

Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation

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ABSTRACT

Aim We characterized changes in reporting rates and abundances of bird species over a period of severe rainfall deficiency and increasing average temperatures. We also measured flowering in eucalypts, which support large numbers of nectarivores characteristic of the region.

Location A 30,000-km² region of northern Victoria, Australia, consisting of limited amounts of remnant native woodlands embedded in largely agricultural landscapes.

Methods There were three sets of monitoring studies, pitched at regional (survey programmes in 1995–97, 2004–05 and 2006–08), landscape (2002–03 and 2006–07) and site (1997–2008 continuously) scales. Bird survey techniques used a standard 2-ha, 20-min count method. We used Bayesian analyses of reporting rates to document statistically changes in the avifauna through time at each spatial scale.

Results Bird populations in the largest remnants of native vegetation (up to 40,000 ha), some of which have been declared as national parks in the past decade, experienced similar declines to those in heavily cleared landscapes. All categories of birds (guilds based on foraging substrate, diet, nest site; relative mobility; geographical distributions) were affected similarly. We detected virtually no bird breeding in the latest survey periods. Eucalypt flowering has declined significantly over the past 12 years of drought.

Main conclusions Declines in the largest woodland remnants commensurate with those in cleared landscapes suggest that reserve systems may not be relied upon to sustain species under climate change. We attribute population declines to low breeding success due to reduced food. Resilience of bird populations in this woodland system might be increased by active management to enhance habitat quality in existing vegetation and restoration of woodland in the more fertile parts of landscapes.

Keywords

Australia, birds, breeding failure, drought, eucalypt woodlands, flowering.

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INTRODUCTION

Many regions of the world have been subjected to profound change in management over the past few centuries, with loss and fragmentation of native vegetation cover counting as the most threatening of processes for declines in biological diversity (Fahrig, 2003; La Sorte, 2006). Conservation biologists have predicted an acceleration of species extirpations and

extinctions due to an ‘extinction spiral’, where negative feedbacks affect demographical processes and recruitment fails (Caughley, 1994). Another primary agent of negative impacts on biological diversity is human-induced climate change (Root *et al.*, 2003; Thomas *et al.*, 2004), which has been linked with many biological effects, including changes in geographical and elevational distributions and altered seasonal breeding activity (Parmesan & Yohe, 2003; Parmesan, 2007; Rosenzweig *et al.*,

2008). There seems to have been little attention paid to possible population-dynamic effects of climate change, including adverse impacts on breeding success (Mac Nally *et al.*, 2009a). Under current climate change scenarios, southern Australia is projected to experience a 1–5 °C temperature increase and a $\geq 10\%$ decrease in rainfall in all months by 2070 (CSIRO, 2007; Timbal & Jones, 2008).

Human effects on the avifauna of the woodlands of south-eastern Australia have been extensively reported (Recher, 1999; Ford *et al.*, 2001; Mac Nally, 2007b). These largely stem from widespread clearance of forests (Radford *et al.*, 2005), harvesting practices (Mac Nally *et al.*, 2000) and water loss from landscapes (Lemly *et al.*, 2000; Cai & Cowan, 2008b). Structurally complex forests with mature trees are scarce. Most of the few existing large, old trees in the region pre-date widespread European settlement in the 19th century (Gibbons *et al.*, 2008). Many of these trees are on private land, in small remnants or scattered across farmland and are likely to die in the next 50–100 years even without climate change; there are few replacements (Gibbons & Boak, 2002). In larger blocks on public land, old trees are rare due to past management; forests mainly consist of small, coppiced trees (Mac Nally *et al.*, 2000). Old trees are especially significant in southern Australia because of the dependence of many birds, mammals, reptiles and invertebrates on tree hollows (Gibbons & Lindenmayer, 2002), which take around 100 years to form (Vesk *et al.*, 2008). Rates of tree growth are slow due to low rainfall and poor soils in the parts of the landscape where remnant vegetation occurs (Vesk & Mac Nally, 2006). Tree growth-rates are likely to decline further in a drying climate (Vesk & Mac Nally, 2006). From broad-scale modelling, there appears to have been substantial decline in stand condition of remnant vegetation coincident with the 12+ year drought (Department of Sustainability and Environment, 2008; Cunningham *et al.*, 2009).

In this article, we present evidence for the collapse of the avifauna of interior eucalypt woodlands of south-eastern Australia collected from three sets of data representing a gradient in spatial scale. First, at the regional scale, we conducted surveys in the largest remnants of woodlands (box and ironbark forests, $> 10,000$ ha) (Thomson *et al.*, 2007) in 1995–97, 2004–05 and 2006–08. Second, we conducted surveys in 24 landscapes (each of 10^4 ha) in 2002–03 (Radford *et al.*, 2005) and in 2006–07. Third, we visited 12 sites situated in the largest remnant forest (40,000 ha) 64 times each over the period from 1997 to 2008 (five to eight surveys p.a. evenly spread). We used a very conservative threshold for assessing change – a 90% probability of change in abundance or reporting rate (proportion of surveys in which a species is recorded). We also show data on drying and much reduced flowering by *Eucalyptus* spp., which provides the primary food resource for a large number of species and individual birds in the region (Keast, 1968) and supports invertebrates that are prey for other bird species. Flowering is a useful indicator over such large scales given the difficulties in measuring invertebrate prey even over small areas (Recher *et al.*, 1996; Timewell & Mac Nally, 2004).

METHODS

The region

The region (30,000 km², central Victoria, Australia, Fig. 1) is characterized by box and ironbark forests and woodlands (mainly red ironbark *Eucalyptus tricarpa*, grey box *Eucalyptus microcarpa*, yellow gum *Eucalyptus leucoxylon*) on gentle slopes and hills (elevation 150–400 m) and currently is an agricultural-forest mosaic, with only 17% of the original vegetation cover remaining (ECC, 2001). The historical mean annual rainfall ranged from 400 to 700 mm, mostly occurring in winter and spring; summers are hot and dry (Mac Nally *et al.*, 2000). For > 160 years, the region has been much modified by gold mining, timber harvesting and agriculture. Most of the remaining native vegetation is located predominantly on sites characterized by shallow, infertile soils (Mac Nally *et al.*, 2000), while on the better soils of the plains, remnant vegetation occurs as highly fragmented patches or linear strips along roads and streams (van der Ree, 2002; Johnson *et al.*, 2007).

The box and ironbark forests and woodlands are open-canopied forests and woodlands of moderate height (10–25 m). The local composition of the forest depends on aspect, elevation, soils and drainage (Mac Nally & Horrocks, 2002). Understorey usually is low and sparse and is dominated by heaths (Epacridaceae), bush-peas (Fabaceae) and small acacias (Mimosaceae, especially Golden Wattle *Acacia pycnantha*). In woodland areas, perennial tussock grasses (*Austrodanthonia* spp., *Poa* spp.) occur.

Rainfall and temperature data

Detailed rainfall (mm) data were obtained for four stations in the region from 1970 to 2007 (Bureau of Meteorology, Australia, <http://www.bom.gov.au>): Bendigo (36°42' S, 144°05' E), Muckleford (37°02' S, 144°05' E), Rheola (36°37' S, 143°40' E) and Rushworth (36°43' S, 145°00' E). Temperature data were obtained for the bounding box including the four stations listed (http://www.bom.gov.au/cgi-bin/silo/cli_var/area_timeseries.pl).

Sources of bird occurrence data

Sampling units were 2-ha strip transects (250 × 80 m). Data are from six major survey programmes (Table 1). In each programme, ≥ 2 survey rounds were conducted in both the 'cooler' (May–September) and the warmer (October–April) parts of the year to capture seasonal variation in the avifaunas (McGoldrick & Mac Nally, 1998). The regional-scale sites were surveyed between 1995 and 1997. A subset of these (25 sites) was resurveyed in 2004–05, as were 40 additional sites used for validating spatial predictive models of species' occurrence (Thomson *et al.*, 2007). There were no apparent differences between the original and additional sites vis-à-vis their avifaunas (Mac Nally, 2007b). Fifty-five sites were surveyed

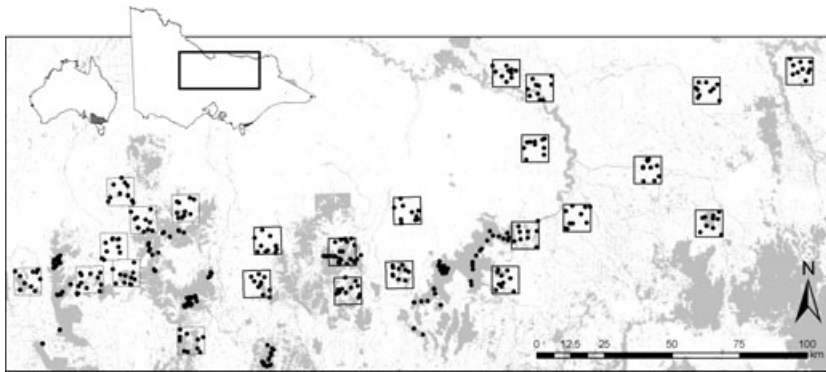


Figure 1 Location of all survey locations across the box and ironbark region of north-central Victoria, Australia, with remnant vegetation in grey shade. Study sites in boxed regions are the landscapes of the landscape-scale study (Radford *et al.*, 2005).

Scale	No. sites	No. surveys per site	Years	Authorities
Regional	213	8	1995–97	Mac Nally <i>et al.</i> (2000), Mac Nally & Horrocks (2002)
Regional	65	8	2004–05	Thomson <i>et al.</i> (2007)
Regional	55	5	2006–08	Radford & Bennett (2007)
Landscape	240	4	2002–03	Radford <i>et al.</i> (2005), Radford & Bennett (2007)
Landscape	240	4	2006–07	Unpublished data
Remnant forest	12	64	1997–2008	Radford & Bennett (2007)

Table 1 Details of bird-occurrence studies.

in 2006–08. In the landscape-scale study, 240 sites were surveyed between 2002 and 2003; these were arranged as 10 sites in each of 24 different 100 km² (10⁴ ha) landscapes (Radford *et al.*, 2005). These 240 sites were resurveyed in 2006–07. The sixth survey programme is a long-term, intensive study of 12 sites located in the largest remnant forest block in the region (> 40,000 ha), which we refer to as the remnant forest survey programme.

Bird-occurrence surveys

All studies used a standard procedure for bird surveys. Observers proceeded along the mid-line of the transect for 20 min (over 2 ha) per survey. Individual birds on the transect ahead of the observer were used for the analyses reported here. Surveys were not conducted in rain, high wind or in high temperatures. There were four to eight repeated surveys at each location except sites in the remnant forest block, which were surveyed 64 times each. For each species, we characterized occurrence as the 'reporting rate' = (number of surveys in which detected)/number of surveys, and 'abundance' = total records (every individual detected) summed over all surveys. Abundance was rescaled to total records per 100 surveys in a given survey programme (Mac Nally, 2007b). With repeated surveys per site, some individuals may be counted more than once. However, we use total records because this indicates 'intensity of use' over the annual cycle.

For each set of survey types, the same sets of observers undertook the work. The habitats are easy to survey for birds because the vegetation is open and tree-heights usually are < 20 m. The use of reporting rates includes adjustments for different numbers of visits. We used different analytical models for each of the data sets that were most appropriate for the survey designs.

Our analyses excluded several groups of birds, such as non-native, nocturnal and largely aquatic species, but still included 159 species. We classified species by several criteria that might be expected to lead to different responses. These include degree of dependence or tolerance to amounts of remnant vegetation in landscapes, foraging guild (diet and substrate), nesting guild, general mobility (e.g. resident vs. seasonal migrant), degree of conservation concern (Radford & Bennett, 2005) and a broad measure of distribution: whether a species' geographical range is associated mainly with drier (semi-arid, arid) or mesic environments or if it is widespread throughout Australia (Blakers *et al.*, 1984).

For a given survey programme (e.g. regional, 1995–97; landscape, 2002–03), we summed all records per species and expressed totals as records per 100 surveys. Species were arranged in decreasing rank-abundance order for the first survey in the sequence to create an abundance spectrum (Mac Nally, 2007b), which provided a frame of reference against which subsequent species-specific abundances were compared. We undertook similar calculations for later surveys of the same programme. Delta-spectra, differences between subsequent and

reference spectra in a given series of survey programmes, were computed and these provided graphical representations of species-specific changes in abundance.

Method for scoring breeding

For a subset of 41 of the regional 2006–08 programme sites, breeding behaviours were recorded using a consensus-weighted, evidence-of-breeding rating by 25 expert Australian ornithologists (Mac Nally, 2007a). These surveys were conducted in addition to the regular surveys outlined above. Each score is based on the ranked importance of a suite of breeding behaviours in relation to realized breeding success. Behaviours with high scores, such as direct observation of feeding young in the nest, indicate breeding success (Mac Nally, 2007a). Behaviours with low scores, such as male and female courting pairs and male territorial behaviours, suggest that birds perceive the site as potentially suitable for breeding, but it remains unknown if this translates into actual production of fledglings. We used only the highest observed scored behaviour for a particular nest. If there were multiple nestlings or fledglings, this was only recorded as a single value (Mac Nally *et al.*, 2009b). For the breeding surveys, transects were sampled six times at regular intervals from late August 2007 to mid-November 2007 (breeding season). Each round of surveys was completed within 2 weeks of the previous one to contend with the potentially short intervals between hatching and fledging of some bird species (Mac Nally *et al.*, 2009b).

Flowering in the regional-scale surveys

We estimated eucalypt flowering over the 2-ha sites. For each species of tree, flowering intensity (I) was classified into four intensities: (1) no flowering, $I = 0$; (2) up to 15% of individual trees flowering, $I = 1$; (3) 15–60% of individual trees flowering, $I = 2$; and (4) > 60% of individual trees flowering, $I = 3$. The basal areas of each species of tree measured on each transect (Mac Nally & Horrocks, 2000) were used in conjunction with these estimates of flowering intensity to compute an overall summed measure of transect-wide, eucalypt flowering for a given census (I_{tot}). For example, if there were three tree species with basal areas of 1.8, 3.8 and 1.9 m² ha⁻¹ with flowering intensities of 2, 3 and 1, respectively, the overall flowering index was: $I_{\text{tot}} = (1.8 \times 2) + (3.8 \times 3) + (1.9 \times 1) = 6.9$. We used the maximum values over the set of visits for a particular survey (e.g. the four visits for the 2004–05 surveys) to characterize flowering for each site by survey.

Flowering in remnant-forest surveys

For the 12 sites in the remnant forest, flowering of eucalypt species was recorded on 64 occasions between April 1997 and May 2008. At each site, 25 points were selected in a stratified random manner and marked with wooden stakes. Flowering was assessed within a 3-m radius of each point by scanning the canopy foliage with binoculars. Flowering was scored in relation

to the relative proportion of canopy foliage covered by fresh flowers (0.5 = < 5% canopy foliage, 1 = 5–10%, 2 = 10–20%, 3 = 20–30%, etc.). Two indices of flowering then were calculated for red ironbark, the dominant tree species at all sites, which potentially has a lengthy flowering period during the austral winter months (April–September) (Keatley & Hudson, 2007) and, when flowering, attracts large flocks of nectarivores. First, we calculated $p_{\text{flowering}}$, which was the proportion of the 25 points at which fresh flowers were present. Second, we calculated an index of flowering intensity ($f_{\text{flowering}}$) by summing, across all points at a site, the product of the flowering score and the estimated foliage cover (in 10% increments) at each point. The two indices were highly correlated at all 12 sites ($R^2 = 0.81$ – 0.97) so we consider data only for $p_{\text{flowering}}$.

Statistical analyses

Reporting rates in regional-scale surveys

We assumed a binomial distribution for the total number of observations r_j from n_j surveys in period j . That is, $r_j \sim \text{Binomial}(p_j, n_j)$, where, p_j is the mean estimated reporting rate for survey period j . We used Bayesian estimation to derive posterior means and 95% credible intervals for each p_j . We assigned uninformative Beta (1,1) prior distributions to p_j and updated those priors through the likelihood function using Markov Chain Monte Carlo (MCMC) sampling. We estimated the posterior probabilities $\Pr(p_{2004-05} < p_{1995-97})$ and $\Pr(p_{2006-08} < p_{1995-97})$ for each species, which indicate the weight of evidence for lower reporting rates in 2004–05 and 2006–08, respectively, than in 1995–97. We considered that $\Pr(p_n < p_{1995-97}) > 0.9$ (equivalent to posterior odds > 9) was strong evidence for a decline in reporting rate and that $\Pr(p_n < p_{1995-97}) < 0.1$ provided strong evidence for an increase in reporting rate (Kass & Raftery, 1995), where n is either 2004–05 or 2006–08.

Reporting rates in landscape-scale surveys

For each species, we fitted a logistic regression model with landscape-level random effects (sites were spatially aggregated in landscapes) to compare reporting rates among survey periods. The model was:

$$r_{ij} \sim \text{Binomial}(p_{ij}, n_{ij}); \log\left(\frac{p_{ij}}{1-p_{ij}}\right) = \alpha_j + e_i.$$

Here, p_{ij} is the mean reporting rate for landscape i in year j , n_{ij} is the number of surveys in landscape i in year j , α_j is the mean log-odds for year j and e_i is the systematic (same among years) error associated with landscape i . We assigned uninformative priors to all model parameters. We used independent normal priors, $N(0,1000)$, for the α s, which were restricted to the interval $(-8, 8)$ to prevent the generation of infinite likelihoods (i.e. fitting 0 or 1 exactly). We used exchangeable normal priors, $N(0, \sigma^2)$, for the e s. We assigned a uniform prior $U(0,5)$ to the standard deviation σ of the landscape random

effects (Gelman, 2005). Alternative prior specifications, including $U(0,10)$ on σ and Inverse Gamma(0.001,0.001) on σ^2 , yielded near-identical results for all species. We estimated the posterior probability that $\alpha_{2006-07} < \alpha_{2003-04}$. We considered $\Pr(\alpha_{2006-07} < \alpha_{2003-04}) > 0.9$ (equivalent to posterior odds > 9) very strong evidence for a decline in reporting rate, and $\Pr(\alpha_{2006-07} < \alpha_{2003-04}) < 0.1$ evidence for an increase in reporting rate.

Reporting rates in the remnant-forest surveys

We fitted a logistic regression model for each species to test for a linear trend in mean reporting rates with time. The model was:

$$r_y \sim \text{Binomial}(p_y, n_y); \log\left(\frac{p_y}{1-p_y}\right) = \alpha + \beta y,$$

where r_y is the number of detections in year y of n_y surveys, p_y is the corresponding reporting rate, α is an intercept and β is the slope of any temporal trend. We assigned α and β uninformative normal priors, $N(0,1000)$, with the latter truncated to the interval $(-8, 8)$. We estimated the posterior probability that $\beta < 0$ from the posterior distribution for β . We considered $\Pr(\beta < 0) > 0.9$ (equivalent to posterior odds > 9) evidence for a decline in reporting rate, and $\Pr(\beta < 0) < 0.1$ evidence for an increase in reporting rate.

Software and general modelling information

We fitted all models in WinBUGS, v. 1.4 (Spiegelhalter *et al.*, 2003). Parameters were estimated from three MCMC chains of 100,000 iterations after 20,000 iteration burn-in periods. We checked MCMC mixing and convergence using the 'boa' package (Smith, 2006) in R (R Development Core Team, 2006). We assessed the importance of parameter values using posterior probability distributions as described above.

RESULTS

Climate change

Rainfall data were highly correlated among stations (all pairwise r_s among stations > 0.89) and so were averaged. Five-year moving averages were obtained for both annual (Fig. 2a) and bird breeding-season (July–November) periods (Fig. 2b). These indicated a steep decline in rainfall over the study period. Since 1950, there has been a substantial increase in mean annual temperature (regression coefficient: 0.009 ± 0.002 SE °C year⁻¹). Since 1997, the average temperature anomaly relative to the historical (all-records) average has been 0.38 ± 0.09 SE °C.

Abundances and reporting rates of adult birds

Declines in abundance and reporting rate occurred at all three spatial scales. At the regional scale, while 33 of the 82 species

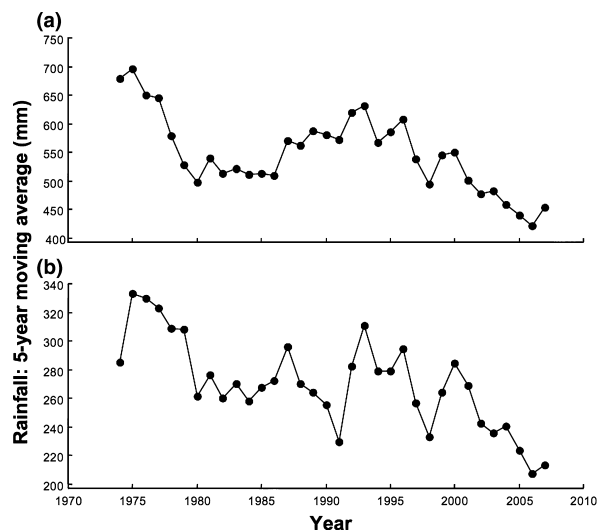


Figure 2 Mean 5-year moving averages of rainfall (mm) for the region for years (a) and for the austral spring (July–November, b).

recorded declined in abundance between 1995–97 and 2004–05, most declines were small (declines of fewer than 20 records per 100 surveys; Fig. 3a). However, data on abundances masked substantial declines in reporting rates over the same period (Fig. 4). The reporting rates of 74% of the species declined between 1995–97 and 2004–05 (Table 2). This result suggests that between 1995 and 2005, a reduced number of individuals of many species congregated in fewer sites. By 2006–07, regional abundances collapsed (Fig. 3b) consistent with substantial reductions in reporting rates (Fig. 4).

At the landscape scale, there were similar major declines in abundances and reporting rates between 2002–03 and 2006–07 (Figs 3c & 4). Of 128 species, reporting rates declined for 84 species (66%) (Table 2). Declines occurred in all landscapes, irrespective of wooded cover (2–60%) (Radford *et al.*, 2005). Reporting rates for a lower proportion of birds declined in the remnant forest sites (54%) (Fig. 3d), but half of these sites were nominally of higher ecological quality (numerous large trees with many hollows, located within the largest remnant, 40,000 ha) (Soderquist & Rowley, 1995; Lada *et al.*, 2007). A weighted average of 66% of species declined in reporting rates across all comparisons (Table 2). Examples of species that declined substantially across all data sets include black-chinned honeyeater (*Melithreptus gularis*), fuscous honeyeater (*Lichenostomus fuscus*), laughing kookaburra (*Dacelo novaeguineae*), rufous whistler (*Pachycephala rufiventris*), restless flycatcher (*Myiagra inquieta*), superb fairy-wren (*Malurus cyaneus*) and white-bellied cuckoo-shrike (*Coracina papuensis*).

The proportion of declining species did not depend on birds' ecological characteristics, feeding or nesting guild, primary habitat type, broad distribution or foraging zone (cf. Jiguet *et al.*, 2007). Moreover, average percentages of declining species differed little between species of current conservation concern and those not so classified (70 vs. 64%, Table 2).

Figure 3 Delta-spectra – changes in abundance (summed records per 100 standard surveys) between the (a) regional-scale surveys in 2004–05 and in 1995–97, (b) regional scale surveys in 2006–08 and 1995–97, and (c) landscape-scale surveys in 2006–07 and in 2002–03. (d) Difference between years 1–3 (1997–99) and 9–11 (2005–07) in the remnant forest programme. The species ordering is the same for (a) and (b) but differs for (c) and for (d). Arrow for fuscous honeyeater (*Lichenostomus fuscus*) in (b) indicates that value extends to –307.

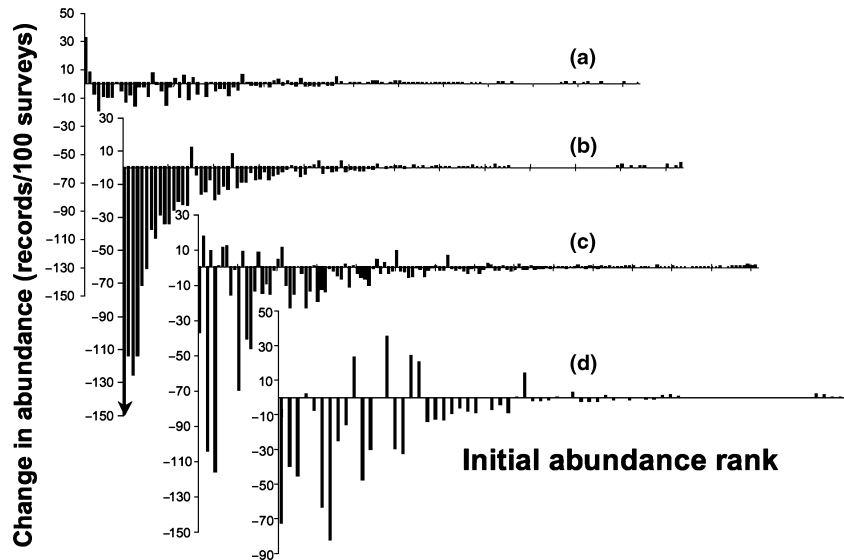
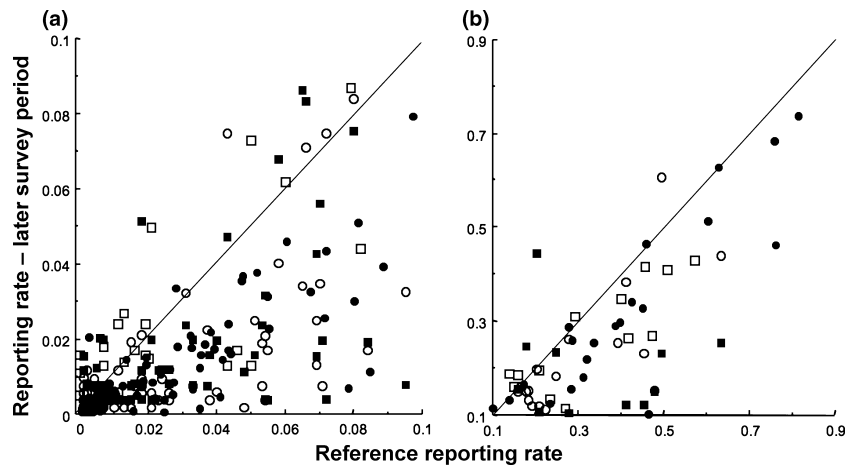


Figure 4 Reporting rates for species in subsequent survey programmes plotted against reporting rates for the earliest corresponding reference survey programme. (a) Data for which the initial reporting rate ≤ 0.1 ; (b) data for which the initial reporting rate > 0.1 . Diagonal lines indicate no change in reporting rates between later and reference programmes. Hollow circles – regional scale, 2004–05 vs. 1995–97; solid squares – regional scale, 2006–08 vs. 1995–97; solid circles – landscape scale, 2006–07 vs. 2002–03; hollow squares – average remnant forest 1997–99 vs. average remnant forest 2005–07.



Breeding

Twenty-eight species displayed breeding behaviours in ≥ 1 of the 41 sites in 2007–08. There were non-breeding records for another 41 species, so only 40% of species showed evidence of breeding. The average number of breeding species per site was 1.4 ± 0.2 (SE). The average total breeding score per site was 5.6 ± 1.0 (SE). At 11 sites, the total breeding score (summed over all species) was 0, and a further 23 sites had total scores < 10 . Across the 41 sites, only nine active nests were seen and only a single scarlet robin (*Petroica boodang*) fledgling was observed. The paucity of observed breeding was not due to the technique used. Using identical methods, 169 fledglings were recorded in 39 small (< 18 ha) revegetation plantings of floodplain vegetation in the austral spring of 2004 (average breeding score per site = 59.3) (Mac Nally *et al.*, 2009b), while 53 fledglings from 18 species were recorded in 21 small (< 55 ha) revegetation plantings in central and western Victoria in the spring 2006 (average breeding score per site = 46.8) (Selwood *et al.*, 2009).

Flowering in the regional-scale sites

Eucalypt flowering varied markedly among survey periods: in 1995–97, the mean index value was 5.69 ± 0.19 (SE), in 2004–05, it was 1.31 ± 0.25 (SE) and in 2006–08, no flowering was recorded (i.e. 0).

Flowering in remnant-forest sites

Flowering of red ironbark occurred seasonally, but irregularly, between 1997 and 2008 (Fig. 5). From 1997 to 2001, moderate or heavy flowering occurred in 4 of 5 years: subsequently, from 2002 to 2007, heavy flowering occurred in 2 of the 6 years, with limited or complete absence of flowering in the other years.

DISCUSSION

We have shown that around two-thirds of the woodland bird species in the region have declined in occurrence and

Table 2 Statistical assessment of changes in reporting rates* based on comparisons between regional-scale and landscape-scale programmes and linear fits to reporting rate trends (remnant-forest programme). Species were characterized according to several criteria relating to levels of vulnerability to habitat loss and fragmentation, foraging and nesting guilds, mobility (Mac Nally, 1995a), conservation concern (Radford & Bennett, 2005) and distributional range (Blakers *et al.*, 1984). Table entries are numbers of species, except where indicated as %.

Classification	Class	Ave. (%)†	Regional 2004–05 vs. 1995–97				Regional 2006–08 vs. 1995–97				Landscape 2006–07 vs. 2003–04				Remnant forest			
			Declining	Total	–	0	+	Total	–	0	+	Total	–	0	+	Total	–	0
Habitat	Open-country	57	9	7	2	0	10	6	4	0	25	14	10	1	4	1	3	0
Habitat	Open-tolerant	66	20	17	3	0	22	16	4	2	33	22	11	0	8	1	7	0
Habitat	Woodland dependent	67	53	37	12	4	51	33	15	3	70	48	22	0	42	27	12	3
Foraging substrate	Aerial	81	5	5	0	0	6	4	2	0	13	11	2	0	2	1	0	1
Foraging substrate	Bark	67	4	2	2	0	4	2	1	1	4	4	0	0	3	2	0	1
Foraging substrate	Canopy	67	29	20	6	3	28	20	6	2	35	25	10	0	27	15	12	0
Foraging substrate	Ground	63	39	30	9	0	41	27	12	2	67	40	26	1	19	8	10	1
Foraging substrate	Low shrubs	50	2	2	0	0	2	1	1	0	4	1	3	0	1	1	0	0
Foraging substrate	Tall shrubs	62	3	2	0	1	2	1	1	0	5	3	2	0	2	2	0	0
Food	Frugivore	44	2	1	0	1	1	1	0	0	4	2	2	0	2	0	2	0
Food	Insectivore	71	43	35	7	1	45	30	12	3	64	45	18	1	29	19	8	2
Food	Nectarivore	63	15	8	5	2	14	11	3	0	19	13	6	0	14	8	6	0
Food	Raptor/vertebrate	53	11	8	3	0	12	6	4	2	23	13	10	0	4	1	3	0
Food	Granivore	63	11	9	2	0	11	7	4	0	18	11	7	0	5	1	3	1
Nesting	N/A	80	1	1	0	0	2	1	1	0	1	1	0	0	1	1	0	0
Nesting	Burrow	85	3	3	0	0	3	1	2	0	5	5	0	0	2	2	0	0
Nesting	Ground	61	4	3	1	0	4	3	1	0	12	6	5	1	2	1	1	0
Nesting	Hollows	72	16	12	4	0	16	14	1	1	25	20	5	0	11	3	7	1
Nesting	Shrub/canopy	64	56	41	11	4	56	36	16	4	83	51	32	0	37	22	13	2
Nesting	Parasite	33	2	1	1	0	2	0	2	0	2	1	1	0	1	0	1	0
Conserv. concern	No	64	59	44	11	4	60	39	16	5	95	61	33	1	41	21	17	3
Conserv. concern	Yes	70	23	17	6	0	23	16	7	0	33	23	10	0	13	8	5	0
Mobility	Migrant	70	23	19	3	1	24	18	5	1	31	21	9	1	13	6	6	1
Mobility	Itinerant	55	13	7	6	0	13	9	4	0	20	11	9	0	8	3	4	1
Mobility	Resident	66	46	35	8	3	46	28	14	4	77	52	25	0	33	20	12	1
Distribution	Dry	57	4	3	1	0	4	1	3	0	13	8	5	0	2	1	1	0
Distribution	Mesic	66	39	26	10	3	39	27	10	2	50	31	19	0	32	22	10	0
Distribution	Widespread	67	39	32	6	1	40	27	10	3	65	45	19	1	20	6	11	3
Totals		66	82	61	17	4	83	55	23	5	128	84	43	1	54	29	22	3

‘–’ Denotes decrease; ‘0’ denotes no evidence of change; ‘+’ denotes increase.

*Only species with ≥ 5 records in a given study.

†Weighted by ‘total’ values in each row.

abundance. A key finding was that the proportion of species that declined was very similar, irrespective of foraging or nesting guilds, spatial dynamics or conservation concern. Other reports of widespread change in avifaunas have found differences attributable to these kinds of classification (e.g. Woinarski & Catterall, 2004; La Sorte, 2006). In our case, it seems likely that these declines are climate-driven or at least reflect the added stresses of sharp reductions in rainfall and increases in temperatures (hence higher evapotranspiration) over the past decade in southern Australia. We do not believe that these sharp declines in abundance and reporting rates of birds are artefacts of survey methodologies because the same sets of observers were involved in each of the three major programmes and the same survey approach (i.e. transect size, time) was employed.

While our observed bird declines are consistent with the expectation of an ‘extinction debt’ (Tilman *et al.*, 1994) due to past land-cover change, the magnitude of decline was similar in extensive forest remnants to sites with little remnant woody cover (c. 2%). This is counter to expectations under extinction debt, specifically accelerated declines in smaller, poorer fragments, and suggests a more pervasive driver. South-eastern Australia has been gripped by drought since 1996 (Fig. 2). However, trends in precipitation more probably reflect a decline of c. 40% relative to long-term averages since the 1950s, which is consistent with projections from climate-change models (Cai & Cowan, 2008a). Our results may foreshadow comparable impacts to other drying regions, such as western North America (Fleishman *et al.*, 2003; Seager *et al.*, 2007; Mac Nally *et al.*, 2008).

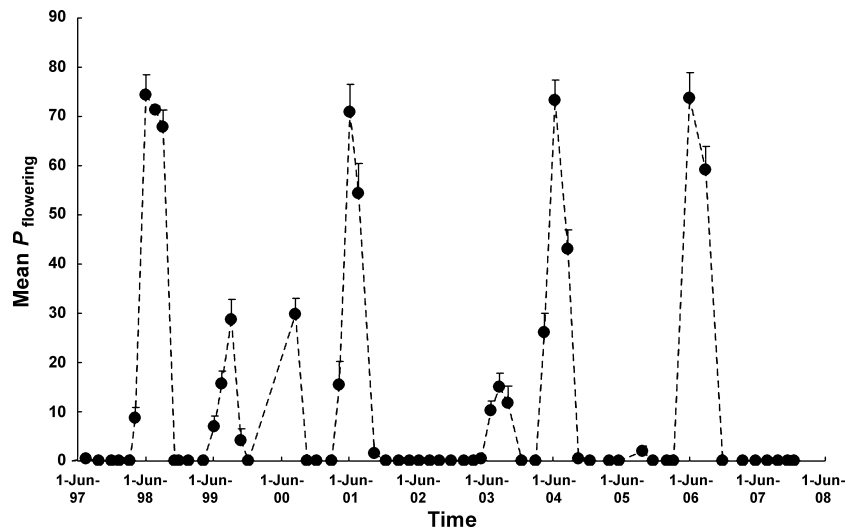


Figure 5 Pattern of flowering of *Eucalyptus tricarpa* in the remnant-forest sites since 1997 as the proportion of sample points with flowering, $p_{\text{flowering}}$. Standard errors.

The mechanisms by which this marked decrease in rainfall influences the abundance and reporting rate of the avifauna are likely to be related to on-going reduction in habitat quality and food availability. At a regional scale, there has been relatively little loss of wooded vegetation in recent decades, but habitat quality continues to decline (Department of Sustainability and Environment, 2008; Cunningham *et al.*, 2009). The collapses in bird reporting rates and abundances suggest strongly that the availability of all types of food has crashed.

Nectar and insect feeders probably are responding in different ways to this same major stress. The avifaunas of the box and ironbark forests numerically are dominated by nectarivorous species (honeyeaters, family Meliphagidae, and lorikeets, family Psittacidae), which depend on regional patterns of flowering of the dominant eucalypt species (e.g. mostly cool-season-flowering species such as *E. tricarpa* and *E. microcarpa* (Mac Nally & McGoldrick, 1997). Most nectarivores are highly mobile, tracking temporal variation in nectar production across large areas. Historically, nectarivore abundances fluctuate in response to the changing spatial mosaic of eucalypt flowering. In the regional-scale study sites, eucalypt flowering was much reduced during surveys in 2003–04 compared with those in 1995–97 and in 2006–07, flowering was not seen. In the remnant forest sites, the frequency of flowering, particularly peak flowering events, of red ironbark was greatly reduced in 2002–07 compared with 1997–2001, with failure to flower in three of these latter 6 years. This pattern contrasts markedly with a 25-year data set (1945–70) from this region (Keatley & Hudson, 2007) in which red ironbark failed to flower in only 4 of 25 years (i.e. failure recurrence of 6.4 years). The outcome is that the seasonal abundance of flowers, and hence nectar, has been much reduced in recent years, which can be clearly associated with the drying climate through rainfall-flowering-nectar-honey production models (Porter, 1978).

When sampling coincides with poor flowering years, nectarivore occurrence and abundance are dramatically reduced

because much of the population emigrates. In 2002, for example, flowering of red ironbarks failed and there was a mass exodus of the red wattlebird (*Anthochaera carunculata*), musk lorikeet (*Glossopsitta concinna*) and other nectarivores from the 40,000 ha Rushworth forest (remnant forest study). This coincided with greatly increased abundance of the musk lorikeet in urban Melbourne, 120 km to the south (Fitzsimons *et al.*, 2003), although we have no evidence that the same birds moved between the regions. In winter 2007, there were very few records of the usually abundant fuscous honeyeater (*Lichenostomus fuscus*) and yellow-tufted honeyeater (*Lichenostomus melanops*) in central Victoria, while irruptions of these species were observed in south-western Victoria, beyond their usual geographical range (R. Clarke, pers. comm.; J.Q. Radford, pers. obs.). Although many birds may return, such mass movement incurs energetic costs, mortality and foregone breeding opportunities. If individuals are required to undertake such movements more often because of more frequent flowering failure in a drying climate, the associated costs will be realized as declining regional populations. Reduced flowering, and possibly reduced pollination due to decline of pollinators, would lead to reduced seed set, and perhaps ultimately to a change in the composition of the plant community.

Temporal comparisons at all spatial scales are consistent in indicating considerable declines in insectivore abundance and reporting rates. The avifaunal declines reflect on-going and consistent erosion of their resource base. Many insectivores, especially residents, have limited capacity to move to alternative habitats (Mac Nally, 1995b; Ford *et al.*, 2001). Their decline signals mortality without replacement rather than movement. The abundance of arthropods, particularly those associated with the foliage of canopy trees, is greatly reduced during drought (Bell, 1985). Biomass of ground-litter invertebrates is linked to soil moisture (lower in drier soils) (Taylor, 2008), which, together with depletion of understorey vegetation, may explain strong declines in ground-feeding birds

(Table 2). There is extensive loss of shrubs across much of the region and the onset of tree death on higher ridge areas (A.F. Bennett, pers. obs.; J.Q. Radford, pers. obs.). We hypothesize that the compounding effects of diminishing food resources and deteriorating nest-site quality (fewer sites and increased exposure) have severely limited recruitment over successive years, culminating in the observed population collapses. Given the low reproductive rates of Australian passerines (Yom-tov, 1987), the occasional average or good year is unlikely to compensate for breeding failure in the increasingly frequent dry years, leading to population growth rates less than replacement levels.

The climatic conditions expected under rapid climate change render avifaunal populations even less resilient to land-use change than previously thought. Current methods for protection of remnant habitat and increases in revegetation will be insufficient to prevent regional extirpations. The urgency and magnitude of remedial action required are many-fold greater than current practice. Increased awareness of the current situation is a prerequisite to policy reform, and policy levers, such as carbon trading (Harper *et al.*, 2007), might induce radical land-use change.

There are several options for enhancing resilience of birds in the box and ironbark system in the face of altered climate. First, measures to restore habitat quality in existing forested blocks will facilitate breeding if and when more favourable seasons occur. Practices related to fire and extractive industries can be managed to promote structural complexity by retaining large old trees, thinning overly dense stands of regrowth to engender more rapid tree growth of retained stems (Vesk *et al.*, 2008), protecting fallen timber from firewood harvesting and recreating spatial patchiness in ground layers (Lindenmayer *et al.*, 2006).

The greatest gains will accrue from preferential restoration in more-fertile areas, particularly those adjacent to existing remnants (e.g. drainage lines and broad riverine flats, Thomson *et al.*, 2009). Revegetation in fertile areas offers multiple benefits. Tree growth rates will be faster than on poor soils (Mac Nally, 2008) and warm-season flowering of eucalypts associated with these sites (e.g. yellow box *Eucalyptus melliodora*, river red gum *Eucalyptus camaldulensis*) will increase the temporal complementarity of nectar resources across the region. Nectarivores range across the entire region (McGoldrick & Mac Nally, 1998), so temporal variability of flowering is important. Regrowth appears to support greater breeding activity of birds, from which recruits may disperse to other parts of the landscape. Multiple pathways for movement at multiple scales (from inter-patch to sub-continental) can be created through strategic enhancement of existing habitat and revegetation (Brereton *et al.*, 1995).

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