I used Generalised Additive Models (GAM) within CANOCO to construct “preference surfaces” in ordination space. This was done for selected species (and abundance groups) that showed a strong primary preference for UW site types.

5.3 Results

5.3.1 Bird abundance and diversity

5.3.1.1 Abundance of individual species

Over the four sampling periods, 7694 observations were made of 13559 individuals from 119 species (Appendix 4). Of 39 species for which a response to riparian status was made, 22 were more abundant in Riparian habitats, 15 in Upslope habitats and two species (crested pigeon and spiny-cheeked honeyeater) were classified as *indifferent* (Table 5.2). Responses to surface water availability were determined for 35 species, 23 of which were most abundant at Watered sites. Three species (crested pigeon, Australian ringneck and black-faced cuckoo-shrike) appeared *indifferent* to the presence of surface water. Nine species were more abundant in Dryland habitats (irrespective of the presence of surface water) than in riparian sites. A range of representative species responses to riparian status and surface water availability is illustrated in Fig. 5.1.

A total of 18 species were more than five times as abundant (after adjustment for covariates), in either Riparian (10 spp.) or Upslope (8 spp.) habitats and 11 species were more than five times more abundant in either Watered (7 spp.) or Dryland (4 spp.) sites (count ratio > 5; Table 5.2). Tests of whether the effect size differed significantly between species responses to riparian status and their responses to the availability of surface water could be determined for 21 species, six of which showed a non-*indifferent* response favouring the effect of riparian status. Thus, for most species the strength of the effects of riparian status and water availability were

similar. Four of the six statistically significant species were most abundant in Upslope rather than Riparian habitats (chestnut-rumped thornbill, singing honeyeater, weebill and splendid fairy-wren).

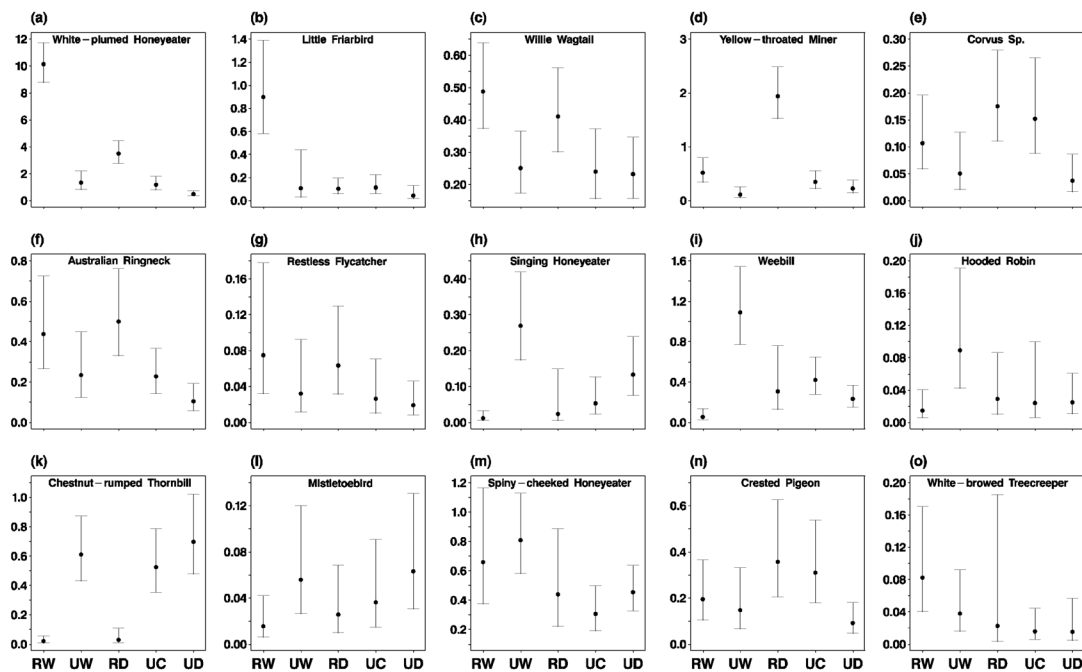


Figure 5.1 Site type variation in the abundance of representative species. Abundance based on mean number of individuals at each site-visit ($n = 865$, 30 min samples). Error bars are 95% confidence limits.

The preference for riparian habitats was split between six species most abundant in Riparian areas with permanent water (specialised “Rip(RW)” response, Table 5.1; white-plumed honeyeater, brown treecreeper, sacred kingfisher, little friarbird, fairy martin, peaceful dove), five species most abundant in Riparian areas without permanent water (specialised “Rip(RD)” response; white-winged chough, noisy miner, yellow-throated miner, cockatiel, mulga parrot) and 11 others that more generally favoured Riparian over Upslope sites (Table 5.2). The clear preference by

some species for RD habitats indicates that riparian preferences were not simply related to the presence of water.

Upslope species were divided among eight that showed a specialised preference for Upslope areas with permanent water (“Ups(UW)” response) and seven species showing a more generalised preference for Upslope habitats irrespective of the presence of water (“Ups” response; Table 5.2). No species showed a specialised preference for Upslope sites away from water (i.e. “Ups(UC,UD),Dry(UC,UD)” response) although the chestnut-rumped thornbill, yellow-rumped thornbill and jacky winter showed a specialised *dryland* (“Dry(UC,UD)”) response but were still influenced by UW sites resulting in a generalised *upslope* response. As UW habitats would not have occurred naturally in the landscape, the observed preference for these areas by many species indicates a strong influence of artificial water on many *upslope* species. Preferences for Watered habitats were divided among those showing specialised (19 spp., 10 associated with RW sites and 9 associated with UW sites) and generalised responses (4 spp.; Table 5.2). No species showed a generalised *dryland* response, and of the nine that showed a specialised preference (6 for RD sites and 3, UC, UD sites; Table 5.2) all showed strong secondary preferences for watered sites (e.g. see Figs. 5.1 d, e and k).

Tests of independence among the 33 species for which a response to both riparian status and surface water availability were determined (Table 5.2) failed to reveal an overall deviation from mutual independence either for a full three by three table with each response classed as positive, indifferent or negative ($P = 0.33$), or for the two by two subset of 29 species showing a non-*indifferent* response ($P = 0.69$). Furthermore,

Table 5.2 Riparian status and surface water availability responses for the abundance of individual bird species: results of generalised linear modelling. Abundance estimates are based on mean number of individuals at each site-visit (n = 865, 30 min samples). Count and difference ratios are presented in favour of effect indicated (R, Riparian; U, Upslope; W, Water; D, Dryland; Ind, Indifferent; ND, Not determined). Count and difference ratio values in parentheses indicate 95% confidence interval. The difference ratio quantifies the difference in the magnitude of the Riparian/Upslope and Water/Dryland count ratios. For example the riparian/upslope influence on the singing honeyeater was 3.4 times greater than the water availability influence, in this case in favour of its abundance in Upslope habitats. Site types in parentheses in the Response group column indicate specialised responses (see text). Riparian and water availability response groups are separated by a comma in the Response group column. Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Bird species	Site-visits (n = 865)	Count ratio		Difference ratio	Response group
		Riparian/Upslope	Water/Dryland		
<i>Riparian/Water response (11 spp.)</i>					
White-plumed Honeyeater	409	11.0*** (8.4- 14.5)R	8.0*** (6.3- 10.1)W	1.4*** (1.1- 1.7)R	Rip(RW),Wat(RW)
Brown Treecreeper	101	6.3*** (3.6- 11.0)R	4.8*** (2.8- 8.3)W	1.3* (1.0- 1.7)R	Rip(RW),Wat(RW)
Sacred Kingfisher	84	6.3*** (3.3- 12.0)R	5.2*** (2.9- 9.6)W	1.2 (0.8- 1.8)RInd	Rip(RW),Wat(RW)
Little Friarbird	125	11.3*** (5.5- 23.2)R	11.5*** (6.1- 21.4)W	ND	Rip(RW),Wat(RW)
Fairy Martin	22	15.2*** (5.7- 40.9)R	15.8*** (5.6- 44.5)W	ND	Rip(RW),Wat(RW)
Peaceful Dove	32	6.7*** (2.9- 15.6)R	7.4*** (3.2- 17.2)W	1.1 (0.7- 1.7)WInd	Rip(RW),Wat(RW)
Laughing Kookaburra	44	4.5*** (2.3- 8.8)R	3.6*** (1.8- 7.2)W	1.3 (0.7- 2.4)RInd	Rip,Wat(RW)
Willie Wagtail	216	1.8*** (1.3- 2.5)R	1.7** (1.2- 2.4)W	1.1 (0.8- 1.5)RInd	Rip,Wat(RW)
Red-winged Parrot	94	2.9*** (1.6- 5.5)R	3.5*** (1.9- 6.5)W	1.2 (0.6- 2.3)WInd	Rip,Wat(RW)
Whistling Kite	23	2.7* (1.2- 6.0)R	3.9*** (1.8- 8.5)W	ND	Rip,Wat(RW)
Little Corella	20	2.8* (1.2- 6.5)R	3.9** (1.5- 9.7)W	ND	Rip,Wat
<i>Riparian/Dryland response (6 spp.)</i>					
White-winged Chough	18	16.6** (2.8- 97.4)R	8.2** (1.9- 34.8)D	ND	Rip(RD),Dry(RD)
Noisy Miner	53	32.2*** (16.1- 64.2)R	22.1*** (10.0- 48.7)D	1.5 (0.8- 2.5)RInd	Rip(RD),Dry(RD)
Yellow-throated Miner	216	9.5*** (6.4- 13.9)R	8.2*** (5.2- 13.2)D	1.1 (0.9- 1.5)RInd	Rip(RD),Dry(RD)
Maggie-lark	102	3.1*** (1.8- 5.4)R	2.1* (1.1- 4.1)D	1.5 (0.8- 2.9)RInd	Rip,Dry(RD)
Grey Shrike-thrush	124	3.8*** (2.4- 6.1)R	2.9*** (1.6- 5.3)D	1.3 (0.8- 2.1)RInd	Rip,Dry(RD)
Corvus Sp.	75	2.1* (1.2- 3.7)R	2.4* (1.2- 4.9)D	ND	Rip,Dry(RD)
<i>Riparian/Water indifferent response (2 spp.)</i>					
Australian Ringneck	167	2.6*** (1.7- 4.0)R	1.4 (0.9- 2.2)WInd	1.9 (1.0- 3.6)RInd	Rip,WatInd
Black-faced Cuckoo-shrike	72	2.3** (1.4- 4.0)R	1.7 (1.0- 3.0)WInd	1.4 (0.7- 2.8)RInd	Rip,WatInd
<i>Riparian/Water not determined response (3 spp.)</i>					
Cockatiel	17	5.2* (1.4- 19.5)R	ND	ND	Rip(RD)
Mulga Parrot	38	4.1* (1.0- 16.8)R	ND	ND	Rip(RD)
Restless Flycatcher	43	2.7* (1.3- 6.0)R	ND	ND	Rip
<i>Upslope/Water response (9 spp.)</i>					
Singing Honeyeater	72	17.1*** (5.9- 49.7)U	5.0*** (2.3- 10.9)W	3.4*** (1.7- 6.6)U	Ups(UW),Wat(UW)
Weebill	142	8.5*** (4.3- 17.2)U	3.5*** (2.2- 5.6)W	2.4*** (1.4- 4.1)U	Ups(UW),Wat(UW)
Splendid Fairy-wren	29	10.4*** (3.9- 27.9)U	4.9*** (2.0- 11.6)W	2.1* (1.1- 4.1)U	Ups(UW),Wat(UW)
Red-capped Robin	44	5.9*** (2.5- 14.0)U	3.9** (1.5- 9.9)W	ND	Ups(UW),Wat(UW)
Double-barred Finch	36	17.3*** (6.1- 48.6)U	12.7*** (5.4- 29.7)W	ND	Ups(UW),Wat(UW)
Hooded Robin	26	4.5** (1.5- 12.9)U	3.5* (1.3- 9.6)W	ND	Ups(UW),Wat(UW)
Common Bronzewing	78	2.5** (1.3- 5.0)U	2.5** (1.3- 4.8)W	1.0 (0.6- 1.6)UInd	Ups(UW),Wat(UW)
Zebra Finch	12	4.3* (1.3- 13.7)U	4.6* (1.2- 17.7)W	ND	Ups(UW),Wat(UW)
Striped Honeyeater	35	3.1** (1.4- 7.1)U	2.5* (1.1- 5.7)W	ND	Ups,Wat(UW)
<i>Upslope/Dryland response (3 spp.)</i>					
Chestnut-rumped Thornbill	122	26.2*** (11.2- 61.4)U	5.4*** (3.0- 9.7)D	4.8*** (2.3- 10.0)U	Ups,Dry(UC,UD)
Rufous Whistler	117	3.5** (1.6- 7.6)U	2.2* (1.2- 4.0)D	1.6 (0.8- 3.2)UInd	Ups,Dry(UC,UD)
Jacky Winter	53	5.9*** (2.7- 12.8)U	2.9** (1.4- 5.9)D	ND	Ups,Dry(UC,UD)
<i>Upslope/Water not determined response (3 spp.)</i>					
Grey-crowned Babbler	27	4.1* (1.3- 12.4)U	ND	ND	Ups
Yellow-rumped Thornbill	32	5.3*** (2.2- 12.5)U	ND	ND	Ups
Mistletoebird	31	2.5* (1.1- 5.7)U	ND	ND	Ups
<i>Riparian indifferent/Water response (1 spp.)</i>					
Spiny-cheeked Honeyeater	243	1.1 (0.7- 1.8)RInd	1.8** (1.2- 2.8)W	1.6 (0.8- 3.1)WInd	RipInd,Wat
<i>Riparian indifferent/Water indifferent response (1 spp.)</i>					
Crested Pigeon	93	1.7 (0.9- 2.9)RInd	0.8 (0.4- 1.4)WInd	2.1 (0.9- 4.8)RInd	RipInd,WatInd
<i>Riparian not determined/Water response (2 spp.)</i>					
White-browed Treecreeper	28	ND	3.2* (1.3- 8.1)W	ND	Wat
White-browed Woodswallow	15	ND	2.5* (1.0- 6.2)W	ND	Wat

the dominant contrasts for all but the little corella in each of the non-*indifferent* response categories involved at least one of the specialised contrasts (Table 5.2). Such

cases are indicative of elevated abundances in a specific site type rather than a generalised response formed by the average of the treatments involved in the initial contrast. For example, the dominant contrasts for eight of the nine species showing both *upslope* and *water* responses were due to higher abundances in the UW sites alone, rather than higher average abundances in both upslope (UW, UC, UD) and watered (UW, RW) sites. Similarly, a suite of six species consisting of the white-plumed honeyeater, brown treecreeper, sacred kingfisher, little friarbird, fairy martin and peaceful dove all appeared to favour RW sites over the alternative Riparian and Watered site types (RD and UW respectively).

5.3.1.2 Species group responses

Due primarily to high numbers in RW sites, total bird abundance was strongly influenced by both riparian status and surface water availability, although the riparian influence was 7% to 20% stronger than the influence attributable to the presence or absence of surface water (Table 5.3, Fig. 5.2a). The statistical modelling suggests that there were about twice as many birds at RW sites compared to the Upslope sites (UW, UC, UD; Table 5.3), however this result was strongly influenced by the white-plumed honeyeater. Without its influence, abundance was highest at RD sites (Table 5.3, Fig. 5.2b). The results for overall sub-asymptotic species richness favoured Upslope sites generally and UC, UD sites specifically (Table 5.3, Fig. 5.3a). About 20% more species were found in Upslope habitats and about 10% more in Dryland habitats, although the difference between the riparian status and water availability effect was not significant ($P > 0.05$; Table 5.3).

Differences in abundance and sub-asymptotic species richness were detected within many species groups, most often showing contrasting responses for these two metrics (see Table 5.3). Pigeons, Parrots and Cockatoos were most speciose in RD site types (specialised “Rip(RD),Wat(RD)” response, Table 5.3, Fig. 5.3e), but were most abundant in Riparian areas and at UW sites (Fig. 5.2f). Larger Bushbirds were more abundant and speciose in RD sites (Table 5.3, Fig. 5.2h, Fig. 5.3h). Bushbird Insectivores showed a similar sub-asymptotic species richness response to overall sub-asymptotic species richness, but were more abundant in Upslope sites especially the bore drains (UW site types; Fig. 5.2e, Fig. 5.3d). Bore drain sites were also favoured by the Uncommon species (Fig. 5.2j, Fig. 5.3j), Ground Generalists (Fig 5.3f), and many of the Honeyeaters (Fig. 5.3b, c). The white-plumed honeyeater was primarily responsible for the strong RW abundance response within that group (Table 5.3, see Figs. 5.2b and c). Without its influence Honeyeater abundance was highest at RD sites, although this was in turn a partial reflection of the second most abundant species, the yellow-throated miner. Despite a strong abundance response favouring the RW sites (Table 5.3, Fig. 5.2i), similar numbers of Aerial Insectivore species were recorded in Riparian and Upslope, and between Watered and Dryland sites (Fig. 5.3i). None of the species richness groups showed a specialised or generalised response favouring both Riparian and Watered sites (Table 5.3). In contrast, all of the abundance groups were observed in higher numbers in either Riparian or Watered (often both) and none were most abundant in Upslope sites away from water.

Table 5.3 Riparian status and surface water availability responses for the abundance and sub-asymptotic species richness of species groups: results of generalised linear modelling. Abundance analyses are based on mean number of individuals at each site-visit (n = 865, 30 min samples). Sub-asymptotic species richness estimates are based on site-sampling periods (n = 433, 60 min samples) calculated after rarefaction using the number of samples and individuals indicated (see text for details). Count and difference ratios are presented in favour of effect indicated (R, Riparian; U, Upslope; W, Water; D, Dryland; Ind, Indifferent; ND, Not determined). Count and difference ratio values in parentheses indicate 95% confidence intervals. Site types in parentheses in the Response group column indicate specialised responses (see text). Riparian and water availability response groups are separated by a comma in the Response group column. Significance levels: * P < 0.05; ** P < 0.01; *** P < 0.001.

Species grouping	Site-visits	No. of species	% of total abundance	Post-rarefaction site-sampling periods (individuals sampled)	Count ratio		Difference ratio	Response group
					Riparian/Upslope	Water/Dryland		
<i>Abundance responses</i>								
Total Abundance	863	138*	100	-	2.05*** (1.82- 2.31)R	1.81*** (1.61- 2.04)W	1.13*** (1.07- 1.20)R	Rip(RW),Wat(RW)
Excluding white-plumed honeyeater	862	137*	76.9	-	1.51*** (1.28- 1.78)R	1.26** (1.06- 1.50)D	1.20*** (1.10- 1.31)R	Rip(RD),Dry(RD)
Aerial Insectivore	268	7	4.1	-	3.88*** (2.47- 6.10)R	3.45*** (2.22- 5.37)D	1.12 (0.97- 1.31)RInd	Rip(RW),Wat(RW)
Larger Bushbird	302	11	4.6	-	3.04*** (2.16- 4.28)R	2.35*** (1.56- 3.53)D	1.29* (1.02- 1.64)R	Rip(RD),Dry(RD)
Raptor	42	10	0.4	-	3.25*** (1.67- 6.32)R	4.46*** (2.35- 8.44)W	ND	Rip,Wat(RW)
Pigeons, Parrots & Cockatoos	446	16	15.6	-	1.60*** (1.25- 2.05)R	1.33* (1.02- 1.75)W	1.20 (0.82- 1.76)RInd	Rip,Wat
Ground Generalist	93	6	5.4	-	ND	2.96* (1.21- 7.27)D	ND	Dry
Bushbird Insectivore	642	37	20.1	-	1.57*** (1.31- 1.88)U	1.37** (1.11- 1.70)W	1.15 (0.92- 1.43)RInd	Ups,Wat(UW)
Honeyeaters, Flowerpeckers etc.	697	17	44	-	4.33*** (3.62- 5.19)R	1.47*** (1.19- 1.80)D	2.96*** (2.27- 3.85)R	Rip(RW),Dry(RD)
Excluding white-plumed honeyeater	564	16	20.9	-	3.38*** (2.69- 4.24)R	2.43*** (1.88- 3.13)D	1.39*** (1.19- 1.63)R	Rip(RD),Dry(RD)
Finch	49	3	1.2	-	20.25*** (8.48- 48.37)U	13.58*** (5.33- 34.59)W	ND	Ups(UW),Wat(UW)
Nomad	97	12	3.2	-	2.38* (1.09- 5.21)R	ND	ND	Rip
Uncommon Species	206	58	4.8	-	1.93* (1.16- 3.20)U	2.39*** (1.48- 3.86)W	1.24 (0.89- 1.73)WInd	Ups(UW),Wat(UW)
<i>Sub-asymptotic species richness responses</i>								
All species	840	119	98.6	258 (21)	1.17*** (1.09- 1.25)U	1.15** (1.05- 1.25)D	1.02 (0.94- 1.11)RInd	Ups,Dry(UCUD)
Excluding white-plumed honeyeater	837	118	76.5	193 (21)	1.12** (1.03- 1.22)U	1.04 (0.96- 1.13)W	1.08 (0.95- 1.22)RInd	Ups,WatInd
Aerial Insectivore	268	7	4.1	46 (4)	0.98 (0.85- 1.13)R	0.95 (0.85- 1.07)W	1.03 (0.86- 1.23)RInd	RipInd,WatInd
Larger Bushbird	302	11	4.7	35 (6)	1.26*** (1.10- 1.44)R	1.47** (1.14- 1.90)D	1.17 (0.95- 1.45)WInd	Rip,Dry(RD)
Pigeons, Parrots & Cockatoos	446	16	15.8	85 (8)	1.38*** (1.19- 1.60)R	1.30*** (1.13- 1.49)D	1.06 (0.95- 1.18)RInd	Rip(RD),Dry(RD)
Ground Generalist	93	6	5.5	60 (3)	1.23*** (1.12- 1.35)U	1.20*** (1.08- 1.32)W	1.03 (0.99- 1.08)RInd	Ups(UW),Wat(UW)
Bushbird Insectivore	642	37	20.3	70 (12)	2.13*** (1.87- 2.43)U	1.77*** (1.57- 2.00)D	1.20*** (1.09- 1.33)R	Ups(UCUD),Dry(UCUD)
Honeyeaters, Flowerpeckers etc.	697	17	44.7	224 (8)	1.50*** (1.33- 1.69)U	1.36*** (1.20- 1.55)W	1.10* (1.02- 1.18)R	Ups(UW),Wat(UW)
Excluding white-plumed honeyeater	564	16	21.2	142 (7)	1.59*** (1.36- 1.85)U	1.45*** (1.20- 1.76)W	1.09 (0.96- 1.25)RInd	Ups(UW),Wat(UW)
Nomad	97	12	3.2	33 (4)	1.19** (1.05- 1.35)U	1.15** (1.04- 1.28)D	1.03 (0.98- 1.09)RInd	Ups(UCUD),Dry(UCUD)
Uncommon Species	206	58	4.9	47 (5)	1.27** (1.06- 1.52)U	1.25* (1.02- 1.55)W	ND	Ups,Wat(UW)

* includes 19 taxa not identified to species level

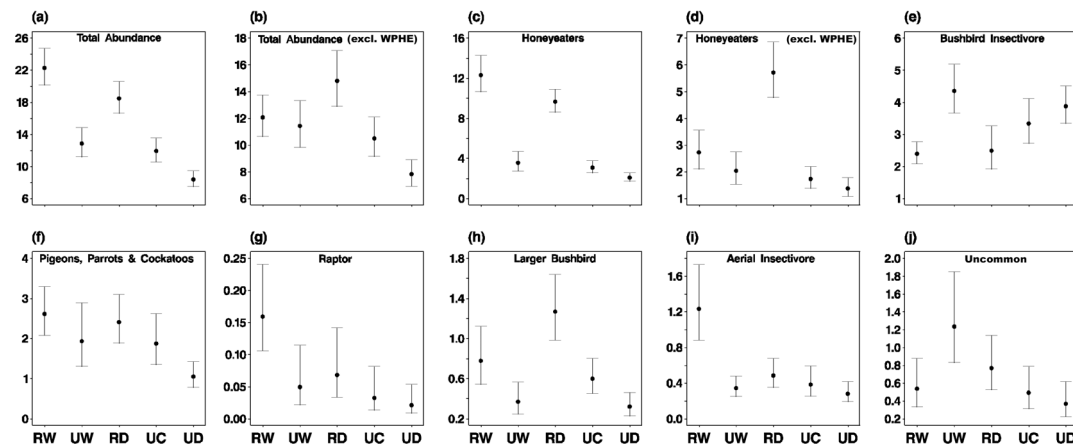


Figure 5.2 Site type variation in the abundance of selected species groups. Abundance based on mean number of individuals at each site-visit ($n = 865$, 30 min samples). Error bars are 95% confidence limits. “excl. WPHE” in parenthesis indicates analyses that excluded the white-plumed honeyeater.

Significant differences in the strength of the effect for riparian status and water availability were observed within the following groups; total abundance, abundance and richness of Honeyeaters, abundance of Larger Bushbirds, and sub-asymptotic species richness within the Bushbird Insectivores (Table 5.3). In all cases the riparian status effect was stronger, favouring Riparian sites for the abundance groups and Upslope sites for the species richness groups. Other than these examples, most other groups showed an *indifferent* response indicating the similarity in the relative strength of these influences.

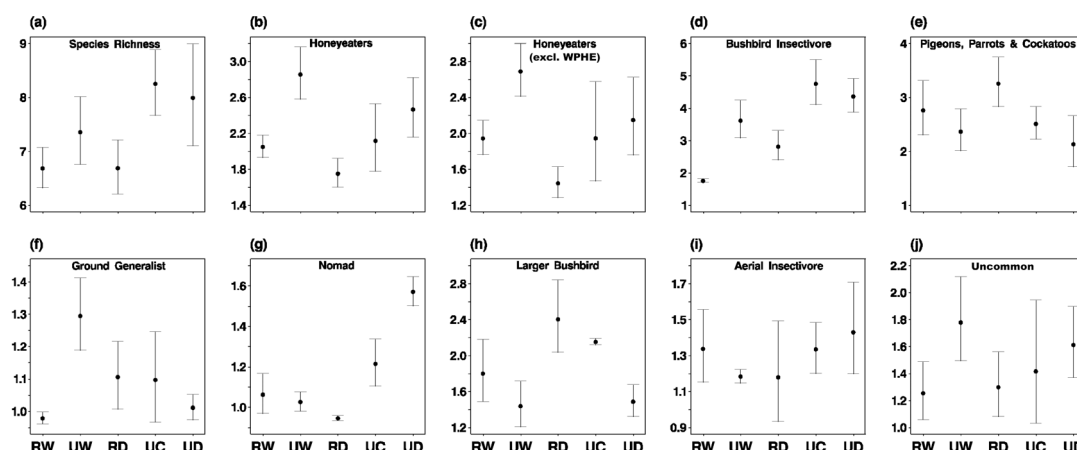


Figure 5.3 Variation among site types in sub-asymptotic species richness of selected species groups. Number of species is based on site-sampling periods ($n = 433$, 60 min samples) calculated after rarefaction using the number of samples and individuals indicated in Table 5.3 (see text for details). Error bars are 95% confidence limits.

5.3.2 Bird community composition

There was a clear separation of site types in ordination space (Fig 5.4a) illustrating the influence of both riparian status and surface water availability on species composition. Together both variables accounted for a statistically significant proportion of overall variation (3.7%, $F = 6.7$ $P < 0.002$). Although small, this variation represented 47.7% of that explained (i.e. environmental variables and co-variables). Individually, both environmental variables were significant at $P < 0.05$; RIPARIAN accounted for 30.1% ($F = 8.4$, $P < 0.002$), and WATER for 17.6% ($F = 4.9$, $P < 0.002$) of explained variation. The locations of the species shown in the ordination were generally consistent with the responses determined from the univariate analyses. Together, the four vegetation variables accounted for 44.6% and 12.7% of the variation in species composition due to riparian status (RIPARIAN, $F = 271.8$, $P < 0.002$; Table 5.4) and surface water availability (WATER, $F = 48.9$, $P < 0.002$; Table 5.4) respectively. Nearly all of this

could be accounted for by differences in upper canopy height (UPPER_HT; Table 5.4) although the vegetation cover estimates for each of the lower, mid and upper strata (UPPER_COV, MID_COV, LOW_COV respectively; Table 5.4) also explained small but significant components of variation in species composition for both RIPARIAN and WATER.

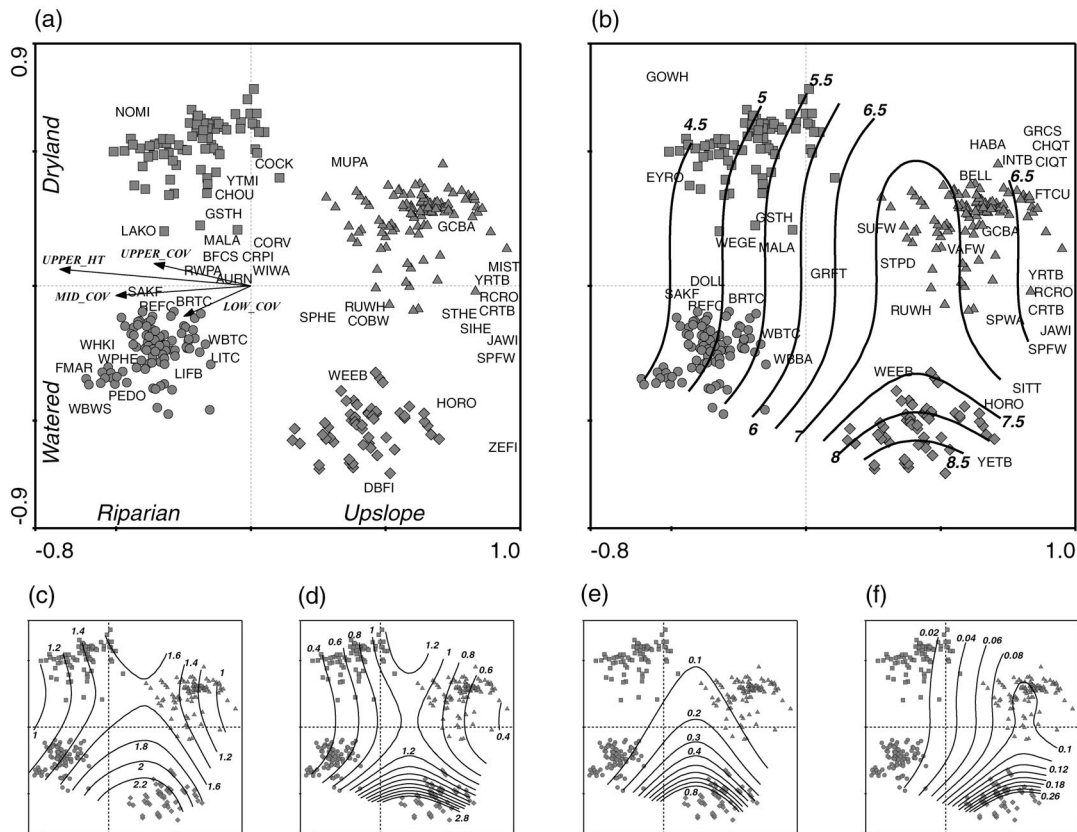


Figure 5.4 Ordination biplots based on partial canonical correspondence analysis (pCCA) showing variation in bird species composition with respect to riparian status and surface water availability. (a) Samples in relation to species identified in Table 2 and passive vegetation variables (arrows); (b) samples in relation to modelled abundance (isolines) of Bushbird Insectivores; (c) Uncommon species; (d) weebill; (e) double-barred finch, (f) hooded robin. Points represent site-sampling periods and are the same for each biplot: circle, RW; square, RD; triangle, UD; diamond, UW (n = 343, 60 min samples). Species abbreviations detailed in Appendix 4.

Among those species and groups that showed a specialised preference for bore drains (“Ups(UW)” or “Wat(UW)” abundance response; Tables 2 and 3) a variety of “preference landscapes” were evident. Species such as the weebill (Fig. 5.4d), double-

barred finch (Fig. 5.4e), common bronzewing, and many of the Uncommon species (Fig. 5.4c) showed a clear preference for UW sites without distinct secondary preferences. This contrasts with the Bushbird Insectivores (Fig. 5.4b) and individual species such as the hooded robin (Fig. 5.4f), singing honeyeater, zebra finch, splendid fairy-wren, red-capped robin which all displayed strong secondary preferences for the other Upslope treatment (UD) over either of the Riparian site types (RW, RD).

Table 5.4 Marginal contributions of four vegetation variables to the variance in species composition explained by differences in riparian status and surface water availability status. *P* = significance level of the effect, as obtained from a Monte Carlo permutation test with 499 random permutations.

Variable	RIPARIAN		WATER	
	% Variance explained	<i>P</i>	% Variance explained	<i>P</i>
Upper canopy height (UPPER_HT)	43.0	< 0.002	12.6	< 0.002
% cover - upper statum (UPPER_COV)	7.0	< 0.002	2.2	0.05
% cover - mid statum (MID_COV)	17.0	< 0.002	1.2	< 0.002
% cover - lower statum (LOW_COV)	2.0	0.006	4.9	< 0.002
Variables combined	46.6	< 0.002	12.7	< 0.002

5.4 Discussion

5.4.1 Influences of riparian status and water availability

In the present study, both riparian status and surface water availability exerted a strong influence on the terrestrial avifauna of the Mulga Lands region. For many species and groups the magnitude of these influences was similar, however there were numerous significant differences, all of which favoured the effect of riparian status. For example, the influence of riparian status on species composition was about twice that attributable to the presence (or absence) of water. Similarly, the riparian influence on overall abundance was about 13% higher than that due to water (Table 5.3). For some individual species (chestnut-rumped thornbill, singing honeyeater, weebill, splendid fairy-wren; Table 5.2), and for sub-asymptotic species richness within the Bushbird Insectivores and Honeyeaters (Table 5.3), the preference for Upslope sites was significantly greater than their preference for either Dryland or Watered habitats.

However, rather than responding primarily to one factor or the other (i.e. directional response to one factor and an indifferent response to the other) birds generally responded to both. This is significant because it meant that high numbers of birds and species showed specialised responses to specific site types, rather than generalised independent responses to one factor or the other. Although the observation that riparian areas with permanent water (RW site types) were commonly favoured while upslope areas away from permanent water (UD site types) were commonly avoided was consistent with previous research on the separate influence of these factors (riparian, Chapter 3; water availability, Davies, 1972, Fisher *et al.*, 1972, Landsberg *et al.* 1999),

the more sophisticated analysis used in the present study have revealed more subtle, but strong interactions. Most significantly, there was: (1) a very marked water availability influence among species and groups preferring upslope habitats (UW site types); (2) a relatively large group of species associated with ephemeral riparian habitats (RD site types); and (3) contrasting abundance and sub-asymptotic species richness responses within some groups (see Chapter 3 for discussion on this latter point). Clearly, the two factors were not entirely independent, however the responses indicate that while the presence of surface water was important, it could not alone explain differences due to riparian status.

While far from comprehensive, the analysis of the four vegetation variables provides useful insights into the possible source of the additional variation in riparian and upslope bird assemblages. In particular, the height of the upper canopy was strongly correlated with riparian status, accounting for nearly half of the variation in species composition due to riparian status but only one eighth of that due to differences in water availability. Both types of riparian habitat (RW, RD site types) supported taller vegetation than the surrounding upslope areas. The projective foliage cover of the upper, mid and lower strata also showed positive associations with the riparian effect suggesting that together these measures are more generally indicative of higher productivity and structural complexity at the riparian sites. Many studies have attributed differences in bird abundance (and richness, but see Chapter 3) to these factors (Stauffer and Best, 1980; Loyn, 1985; Finch, 1989; Recher *et al.*, 1991; Mills *et al.*, 1991; Douglas *et al.*, 1992; Sanders and Edge, 1998). Indeed, there is widespread agreement that such conditions provide resources that can be simultaneously utilised by many individuals and species (Hewitt, 1990; McGarigal and McComb, 1992; Catterall, 1993;

Naiman *et al.*, 1993; Naiman and Décamps, 1997). In turn, the ability of riparian zones to support a more productive and complex vegetation habitat than the surrounding landscape is likely to be a consequence of geomorphology and climate, in particular their greater retention and concentration of nutrients, sediment, surface and sub-surface water (Gregory *et al.*, 1991; Ludwig *et al.*, 1997).

In addition to their dominant (primary) responses, strong riparian influences were also apparent in species' secondary and other lower order preferences. Rather than occurring exclusively (or even near-exclusively) in one habitat type or another, almost all common species and groups were observed in varying abundances across the range of site types surveyed. However, because of the stronger underlying influence of riparian status (see above) secondary preferences for many species and groups favoured site types of the same riparian (rather than water availability) status. For example, species and groups showing a strong primary association with RW site types were more closely associated with RD than UW site types. Similarly, species and groups showing a strong primary association with UW site types were secondarily associated with other upslope site types (UC, UD). This suggests that most species and groups have a dominant association with riparian or upslope habitats and will preferentially seek to meet their need for water within these areas.

Notwithstanding the interactions with riparian status, the results support the widely held view that water availability is a critical factor in the distribution of birds in the arid zone (Fisher *et al.*, 1972; Schodde, 1982; Landsberg *et al.*, 1999; James *et al.*, 1999; Roshier *et al.*, 2002). Almost without exception, individual species and groups showed strong primary and/or secondary associations with at least one of the watered site types (RW or

UW). However, the strength of these associations was not always a simple reflection of the apparent behavioural and/or physiological adaptations commonly attributed to specific groups of species. For example, some of the strongest responses to watered sites were observed among small insectivorous passerines (e.g. Bushbird Insectivores and many of the small honeyeaters; Appendix 4), even though most are considered least water-dependent (Fisher *et al.*, 1972; Dawson, 1976; Schodde, 1982). In contrast, the response of the seed eating and apparently highly water-dependent Pigeons, Parrots and Cockatoo group (Fisher *et al.*, 1972; Dawson, 1976; Schodde, 1982) was complicated by differences in the riparian and upslope responses. It was suggested in Chapter 3 that this was due to strong inter-habitat movements reflecting their need to forage in upslope habitats and roost in riparian habitats.

The results for many individual species were also inconsistent with those reported by Landsberg *et al.* (1999) for the Queensland Mulga Lands. By comparing relative species abundances between UW and UD sites (not shown) among the 16 species for which determinations were made in both studies I found only seven species that showed consistent trends (all of which were observed at their highest abundances near bore drains; common bronzewing, hooded robin, restless flycatcher, singing honeyeater, white-browed woodswallow, white-plumed honeyeater, zebra finch). In this study, the mulga parrot and grey shrike thrush, both decreased near bore drains whereas Landsberg *et al.* (1999) found significant increases near artificial water. For the remaining seven species (4 “increasers”, *sensu* Landsberg *et al.*, 1999; crested pigeon, jacky winter, mistletoebird, willie wagtail; 3 “decreasers”; chestnut-rumped thornbill, red-capped robin, yellow-rumped thornbill) I found no significant difference in their abundance despite ample observations. As a further complication, five of the 16 species

(grey shrike-thrush, restless flycatcher, white-browed woodswallow, white-plumed honeyeater, willie wagtail) were much more strongly influenced by riparian status than either artificial water or distance away from it, suggesting that these species are unlikely to be strongly influenced by artificial water despite showing an apparent preference for it over other upslope habitats. It is highly likely that such discrepancies are due to differences in the approaches to sampling; this study sampled bore drains at numerous locations in space and time within the Queensland Mulga Lands whereas Landsberg *et al.* (1999) were focussed on grazing impacts and sampled point water sources which were replicated more generally across the arid zone, taking only a single snapshot within the study area. Nonetheless, these differences highlight the potential for spatial and temporal variation in bird responses (see also Chapter 4) and the importance of sampling all relevant sources of a factor of interest, in this case water.

5.4.2 Management implications

Although there are numerous sound reasons for the closure of bore drains (water conservation, pasture and vegetation management, control of overabundant macropods and feral animals), the results suggest that most of the impacts on terrestrial birds will be negative. This is essentially because species and groups that prefer upslope habitats make extensive use of bore drains, presumably as a source of surface water, but appear reluctant to use riparian areas which potentially provide the only alternative reliable source of water once the bores are capped. Of the 15 upslope species I was able to analyse (typically Bushbird Insectivores and other small passerines; Table 5.1) and 3 upslope groups (Bushbird Insectivores, Finches, Uncommon species; Table 5.3), all

were found: (1) at their highest, or equally highest, densities near bore drains; and (2) at their lowest, or equally lowest, densities near riparian areas with permanent water.

While these observations do not necessarily preclude a significant shift in the habitat preference of these groups toward riparian areas following the closure of bore drains, there are a number of factors likely to impede the ability of the small passerines to do so. It was suggested in Chapter 3 that low densities of these birds in RW site types was due, in part, to competitive interactions especially with the white-plumed honeyeater which dominates these habitats and aggressively excludes other small birds. Moreover, Chapter 4 showed that riparian-upslope habitat partitioning was most apparent during periods of low rainfall, when water would be most difficult to obtain in non-riparian habitats. In addition, many areas serviced by bore drains are large distances (tens of km) from riparian areas with permanent water, and the small passerines are typically sedentary with relatively small home ranges (a few hectares or more; see Blakers, *et al.*, 1984; Schodde and Tidemann, 1986). It is also significant that I found no evidence of species or groups likely to directly benefit from bore drain closures. For this to be the case, I would have expected to observe upslope species in higher abundance away from the bore drains than near them.

It is possible that some of the species affected by bore drain closures may make use of water reticulated to stock troughs and the like, however it is not clear whether this will in fact occur. Although these systems may distribute water more evenly and frugally throughout the landscape, the sources themselves will need to be more concentrated to yield water conservation benefits and as a consequence higher numbers of livestock, and other biota including birds, would need to compete for access to these areas.

Trampling and grazing by stock around watering points is also likely to reduce habitat suitability for birds (James *et al.*, 1999). In addition, the ability of land managers to regulate total grazing pressure by controlling access to water may affect sedentary birds by forcing them to travel long distances to water or by limiting their distributions to areas proximate to sources of permanent water (e.g. riparian areas, dams, homesteads, natural wetlands etc.). Indeed, providing water to areas where it was not previously available may simply encourage overgrazing (Cowley and Rogers, 1995).

For native species, one of the essential arguments in support of the regulation of artificial water sources is that its provision has directly favoured some species while others have declined (Davies, 1977; James *et al.*, 1999). The implication of this is that restricted access to artificial water will restore a previous (pre-European) ecological balance. There are problems with this proposition. Firstly, the argument is most compelling where there is overwhelming evidence of decreasing abundance of native species with distance from water, or increasing abundance leading to land degradation or other negative consequences (e.g. macropods). However, it is least appealing where there appears to be a benign increase in the population of many species.

The results show very little evidence of decreased abundance of birds near bore drains and, to my knowledge, no negative consequences are known among the upslope species that appear most reliant on the bore drain resource. On the contrary, the birds that appear most vulnerable to bore drain closures are typical of those thought to be declining in more agriculturally developed neighbouring regions (Reid and Flemming, 1992; Smith and Smith, 1994; Reid, 1999; Seddon *et al.*, 2003; Woinarski and Catterall, 2004). Based on the results of 11 studies across the adjacent sheep-wheat belt of NSW,

Reid (1999) diagnosed the decline of 20 species that were formerly common widespread, finding that small passerines (18 spp., including 15 Bushbird Insectivores) were strongly over-represented. Most of the individual Bushbird Insectivore species identified as “decliners” by Reid (1999) that were also common enough to be analysed for this study, were found most frequently near bore drains (6 of 8 spp.; chestnut-rumped thornbill, jacky winter, red-capped robin, hooded robin, grey-crowned babbler, rufous whistler).

Secondly, the results highlight the possibility that factors other than water may also be important. The advent of artificial water was but one of a number of inter-related changes to arid zone habitat conditions that accompanied European settlement. Other factors included the effects of land clearing and fragmentation, overgrazing, changes to the fire regime and competition and predation by exotic species (Davies, 1977; Morton, 1990; James *et al.*, 1995). Mulga Land habitats appear to have been particularly prone to grazing-related changes in vegetation (Wilson 1999) and this has led to the transformation of extensive areas of native grasslands and open woodland to mulga and other shrublands (Hodgkinson and Harrington, 1985; Witt and Beeton, 1995; James *et al.*, 1999; Witt *et al.*, 2000). Given the strong influence of vegetation structure on the bird community shown in this study I expect that such wholesale changes to the regional vegetation would have resulted in equally dramatic shifts in the regional bird community. Indeed, most authors reviewed by James *et al.* (1999) regard habitat change arising from overgrazing as the primary cause of historic shifts in bird abundance and distribution in arid Australia. For many birds, access to artificial water has probably helped maintain (or increase) their populations despite the advent of pastoralism. In these circumstances it would be misleading to assume that closure of the bore drains

will move the ecological conditions for terrestrial birds any closer to the pre-European state without simultaneously addressing the other changes to the landscape. In fact, it seems possible that such action could realise latent pastoral impacts causing further decline in many species.

Thirdly, the removal of artificial water sources may refocus the activities of stock, macropods and feral animals onto the riparian zone. These concerns are amplified by the facts that riparian areas: (1) occupy such a small proportion of the landscape (Knopf, *et al.*, 1988; Hewitt, 1990); (2) are amongst the most degraded habitats in the Mulga Lands (Wilson, 1999); (3) are thought to be a critically important habitat for terrestrial birds including those that spend most of their time in upslope habitats (Chapter 3); and (4) in many locations are likely to offer the only other source of water available to many of the birds that currently occupy upslope habitats.

Our understanding of the pre-European environment and its avifauna is poor and historical changes in the avifauna have been as complex and varied as the range of factors that have contributed to changed habitat conditions (Woinarski and Catterall, 2004). Hence addressing and reversing species declines may require environmental solutions other than a return to a pre-European state. I acknowledge that measures for the conservation of artificial water resources are necessary to prevent the effective exhaustion of the artesian water resource. However, the results presented here indicate that there is clearly cause for concern in relation to the possible consequences of bore drain closures for the regional avifauna. I suggest careful monitoring of the effects of bore drain closures including the implementation of complementary programs to: (1) gain a better understanding of the ecological processes that affect wildlife communities

in semi-arid environments that are used for the production of grazing livestock; (2) consider making environmental allocations of artificial water to support vulnerable native species; and (3) safeguard riparian areas from secondary impacts.

6.0 General Discussion

Although many factors have been identified that may be involved in observed differences in riparian and upslope avifaunas (Chapter 1), this thesis is primarily concerned with the role of riparian areas in the broader landscape. Knopf and Samson (1994) argued that despite the commonly observed riparian-upslope differences (which have led to a disproportionate conservation focus toward riparian areas themselves), many species make extensive use of both riparian and upslope components of the landscape. Accordingly, this chapter is focused on the landscape-scale interrelationships observed between riparian and upslope bird communities in the Mulga Lands, and the likely ecological processes involved in their creation. This is approached: (1) by drawing on the major findings from the previous chapters to describe the overall spatial and temporal patterns of riparian-upslope occupancy and the apparent linkages between them; and (2) by considering these patterns in the context of a conceptual model to explain spatial and temporal processes that may structure terrestrial bird communities in the Australian arid zone, and perhaps more broadly. The estimation of species richness in circumstances where there are major differences in abundance emerged as an important issue for riparian-upslope comparisons (Chapter 3), and is also discussed further.

6.1 Riparian-upslope patterning and linkages

In this study, the bird assemblage (Chapter 3) was generally characterised by high riparian abundances, but both low alpha and beta diversity. Compared to the relatively even abundance distributions observed in upslope areas, riparian habitats were also typically dominated by high densities of a few species (e.g. white-plumed honeyeater,

yellow-throated miner). This in turn contributed to a relatively high similarity in riparian species composition among riparian sites (Fig 3.4). However, these patterns were not a simple reflection of greater spatial heterogeneity among upslope habitats. Even within restricted localities (containing similar habitats under the same climatic conditions) the composition of upslope bird communities was highly variable. Consistent with the idea that arid zone birds (and other fauna) respond to spatio-temporal differences in productivity (Stafford Smith and Morton, 1990, James *et al.*, 1995), this pattern is likely to reflect strong spatial and temporal limitations on upslope resources that prevent multiple resource preferences from being satisfied simultaneously in the same locality. As a consequence upslope birds need to move about constantly to meet their resource needs.

Although it could be argued that movement might “iron out” spatial heterogeneity, upslope sites were characterised by low bird densities with relatively even abundance distributions. In these circumstances even small turnovers in the number of individuals at a site may cause significant change in species composition. Notwithstanding this, at broader spatial and temporal scales patterns of upslope species composition are likely to reflect local or regional variations in habitat conditions. These broader-scale patterns were observed in relation to spatial variation in vegetation structure (Chapters 3 and 5) and temporal variation in localised rainfall, season and year (Chapter 4).

The strong overall riparian effect in relation to species occurrence and abundance observed in this study were also consistent with existing literature for studies from semi-arid regions and more mesic biomes throughout the world (see reviews of Brinson *et al.*, 1981; Knopf *et al.*, 1988; Catterall, 1993; Malanson, 1993; Naiman and Décamps,

1997; National Research Council, 2002). Exceptions to this pattern appear to occur where riparian habitats support lower or less complex vegetation (Chapter 1), which in turn may reflect spatial differences in productive capacity. For example, McGarigal and McComb (1992) observed lower bird abundances in riparian areas, however their riparian sites may have been less productive because they were associated with low-order, high energy streams, whereas their upslope sites were associated with much taller forests on a more fertile soil substrate. In this study, riparian habitats supported taller and more complex vegetation (Fig 5.4), and are presumably more productive for birds over the long term.

Many birds also appeared to respond strongly to longer-term temporal fluctuations in seasonal and inter-annual climatic conditions, and localised rainfall (Chapter 4). In general, sub-asymptotic species richness (as defined previously; see Section 3.2.1.1) was higher in summer than winter, but lower during drought (1997). Overall bird abundance remained relatively stable during summer but decreased during drought. Riparian areas were generally favoured during periods of low rainfall and drought but not necessarily during summer. Patterns of bird species composition also reflected fluctuations in the temporal variables, with the strongest overlap of riparian and upslope assemblages observed during the drought-affected summer of 1997. Since this increased overlap was due to greater use of riparian areas during drought, this suggests that these areas may be critically important when surface water is scarce.

Although the availability of water was clearly important in determining these spatial and temporal patterns (Chapter 5), the value of riparian areas was not simply due to water availability. Birds responded strongly to the presence of surface water, but this was

insufficient to account for differences observed between riparian and upslope habitats. Indeed, most species and functional groups preferentially sought to meet their need for water in the habitat (riparian or upslope) in which they were most frequently observed. Whether or not surface water was present, riparian and upslope habitats were strongly differentiated by vegetation structure; riparian areas typically supported taller and denser vegetation. This suggested that riparian-upslope differences in productivity and/or structural complexity were probably responsible for the “residual” riparian influence.

Furthermore, strong riparian-upslope linkages were implied by overlapping species assemblages. Despite distinct preferences for one habitat or another, very few species were found exclusively in either riparian or upslope habitats, many were dominant in both, and as a consequence riparian and upslope species assemblages overlapped. However, rather than a pattern of species distributions characteristic of a simple riparian-upslope gradient, species associated with riparian sites were centred within a broader constellation of upslope sites and species (Fig. 3.4). It seems most likely that this occurred as a result of extensive interhabitat movements. Furthermore, temporal influences of season, year and localised monthly rainfall were associated with fluctuations in the strength of this overlap (Fig 4.6), suggesting that birds were adjusting their use of the landscape in accordance with prevailing conditions (e.g. making greater use of riparian zones during drought). In the only other comparable study, Szaro and Jakle (1985) also report overlap in riparian and upslope species assemblages from an Arizonan desert.

Thus, despite an apparently steep gradient in riparian-upslope habitat conditions, the overall picture is one of a shared avifauna. Rather than adapting to conditions at either end of this gradient, which would result in strongly differentiated assemblages, it is suggested that many Australian arid zone birds (and perhaps other fauna) use movement to dampen spatial and temporal variations in resource availability. This means that, resources available in either the riparian or upslope components of the landscape, may be potentially available to the entire bird community. As a consequence, many of the common micro and meso-scale explanations for riparian-upslope differences in the bird response (e.g. productivity, disturbance, habitat complexity, spatial heterogeneity, microclimate, provision of essential resources etc.; see Chapter 1) need to be considered in the context of overwhelming inter-habitat exchange.

6.2 Riparian-upslope biodiversity comparisons

The use of rarefaction to adjust for density differences, and thus compare sub-asymptotic species richness from riparian and upslope treatments has not been previously attempted in the riparian wildlife literature. Almost all of the quantitative studies that claim higher wildlife diversity in riparian areas use species density (species per unit area; Simpson, 1964) as a measure of diversity. For the purpose of this discussion, I use the term “species diversity” to describe measures that incorporate the number of species and/or the distribution of individuals among species (see Krebs, 2001). Thus, species richness is a measure of species diversity. I also make the same distinction between asymptotic and sub-asymptotic species density as I did for species richness (Section 3.2.1.1). Although it is clear that the asymptotic species density is the same quantity as asymptotic species

richness, the sub-asymptotic variants of species richness and density do not necessarily measure the same quantity. It is sub-asymptotic species density estimates that have been most commonly used to estimate diversity in the riparian wildlife literature.

Claims of higher wildlife diversity in riparian areas are surprising given that: (1) the problem of comparing diversity from different-sized samples has a long history (Fisher *et al.*, 1943; Sanders, 1968; Hurlbert, 1971; Gotelli and Colwell, 2001); (2) the techniques for making the necessary adjustments are well-understood (see basic texts of Rosenzweig, 1995 and Krebs, 2001 and recent review by Gotelli and Colwell, 2001); and (3) riparian areas typically support higher numbers of individuals than upslope habitats (see Table 3.4 and Brinson *et al.*, 1981). This oversight may be due to a number of factors including: (1) a lack of understanding of the potential consequences of not addressing differences in abundance and; (2) a widespread perception that species density when calculated from samples (i.e. sub-asymptotic estimates) is a useful measure of species diversity. The widespread use of sub-asymptotic species density as a measure of diversity in riparian-upslope systems may have contributed to the generalisation that riparian areas are more diverse than upslope habitats, and consequently distorted our understanding of the mechanisms underlying biodiversity differences in these areas.

Calculations for this study (see Chapter 3) showed that the use of sub-asymptotic species density as a measure of diversity showed the familiar pattern of higher riparian “richness”, but after rarefaction this pattern was reversed. McCabe and Gotelli (2000) showed the same effect in an assemblage of stream macroinvertebrates. The problem of using sub-asymptotic species density in this way is easily explained. Consider two area-based samples taken from two separate populations. The first sample consists of 2000 individuals

evenly distributed among 40 species, the other 1000 individuals evenly distributed among 30 species. Using sub-asymptotic species density as a measure of diversity we would conclude that there were one third more species in the first population (40/30). However, the sample sizes were unequal; twice as many individuals were sampled in the first sample, simply because they were present at higher density. Had we restricted our sampling to 1000 individuals from both populations we would conclude that there were 50% more species in the second sample (30/20). Moreover, because the species accumulation curve is steeper in more even populations (Gotelli and Graves, 1996), assuming a more realistic pattern of relative abundance (i.e. few common species and many rare species) would actually yield fewer than 20 species in the rarefied sample of 1000 individuals, suggesting that diversity was somewhat more than 50% higher than the first. Gotelli and Colwell (2001) claim that most ecological comparisons of biodiversity are actually comparisons of (sub-asymptotic) species density.

However, the problem with using sub-asymptotic species density as a measure of diversity is not simply one of clearly specifying the technique and interpreting the results accordingly. Consider a single population consisting of 500 species distributed evenly among 1000 individuals. Out of this population take two random samples, one of 200 individuals, the other of 100 individuals. Place each of these samples into one-hectare plots and count the number of species in each. On average, the plot of 200 individuals will have 100 species and the other 50 species. Since the plots are the same size, the first plot has a sub-asymptotic species density twice that of the second. Again if we assume a more realistic pattern of relative abundance the species density of the first plot would be more than twice that of the second. This is because the smaller sample would yield proportionally fewer species than the larger. Whatever the pattern of relative abundance,

the problem here is that both plots are merely different-sized samples from the same population. In this case, the differences in sub-asymptotic species density are solely due to differences in abundance rather than differences in species richness or any other measure of diversity. To resolve this and make valid diversity comparisons, the sub-asymptotic species density samples must be rarefied (Gotelli and Colwell, 2001), at which point they become sub-asymptotic species richness comparisons. There seems little point in reporting a statistic that may or may not reflect the attribute of interest (diversity), when the contributing parameters (abundance and species richness) can be easily be expressed separately from the same data.

It may also be argued that sub-asymptotic species richness and density are simply different quantities that tell us different things about the target population. This may be true, however it is clear that sub-asymptotic species density estimates do not necessarily measure species diversity (at least as defined here). Notwithstanding this, there are clearly cases where comparisons of species diversity in relation to area are ecologically relevant. For example, if we wish to compare the number of species between two similar sized areas, it would be prudent to sample a similar number of individuals from each area to make the comparison rather than similar sized sample plots. The first approach would yield useful information on sub-asymptotic species richness (and relative abundance). The second approach would yield only absolute and relative abundance data, and unless rarefaction techniques were used to obtain an estimate of sub-asymptotic estimate of species richness these quantities may not shed light on the question.

Riparian habitats are another pertinent example; they occupy a very small proportion of the landscape but support many of its species (Hewitt, 1990). Indeed, a simple calculation

based on the asymptotic species richness estimates presented in Chapter 3 (Upslope, 126 spp. estimated over 92% of the Mulga Lands compared to Riparian, 104 spp. estimated over 8% of the landscape), suggests that the number of species per unit area (i.e. species density) in riparian habitats was nearly ten times (i.e. $(104/0.08)/(126/0.92) = 9.49$) that of the upslope habitats, despite only slight differences in species richness. Although there are other issues involved (e.g. riparian-upslope linkages), this sort of statistic may be crucially important for conserving biodiversity (e.g. reserve acquisition). For example if the goal is to maximise the number of species conserved, and that it can be assumed that this is best achieved by maximising the proportion of habitat committed to reservations, then acquiring 1000 ha of riparian habitat would be much more effective than acquiring a similar area of upslope habitat. Indeed, such statistics may also suggest that conserving upslope habitats may be best achieved by landholder incentives, clearing controls, or by other means not involving acquisition.

Comparisons of riparian and upslope diversity may also be complicated by other sources of bias. Although riparian habitats are commonly characterised as diverse and heterogeneous (see Chapter 1) most riparian-upslope comparisons sample only a limited number of upslope communities within a bioregion. In many landscapes, upslope areas potentially support a much greater range of habitat types, patch sizes, successional stages and may experience strong temporal resource fluctuations leading to a complex spatio-temporal habitat mosaic. In the same way that habitat heterogeneity has been linked to diversity in riparian areas (see Chapter 1), such configurations of upslope habitats should lead to similar patterns of upslope beta diversity among wildlife assemblages. Although it is not possible to generalise this to upslope areas in all landscapes, it is notable that sites for this study were spread (in space and time) across the entire bioregion and sampled a range of

upslope habitats, with the consequence that overall bird diversity was strongly influenced by high beta diversity in upslope areas (Chapter 3).

Interhabitat linkages will also influence riparian-upslope diversity comparisons. In general, interhabitat movements should decrease diversity differences between habitats; the more movement that occurs the more similar the assemblages will appear. This is likely to be particularly so for species richness which is insensitive to variations in relative abundance (see Brown *et al.*, 2001). In this study, very few species were found exclusively in either habitat (Chapter 3). In fact, only one of 38 species that were common enough to be analysed was found exclusively in either habitat (splendid fairy-wren; Table 3.2), despite apparently larger differences in the asymptotic estimates (104 species from riparian sites compared to 126 species from upslope sites; Figure 3.3). As noted (Chapter 3), this apparent anomaly is likely to reflect the short (two-year) duration of the study. However, in the context of substantial interhabitat exchange and longer-term observations, we might expect these “asymptotic” estimates to converge, as individuals respond to temporal variation and larger samples reveal that rare species also use both components of the landscape. Even if some rare species do not use riparian habitats, riparian-upslope comparisons of species richness based on short-term snapshots will underestimate the similarity in species richness between riparian and upslope areas. Clearly, the use of species richness will emphasise similarities in riparian and upslope habitats but this measure of diversity does not account for the relatively large variations in relative abundance that may exist between riparian areas and other parts of the landscape (Chapter 3).

While problems with the way in which diversity has been measured suggest the need to question the universality of high wildlife diversity in riparian habitats, there is also an important point underlying the interpretation of riparian-upslope biodiversity comparisons. Observations of high riparian diversity have typically been used to imply that these habitats are in some way “superior” (see Knopf and Samson, 1994; Chapter 1). High species diversity is thought to reflect and influence important ecological processes (Naeem, *et al.*, 1994; Tilman, 1996; Chapin, *et al.*, 1998), and implicitly or explicitly underpins many conservation studies (May, 1988). Since the results of this study suggest that, at least over short time scales, upslope species richness is higher, then perhaps upslope habitats are “superior” and should be a priority for conservation. Clearly however, if as suggested in this study, riparian habitats have an important, if not critical, role in sustaining upslope bird assemblages, the neglect of riparian habitats could have disastrous and counterproductive consequences for the regional avifauna. Although few would advocate making conservation decisions on diversity comparisons alone, this scenario highlights the need to understand the processes that regulate the community, and interpret such comparisons accordingly.

6.3 A conceptual model of avifaunal community organisation in the Australian arid zone.

6.3.1 Introduction

Although there is a clear conceptual understanding of the ways in which the surrounding landscape influences the form and function of riparian areas (e.g. Gregory *et al.*, 1991; Malanson, 1993) much less is known about the ways in which terrestrial

wildlife use both riparian and upslope components of the landscape, despite a large body of literature dealing with riparian-upslope differences (Chapter 1). It is clear from this study, that there may be strong interrelationships suggesting that many species (almost all in this study) use both components of the landscape, but no attempt appears to have yet been made to develop general or regional models to explain (and ultimately predict) the ways in which birds (or other wildlife) utilise the riparian-upslope habitat complex. In many arid zones (including those in Australia; see Chapter 1) spatial variation in edaphic conditions and strong temporal controls on productivity have a dominant influence on ecosystem processes (Wiens *et al.*, 1985; James *et al.*, 1995; Ludwig *et al.*, 1997; Huxman *et al.*, 2004). Is it possible that a set of relatively simple rules underpin avian community organization in the Mulga Lands and elsewhere in the Australian arid zone?

The purpose of the conceptual model outlined below is twofold; firstly to synthesise the findings of the previous chapters in this study, and secondly to provide a framework to advance our understanding of some of the processes that may structure terrestrial bird communities in the Australian arid zone. In this context it is a conceptual tool, which provides a landscape-scale rationale to test specific ideas about the overall bird community. More detailed models are clearly needed to predict individual species and fine-scaled responses. Accordingly, in this section I: (1) use the results of this study to develop a conceptual model to predict relative differences in a number of key attributes of the regional bird assemblage (abundance, dominance, the probability of inter-habitat movement, species richness) and; (2) use the model to consider how birds might vary their use of the landscape in response to two extremes of environmental variability

(drought and production arising from extensive rainfall). I also discuss the model's broader applicability to terrestrial bird communities in other biomes.

6.3.2 The model and its underlying gradients

Spatial variations in productivity have often been used to explain differences in riparian and upslope bird assemblages (Chapter 1). However, rather than considering differences in productivity as static feature of a specific habitat or biome, productivity may be as much a temporal concept as it is a simple reflection of spatial patterns. This may be especially so in arid and other resource-limited biomes where the temporal availability of a limiting resource (e.g. rainfall) has a major influence on biological production (Barker and Greenslade, 1982; James *et al.*, 1995; Ludwig *et al.*, 1997; Roshier *et al.*, 2002). As noted in Chapter 4, arid zone birds make use of a wide variety of adaptive strategies to cope with harsh and uncertain conditions (Davies, 1976; Dawson, 1976; Rowley, 1976; Schodde, 1982; Astheimer and Buttemer, 2002) but almost all birds are capable fliers, giving many the potential to avoid stressful situations and exploit productive resources when and where they occur (Schodde, 1982; Chan, 2001; Griffioen and Clarke, 2002; Kingsford and Norman, 2002). In a landscape with weak inter-habitat linkages, temporal fluctuations in community attributes such as abundance, dominance and species richness might be seen primarily as a function of differential mortality and local recruitment. However in a landscape characterised by strong spatial and temporal variability, the ability to move between habitat patches will also influence these attributes. Many of the results of this study suggest that inter-habitat movements may have a significant role in structuring Mulga Land bird assemblages over both space (Chapter 3) and time (Chapter 4). The response of the bird community can thus be seen

as a dynamic function of spatial and temporal resource gradients largely mediated by movement (Fig. 6.1).

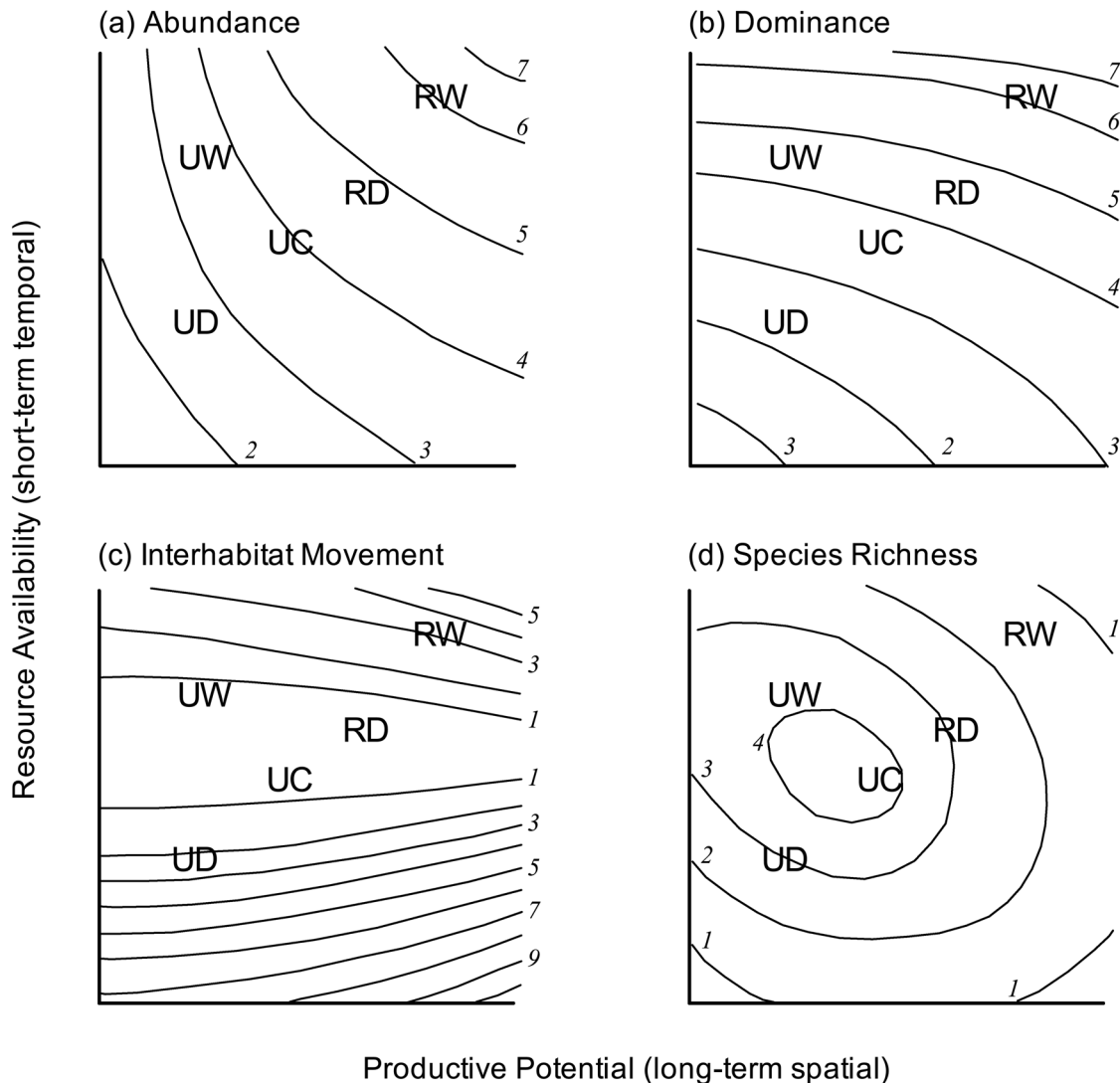


Figure 6.1 Hypothesised responses of the Mulga Land terrestrial bird community to spatial and temporal variation in productive resources. The Productive Potential axis represents long-term cumulative outcomes of prevailing spatial and temporal productive processes (e.g. spatial variation in nutrient status, soil moisture, vegetation biomass). The Resource Availability axis reflects the short-term availability of productive resources (e.g. rainfall) relative to other habitats in the landscape. The scaling of the axes on all four graphs are the same. Isolines represent a mean response surface for the relevant attribute (abundance, dominance, interhabitat movement, species richness) across the entire landscape. Isoline values are indicative only and do not imply a specific origin. Site types used in this study are located with respect to their presumed mean levels of long-term productive potential and short-term resource availability. The model predicts that on average, birds will be more abundant (a), have higher levels of species dominance (b) but lower species richness (d) in RW than UD habitats. Compared to the other site types, birds in RW and UD habitats also will be more likely to move to another habitat (c). See text for further explanation.

The spatial gradient reflects the functional continuum in the Australian arid zone (noted previously; Chapter 1) that extends from dry, infertile and sparsely vegetated parts of the landscape to depositional areas such as riparian zones where nutrients concentrate, water is more readily available, and the vegetation is tallest and most structurally complex (Stafford Smith and Morton, 1990; Ludwig *et al.*, 1997). The model assumes that spatial differences in above-ground vegetation structure (cover and height) reflect: (1) the long-term cumulative outcomes of the prevailing spatial and temporal productive processes; and (2) resources available directly to animals such as terrestrial birds that exist higher up the food chain. The implicit assumption that standing crop reflects productive potential is based on studies of the Australian rangelands (see review of Ludwig *et al.*, 1997) which have revealed that “runon” areas produce more growth for a given rainfall trigger and also support a higher standing crop than similar “runoff” parts of the landscape. An important consequence of this is that the spatial gradient also reflects long-term temporal variations. Clearly, poorly vegetated parts of the landscape may experience strong production pulses but overwhelming temporal limitations on resources prevent the accumulation of biomass. Such ephemeral habitats are considered to have relatively low long-term productive potential but may periodically have high resource availability (see below).

At any point in time, the temporal gradient (Fig. 6.1) reflects the short-term availability of productive resources (light, water, nutrients, temperature etc.) relative to other habitats within the bioregion. For any given habitat, resource availability will fluctuate about a mean, but different habitats may have different means and variances. When resources are abundant there are few temporal restrictions on production, whereas at low levels of resource availability, one or more temporal factors severely limit

productive outcomes. There are many temporal factors that may affect productive outcomes for arid zone birds (James *et al.*, 1995). These include abiotic factors such as rainfall, seasonal and diurnal temperature and humidity fluctuations, disturbance by fire, storms and flooding, and temporal variation in biotic phenomena such as flowering, nectar and seed production, grazing impacts, competition and predator-prey dynamics.

For each bird community attribute (abundance, dominance, the probability of inter-habitat movement, species richness; Fig 6.1 a-d respectively), isolines were used to define a response surface where differences in “elevation” represent relative differences in the attribute. The shape of each surface was informed by empirical observations made during this study (site type responses; see Chapters 3, 4 and 5) combined with theoretical considerations (outlined below). Site types were located within the response domain formed by the two gradients, on the basis of the following a priori classification: highest to lowest, presumed average productive potential, $RW > RD > UC > UW \geq UD$; highest to lowest, presumed average resource availability $RW > UW > RD \geq UC > UD$. Site type rankings along the productive potential (spatial) axis were based on a biomass index calculated as the sum of the percentage cover estimates for the lower, middle and upper vegetation strata multiplied by the height of the upper strata. Site type rankings along the resource availability (temporal) axis were based on the amount of water present near each site. For the purposes of describing the model further, each site type is initially represented as a fixed average location to consider overall patterns of response (Section 6.3.3 below). The ways in which environmental variability may influence these attributes are discussed in Section 6.3.4.

6.3.3 Predicted responses for key bird community attributes

The model (Fig. 6.1) predicts that for any given level of productive potential (e.g. nutrient status) bird abundance should vary with patterns of resource availability and *vice versa*. Maximum abundance is predicted at sites of high productive potential when limiting resources are constantly available (e.g. RW site types; Fig 6.1a) whereas the lowest abundances are expected at less productive sites when one or more important resources are limiting (e.g. UD site types; Fig 6.1a). However the relationship between the gradients may not be linear. As resource limitations decrease, abundance increasingly reflects productive potential. Similarly, at high productive capacity, differences in abundance should increasingly reflect resource availability patterns, and at low levels of resource availability abundance is inhibited, most noticeably at low levels of productive potential. These predictions are consistent with the responses observed in this study (see Fig 5.3a), and when considered in terms of a simple riparian-upslope dichotomy, the vast majority of studies from other taxa and biomes (see Chapter 1).

The gradients also have consequences for patterns of species dominance (Fig. 6.1b). Increasing resource availability implies less abiotic disturbance (Krebs, 2001), allowing biotic processes to play a more significant role in structuring the bird community (Wiens, 1984). At high levels of resource availability (low disturbance), the processes that lead to competitive exclusion are likely to be favoured, and it is predicted that this will lead to increases in species dominance (Tilman, 1982). The numerical dominance of species such as the white-plumed honeyeater and the yellow-throated miner was particularly evident in riparian habitats (Chapter 3). Both species were commonly

observed in large aggregations where they aggressively mobbed intruders, repelling them from their preferred habitat. At lower levels of resource availability (high disturbance) biotic interactions (such as competition) are likely to be less important, and consequently dominance is predicted to decrease. However, in extremely harsh and unpredictable environments (very low resource availability and productive potential) dominance may again increase as stochastic reductions in species abundance cause local extinctions and extant species account for progressively larger proportions of overall abundance. Thus, providing disturbance affects most species, more even abundance distributions should arise at some intermediate level of resource availability. The more even upslope abundance distributions observed in this study (Fig 3.2) are consistent with this prediction.

Over small spatial scales, a further consequence of the interplay between biotic and abiotic forces is the facilitation of inter-habitat movements. Competitive interactions that are likely to prevail when and where many resources are abundant and predictable (e.g. riparian areas) should put pressure on birds to seek to meet their needs in adjacent upslope habitats. On the other hand, if some essential resources are available exclusively or more reliably in riparian habitats then many of the species that spend most of their time in upslope habitats may need to visit riparian areas on a regular basis. Between these extremes it is likely that the probability of inter-habitat dispersal will be lower. Thus, the hypothesised response surface (Fig. 6.1c) strongly reflects the resource availability gradient especially at higher and lower values. The model also predicts that the probability of interhabitat movement will be highest in highly ephemeral (i.e. low resource availability, high productive capacity) and highly productive habitats (i.e. high resource availability and productive capacity). Although the probability of interhabitat

movement was not assessed directly in this study, the spatial (Fig. 3.3) and temporal (Fig. 4.4) patterns of species composition observed appeared to be generally consistent with these predictions.

The hypothesised response for species richness is more speculative (Fig. 6.1d). This is because the potential mechanisms that determine species richness (and other measures of diversity) are many, and their interactions and relative importance cannot easily be predicted (see Rosenzweig, 1995; Krebs, 2001). Nonetheless, a likely pattern can be approximated by considering the common gradients in relation to: (1) productivity-diversity patterns evident from the literature at local and regional scales; (2) directions suggested by the hypothesised responses for abundance, dominance and inter-habitat dispersal (Figs. 6.1a, 6.1b and 6.1c respectively) and; (3) observed variation in sub-asymptotic species richness across site types (Fig 5.3a). As there is also uncertainty related to the long-term differences in species richness between site types (Section 6.2 and Chapter 3), Figure 6.1d assumes a timeframe and sampling intensity similar to this study.

Recent reviews of productivity-diversity relationships suggest that different patterns emerge at different scales, across habitats and taxa, although among birds and mammals both positive and unimodal relationships seem to be most common (Waide *et al.*, 1999; Mittelbach *et al.*, 2001). In terms of the axes, a positive productivity-diversity relationship would mimic the shape of the hypothesised abundance response (Fig. 6.1a), and a unimodal response would peak at some intermediate level of resource availability. Although it is likely that some of the positive relationships reported in the literature arise from comparisons of productivity samples taken from the rising portion of an

underlying unimodal relationship (Waide *et al.*, 1999), a unimodal relationship is favoured here for the following reasons. First, in this study, species richness was lower at riparian sites, even though these areas are likely to be more productive (see Chapter 1). Second, for any given level of abundance, changes in diversity (including species richness) are an inevitable outcome of changes in species dominance. Indeed, unless the probability of local extinction is inversely proportional to species abundance, increases in species dominance will lead to decreases in species richness as the less common species are extirpated. This should put downward pressure on species richness at higher abundances and in very harsh and unpredictable environments (Fig 6.1b). Third, this pattern is likely to be further reinforced by inter-habitat movements, which suggest maximal faunal mixing at intermediate levels of resource availability and productive potential (resulting from higher dispersal probabilities at UD and RW sites, Fig. 6.1c). Fourth, although higher concentrations of species (and individuals) in riparian areas have been widely attributed to enhanced structural and/or floristic diversity in riparian habitats (Chapter 1) this influence, if it occurred, was not sufficient in this study to suggest a positive productivity-diversity relationship.

6.3.4 The influence of environmental variability

In the Australian arid zone, extreme events such as drought and production arising from extensive rainfall have a major role in structuring biotic assemblages (Stafford Smith and Morton, 1990; James *et al.*, 1995). Any conceptual framework that attempts to describe differences in biotic organisation and inter-relationships between different parts of the landscape must also be capable of predicting responses to such events. To illustrate some of the ways in which birds might respond to environmental variability,

the model is used to develop a set of predictions for each of the community attributes based on two extreme but relatively common Australian arid zone scenarios, drought and production pulses after extensive rainfall (Figs. 6.2, 6.3, 6.4, 6.5).

Due to the explicit specification of a temporal axis, the model described above (Fig. 6.1) can readily accommodate temporal variation. However, as changes in relative abundance arise from two processes, movement and the balance between mortality and local recruitment, it is convenient to model this dynamic as a two-step process. The first step involves the relocation of individual site types on the resource availability axis to reflect the desired deviation from the mean (e.g. due to drought). This causes changes to the absolute and/or relative positions of the site types on the abundance response surface (Fig. 6.2), initiating passive changes in mortality and recruitment. However, this is not instantaneous, and changes to the positions of the site types also imply changes to interhabitat movement probabilities (Fig 6.4). In the second step, individuals react to these new conditions by actively moving. As a result, interhabitat movement may alter the patterns of initial abundance (Fig. 6.2) and hence the abundance response surface itself. Changes to abundance arising from temporal deviations in environmental conditions will therefore, consist of an increment due to recruitment and mortality, and another arising from the movement feedback.

Although the balance of mortality and recruitment ultimately determines absolute abundance, it is proposed that patterns of relative abundance within arid zone bird communities are most strongly influenced by dispersal. This is because movement responses can be almost instantaneous, whereas mortality and local recruitment processes for birds (and other mobile fauna) are likely to operate at longer and less

responsive time scales. In theory, feedback imbalances of this nature have the potential to destabilise abundances by facilitating unchecked population growth or decline (DeAngelis and Waterhouse, 1987). However, in highly variable environments stochastic forces may dampen or extinguish these influences (Wiens, 1984). Nonetheless, it is suggested that temporal fluctuations in the environment will cause site types to move up and down the resource availability axis (within the range of their variation) and response surfaces to deform and reform.

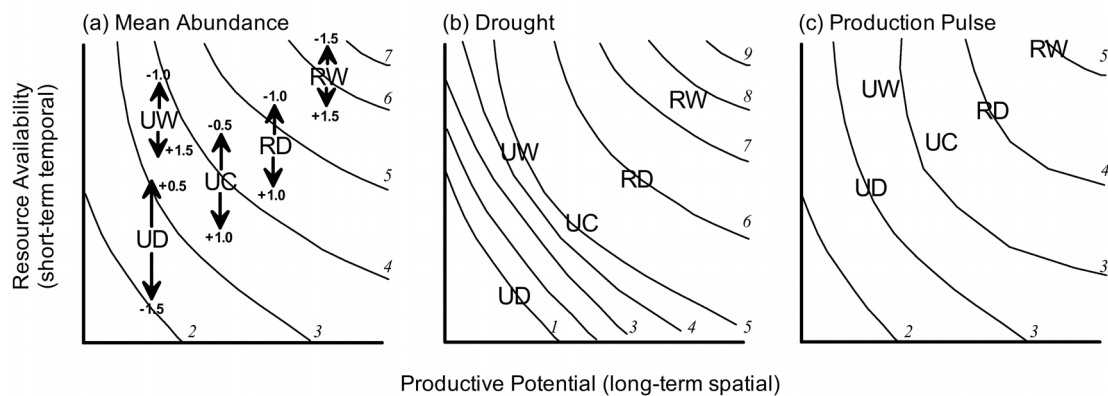


Figure 6.2 Hypothesised abundance responses of the Mulga Land bird community to spatial and temporal variation in productive resources: effects of drought and production pulses. (a) Mean abundance response from Figure 6.1. The arrows associated with each site type represent the expected magnitude and direction of change in resource availability under the drought and production pulse scenarios. Under drought it is assumed that resource availability will decrease in all site types (downward arrows) but most notably at upslope locations away from water (e.g. UD site types). Similarly, during production pulses resource availability is assumed to increase (upward arrows) compared to the mean position. Numbers associated with each arrow indicate the predicted change in abundance, with respect to the predicted mean response as interpolated from the isolines (the sign indicates the direction of change). The “new” response surfaces and positions of the site types and are shown for each scenario; (b) drought and (c) a production pulse following extensive rainfall. Under drought it is predicted that abundances at UD site types will decrease markedly (2.5 to 1.0; 2.5 from the mean response isoline less 1.5 due to mortality and movement to drought refuges such as riparian habitats; see graph (a)) whereas RW habitats may experience a slight increase in abundance (6.0 to 7.5; 6.0 from the mean response isoline plus 1.5 due to individuals seeking refuge in these areas; see graph (a)). Thus, under drought (b) the abundance response surface will be steeper than the mean response surface (a). The opposite pattern is expected for abundance under a production pulse (c) where the response surface will be flatter than the mean response surface (a). See text for further explanation.

Under drought conditions all site types would be expected to suffer production losses, although the most acute decreases in resource availability are likely to be associated with upslope habitats away from water (e.g. UD site types; see Ludwig, *et al.*, 1997). All site types will thus “migrate” varying distances down the resource availability axis, and in doing so, will be repositioned on the mean response surfaces (downward arrows, Fig. 6.2). However, the new positions of the site types on the mean dispersal surface (Fig 6.4) suggest that birds in the UD, and to a lesser extent UC, sites will experience a substantial increase in the need to move, whereas change in the other site types will be negligible (RD, UW) or may reduce in RW habitats, as individuals avoid expensive forays into the drought-affected landscape. This should cause a decrease in the UD abundances as individuals move out, and may also contribute to increased abundances of the other site types, if these upslope species seek refuge in UW, riparian, or nearby UC habitats. Under this scenario, the abundance response surface will therefore steepen toward the UD site types (Fig. 6.2b).

This pattern of abundance contrasts strongly with that predicted during production pulses (Fig. 6.2c). In this case, bird densities in riparian areas are expected to decrease, as riparian species seek to take advantage of upslope resources and upslope species repopulate. There may also be decreases in UW and perhaps UC habitats as individuals disperse into the surrounding landscape. In response to these changes, the abundance response surface is expected to flatten (Fig. 6.2c). Riparian-upslope variations in abundance observed between 1997 (drought) and 1998 and during low rainfall in this study were generally consistent with these predictions (Chapter 4).

The predicted pattern for species dominance under these scenarios remains speculative (Fig. 6.3). Riparian sites (RW and RD site types) are expected to experience modest declines in dominance in both circumstances. This is because favourable conditions should encourage riparian-preferring species to exploit upslope resources, decreasing dominance, but when conditions are difficult many upslope species may seek refuge in riparian habitats, also decreasing dominance. These predictions are consistent with the observations from Chapter 4; during high rainfall many riparian-preferring species appeared to disperse into upslope habitats while higher numbers of birds and species were observed in riparian areas during extended drought (1997) than at other times.

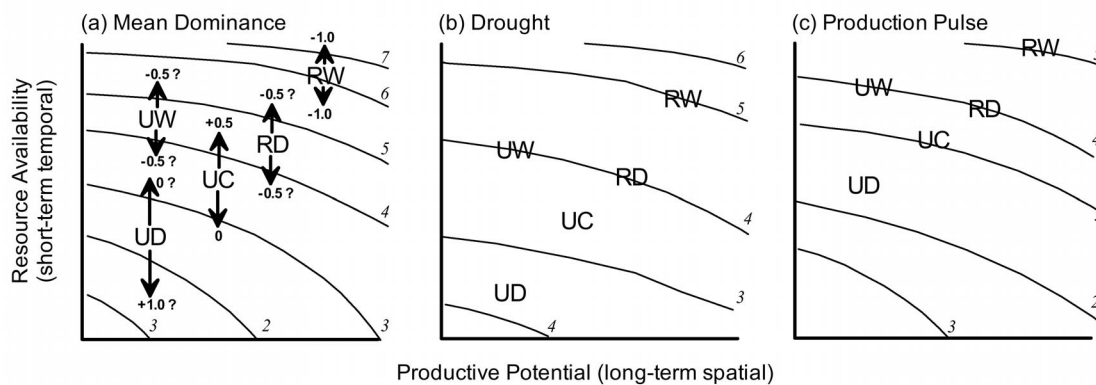


Figure 6.3 Hypothesised dominance responses of the Mulga Land bird community to spatial and temporal variation in productive resources: effects of drought and production pulses. (a) Mean dominance response from Figure 6.1. The arrows associated with each site type represent the expected magnitude and direction of change in resource availability under the drought and production pulse scenarios (downward and upward arrows respectively). Numbers associated with each arrow indicate the predicted change in dominance, with respect to the predicted mean response as interpolated from the isolines (the sign indicates the direction of change). The “new” response surfaces and positions of the site types and are shown for each scenario; (b) drought and (c) a production pulse following extensive rainfall. See text for further explanation.

During severe drought the number of individuals (Fig. 6.2) and species (Fig. 6.5) able to persist in UD habitats is expected to decline. As species die out or seek refuge elsewhere, dominance might increase as the extant species will account for progressively larger proportions of overall abundance. Conversely, at upslope sites near

riparian areas (UC site types), favourable conditions are expected to result in modest increases in dominance due to a proportionally stronger influence from riparian species. But during drought, these areas are likely to host additional individuals of similar species composition from other upslope areas, resulting in little or no change in average dominance. As a result of these patterns it is suggested that under the production pulse scenario the response surface may shift up the resource availability axis and flatten, but during drought the mean response surface may flatten at high resource availability and steepen at low resource availability.

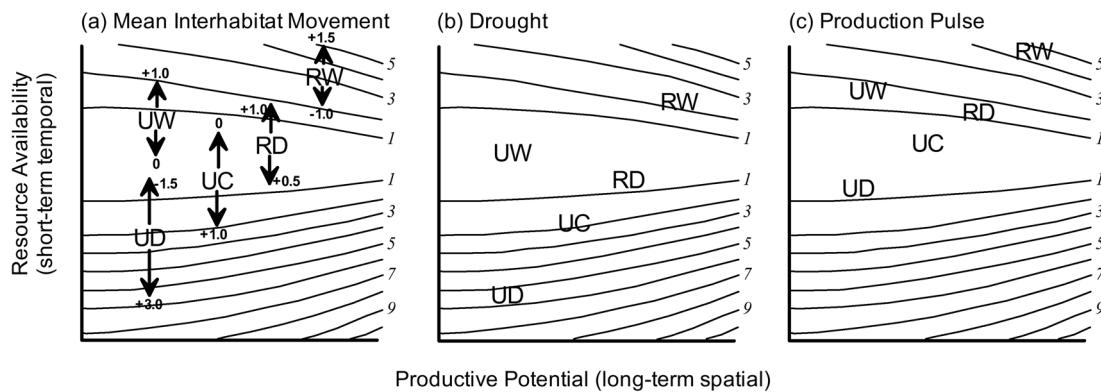


Figure 6.4 Hypothesised Interhabitat movement responses of the Mulga Land bird community to spatial and temporal variation in productive resources: effects of drought and production pulses. (a) Mean interhabitat movement response from Figure 6.1. The arrows associated with each site type represent the expected magnitude and direction of change in resource availability under the drought and production pulse scenarios (downward and upward arrows respectively). Numbers associated with each arrow indicate the predicted change in interhabitat movement, with respect to the predicted mean response as interpolated from the isolines (the sign indicates the direction of change). The “new” positions of the site types and are shown for each scenario; (b) drought and (c) a production pulse following extensive rainfall. In this case the response surface is the same for all scenarios (a-c) See text for further explanation.

Unlike abundance and dominance (Figs. 6.2 and 6.3 respectively), which were both assumed to respond to the interhabitat movement surface, predicted changes to the propensity of individuals to move between habitats (Fig. 6.4) can be obtained directly from the mean response surface for this attribute (i.e. the model does not assume any

feedbacks that would deform the response surface under either scenario). Under the drought scenario, the probability of interhabitat movement is thus predicted to increase at UD and to a lesser extent UC site types as species and individuals seek refuge in less hostile parts of the landscape (e.g. riparian areas). The model predicts that RW site types will experience a slightly reduced dispersal probability under drought, reflecting the interplay between the refuge provided in these areas and the need to relieve increased competitive interactions at this time. On the other hand, when conditions are good, proportionally greater increases in production away from riparian areas are expected to increase dispersal into the surrounding landscape, especially for RW site types. However, at this time, individuals from UD site types are predicted to experience a reduced need to move outside their preferred habitats. These temporal predictions are generally consistent with the findings detailed in Chapter 4.

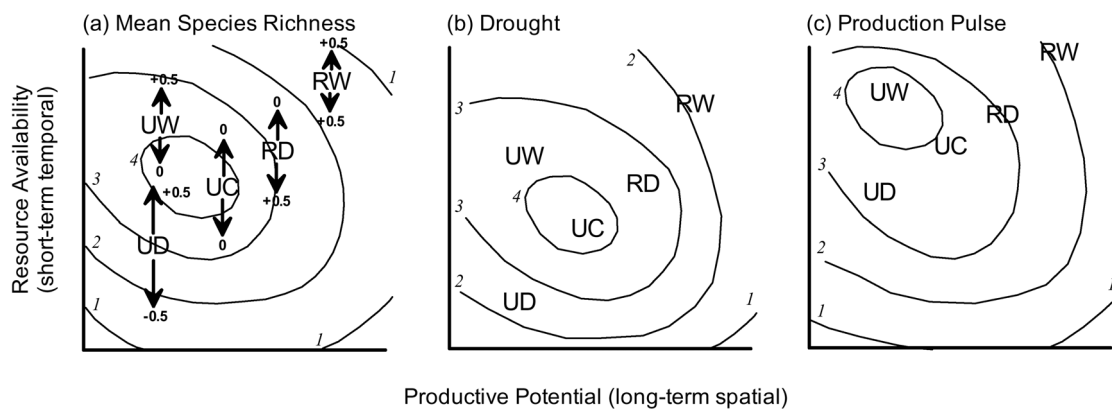


Figure 6.5 Hypothesised species richness responses of the Mulga Land bird community to spatial and temporal variation in productive resources: effects of drought and production pulses. (a) Mean species richness response from Figure 6.1. The arrows associated with each site type represent the expected magnitude and direction of change in resource availability under the drought and production pulse scenarios (downward and upward arrows respectively). Numbers associated with each arrow indicate the predicted change in species richness, with respect to the predicted mean response as interpolated from the isolines (the sign indicates the direction of change). The "new" response surfaces and positions of the site types and are shown for each scenario; (b) drought and (c) a production pulse following extensive rainfall. See text for further explanation.

The general prognosis for species richness is one where the response shifts up and down the resource availability axis during landscape-wide production pulses and drought respectively (Fig. 6.5). During drought, species richness is expected to increase in riparian areas and UW site types, as many will need to visit these areas to obtain water or other resources. Local extinctions appear most likely in UD site types, and this is expected to reduce species richness in these areas. Due to their closer proximity to essential resources, local extinctions should be much less likely in other site types. During widespread production pulses, species richness is predicted to increase in UD and UW sites as result of dispersing riparian species. It is also expected to rise in RW (and perhaps RD) site types, as upslope species exploit riparian resources while riparian bird densities are low (Fig. 6.2). This switching effect was observed in Chapter 4 in response to variations in rainfall. Rises in UC site types are expected to be less likely because of similar species compositions to riparian and other upslope habitats. In general, because of strong linkages between site types (Chapter 3), it is predicted that temporal changes in species richness even under extreme conditions will be modest. This prediction is consistent with Brown *et al.* (2001) who reviewed global long-term trends in taxonomic richness and species composition and found that species richness was relatively insensitive to environmental variability, even those involving large changes in species composition.

6.3.5 Model limitations and application to other biomes

The axes of productive potential and resource availability are spatially and temporally explicit, and probably reflect many of the factors thought to structure avifaunal communities at the landscape scale (e.g. productivity, habitat complexity, spatial heterogeneity and configuration, disturbance, biotic interactions such as competition

and predation). For example, spatial heterogeneity may arise from fine-scale spatial differences in productive potential, especially where resources are less predictable (Stafford Smith and Morton, 1990). Habitat complexity may be promoted by more extended successional development of the plant community in more productive areas such as riparian areas (Thomas *et al.*, 1979a; Brinson *et al.*, 1981). The consequences of biotic feedbacks (such as competitive exclusion) may also be more apparent in riparian areas (or other refuge habitat) where resources may be more reliable (see Pollock, 1998). Disturbance can also be viewed as a limitation on resource availability; disturbance prevents resources from being exploited (Huston, 1979). For birds, inter-habitat movements can compensate for both spatial and temporal limitations on resource availability (this study) and help stabilise communities whose persistence may be threatened by environmental stochasticity or biotic feedbacks (see DeAngelis and Waterhouse, 1987). Indeed, in biomes characterised by climatic uncertainty, the resource availability gradient may represent a broad continuum from equilibrium to non-equilibrium conditions (see Wiens, 1984). As a consequence of these interrelationships, the response domain used for the model may be applicable to many cases where it is necessary to explain local spatio-temporal patterns in bird community structure. However, as the model's response surfaces are expected to vary with fluctuations in the environmental conditions, this component of the model is clearly more fluid, and may need to be "customised" to suit other biomes. Nonetheless, it is notable that even under extreme conditions (Figs. 6.2, 6.3, 6.4, 6.5), hypothesised changes to the mean response surfaces for each bird community attribute retained their general shape, and hence the general spatial and temporal relationships proposed under the mean scenario (Fig 6.1).

The model makes a number of assumptions (noted previously) that will affect its efficacy both in the Australian arid zone and elsewhere. In broad terms these involve the assumptions: (1) that birds will respond to spatio-temporal variations in the availability of productive resources; and (2) that this can occur rapidly because birds are capable of landscape-scale movement.

Perhaps the most significant weakness relates to the link between primary production and bird responses. Although the model does not rely heavily on secondary production, trophic efficiencies for higher level consumers such as terrestrial birds are typically very low (<2% Humphreys, 1979, 1984) and it is possible that many increments in plant growth will have little or no influence on either patterns of bird recruitment and mortality, or movement. This can be partially offset by using aspects of vegetation structure (eg biomass, cover, height etc.) as proxies for the longer-term spatial influence of productive potential, however this has its own problems. In particular, this approach equates very simple measures of vegetation structure with habitat quantity and quality. In many arid systems this may be reasonable as there are quite straightforward relationships with productive potential (e.g. nutrient status, soil moisture etc.). In many arid areas, as productive capacity increases vegetation structure also increases, firstly in terms of cover and then height (Ayal *et al.*, 1999) with the consequence that fertile sites support taller and more complex vegetation. In addition, this relationship is also commonly reflected in broad spatial patterns of floristic composition. For example in the Australian arid zone, eucalypts are typically associated with woodland and forest formations, acacias such as mulga dominate the taller shrubland communities while chenopods dominate low shrublands. Therefore, in such environments, crude measures of vegetation structure are likely to reflect many important habitat features (e.g. biomass,

vegetation volume, structural complexity and even floristic differences). However, the model will be less successful where important habitat features are not so strongly correlated. For example, because of differing metabolic processes, some wetlands may be consistently productive without the long-term development of tall and complex vegetation. It may also fail where there are other overriding influences on bird habitats. For example in highly fragmented habitats, the bird response due to simple structural or floristic characteristics of the vegetation may be overwhelmed by fragmentation effects (e.g. edge, matrix, area and connectivity influences) and consequently account for only a limited proportion of overall variation.

As the model was designed as a general tool to describe an entire regional bird assemblage, difficulties may also arise if attempts are made to predict movement responses of specialised species groups or individual species. Specialised groups (e.g. granivores, nectarivores etc) and individual species are much more likely to respond to specific habitat components which may not be correlated with overall patterns of vegetation structure. In addition, reproductive or behavioural constraints (such as breeding, raising young or maintaining territories) may effectively prevent some species from being able to exploit available resources in other parts of the landscape. In these cases it may be possible to revise the response surfaces to more accurately reflect the observed responses of individual species or functional groups.

Also, in its current state, the model does not explicitly accommodate larger scale inter-bioregional movements (migration). Although patterns of inter-bioregional movement were inferred in this study (Chapter 4) there was no assemblage-wide response and as a consequence net turnover was modest. However, as the model is concerned with relative

(rather than absolute) differences in the community attributes, strong patterns of migration should only be problematic if migrants have highly specialised needs that are not reflected in overall vegetation structure.

Although the model was constructed as a conceptual framework to explain and synthesise the observations and processes thought to influence the avifaunal community in the Mulga Lands, it may nonetheless provide a useful framework for evaluating spatial and temporal variation in bird communities from other biomes. In other biomes the relative placement of site types (representing habitats in the landscape) and their expected movement on the response surfaces in relation to temporal change, will vary from those used in this study. Moreover, (as noted previously) the response surfaces themselves may need to be adjusted slightly. Nonetheless, the placement of sites on the axes may be achieved, as it was in this study, by ranking them on both axes in relation to overall bioregional variation.

As an example, the projection of riparian and upslope sites on the response surfaces of the model (Fig. 6.1) is described below for the study of McGarigal and McComb (1992). Although a more thorough analysis might consider minor variations to the response surfaces outlined in Figure 6.1, this approach allows the model to be superficially applied in a very different bioregional setting (central Oregon Coast Range, Pacific north west USA) from the present study.

According to McGarigal and McComb (1992), the central Oregon Coast Range is characterised by mild wet winters and cool dry summers with annual precipitation in the range of 1500 mm to 3000 mm. In a completely forested study area, they observed that

the upslope vegetation supported much higher densities of large tall trees (mostly conifers) and associated snags than the riparian habitats. On the other hand, riparian habitats showed more even stratification of vegetation, with higher densities within herbaceous, tall shrub and mid-story strata. However, unlike riparian floodplains, which concentrate sediments and nutrients, riparian areas in this study area (as noted previously) were associated with deeply incised high-energy streams, indicating a strongly erosional character. This, together with the observations of high upslope biomass, suggest that productive capacity is likely to be lower the riparian habitats. As this study (1) took place in a mesic environment with a relatively predictable temperate climate and (2) both riparian and upslope areas showed different but important habitat characteristics, it is suggested that overall resource availability is likely to be relatively high in both cases. If it can be further assumed that their upslope habitats represent moderately high productive potential within the bioregion, then these site types (riparian and upslope) can be projected onto the hypothesised response domain (Fig. 6.6).

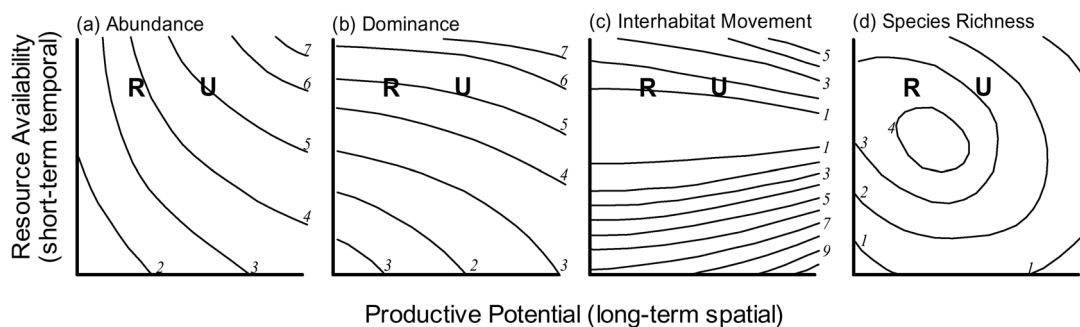


Figure 6.6 Predicted responses of the central Oregon Coast Range bird community studied by McGarigal and McComb (1992) to spatial and temporal variation in productive resources. Site types (R=Riparian, U=Upslope habitats) are located with respect to their presumed mean levels of long-term productive potential and short-term resource availability. Isolines represent a mean response surface for the relevant indicator. Isoline values are indicative only and do not imply a specific origin. The model predicts that on average, birds will be less abundant (a), but more speciose (d) in riparian areas. Similar levels of species dominance (b) interhabitat movement pressure (c) are predicted in both site types. See text for further explanation.

Based on the riparian-upslope configuration and the assumptions noted above, the model (Fig. 6.6) predicts that: (1) bird abundances will be higher in upslope habitats; (2) riparian and upslope levels of species dominance will be similar; (3) both habitats will be subject to modest dispersal pressure; and (4) species richness will be higher in riparian areas than in the adjacent upslope habitat. As predicted, McGarigal and McComb (1992) found higher upslope abundances, but similar levels of riparian and upslope dominance. Although a number of species were observed more frequently in one habitat or the other, they also found considerable overlap in the species composition. Since their riparian and upslope transects were separated by only 400m, it is likely that some of this overlap is due to interhabitat movements, although they did not consider this option. Contrary to the fourth prediction, McGarigal and McComb (1992) reported higher species richness in upslope areas. However, their “richness” estimates were based on sub-asymptotic species density (not richness) and thus did not account for the substantial (app. 60% greater) differences in abundance (see Section 6.2 above). As was the case in the present study, it is possible that their sub-asymptotic species density comparison was inversely related to the result they would have achieved using sub-asymptotic species richness. If this were the case, then Figure 6.3b would correctly predict species richness for their data. Although this single example does not prove the universality of the model, its ability to correctly characterise a bird community from such a different bioregional setting using only a very basic understanding of the habitats suggests that the model may have broader application than the Australian arid zone. Clearly, further work is needed to establish the scope of the model’s applicability.

6.4 Conclusion

This study suggests that, as far as the Mulga Land birds are concerned, the bird communities of riparian and upslope components of the landscape are functionally interrelated. This is despite strong structural and floristic differences in habitat, and the fact that many bird species show distinct preferences for one habitat or the other. Almost all terrestrial species were found in both the riparian and upslope habitats, although their use appeared to be strongly related to spatial and temporal variations in resource availability. As most birds are capable fliers, and changes in relative abundance were rapid, these patterns are likely to more strongly reflect movement between habitats (and in some cases, bioregions), than differences in recruitment and mortality. In fluctuating and unpredictable environments the ability to move between habitats may be an important adaptive strategy to dampen spatial and temporal variations in resources and facilitate species persistence. The overall picture is one of a shared and responsive avifauna.

Variations in the way in which species richness has been measured in riparian and upslope habitats may have contributed to the generalisation that riparian habitats support richer wildlife communities than upslope habitats. The approach taken to measuring richness in this study suggests that this generalisation needs to be reviewed. Indeed, the way in which area-based assessments of diversity are made may have distorted our understanding of the mechanisms that underlie riparian-upslope community structure across different landscapes. It is hoped that the conceptual model developed for this study makes some progress in this direction.

The existence of strong riparian-upslope linkages clearly implies that strategies for the long-term persistence of regional avifaunas require a holistic approach to management (Knopf and Samson, 1994). However, riparian areas occupy only a small proportion of the landscape. For management this may be a double-edged sword; small improvements in management may have far-reaching consequences, but so may minor neglect or habitat loss. It is from this perspective that riparian areas can be seen as critical components of the landscape.

7.0 References

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Appendix 1

Reprint of an article published in *The Sunbird*, Volume 32, No. 1 April 2002 entitled:

Use of riparian areas by terrestrial birds of the Mulga lands – South West Queensland, by Mark B. Kingston, Carla P. Catterall and George S. Kordas.

This reprint has been removed from the thesis.