

Chapter 9. GENERAL CONCLUSIONS

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9.1 The Peery bird community - structure, dynamics and spatial heterogeneity

The Peery study area supported a rich avifauna. A total of 95 native land bird species was recorded in the four year study period which included a severe drought. As expected, the native avifauna was dominated by species of Eyrean and Multifaunal origin. The birds derived from 32 families (Simpson & Day 1993) and well represented families included the cockatoos and parrots, honeyeaters, woodswallows and allies, pardalotes, thornbills and allies, and pigeons and doves.

As in most Australian habitats, the avifauna was dominated by resident species. Over half the birds recorded in censuses were resident and 35% were nomadic. The proportion of nomads at Peery was only slightly higher than the figure of 26% estimated by Keast (1959) for the entire Australian avifauna. The findings of this study contradict early reviews, e.g. Keast (1959), Immelmann (1963) and Serventy (1971), of the Australian arid zone avifauna which suggested that nomadism was the most common strategy adopted by birds in the arid zone in response to environmental unpredictability. A number of other more recent studies in the arid zone, e.g. Wyndham (1978), Brooker *et al.* (1979), Henle (1989) and Badman (1991), do the same. Thirteen per cent of species recorded in censuses were winter or spring-summer

migrants. Numbers of migrants were always low and migrants tended to be specialised aerial feeders. Possibly the variability and unpredictability of the arid environment makes it unsuitable for specialised feeders which are constrained by regular movement patterns.

The composition of the Peery bird community was highly variable through time and variability between years was greater than seasonal (winter-spring) variability. High temporal variability has also been demonstrated in bird communities in more mesic forests and heathlands (e.g. Ford *et al.* 1985, Pyke & Recher 1988, Hardy & Farrell 1990, Osborne & Green 1992, Slater 1995, Mac Nally 1996). The findings at Peery lend further support to the view that bird communities may fluctuate too greatly to be considered equilibrial (Mac Nally 1996).

Overall, spring breeding predominated, but levels of breeding activity were reduced during the drought. An underlying seasonal pattern to breeding has also been reported in more mesic areas (e.g. Marchant 1992) as have reductions in breeding effort associated with drought. Levels of cooperative breeding at the study site were intermediate between those reported in semi-arid woodland and desert (Ford *et al.* 1988). Opportunistic observations at nests indicated that most known cooperative breeders in the study area were facultative rather than obligate cooperative breeders. As reported by Ford *et al.* (1988) for more mesic eucalypt woodland and forest, cooperative breeders tended to be insectivorous species, which were active rather than passive feeders. Cooperative breeding at Peery was not associated with a ground-feeding habit, as found by Ford *et al.* in their more mesic study area. Cooperative species at Peery were mainly residents and cooperative breeding would enable these birds to receive help and thus make it feasible to attempt nesting even if food was scarce.

Within the study area there was marked spatial variability in the avifauna and this reflected the spatial heterogeneity of the local environment. Avian densities and species richness were especially low on the open plains. Creekline habitats supported the densest and richest populations of birds. Creekline habitats were structurally more complex and more productive than run-off habitats and provided birds with greater and more diverse opportunities for feeding, nesting, roosting and sheltering. About two-thirds of the bird species in the study area drank regularly or occasionally and creeklines provided the most reliable natural sources of drinking water. In more mesic forests and woodlands the species composition and density of

the avifauna is also variable. Gullies tend to support higher densities of birds than drier ridges (e.g. Loyn 1985, Smith 1984). However, the degree of difference between run-on and run-off habitats in arid areas appears to be more pronounced, presumably because there is greater dissimilarity in run-off and run-on habitats in arid areas.

Creeklines supported wide-ranging species such as the Blue Bonnet, Crested Pigeon and Apostlebird, as well as species associated with particular habitat features, such as the Grey-shrike Thrush, White-plumed Honeyeater and White-winged Fairy-wren. The composition of the creekline avifauna reflected an uphill gradient from wetter, eucalypt-fringed creeklines to drier, non-eucalypt creeklines surrounded by shrubland. A number of broader scale studies in more mesic regions of eastern Australia (e.g. Kikkawa 1968, Loyn 1985, Shields *et al.* 1985) have also documented changes in the composition of the avifauna along mesic-xeric gradients. The most mesic creeklines in the study area supported the tallest and most extensive eucalypt woodland and a number of bird species were restricted to them. The 'best' eucalypt creeklines at Peery supported bird densities that matched those recorded in the richest communities in mesic eucalypt forests. The avifauna of the arid eucalypt woodland, however, was less diverse, as it was dominated by just two species, the White-plumed Honeyeater and Tree Martin, and it lacked the large suite of eucalypt specialists which characterise more mesic eucalypt communities. The dominance of the eucalypt bird community in the study area by only two species may reflect the relative lack of floristic and structural diversity in arid eucalypt woodland. In the study area, eucalypt woodland was dominated by River Red Gum and Black Box. Only two other eucalypts, Bimble Box *Eucalyptus populnea* and Gum Coolibah *E. intertexta* occurred rarely in the study area. Eucalypt woodland was confined to narrow strips along creeklines and was surrounded by extensive treeless areas. In arid eucalypt woodland the range of foraging opportunities may not be as great as in more mesic woodland and forest which generally contain more eucalypt species and are a mosaic of different and intergrading woodland or forest types. The White-plumed Honeyeater's consistently high level of indiscriminate aggression may have led to the exclusion of smaller species from the most mesic sections of creekline at Peery. Cases of indiscriminate interspecific aggression leading to the exclusion of species have been documented in more mesic environments in two larger colonial honeyeaters, the Noisy Miner *Manorina*

melanocephala (Dow 1977) and Bell Miner *M. melanophrys* (Loyn *et al.* 1983, Clarke 1984), and noted in the similar-sized and semi-colonial Fuscous Honeyeater *Lichenostomus fuscus* and White-naped Honeyeater *Melithrepius lunatus* (Davis & Recher 1993).

The study area adjoined Peery Lake. In the study period, 55 species of waterbirds were noted on the lake and it supported many thousands of individuals. The lake, however, seemed to have little effect on the terrestrial bird community. When the study began, Peery Lake was full and the salinity of its water was low. Bird densities in transects adjacent to the lake margin may have been increased by the proximity of fresh water. Birds in these transects were occasionally noted drinking at the lake edge. Numbers of Tree Martins were particularly high at this time. The Tree Martins skimmed the lake to drink and hawk, and roosted and nested in eucalypts fringing the lake. As the study progressed, the lake receded and became more saline. In summer 1992-93 it was recharged by local flooding rain. In all censuses subsequent to the first, the lake was at least a quarter of a kilometre from the nearest transect, its margin was bereft of trees and shrubs, and few birds drank from it. A few terrestrial species, for example the Orange Chat and Blue-winged Parrot, favoured the patches of vegetation that grew on the lake bed after the lake receded and probably occurred in the study area proper only incidentally. Several resident and wide-ranging species flew out to feed on the lake bed. The Little Corella, Galah and Pink Cockatoo fed on the fruits of saltbushes which grew on the lake bed and congregated to drink at the exposed lake edge.

Although the highest bird densities occurred in creeklines with a cover of perennial trees or shrubs, the most important feeding substrate in the study area was the ground. Almost half of all feeding observations were made of birds foraging on or from the ground. Different species appeared to prefer to feed on ground with differing covers of herbage, stone and litter, and tended to be selective in the distances from cover at which they fed. Compared to communities of more mesic forest and woodland in eastern New South Wales (Recher *et al.* 1985, Ford *et al.* 1986, Smith & Smith unpublished data), the Peery community was well endowed with specialised ground and aerial feeders, but had fewer representatives from the large suite of birds that specialise on the bark, fruit, flowers and foliage of eucalypts in more mesic areas. The differences between the Peery and more mesic communities reflect differences in foraging opportunities. At Peery, eucalypt woodland was restricted to creeklines

and, as noted above, virtually the only eucalypts present were the River Red Gum and Black Box.

Although many species at Peery were ground-feeders, few nested on the ground. Possibly a heavier predation pressure at ground level than in trees or shrubs has selected against ground-nesting. Only the Emu and the Spotted Nightjar nested on open ground. The large size of the Emu and the cryptic colouration of the Spotted Nightjar and its eggs may have afforded these birds protection from predators. Predation pressure may have been one reason why birds drank mainly from creekline waterholes with a good cover of trees and shrubs. Only aerial drinkers, such as the Tree Martin and Rainbow Bee-eater, and larger birds, such as the Emu, Galah and Little Corella, drank from exposed situations along Peery Lake.

This study has allowed generalisations to be made about the nature of the Peery bird community. An equally, if not even more, interesting revelation of the study has been the number of exceptions at the level of the individual species to these generalisations. The magnitude and direction of population fluctuations of individual species were not consistent. Individual species showed differing degrees of habitat specificity and were associated with different habitat variables. Patterns in the timing and magnitude of the breeding effort of individual species also were inconsistent. The differences between individual species within the community were complex and involved differences not only in resource use and habitat specificity, but also differences in the nature and timing of their responses to environmental variability.

9.2 Factors influencing patterns in the avifauna

The role of competition in determining the structure of communities has been much debated (e.g. Noy-Meir & van der Maarel 1987, Wiens 1989). Classical competition theory developed from the ideas of early naturalists such as Grinnell (1904), Ortmann (1906) and Hiltzheimer (1909). Indeed, it has been claimed (e.g. Hutchinson 1975, Diamond 1978) that a recognition of the importance of competition is implicit in the writings of Darwin. Gause (1934, 1935) used laboratory experiments to show that species too similar in resource use could not coexist, one will eventually competitively exclude the other. By the 1970s the belief that competition is

the dominant biological interaction and that the number of species that can coexist is determined by the number of limiting resources had become widely accepted by ecologists (e.g. Hutchinson 1959, MacArthur & Levins 1967, MacArthur 1972, May 1974).

More recently, the notion that competition is the single predominant factor determining community structure has been questioned. Results of this study at Peery suggested that a number of factors play a part in determining the structure of the avian community. Such a finding is in keeping with a now general acceptance that a range of factors is important (Dunson & Travis 1991). These factors include competition, predation, disturbance, resource heterogeneity in time and space and other types of patchiness, individualistic responses of species to environmental variation, chance, symbiosis, parasitism and disease (e.g. Wiens 1977, 1989, Dunson & Travis 1991, Drake 1991).

Patterns revealed in the Peery study suggested individualistic responses of species to temporal and spatial variability. Population trends of different species over the pre-drought, drought and post-drought periods of the study were not consistent. Among residents, for example, populations of White-plummed Honeyeater and Grey Shrike-thrush were not diminished after the drought, while populations of Chestnut-rumped and Yellow-rumped Thornbills declined by factors of 11 and eight respectively. The differential responses of species to drought may have been a consequence of the different species unique habitat requirements coupled with factors such as the species mobility and the different lags in response to rainfall of the varied plant life forms that provided food. The continuous variability found in the avifauna of creeklines was in keeping with a species-specific response to habitat variability along the arid-mesic creekline spectrum. Species groups were identified in creeklines, but there was considerable overlap between groups and they did not form discrete units. Several factors, for example total eucalypt density, width and height of creekline vegetation, and distance from Peery Lake, were important in determining patterns in avian density and species richness in creeklines, but these were not always the most important factors at the level of the individual species. The considerable variability in the timing and magnitude of the breeding effort of individual species was also indicative of an individual response to environmental variability.

At Peery, interactions between species may also have played a part in determining

the structure of the community. The concerted aggression of the White-plumed Honeyeater, for example, was notable throughout the study. The White-plumed Honeyeater concentrated in eucalypt woodland in the most mesic sections of creekline. Its indiscriminate aggression may have affected the distributions of other species and led to their exclusion from what was most likely a drought refuge. The absence of small species, such as the Chestnut-rumped and Yellow-rumped Thornbills (which fared so badly in the drought), Crimson Chat, White-fronted Honeyeater, Black Honeyeater and White-winged Triller, in eucalypt woodland with high concentrations of White-plumed Honeyeaters was more likely a consequence of the indiscriminate aggression of the White-plumed Honeyeater than a response to a lack of suitable habitat.

Positive associations between species were also evident. In winter, mixed-species foraging flocks of small insectivores were frequently noted. The species composition of flocks was not constant, but variously included the White-winged and Variegated Fairy-wrens, Yellow-rumped and Chestnut-rumped Thornbills, Southern Whiteface, Red-capped Robin, Willie Wagtail and Grey Fantail. Presumably these birds incurred mutual benefits by forming mixed foraging flocks. It has been hypothesised that birds joining these flocks may benefit by increasing foraging efficiency (Krebs 1973, Morse 1978) or by increasing vigilance against predators (Lack 1968, Goss-Custard 1970). Evidence of active predation was encountered in every study period. Predators of adult birds, nestlings and eggs in the study area included avian predators, such as the Collared Sparrowhawk, Black Falcon and Australian Hobby, as well as feral cats, foxes, snakes and goannas. The Willie Wagtail provided a further and simple example of a species appearing to gain a positive benefit by associating with other species. The Willie Wagtail occasionally tagged along with groups of ground-feeding Apostlebirds or Yellow-throated Miners apparently to take advantage of the invertebrates flushed by the larger birds.

There has long been a belief that fluctuations in the densities and relative densities of organisms and in the environments in which they live will influence the structure of communities. A body of theory has developed to address this question and, since most models assume that fluctuations in population densities originate with environmental fluctuations, it has been termed 'variable environment theory' (Chesson 1994). Chesson (1994) outlined a model

to explain the co-existence of many species in temporally variable environments. His theory, like classical theory, requires that species must be sufficiently ecologically distinct to coexist. Chesson's model, however, considers a much broader range of ways than use of resources (which is the major concern of classical theory) in which species can be ecologically distinct. His model predicts that in a fluctuating environment species can use the same limiting resource and coexist if they respond differently to environmental fluctuations. If responses to environmental fluctuations are species-specific, then responses to a fluctuating environment will be asynchronous between species. Environmental fluctuations are then compatible with continuous interspecific competition, but competitive rankings of species may vary through space and time and trends towards competitive exclusion may thus be slowed or reversed (Chesson & Case 1986, Chesson 1994). Variable environment theory emphasises the importance of dynamic features of communities and emphasises species characteristics such as functional responses and life history traits. In the Peery study area, different species had varied life history strategies and responded to environmental variability at different scales and levels. Such differences between species are an integral part of variable environment theory and are discussed in the following section.

9.3 Life history strategies in an arid environment - residency, nomadism and migration

In arid Australia rainfall determines the availability of food, water, shelter and nest sites for birds. The unpredictability of rainfall (Stafford Smith & Morton 1990) coupled with the spatial patterning of landscapes (Friedel *et al.* 1993) results in environmental variability on many spatial and temporal scales. The arid environment also fluctuates asynchronously at different spatial locations and such variability has been termed spatio-temporal (Chesson 1985).

Birds respond to the spatial, temporal and spatio-temporal environmental variability at different scales and levels by employing three different broad life history strategies: residency, nomadism and migration. Nomads and migrants are distinguished on the basis of the regularity and direction of their movements (Davies 1983). In the Peery study area, of birds recorded in censuses, 52% were resident, 35% nomadic and 13% migratory.

The composition of the bird community changed constantly in the study area. The

relative importance of residents, nomads and migrants was temporally variable and the mobile elements were not always present. For residents and nomads year-to-year variations in numbers were greater than seasonal variations. Numbers of winter and spring-summer migrants varied little between years and their comings and goings provided an element of seasonal variation. However, their low numbers made it difficult to discern trends. Like nomads, their numbers are influenced by conditions outside the study area, and possibly beyond the arid zone. The regularity of their movements compared to those of nomads means that, like residents, they must endure the prevailing conditions for a fixed part of the year.

Residents dominated the avifauna before the drought, declined quickly with the onset of drought and were slow to recover after the drought. Before the drought, when conditions were considered average seven nomadic species were present in the study area, the Black-eared Cuckoo, Chirruping Vedgebill, Fairy Martin, Rufous Songlark, Brown Songlark, Mistletoebird and Zebra Finch, but each only in low numbers. During the drought nomads were largely absent. There was a general link between the breaking of the drought and the appearance of large numbers of nomads, especially Zebra Finches and Budgerigars. However, not all nomads fluctuated on the time scale of local rainfall. The population peaks of the various nomads were asynchronous and relatively short-lived. Nomads came and went even when conditions appeared to be good. Species peaked for different reasons. White-fronted Honeyeaters, for example, peaked at the height of the drought in winter 1992 when the Harlequin Eremophila flowers, on which they fed almost exclusively, were abundant. In winter 1992, flocks of Blue-winged Parrots invaded the fringes of the study area and fed on the then prolific fruits of saltbushes growing on the drying bed of Peery Lake. White-browed Woodswallows were most abundant in spring 1992, just before the drought broke, but following a localised thunderstorm.

Trends in the populations of resident species were influenced primarily by local conditions. They may be indirectly influenced by regional conditions through their effect on levels of predator populations. At Peery, residents persisted when conditions deteriorated during the drought by exploiting local spatial habitat variability and by eating a variety of foods. Residents concentrated on the relatively stable food supplies offered by perennial plants which grew in the more mesic portions of the site. Residents were found in all feeding guilds

identified in the study. The foliage, flowers, fruits, seeds and bark of perennials were important feeding substrates for residents. Ground-feeding residents, which tended to be larger than ground-feeding nomads, used a wider range of foods than the nomads. The seasonal differences found in the relative use of feeding substrates by a number of residents illustrated their dietary opportunism. Resident flower/foilage feeders suffered less than other residents in the drought, probably due to the relatively greater stability of their food supply. They fed extensively at eucalypts which tap the most reliable supplies of subterranean water, and like the eucalypts, they were buffered from the effects of short-term drought.

Temporal environmental variation has generally been thought to favour generalists by forcing all individuals to perform a range of activities (Wilson & Yoshimura 1994, see also Schoener 1969, Roughgarden 1972, Slatkin & Lande 1976, Taper & Case 1985, Lynch & Gabriel 1987, Seger & Brockman 1987), whereas more stable environments allow individuals to specialise and have narrower niches. In the absence of temporal variation, habitat choice and negative density dependence favour specialisation, even when the costs (performing activities less well than specialists) of being a generalist are low (Wilson & Yoshimura 1994). In contrast to residents, the greater mobility of nomads allows them to exploit habitat variability at a regional level. Random spatio-temporal variation in rainfall provides nomads with a fair chance that favourable conditions will exist at least in some part of their range and dietary specialisation becomes possible. At Peery, nomads concentrated on a narrower range of food resources than residents. All specialised aerial feeders, apart from the Tree Martin, and the one obligate specialised nectar feeder, the White-fronted Honeyeater, were nomads. All small granivorous birds which specialise on grass seeds, such as the Budgerigar, Zebra Finch, Diamond Dove and Peaceful Dove were also nomadic. For nomadic granivores, short-lived plants were more important providers of seed than perennials.

Resident species at Peery generally showed a regular seasonal pattern of breeding, but the magnitude of the breeding effort was influenced by prevailing conditions. The breeding effort of residents declined when conditions at the site deteriorated and only small numbers attempted to breed during the drought. After two dry years, a localised thunderstorm in spring 1992 was sufficient stimulus to promote breeding in residents and, at this time, residents reached their greatest breeding effort on a per bird basis. Their tendency to breed regularly

could be related to their generalized and opportunistic feeding habits and their exploitation of the relatively stable food supplies found in the mesic parts of the study area. A further factor promoting regular breeding, especially among insectivorous residents, could be their tendency to breed cooperatively. Cooperative breeding behaviour would enable them to receive help and thus make it feasible to attempt nesting even when food was scarce. Scarcity may also discourage dispersal and breeding by helpers/young birds. Residents nested either in perennial plants or on open ground and so, unlike a number of nomads which nested in dense ground-layer vegetation or short-lived plants, for example the Rufous Songlark, Little Button-quail and Crimson Chat, their nesting efforts were not curtailed by a lack of suitable nest-sites during the drought. Residents did not respond to the breaking of the drought with prolonged or aseasonal breeding and a rapid population increase. There was no evidence of a boom-and-bust cycle among residents in response to the sudden flush of plant growth after the drought.

The breeding season of nomads was less predictable than that of residents. In this study nomads did not breed cooperatively and only bred when their relatively specialised foods were abundant. Following the thunderstorm in spring 1992, the only nomad to arrive in large numbers and show a concerted nesting effort was the White-browed Woodswallow, an aerial insectivore. In 1993, when drought breaking rains brought a substantial and sustained improvement in conditions, the nomads that invaded the study area nested in large numbers soon after arrival. The White-browed Woodswallow and Zebra Finch were striking examples of the rapidity with which nomads could complete a breeding cycle.

The three broad categories, residency, nomadism and migration, summarise the different life history strategies in the arid zone. In reality, there is considerable variation within these categories and the categories merge. At Peery, resident species varied considerably in their ability to withstand drought. Of the nomads, the White-browed Woodswallow was the only nomad to take advantage of a temporary improvement in conditions following the thunderstorm during the drought. There was considerable individual variation in the timing and magnitude of the breeding effort within the broad strategy types. Though residents tended to breed in spring, a number, including the Yellow-throated Miner, White-plumed Honeyeater, and Southern Whiteface, also nested in winter. The breeding effort of most residents increased after the drought, but the resident Chestnut-rumped Thornbill and Striated Pardalote, which

nested in each winter and spring of the drought, were not found nesting during post-drought surveys. Though residents were more generalised in their foraging habits compared to nomads, there was considerable variation in the degree of foraging specialisation of species within the two groups. Among residents, for example, the Apostlebird, Australian Magpie-lark and Australian Magpie, fed almost exclusively from a single substrate, the ground. In contrast, the Spiny-cheeked and White-plumed Honeyeaters used each of the six foraging substrates defined in this study.

The three broad strategies appear to lie along a continuum. At Peery, a number of birds classified as residents moved between habitats within the study area as they tracked localised resource fluctuations. The difference between residents and nomads is then only a matter of scale. Such a pattern of behaviour was exhibited by the Spiny-cheeked Honeyeater, a number of which were individually colour-banded. Spiny-cheeked Honeyeaters congregated on the plains when the Harlequin Eremophila flowered, in the lower reaches of the most mesic creeklines when the River Red Gum and Black Box flowered, and in the more ephemeral creeklines when the Boobialla bushes fruited. Some species that are typically resident may desert an area when conditions are extremely poor. A number of residents in the study area experienced large population fluctuations which suggested a nomadic or migratory component in their populations. The Tree Martin, for example, was especially numerous when Peery Lake was full, suggesting a nomadic component, and was consistently more abundant in the spring than the winter of each year, suggesting a migratory component. The use of the same nesting hollow by a banded pair of Tree Martins over consecutive springs demonstrated at least site fidelity, if not residency. Other residents whose population fluctuations suggested that they were partial migrants or nomads included the Spiny-cheeked Honeyeater which was more abundant in winter than spring and especially numerous in winter 1992, the Yellow-throated Miner which peaked in spring 1991 and the Apostlebird and Galah which both peaked in winter 1992.

Individual species may have different life history strategies in different parts of their geographic range. A species resident in areas offering reliable food supplies might be forced to move nomadically in areas of marginal habitat in which the availability of food fluctuated. Such differences may explain why, for example, the Zebra Finch is apparently nomadic and

breeds opportunistically in central Australia (Zann *et al.* 1995), but is resident and breeds regularly in parts of arid Western Australia (Davies 1977). Birds which must drink regularly may be resident in areas, such as Ptery, where pastoral development has led to the provision of permanent supplies of water, but could only occur nomadically in areas that are waterless in drought.

Classifications of life history strategies derived from short-term observations may reflect the habitat quality for a particular species over the observation period. Observations made when resources are abundant could suggest that nomadic species are resident, since there may be no impetus for them to quit an area. Alternatively, when conditions deteriorate residents may die out and later recolonise, giving the impression of desertion or nomadic behaviour. Classifications will also reflect the spatial scale of observations. Observations made at the local level of this study indicated that the Black Honeyeater, Budgerigar and White-browed Woodswallow were nomadic. Continental-scale overviews of the movements of these species (Ford 1978, Wyndham 1982, Wood 1994), however, have indicated an underlying seasonal component to their movements.

In conclusion, the simultaneous existence of temporal, spatial and spatio-temporal variability in the arid zone allows the co-existence of species employing a continuum of life history strategies. Resident species persist because they exploit local spatial variability or concentrate on resources which are relatively predictable and, in accord with theoretical predictions, they tend to be generalists. Generalists are able to survive temporal variation by modifying their choice of diet or habitat. Nomads by virtue of their superior mobility are able to track resources at a regional level and can afford to specialise on locally fluctuating resources. At a local level, temporal variation causes the abundance of specialists to fluctuate, but may not change their habitat choice (Wilson & Yoshimura 1994). The occurrence of nomads coincides with periods of super-abundant food and they are unlikely to compete with resident birds for food resources. They tend to be non-aggressive, perhaps because there is no need to defend resources which are super-abundant. In theory (Allen *et al.* 1993), apparently chaotic or spatio-temporal variability should promote the persistence of birds at the regional level. Local populations fluctuate asynchronously and provided that local extinctions are balanced by colonisation events elsewhere the species will persist.

Andersson (1980) derived a theoretical model which predicted that nomadism would be superior to site tenacity when there are cyclic fluctuations in resource levels and long intervals between periods of abundance. Under these conditions periods of abundance would be followed by a long poor period and it would be advantageous for a bird to move. Where resource fluctuations are erratic, the advantages of moving and possibly finding a better site must be weighed against the possibility that good conditions might return to the original site sooner rather than later. Short intervals between periods of abundance would make it more attractive to wait out the bad times. Andersson's model suggests that the "decision" to stay or go is a critical one. His model seems to assume that birds will stay at a site until driven from the site by a lack of resources. At Peery birds were more nomadic than Andersson's model would seem to imply was optimal. Different nomads peaked at different times and nomads came and went even when conditions appeared favourable. Nomads, by virtue of their mobility, may have access to abundant food resources and may not be constrained by the need to save energy wherever possible and live their lives in the most energy efficient manner. All nomads, as indeed all birds, must find a continuous supply of resources for survival and periodic abundances of them for successful breeding (Davies 1984a). However, nomads differ in their habitat requirements and responses to environmental variation. A single theoretical model may not adequately predict the behaviour of nomads which form part of a continuum of life history strategies rather than a discrete group.

9.4 Implications for conservation of the avifauna in arid western New South Wales

A number of authors, e.g. Recher & Lim (1990), Reid & Fleming (1992) and Smith & Smith (1994), have voiced concerns regarding the future of birds in arid Australia. In arid New South Wales, Smith & Smith (1994) identified population decreases in 48 bird species, including at least 20 species in which major decreases have occurred, since European settlement. The situation has by no means stabilised, as shown by the recent declines in the Malleefowl (Brickhill 1985), Bush Thick-knee (Maher 1988), Grey Falcon (Olsen & Olsen 1986) and others.

In order to discern trends in the arid zone avifauna, long-term surveys which take

account of the variable and unpredictable nature of the environment are required. The temporal variability demonstrated in this study is indicative of the limited value of short-term one-off surveys. Such surveys produce an unrepresentative and incomplete account of the bird species that use an area. Surveys need to take account of the spatial variability of the avifauna. A comparison, for example, of the avifauna in a run-off situation in one area with the avifauna of a run-on situation in another has little, if any, validity.

The detrimental effects of drought on the avifauna recorded in this study are supported by numerous earlier accounts, e.g. Barnard (1917, 1927), Berney (1906, 1928), MacGillivray (1929), McGilp (1929) and Robertson (1987). This study spanned a period of drought considered locally to be the worst in at least 40 years. In two years the numbers of birds recorded in censuses declined by over 50%, but no resident bird species were lost from the site. As irregular droughts are a feature of the Australian arid zone (Foley 1957), birds are, no doubt, adapted to cope with such events. The ability of birds to cope with drought in conjunction with European pastoral activities and feral predators is less certain. Barnard (1917) linked the disappearance of the Paradise Parrot *Psephotus pulcherrimus* in central Queensland around the turn of the century to the coupling of severe overgrazing with catastrophic drought. Prior to the drought of 1901-02 'it was not very uncommon to see a pair of these [now presumed extinct] birds'. Barnard (1927) also noted that 25 years after the severe drought of 1901-02, numbers of birds had still not recovered to pre-drought levels.

Severe overgrazing occurred in parts of western New South Wales during the drought of this study (Pickard & Norris 1994). The drought coincided with a period of low stock prices and there was no short-term financial incentive to remove stock since the cost of transporting the stock to market exceeded the likely financial return from the sale. In many instances stock were left to graze until they starved and overgrazing resulted. The arid rangelands continue to be degraded by erosion (Fanning 1994).

Inevitably, droughts comparable to that of 1901-02 will recur. It is imperative for the effective conservation management of birds that the long-term effects of grazing be considered and that the coupling of drought with overgrazing is not allowed to continue.

The use of plant species at the study site as food sources highlighted the importance to birds of perennial species, especially trees and shrubs. Virtually all feeding observations at

foliage, flowers and bark, involved perennial plants. The sources of fruit and seed of sedentary species, such as the Mallee Ringneck, Spiny-cheeked Honeyeater and Singing Honeyeater, were predominantly perennial species. Ephemerals, annuals and biennials produced abundant, but erratic supplies of seed and fruit. Their importance was affirmed by frequent congregations of fruit and seed-eating birds on ground well away from the cover provided by perennial plants. Such birds were generally nomadic or wide-ranging species, rather than residents, especially small residents.

This reliance on perennial species has considerable management implications. Though the rate of land degradation is generally perceived to have slowed in the arid zone since the 1950s (Condon 1986, Palmer 1994, Pickard & Norris 1994), widespread and effective regeneration of perennial trees and shrubs is not occurring in arid New South Wales, largely due to overgrazing by stock, feral animals and kangaroos. Many of the mature trees in the area probably became established prior to European pastoral settlement. The Beefwood Tree *Grevillea striata* marking the burial site in the north-west corner of the state of the early explorer, James Poole, in 1845, still stands today and is evidence of the longevity of arid zone trees. The Soil Conservation Service (1989) reported an absence of effective tree regeneration in 69% of the Western Division of New South Wales compared with 37% for the rest of New South Wales. Within the Western Division the lack of regeneration is most pronounced in the arid areas west of the Darling River. This lack of regeneration has been so aptly described by Reid & Fleming (1992) as, for birds, 'a time bomb quietly ticking away'. Reid & Fleming (1992) argued that adverse effects on birds would be mitigated by virtue of their mobility. However, many arid zone species are sedentary. Over half of the species in the Peery study area were residents and their ability to move is questionable. Besides, given the widespread nature of the problem, where would they move to? Such is the extent of the problem that it is likely that mobile species will also be affected.

The food resources of arid zone birds are also threatened by continued erosion. Frequent and sometimes severe dust storms occurred in western New South Wales in dry periods during, and immediately after, this study. Removal of topsoil removes nutrients, thus stunting future plant growth, and the stored seed bank on which many ground-feeding birds are dependent. Badly scalded areas were quite extensive in the study area, particularly on the open

plains of the Fowlers land system. Birds were noted feeding widely over the open plains within the study area and in the surrounding district, but never in badly scalded areas where there was virtually no ground vegetation. A number of ground-feeding species, including the Australian Magpie, Zebra Finch and Crimson Chat, in addition to their avoidance of bare scalds, also tended to avoid sparse ground vegetation.

The arid zone avifauna may be dominated by ground-feeding species, but most species nest in trees and shrubs. In this study, 44 of the 51 birds that I found breeding built their nests in trees or shrubs and over one quarter of nesting species were obligate hollow-nesters. All but three of the 24 tree and shrub species which provided nest sites were perennials and all of the main nest plants were perennials.

The continued availability of suitable nest sites for arid zone birds is, as is the case for food, dependent on adequate regeneration of trees and shrubs and protection of ground layer vegetation. Hollow-nesting species are reliant on a continued availability of mature hollow-bearing trees. At Peery, birds nested in a range of plant species, but certain plants, for example River Red Gum, Whitewood, Black Box and Harlequin Eremophila, were especially important. Plant species diversity needs to be maintained in order to meet the individual requirements of different birds. The characteristics of trees and shrubs which make them suitable nest sites warrant further study. The requirements of some hollow-nesting species have already been investigated, e.g. Saunders *et al.* (1982), Rowley (1990) and Rowley & Chapman (1991). Open and mud nesters also have specific requirements (Recher 1991) and these require further attention. Conservation of ground-layer vegetation is essential to provide nesting opportunities for ground-nesting species, including the Rufous Songlark and Little Button-quail, which nest in dense herbage.

In arid New South Wales approximately one third of landbirds require regular access to drinking water and a further third drink occasionally. The provision by pastoralists of reliable water sources, mainly bores tapping subterranean water, has probably extended the permanent range of species that are dependent on drinking water, either year round or during hotter periods.

Closure of these bores would lead to a considerable local reduction in the species richness of the avifauna during drought. The closure of bores is unlikely to be an issue in areas

which remain devoted to pastoral activity. However, where existing pastoral leases are acquired for conservation reserves, it has been argued that the bores are artificial and should be removed. Whether to close or maintain bores is a complex question. Closure of bores might be appropriate if the acquired lands were, apart from the existence of bores, in a natural state. Bores help maintain populations of stock, feral herbivores and kangaroos during drought, leading to overgrazing, even in reserves where stock are excluded. Arid areas have, however, been substantially altered by past grazing by domestic and feral animals and all harbour feral predators. It would be extremely short-sighted to close bores to birds without first determining that birds can and will recolonise these essentially unnatural areas after drought.

The potential for, and the long-term effects of, increased competition from water-dependent species on water-independent species are unknown and warrant study. The White-plumed Honeyeater probably persists in many parts of the arid zone during drought where it would previously have been unable to. At Peery, it may exclude small birds from riparian eucalypt woodland which is most likely a drought refuge.

Almost half of the species recorded at Peery were nomadic or migratory species and populations of these birds were influenced by conditions beyond as well as within the study site. If avifaunal biodiversity is to be maintained in the arid zone, then conservation measures must be implemented at a landscape rather than a local level. Most land in arid western New South Wales is leased for pastoral purposes. The long-term survival of birds will be aided by the existence of conservation reserves. In the past, reserve selection has been essentially opportunistic but there is now at least recognition of the need for selection methods to become more systematic. Reserve selection methods designed to obtain a comprehensive sample of the region's natural environments are being developed (Pressey & Nicholls, 1989a,b, 1991; Bedward *et al.* 1992). However, the area of conservation reserves is small. Threatening processes such as overgrazing by feral herbivores and kangaroos, introduced predators and altered fire regimes, also operate in reserves (Smith *et al.* 1994). The health of reserves is influenced by the health of surrounding areas. Morton *et al.* (1995) emphasised the need for a holistic approach to land management in the arid zone. They proposed a hierarchical system of management which focuses on resource rich regions such as riverine strips which provide predictable and reliable drought refuges (Morton 1990). Riverine strips provide more

diverse feeding opportunities for birds and are a richer source of nesting, roosting and watering sites than run-off areas. They support more birds and more species than habitats of run-off areas. However, a number of species in this study, for example the Southern Whiteface, Red-capped Robin, Richard's Pipit and Crimson Chat, were largely confined to run-off areas. Nomadic species are reliant on the ephemeral and unpredictable pulses of increased production which occur in run-on and run-off areas following rain. Preservation of avifaunal biodiversity in the arid zone will not be assured unless there is a greater integration of conservation objectives into land management outside reserves, especially on pastoral leases. For birds, it is essential that permanent, predictable refugia in run-on habitats and ephemeral, unpredictable refugia in run-off habitats be managed sympathetically.

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