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Temporal variation in bird assemblages: how representative is a one-year snapshot?

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ABSTRACT

Bird assemblages generally are no longer regarded as stable entities, but rather as fluctuating in response to many factors. Australia's highly variable climate is likely to result in a high degree of dynamism in its bird assemblages, yet few studies have investigated variation on an inter-annual temporal scale. We compared two year-long samples of the bird assemblages of a series of highly fragmented buloke *Allocasuarina luehmannii* (Casuarinaceae) woodland remnants in south-eastern Australia, the first sample taken in 1994–1995 and the second in 2001–2002. Bird densities were almost three times higher in the second period than in the first. Mean species richness also was significantly higher. Species richness of each individual site was unrelated between the two years. Minimum species turnover was 63% and was higher, on average, for migratory and nomadic than for sedentary species. Therefore, site-level bird assemblage composition was markedly different between the two survey periods and, on average, the assemblage composition of each site bore greater resemblance to those of other sites in the same year than to that of the same site in the other survey period. Most species changed substantially in their distribution among remnants between the two periods. The change in distribution of most species did not differ significantly from that expected if the species had redistributed at random among the sites. This suggests that although the remnant vegetation of the area is highly fragmented with minimal inter-patch connectivity, bird movements among remnants must be relatively frequent. Inter-annual variability in Australian bird assemblages may be higher than is commonly recognized. In such dynamic systems, we must be cautious when extrapolating from the findings of short-term studies to longer temporal scales, especially in relation to conservation management. A greater understanding of the processes driving

distributional patterns is likely to enable better predictions of species' responses to habitat change.

Key Words: inter-annual variation, bird assemblages, buloke woodlands, turnover, fragmentation

INTRODUCTION

Studies in recent decades, mainly in the northern hemisphere, have challenged the idea that most bird assemblages are tightly structured and are, therefore, at or close to an equilibrial state (Wiens 1973, 1981; Rotenberry & Wiens 1980; Wiens & Rotenberry 1981; Holmes et al. 1986; DeAngelis & Waterhouse 1987; Mac Nally 1995; Yahner 1997; Collins 2000; Holmes & Sherry 2001). Not only do bird assemblages change seasonally, they also vary over longer temporal scales. The causes of such changes are often difficult to determine because patterns of variation in abundance and distribution differ among species (Hogstad 1993; Blake et al. 1994; Mac Nally 1996; Yahner 1997; Holmes & Sherry 2001). Factors responsible for changes in bird population densities and local distributions include climatic and/or resource variation on a local, regional or continental scale (Collins et al. 1984; Holmes et al. 1986; Virkkala 1991; Blake et al. 1994), interspecific competition (Holmes et al. 1986), density fluctuations of predators and changes in the type, amount and spatial configuration of available habitat (Blake et al. 1994; Holmes & Sherry 2001). These multiple influences, many of which may be unpredictable and/or difficult to detect, may result in a local bird assemblage exhibiting apparently stochastic variability through their effects on breeding success, juvenile or adult mortality and emigration/immigration of individuals.

Australia has one of the most temporally variable continental climates on an inter-annual scale, with consequent large fluctuations in resource levels (Hobbs et al. 1988). The climatic variability is irregular and difficult to predict, because it is strongly influenced by the El Niño Southern Oscillation (Nicholls 1992). Bird assemblages of regions with variable climates in the northern hemisphere display high inter-annual

variability in composition and species richness (Enemar et al. 1984). However, although much research has investigated seasonal variation in Australian bird assemblages, few studies have focused on variation among years (although see Mac Nally 1996). Australia has many nomadic bird species that respond to fluctuating resource availability (Rowley 1975; Schodde 1982). Many Australian birds, particularly nectarivorous species, are very dynamic in their distribution and local population sizes within years (Collins & Briffa 1982; Recher et al. 1983; Collins et al. 1984; Collins & Newland 1986; Mac Nally & McGoldrick 1997; Griffioen & Clarke 2002). Inter-annual variability of bird assemblages of particular localities is also likely to be pronounced, particularly where the climate is most variable.

Despite this variability, most studies of Australian bird assemblages take "snapshots", such as a series of surveys over one or a few years. We reviewed 65 studies of Australian bird assemblages published in the journals *Emu, Australian Journal of Ecology/Austral Ecology, Pacific Conservation Biology, Corella* and *Australian Wildlife Research/Wildlife Research* from 1993–2003. This survey revealed that the modal period of time over which such studies were conducted was less than six months. Such snapshots are often extrapolated to predict future patterns. However, without an appreciation of how much a bird assemblage varies among years, such extrapolation will often be inaccurate and misleading (Collins 2001). For example, the endangered swift parrot *Lathamus discolor* of eastern Australia displays much variation in its habitat use from year to year. In the winter of one year, parrots foraged in areas of continuous forest (> 6 000 ha), but in the following year, large numbers of birds were found in forest fragments (≤ 80 ha) in an agricultural matrix (Mac Nally & Horrocks

2000). Recommendations for management stemming from only the one year of study would have led to only part of the species' habitat being considered for conservation management.

If the degree of inter-annual variation of Australian bird assemblages proves to be comparable with that commonly observed in northern hemisphere bird assemblages, it would have profound implications for conservation management of the continent's native birds. Here we compare two year-long samples, taken seven years apart, of the bird assemblages of a series of woodland remnants, to characterize inter-annual variation and investigate the degree to which a one-year "snapshot" resembles another such snapshot taken several years later. We document changes in the composition of the bird assemblages of 26 remnants, and assess minimum species turnover and the degree to which species' distributions among remnants had changed.

METHODS

Study Area

The study area is in the Wimmera region of western Victoria, Australia (Fig. 1). The area was originally grassland and open woodland, but has been mostly cleared for agriculture. About 95% of native vegetation has been removed, with the majority of clearing occurring prior to 1940. Woodland dominated by buloke *Allocasuarina luehmannii* (Casuarinaceae), a small tree (to 15 m), was once a common vegetation type in this region, but now is restricted to a series of small, isolated patches. Originally having an understorey of native grass, forb and chenopod species, most remnants have been severely degraded by livestock grazing and introduced pest herbivores (European rabbit *Oryctolagus cuniculus* and brown hare *Lepus capensis*). Regeneration of bulokes is restricted to the few remnants from which grazing is excluded.

The study area is on the fringe of the southern part of Australia's semi-arid zone. The climate is variable and unpredictable from year to year. Mean annual rainfall is 400 mm, but annual totals fluctuated between 221 mm and 580 mm over the 15 y to the end of 2002. Most rainfall occurs in winter. Average daily temperature range at Nhill (36° 33’ 64’’S; 141° 63’ 53’’E) is 12.5°C–28.9°C in the austral summer (December–February) and 3.9°C–14.4°C in the austral winter (June–August).

Bird surveys

Twenty-six buloke woodland remnants were selected for this study (Watson et al. 2000). The remnants ranged in area from 2.5 to 467 ha, although most were < 20 ha (see

Watson et al. 2000). Most remnants were very isolated from other areas of native vegetation by cropping land, and only six of them were connected to nearby native vegetation by narrow (20–40 m) corridors. The distance from each remnant to the nearest patch of native vegetation ≥ 10 ha averaged 1457 m (Maron et al. 2004). The bird assemblages of the 26 remnants were surveyed during each of two survey periods. Survey Period 1 was between April 20 1994 and March 22 1995 and Survey Period 2 was between June 30 2001 and June 14 2002. During each survey period, nine surveys were conducted in each of the 26 remnants at approximately six weekly intervals. Each survey consisted of the observer (DMW in 1994-95 and MM in 2001-02) slowly walking a 200 m transect and recording all individual birds within 25 m of the transect line, yielding a 1 ha sampling area. Each survey took 20 min to complete. Birds seen flying over the remnant were not included in analyses. Surveys were not undertaken in rainy or very windy conditions, within 30 min of sunrise or sunset, or during the hottest part of the day. To minimize survey bias due to time of day, each transect was surveyed at least four times in the morning and three times in the afternoon during each survey period. All transects were located ≥ 20 m from the remnant's edge. Although transects could not be permanently marked because most remnants were privately managed, transects for Survey Period 2 were positioned as close as possible to the locations used in Survey Period 1 by referring to diagrams of their locations made by DMW during the first survey period.

To reduce possible inter-observer differences, the same observer would have conducted all surveys during both survey periods. However, as is often the case in long-term studies, this was not possible, but the observers had a similar degree of familiarity

with the bird fauna of the region and both observers undertook 'mock' surveys prior to data collection to become acquainted with the birds present. The open nature of buloke woodland and the structure of the trees themselves make locating and identifying birds present within a 1 ha transect relatively easy. Survey effort was identical during each survey period.

In addition to bird surveys, we obtained data on mean annual precipitation for the study area, to identify any major climatic events, such as drought, that might have affected the avifauna of the area. These data were obtained for the 15-y period from 1988 (6 years before the start of Survey Period 1) to the end of 2002. We also obtained maps of the deviation from regional long-term mean rainfall totals for Australia for each year during the same 15 y period. Rainfall data and maps were obtained from the Australian Bureau of Meteorology.

Data analysis

Total abundance (the total number of records of each species at each site, summed for the survey period) was compared for each species (excluding those that occurred in fewer than five sites, and those that were not present during one of the survey periods) between the two years using Wilcoxon signed-rank tests. Total species richness for each site was calculated for both survey periods and linear regression was used to determine whether the species richness of individual sites was related between the two survey periods. Species turnover rate could not be determined because the survey periods were not in successive years so numerous undetected instances of extinction and recolonization of remnants (symmetrical movements) may have occurred in the interval

(Diamond & May 1977). Therefore, we calculated minimum turnover (*T*) for each site as:

$$T = \frac{(E_{spp.} + C_{spp.})}{S_{tot.}} \times 100$$

where $E_{spp.}$ = number of local extinctions (number of species not recorded at the site during survey period 2 that had been recorded during survey period 1), $C_{spp.}$ = number of local colonizations (number of species recorded at the site during survey period 2 that had not been recorded during survey period 1) and $S_{tot.}$ = total number of species observed at the site during both survey periods.

Mean minimum turnover per site was calculated for all species combined. Linear regression was used to investigate relationships between mean minimum turnover and a) patch size and b) the distance to the nearest woodland patch ≥10 ha (both log transformed). Bird species were categorized as nomadic, migratory or sedentary based on the classifications of Pizzey and Knight (1997). Where classifications in Pizzey and Knight (1997) were equivocal, the Handbook of Australian, New Zealand and Antarctic Birds (Marchant & Higgins 1990, 1993; Higgins & Davies 1996; Higgins 1999; Higgins & Peter 2001, 2002) was consulted to determine the most appropriate classification for the species in question in the study area. Mean turnover per site was then calculated separately for nomadic, migratory and sedentary species, and paired *t*-tests were conducted between each pair of categories.

We also investigated the degree to which the distributions of individual species had changed between the two survey periods. For each bird species that occurred at

least once during each survey period, we calculated the percentage change in distribution (*D*) between the two periods as:

$$D = \frac{(E_{sites} + C_{sites})}{N_{tot.}} \times 100$$

where E_{sites} = number of local extinctions (number of sites from which the species was not recorded during Survey Period 2 but in which it had been recorded during Survey Period 1), C_{sites} = number of local colonizations (number of sites in which the species was recorded during Survey Period 2 but in which it had not been recorded during Survey Period 1), and $N_{tot.}$ = total number of sites in which the species was recorded during at least one survey period. We conducted pairwise comparisons of the mean percentage change in distribution for each movement category (nomadic, sedentary, migratory) using heterogeneous variances *t*-tests, because of the unequal numbers of species in each category.

In order to assess whether the distribution of a species among sites in Survey Period 2 was consistent with a random reallocation from Survey Period 1, we used a randomization approach (Manly 1997). The method involved holding constant the distribution of each species among sites as observed in Survey Period 1 and then randomly allocating the number of presences observed for the species during Survey Period 2 among the sites. The resultant percentage change in distribution was then computed as described above. This was repeated 1000 times for each species, and the 95% confidence intervals for the randomized distributions of the test-statistics were obtained. If the observed value was less than the lower 95% confidence limit (i.e. 2.5%), then the species was less chaotically distributed during Survey Period 2 than expected by chance, given its distribution during Survey Period 1.

For assemblage-level comparisons, both the total abundance and presence/absence data were represented as sites × species matrices, and Bray-Curtis similarity matrices were calculated for each data set. We investigated whether the bird assemblage of each site in Survey Period 1 was more similar to that of the same site in Survey Period 2 than it was to the assemblages of other sites in Survey Period 2. The similarities between the bird assemblage of each site in Survey Period 1 and that of the same site in Survey Period 2 were determined (hereafter referred to as "site similarity"). We also calculated the mean similarity between the bird assemblage of each site in Survey Period 1 and those of each site in Survey Period 2. For example, similarities between site 1 in Survey Period 1 and site 1, 2, 3,…26 in Survey Period 2 were determined. The mean of these similarities was calculated. The grand mean of these 26 means (hereafter referred to as "overall similarity") was then determined and compared with the site similarity.

Analysis of similarity (ANOSIM) was used to explore differences between the bird assemblages recorded in each of the two survey periods, using both total abundance and presence/absence data. The ANOSIM routine involves calculating a statistic (*R*) representing the differences between groups (in this case, survey periods) compared with the differences among sites within groups, and a randomization procedure is then used to determine the probability of obtaining the observed result. Where significant differences in the bird assemblages between survey periods were found, similarity percentage (SIMPER) analysis was used to identify the species that contributed most to these differences. The PRIMER software package (Clarke & Gorley 2000) was used for these calculations.

RESULTS

Precipitation

The mean annual precipitation in the study area varied between 221 mm and 580 mm (Fig. 2). Both survey periods began during abnormally dry years, although in 1994 there was 99 mm less rainfall than in 2001. Unusually dry conditions were widespread across inland Australia during both 1994 and 2001. The rainfall total in the study area was close to the long-term mean in 1995 during the latter part of Survey Period 1, but conditions remained dry during 2002 in which Survey Period 2 concluded.

Species richness

Seventy-six bird species were recorded during the surveys, 65 in each survey period (for a complete list, contact the corresponding author). The mean species richness per site (± 1SE) during Survey Period 1 was 13.5 ± 0.78, compared with 18.7 ± 0.61 during Survey Period 2, and this difference was statistically significant ($t_{25} = 6.845$, $P < 0.0001$). The increased species richness was due to most species being more widespread among the remnants during Survey Period 2 (see 'species distribution', below). There was no relationship between the species richness of sites in the two survey periods ($R^2 = 0.018$), so that a site with a relatively high species richness during Survey Period 1 did not necessarily also have a high species richness in Survey Period 2, and vice versa.

Abundance

Almost three times as many individuals were observed in Survey Period 2 (2942 or 12.6 per survey) than in Survey Period 1 (1077 or 4.6 per survey). Fifty-four species

(71%) increased numerically in abundance, 16 of which were statistically significant changes (Table 1). The red-rumped parrot *Psephotus haematonotus* increased most in abundance—from 37 individuals recorded in Survey Period 1 to 269 in Survey Period 2. For most species (with the exception of summer migrants), these greater abundances were due to generally higher counts from surveys throughout Survey Period 2, rather than to very high numbers recorded during only a few survey visits. Twenty species decreased in abundance in absolute terms, but none significantly.

Turnover

Mean minimum species turnover per site was 63% (Table 2). Turnover of sedentary species was significantly lower than that of both migratory and nomadic species (Tables 2 and 3), but there was no significant difference in turnover between the latter two groups (Table 3). Turnover was not related to either patch area ($R^2 = 0.001$) or to the distance to the nearest patch ≥ 10 ha ($R^2 = 0.016$).

Species distribution

For species that were recorded during both survey periods, the mean difference in distribution among the sites between the two time periods was 68% (Table 2). This means that, considering all the sites in which a species was recorded in either survey period, on average it occurred in 68% only during a single survey period, and in 32% of sites during both survey periods. For example, the dusky woodswallow *Artamus cyanopterus* was recorded in 16 sites in total during the study, but in only four of them during both survey periods. This means that there were 12 sites of the 16, or 75%, in which the species was recorded during only one survey period. Only two species were

unchanged in distribution, namely the white-eared honeyeater *Lichenostomus leucotis*, which was observed only at Site 1 in both survey periods, and the variegated fairy-wren *Malurus lamberti*, which occurred only in sites 1, 2 and 3. The mean difference in distribution was significantly greater for both migratory and nomadic species than for sedentary species, but there was no significant difference between nomadic and migratory species (Table 3).

The randomization test showed that of the 54 species that were recorded at least once during each survey period, only five had a significantly smaller difference in distribution among sites between the two survey periods than expected if their redistribution was random (Table 4). These species were the brown treecreeper *Climacteris picumnus*, spiny-cheeked honeyeater *Acanthagenys rufogularis*, varied sittella *Daphoenositta chrysoptera*, variegated fairy-wren, and yellow thornbill *Acanthiza nana*. The remaining 49 species were no more likely than expected by chance to be recorded during Survey Period 2 in sites in which they had occurred during Survey Period 1.

Assemblage structure—abundance data

The series of bird assemblages recorded from sites in each survey period were significantly different (ANOSIM Global $R = 0.298$, $P < 0.001$). The average Bray-Curtis dissimilarity between survey periods was 76.9, and the within-group similarities for Survey Periods 1 and 2 were 29.6 and 31.8, respectively. The Global *R* value indicates that the groups overlapped but were clearly different (Clarke & Gorley 2001). The species contributing most to this difference were the yellow-rumped thornbill

Acanthiza chrysorrhoa (accounting for 10% of variation between survey periods), red-rumped parrot (8%), and house sparrow *Passer domesticus* (7%). All of these were species that had significantly different abundances in the two survey periods (Table 1).

The bird assemblage of a particular site (based on abundance data) was more similar to those of the other sites in the same survey period than to that of the same site in the other survey period. The average Bray-Curtis similarity among sites was 29.6 in Survey Period 1 and 31.8 in Survey Period 2. These similarities among sites within years were comparable to the average site similarity (i.e. the similarity between the bird assemblage of a site in Survey Period 1 and that of the same site in Survey Period 2), which was 27.1. Although the mean overall similarity (i.e. the mean similarity between a site in Survey Period 1 and *all* sites in Survey Period 2) was significantly lower at 23.1 ($t_{25} = 2.57$, $P < 0.05$), the bird assemblages of individual sites still differed considerably between the two survey periods.

Assemblage structure—presence/absence

Overall differences between survey periods were driven largely by changes in abundance, because, when only species' presence was considered in the assemblage analysis, the overall differences between the bird assemblages recorded in the two survey periods described above were no longer evident (Global $R = 0.066$, $P > 0.05$). However, bird assemblages of individual sites were still substantially different between survey periods, with a mean Bray-Curtis similarity of 48.4. This was still significantly higher than the mean overall similarity of 40.3 between each site in Survey Period 1 and all sites in Survey Period 2 ($t_{25} = 2.57$, $P < 0.05$).

DISCUSSION

Bird abundance changes

The bird assemblages of these buloke woodland remnants had changed substantially after a period of just 7 years. The change in the avifauna of the area was due largely to a threefold increase in the number of individuals recorded in the second survey period. Similar increases have been recorded in several long-term, continuous studies in the northern hemisphere. The total number of individual birds recorded on a 10-ha study plot in the Hubbard Brook Experimental Forest in New Hampshire, USA, varied from 89–214 over a 16 y period (Holmes et al. 1986), while Enemar et al. (1984) found that the number of breeding bird territories in a Swedish Lapland site fluctuated between 260–550 over a 20 y period. The populations of 78% of bird species considered to be permanent residents in Michigan and Wisconsin, USA, also varied significantly in abundance among years during a 6 y study (Blake et al. 1994).

What might have caused the observed difference in bird abundance in the Buloke system? Unfortunately, the lack of continuous monitoring of both bird populations and potential causal factors limits speculation on the causes of the observed discrepancies. We do not know whether the results of this study represent variation typical of the study area or whether this was an extreme example caused by a large-scale event that may be a rare occurrence, such as an extreme climatic fluctuation. The rainfall data for the study area did not suggest a clear trigger, because although the year in which the first survey period began was the driest in the 15-y period from 1988–2002, Survey Period 2 also had below average rainfall. Given that differences in abundance were evident for

species with a range of movement patterns and foraging strategies, it is difficult to attribute them to any single driver. However, it is possible that climatic conditions, perhaps distant from the study area, were ultimately responsible for the changes in bird abundance, because the study area abuts Australia's semi-arid region. Variability in precipitation has been found to influence fluctuations in abundance in other animal populations (Lake 1995; Post & Forchhammer 2002; Meserve et al. 2003), and local populations of mobile taxa such as birds could be influenced by climatic variability in adjacent or even distant regions of the continent. The study area is likely to sustain fluctuations in bird populations that are driven by the climatic variability that characterizes the arid zone. Unusually dry conditions inland may force birds south into the study area, while at other times, wetter coastal conditions may allow southern birds to move inland to the study region.

Many species underwent substantial changes in abundance, some (e.g. the red-rumped parrot) as much as six-fold. Changes of this magnitude over a period of just seven years are unlikely to reflect absolute changes in population density on a broader spatial scale. To determine whether density changes in one region are representative of broader trends, information on the population dynamics of a species on a much broader spatial scale is required (Virkkala 1991) because population dynamics are not necessarily correlated over large areas (Blake et al. 1994). For example, several of the species that underwent substantial increases in abundance in our study, such as the varied sittella, hooded robin *Melanodryas cucullata* and chestnut-rumped thornbill *Acanthiza uropygialis*, are thought to be generally declining in abundance in many other parts of southern Australia (Reid 1999; Traill & Duncan 2000). It is more likely that the

large differences in abundance that we recorded were due to influxes of individuals into the study area from elsewhere in the region, or even other parts of the continent. Abundance changes of the observed magnitude are not unexpected in nomadic or migratory species. Numbers of individuals of several migratory species, such as the white-winged triller *Lalage sueurii*, reaching Victoria vary from year to year and influxes of several nomadic species into the study region are irregular (Emison et al. 1987). However, the substantial changes in abundance of several species generally considered to be sedentary suggest relatively large-scale movement even for these species. Movement strategies of many Australian birds are not easily categorized because little is known of their large-scale movements (Griffioen & Clarke 2002) and movement strategies of many species differ among populations (Chan 2001). Our results suggest that many species thought to be sedentary may be more vagile than is commonly recognized.

The use of different observers during each survey period also may have contributed to differences recorded in the bird assemblages between the two survey periods. Several studies have found that estimates of bird abundance can be influenced by observer differences (Kavanagh & Recher 1983; Morin & Conant 1994; Sauer et al. 1994; Cunningham et al. 1999), although others have found this effect to be small relative to among-site or inter-annual variation (Smith 1984). Often, observer differences are attributable largely to variation in ability and experience (Link & Sauer 1998; Boulinier et al. 1998*a*). In this study, both observers were similarly experienced in conducting bird surveys, and each undertook trial surveys in buloke woodland prior to their survey period. The small dimensions of the transects and the high apparency of

birds in Buloke woodland also reduced the likelihood of large observer effects. The substantial increase in abundance of red-rumped parrots between the two survey periods was also reported by local residents (K. Boschen, personal communication). The variation in the bird assemblages of individual sites between survey periods was substantial even when only presence/absence data were considered. Such data are likely to be more robust to inter-observer effects than abundance data (Kavanagh & Recher 1983), particularly as nine surveys per remnant were conducted in each survey period. We believe that the effects of observer differences were probably minor relative to the magnitude of the bird assemblage differences between survey periods. Precluding observer effects will always be difficult in long-term studies, because the capabilities of each individual observer change with experience and skill levels over time (Kendall et al. 1996).

Assemblage composition and species richness

The distributions of most species among remnants in our study area changed substantially between the two survey periods, but the distributions of five species differed less than expected if they randomly redistributed between the two survey periods. In general, species whose distributions among sites changed less than expected may be more likely to have particular landscape or habitat requirements, or may simply be more restricted in their inter-patch movements. Four of these five species were recorded during Survey Period 2 from sites in which they had not occurred during Survey Period 1, and they also increased in the number of sites from which they were recorded. Thus restricted inter-patch movement is unlikely to explain the lower degree of distributional change for those species. However, either or both of these factors could

have influenced the distribution of the fifth species, the variegated fairy-wren, which was recorded only from the same three sites in each survey period.

The majority of species, however, appear able to move among patches of remnant vegetation in the area, because their change in distribution among sites was similar to that expected in a random redistribution. These changes in distribution led to considerable differences in the bird assemblages of individual sites between the two survey periods, despite the apparent 'isolation' of the sites by expanses of cropping land. The 63% minimum turnover observed in this study is broadly comparable to the figure of 52–60% average annual turnover in breeding bird species in Kansas tallgrass prairie (Collins 2000). Species richness values of individual sites in our study were also unrelated between survey periods. Fluctuations in bird species richness of 35–40% at a site have been documented in northern hemisphere studies (Enemar et al. 1984; Holmes et al. 1986). This potential for temporal variation in the relative species richness of a site must be recognized, particularly in situations where such information is intended to contribute to conservation management decisions.

Some of the variation in bird assemblages detected in long-term studies has been attributed to vegetation succession (Blake et al. 1994; Holmes et al. 1986). However, it is unlikely that changes in the vegetation characteristics of the remnants that we studied account for the large differences in the bird assemblages between the two survey periods. The buloke, which dominates these woodlands, is a very slow growing tree (L. Morcom, unpublished data), as are the few mature individuals of *Eucalyptus* species present in the remnants. Shrubs are sparse or absent in all sites. The component of

habitat that would be most likely to change is the ground layer. Although grazing regimes had not altered noticeably between survey periods, minor changes in grazing pressure may affect aspects of the ground layer, such as percentage grass cover, proportion of native grasses and mean grass height. It is possible that these relatively subtle changes may have influenced the bird assemblages, although it seems unlikely that so many bird species would have been directly affected by vegetation change to the observed extent. It is also difficult to attribute the differences in the bird assemblages of the Buloke remnants to changes in matrix land use, because broad-scale land clearing no longer occurs in the area, and farming practices have not changed markedly since the first survey period. However, rotation of crops is a common practice in the area and so, while similar crops were grown across the study area, it is possible that the particular combination of crops surrounding each site during winter and spring was different between the survey periods.

Such changes in the landscape immediately surrounding each site, as well as subtle within-site habitat changes, may have influenced the availability of food resources. Availability of both grass seeds and invertebrates could be influenced by relatively minor changes in vegetation or rainfall (e.g. Tanaka & Tanaka 1982). Most bird species present in the sites feed primarily on one or the other of these resources, so changes in resource availability may be at least partially responsible for the distributional changes of bird species among remnants. However, it is also possible that the sites studied do not vary greatly in their suitability as habitat for many species. Persistent ecological relationships are difficult to detect in such generally suitable habitat (Aberg et al. 2000). If all sites are similar in their suitability for a species, if sites

are not ‘saturated’ with individuals at all times, and if individuals can move among patches, as appeared to be the case in this study, such distributional changes may be expected even in the absence of corresponding habitat or resource changes.

Dynamism in Australia

The Buloke woodlands we studied are unlikely to be unusual in terms of the variability of their bird assemblages. A large proportion of the Australian continent is similarly or more arid than our study region and thus experiences similar or greater climatic variability. James et al. (1995) considered it likely that large population fluctuations, local extinction and local colonisation are common events in many arid-zone Australian organisms, and there are indications from other parts of Australia that this level of variability may be widespread. For example, long-term data from the Canberra Garden Bird Survey show large inter-annual variation in abundance of many bird species, including the dusky woodswallow (a 6.5 fold change over 5 years), little raven *Corvus mellori* and restless flycatcher *Myiagra inquieta* (both displayed a 6 fold difference between consecutive years) (Veerman 2003). The number of bird species present in New South Wales forest and woodland remnants during summer differed by up to 50% in consecutive years (and was highest during a year of above-average rainfall), and the number of individuals caught in mist-nets varied from 646 to 273 in consecutive summers (Recher et al. 1983). In consecutive winters, bird densities in a Victorian wet forest varied from 381 to 633 birds/50 ha (Mac Nally 1996). However, while there are numerous published studies with datasets that could be used to investigate inter-annual variation in Australian bird assemblages further, most have

been analysed only with respect to seasonal variation after combining data for all years (Collins & Briffa 1982; Pyke & Recher 1988).

Management implications

The considerable temporal variation in bird species richness and assemblage composition in each remnant, despite a lack of clear habitat change, presents difficulties in determining management priorities. Land managers need rapid and inexpensive assessment of the conservation value of sites and predictive models that can be used to prioritize sites for protection or restoration. However, such assessments rarely take into account long-term variability, and the conservation planning tools that ecologists develop are often based on extrapolation of patterns from "snapshot" data. If inter-annual variability of the magnitude recorded in this study is widespread, such pattern-based extrapolation could result in misleading and inaccurate predictions (Mac Nally & Horrocks 2000). For example, Pearce et al. (2001) developed logistic-regression models to predict the distributions of 59 species of diurnal birds in north-eastern New South Wales. When confronted with new data, only 53% of the individual-species models had a prediction accuracy greater than 70% (< 70% was considered poor to marginal discrimination). In the current study, the lack of relationships between the bird species richness values of individual remnants between the two survey periods means that there cannot be a persistent relationship between the species richness of a site and the landscape characteristics of that site, such as size or isolation, because these did not change between survey periods. Any relationships between bird species richness and habitat characteristics are similarly obscured by this temporal assemblage variability. Statistical relationships between landscape or habitat factors and bird species richness

that may have been derived from the Survey Period 1 data are likely to be misleading, making accurate prediction of species distributions problematic.

In temporally variable systems, strategic conservation plans will be unreliable if developed solely on the basis of "snapshot" data (Wiens 1981; Fuller et al. 1997). However, conservation problems need to be addressed urgently, and in many cases we do not have the luxury of collecting data over a period sufficient to characterize the avifauna of sites accurately, or to determine persistent relationships between the presence of a species and landscape and habitat characteristics. An estimate of assemblage variability may be useful in allowing uncertainty to be explicitly incorporated into models used in conservation planning, but for this to be possible, we need to gain an understanding of continent-wide patterns of assemblage variability. Research in the northern hemisphere has identified several potential correlates of bird assemblage variability, such as latitude (Jarvinen 1979) and habitat fragmentation (Boulinier et al. 1998*b*). Several databases in Australia contain relatively long-term bird survey data, most notably from the Atlas of Australian Birds project (Blakers et al. 1984; Barrett et al. 2004), which would permit investigation of inter-annual variability in bird assemblages across a wide range of habitats, climatic zones and landscapes.

Temporal variability of the magnitude detected in this study is likely to obscure important ecological relationships if only patterns of occupancy or abundance are considered. Therefore, in systems that prove to be highly temporally variable, accurate prediction of the effects of various management actions and habitat changes on bird populations will benefit from an improved understanding of the underlying mechanisms

that influence patterns in bird distribution and abundance (Wiens 1994; Austin 2002). Model predictions based on such an understanding of ecological processes are likely to prove more robust to temporal variability than those based on the extrapolation of correlations between bird presence and habitat variables from snapshots of bird distribution. For example, the influences of patch edges, area, and habitat structure on bird distribution may appear to vary from year to year if these variables are surrogates for factors such as the presence of competitors, predators or particular food sources (Burke & Nol 1998; Piper & Catterall 2003). However, in an environment of high temporal variability, identifying the factors that affect such processes is often a difficult task.

While it is possible that the system of habitat fragments that we studied is peculiar among Australian habitats, it is more likely that variability of the magnitude recorded in this study is a common feature of many bird assemblages because it has been recorded in numerous long-term studies worldwide. Authors of many such studies have concluded that bird populations fluctuate in such an apparently stochastic manner from year to year that no single year's surveying is likely to give a representative picture of 'the' bird assemblage of the area (Enemar et al. 1984; Virkkala 1991). If this is true for Australian bird assemblages, studies that make explicit predictions about habitat requirements and persistence of bird species based on 'snapshots' of their distribution must be interpreted against a backdrop of longer-term fluctuation in local population densities and bird assemblage composition.

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Figure 1. Location of the study area in south-eastern Australia.

Figure 2. Mean annual rainfall averaged across the study area 1988–2002. Broken line indicates the long-term annual mean.

Table 1 Species that changed significantly ($P < 0.05$) in abundance (mean no. individuals recorded per site ± SE) between Survey Period 1 (SP 1) and Survey Period 2 (SP 2) (Wilcoxon signed-rank test). †Introduced species. Effect size is Cohen's *d*.

	Mean no. individuals/site			
Species	SP 1	SP 2	Wilcoxon *z*	Effect size (%)
Crested Pigeon *Ocyphaps lophotes*	0.96±0.29	3.46±0.80	3.039	81.6
Eastern Rosella *Platycercus eximius*	0.27±0.14	1.12±0.39	2.038	56.0
Red-rumped Parrot *Psephotus haematonotus*	1.42±0.28	10.35±1.97	3.900	122.3
Chestnut-rumped Thornbill *Acanthiza uropygialis*	0.96±.26	3.46±0.40	2.206	63.1
Yellow-rumped Thornbill *Acanthiza chrysorrhoa*	2.08±0.33	13.42±2.54	3.867	122.6
Yellow Thornbill *Acanthiza nana*	2.85±0.50	8.04±1.73	3.243	80.1
Southern Whiteface *Aphelocephala leucopsis*	0.15±0.12	2.31±0.93	2.673	63.7
Singing Honeyeater *Lichenostomus virescens*	1.08±0.46	3.00±0.79	3.106	58.4
White-fronted Honeyeater *Phylidonyris albifrons*	0.54±0.13	2.92±0.82	2.632	80.0
Hooded Robin *Melanodryas cucullata*	1.39±0.29	2.62±0.61	2.028	50.1
Varied Sittella *Daphoenositta chrysoptera*	0.58±0.15	4.73±1.01	3.511	112.5
Willie Wagtail *Rhipidura leucophrys*	1.81±0.38	2.96±0.46	2.021	53.6
White-winged Triller *Lalage sueurii*	0.04±0.04	0.65±0.27	2.136	63.6

European Goldfinch *Carduelis carduelis*	0.46±0.21	1.92±0.95	2.222	41.5
House Sparrow *Passer domesticus*†	2.69±0.59	9.19±2.16	3.201	80.5
Rufous Songlark *Cinclorhampus mathewsi*	0.08±0.05	1.27±0.37	2.958	87.4

Table 2 Mean minimum species turnover per site and mean change in distribution per species for all species combined and for sedentary, nomadic and migratory species (± SE). Distribution change considers only those species that were recorded in at least one site during both survey periods.

Category	Turnover	Distribution change
All species	63±2%	68±4%
Sedentary	57±3%	60±5%
Nomadic	79±4%	81±6%
Migratory	78±6%	83±5%

Table 3 Results of paired *t*-test comparisons of mean minimum species turnover and heterogeneous variances *t*-test comparisons of distribution change between bird movement categories. *Significant at $P < 0.05$

Comparison	Turnover		Distribution change	
	d.f.	*t*	d.f	*t*
Sedentary v nomadic	25	4.593*	21.9	2.730*
Sedentary v migratory	25	3.323*	25.3	3.430*
Nomadic v migratory	25	0.232	17.5	0.619

Table 4 Species whose distribution among sites changed significantly less than expected ($P < 0.05$) on the basis of a random redistribution between survey periods.

	Change in distribution (%)			
	Observed	Randomized		
Species		Mean	Lower 2.5% C.I.	Upper 97.5% C.I.
Brown Treecreeper *Climacteris picumnus*	**30**	79	58	94
Variegated Fairy-wren *Malurus lamberti*	**0**	92	80	100
Yellow Thornbill *Acanthiza nana*	**20**	49	29	56
Spiny-cheeked Honeyeater *Acanthagenys rufogularis*	**38**	86	56	100
Varied Sittella *Daphoenositta chrysoptera*	**41**	67	50	83

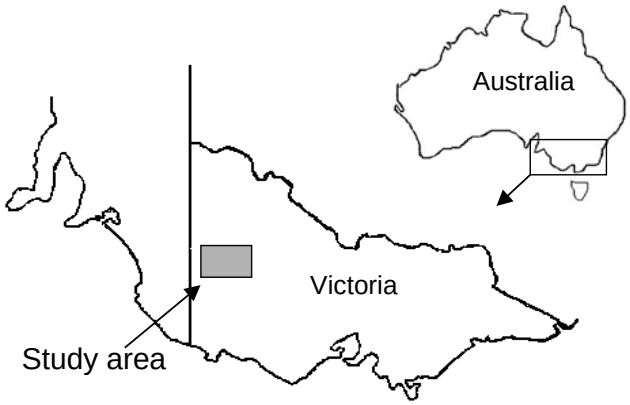

Figure 1.

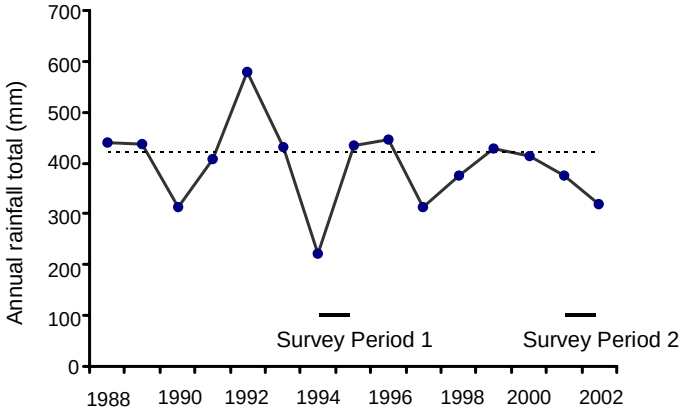
Annual rainfall total (mm)
700
600
500
400
300
200
100
0
1988
1990
1992
1994
1996
1998
2000
2002
Survey Period 1
Survey Period 2

Figure 2.