Response of birds to episodic summer rainfall in the Great Western Woodlands, Western Australia

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From 1999 to 2003, the Great Western Woodlands in Western Australia experienced above average summer and autumn rainfall. Although rainfall from 2004 to 2010 approximated long-term seasonal and annual averages, the soil and litter layer became parched, there was less vegetative growth, and nectar production declined. As habitats became drier, fewer birds nested, although some bred and fledged young. Ground, shrub, and canopy foragers, including migrants, along with nectar-feeders declined in abundance. The numbers of raptors and cuckoos declined in line with declines in abundances of prey and host species. Declines in abundance and breeding were probably linked to declines in food resources, although there were no consistent changes in the foraging behaviour of birds. There was a modest recovery in breeding effort and species abundances in 2010 following above average rainfall in the spring and summer of 2008/2009. These observations indicate that productivity and avian abundance in these semi-arid woodlands (200 – 300 mm annual rain) decline with average rainfall. Episodes of high and possibly prolonged rainfall are required to restore productivity and allow faunal populations to recover.

Climate change models predict less rain and higher temperatures in southwestern Australia. High rainfall events will occur, but there will be longer intervals of average or below average rainfall. As shown by events in 2010, birds can respond quickly to increased rainfall, but with longer periods of drier or even average rainfall numbers may fall to levels below which recovery is not possible. Populations in less productive habitats will disappear and the distribution of species will become increasingly patchy, with increased likelihood of local extinction. To reduce these heightened risks associated with anthropogenic climate change habitat connectivity must be maintained on regional and continental scales not presently provided by existing conservation reserves.

\textbf{Key words:} woodland birds, climate change, drought, episodic rain, eucalypt woodlands, Great Western Woodlands, micro-refuges, habitat connectivity, biodiversity conservation

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\textbf{Introduction}

Climate models predict increased mean annual temperatures, reduced rainfall, changed seasonal patterns of rainfall, and more extreme weather events for southern Australia over the 21st Century (PMSEIC Independent Working Group, 2007; Pittock 2009; Krono et al. 2011; Bureau of Meteorology and CSIRO 2012, 2014). Coincident with increased temperatures and less rain, there will be an increased frequency of fire (Bureau of Meteorology and CSIRO 2014). These changes are expected to have significant adverse effects on continental and regional biodiversity, including globally iconic biodiversity hotspots, such as southwestern Western Australia (Chambers et al. 2005; Wormworth and Mallon 2006; Lunney and Hutchings 2012).

An understanding of the effects on the biota of changes in weather patterns accompanying climate change is critical for long-term conservation management, particularly in the context of on-going habitat loss and fragmentation. Since 1986, we have studied the ecology of woodland birds in Western Australia, including the Great Western Woodlands (GWW) near the towns of Yellowdine, Widgiemooltha, and Norseman from 1997 to 2010. The GWW is the largest remnant of temperate eucalypt woodlands in southern Australia, with an area in excess of 21 million hectares and a core of 7.5 million hectares that has not been grazed by domestic animals and has high biodiversity values (Judd et al. 2008; Watson et al. 2008; Department of Environment and Conservation 2010).

In this paper, we describe the response of woodland birds near Norseman to departures of rainfall from long-term averages. The observations presented were not intended to study the effects of rainfall on birds, but developed from work investigating the foraging ecology of woodland birds and a study of the response of birds to an intense wildfire (Recher and Davis 2013). As such, the study is observational, there was no experimental design nor experimentation, and the data presented in the paper were obtained for other purposes. Investigation of the effects of drought, above average rainfall, or any change in weather patterns on wildlife is necessarily ad hoc; changes in weather patterns can be anticipated, but not planned. Further work is required to fully understand how birds in
these woodlands will respond to and be affected by climate change. Our aim in this paper is to present and interpret some effects of weather patterns on birds, so that others can test our ideas. We discuss our observations in the context of how best to manage the GWW for biodiversity conservation in an era of accelerated climate change on a continent where habitat loss and fragmentation in association with excessive human population growth and resource consumption is an on-going and growing problem for nature conservation.

Study area
The research reported here was conducted on 14 plots along the Hyden-Norseman Road west of Norseman, Western Australia from 32° 10.929' S, 121° 37.846' E to 32° 01.472' S, 121° 30' 903" E and on 16 plots ~ 25 km north of Norseman centred on 32° 00.251' S, 121° 39.305' E. Norseman is centrally located within the GWW (Figure 1). Of the 16 plots north of Norseman, eight were established in 2006 (the 2006 plots) and eight in 2007 (the 2007 plots).

Topography, vegetation, soils
Our study plots at Norseman lie within an elevation range of 311 to 405 m above mean sea level (amsl), with broad, flat ridges, gentle slopes, and wide, flat areas that receive water from the slopes. Drainage is internal and except immediately after rain there is no potable surface water. Soils are primarily soft calcareous earths, sandy loams, and alluvials, with some laterites on ridge lines (Berry et al. 2010; pers. obs.). Most plots have a well-developed biocrust that hydrates rapidly with rain. All plots were located in eucalypt woodlands (Appendix 1). Although there was little topographic relief, the composition and structure of the vegetation changed over short distances with changes in slope and soil. Eucalypts formed open to closed canopies from 15-30 m in height, with emergents to 40-45 m. The most abundant

Figure 1. Southwestern Western Australia showing the location of the Great Western Woodlands and the study sites near Norseman where the effects of rainfall on woodland birds were studied.
eucalypts were Dundas Blackbutt *Eucalyptus dundasii*, Gimlet *E. salubris*, Goldfields Blackbutt *E. lesueufii*, Merrit *E. flocktoniae*, Red Morrel *E. longicornis*, Redwood *E. transcontinentalis*, Ribbon Gum *E. sheathiana*, Salmon Gum *E. salmonophloia*, Sand Mallee *E. eremophila*, Square-fruited Mallee *E. calycogona*, and Yorrell *E. yillagensis*. Mallees (*Eucalyptus* spp.), paperbarks (primarily *Melaleuca uncinata*), and young eucalypts formed a discontinuous understorey. The shrub layer was rich in species, but patchy in distribution. In more open areas shrubs occurred in nearly continuous layers from 50 to 600 cm in height. Paperbarks were the tallest shrubs and formed dense, patchily distributed, monospecific stands. Shrubs in the genera *Acacia*, *Grevillea*, *Eremophila*, *Excoecaris*, *Santalum*, *Mareiana*, and *Atriplex* among others were abundant. Ground vegetation was mainly ephemeral and comprised of low (< 30 cm) fors and shrubs. Grasses were uncommon. As with the shrub layer, the ground vegetation was patchy and rarely continuous. Bare ground formed 30 to 80% of the ground surface, with litter and coarse woody debris, including logs, covering 20 to 70% of the soil surface depending on canopy cover and exposure to wind.

Most plots showed signs of limited selective logging, although none had occurred recently. Firewood removal was common. Four plots established in 2006 north of Norseman were young (< 50 y old), even-aged stands, with scattered mature Red Morrel, regenerating after wildfire or possibly clear-felling. All other plots north of Norseman and those west of Norseman were mature to wind.

There was no surface water on any site and none were grazed by domestic stock nor was there evidence of historic grazing. A small number of plots were used by apiarists, although none were in use during the times we worked at Norseman. Native grazers and browsers other than Emu *Dromaius novaehollandiae* were uncommon.

None of the plots had rabbits or other introduced fauna that we observed, although most had some exotic weeds particularly near road edges and in depressions, such as abandoned bettong *Bettongia lesueurii* warrens.

**Climate**

The CWG has a mean annual rainfall of 200-300 mm increasing from east to west, and north to south, with a long-term (1897-2011) mean at Norseman of 289 mm/year. Monthly rainfall at Norseman occurs through the year averaging from 20 mm in January to 31 mm in May (Figure 2). Long-term mean rainfall is greatest in Autumn (Mar-May) (78 mm) and Winter (Jun-Aug) (82 mm), and least in Summer (Dec-Feb) (66 mm) and Spring (Sep-Nov) (62 mm). The heaviest rains at Norseman fall in Summer and Autumn (Figure 2).

Mean maximum monthly temperatures exceed 35°C during December, January, and February (summer), with mean minimums falling below 15°C in June and July (winter).

Rainfall and temperature data are from the Australian Bureau of Meteorology. We used the Norseman Station (No. 12065; 32° 20' S, 121° 78' E; 277 m asml), with records commencing in 1897. For gaps in the daily records from this station, we used data from the Norseman Aerodrome (No. 12009; 32° 21' S, 121° 75' E; 263 m asml).

**Rainfall 1983 - 2010**

Rainfall at Norseman is highly variable (Figures 2, 3). The mean annual rainfall for the decades 1983-1992 (344 mm) and 1993-2002 (361 mm) exceeded the long-term (1897-2011) average of 289 mm. Mean annual rainfall for 2003 to 2010 was 287 mm. From 1999 to 2003, immediately prior to our study, rainfall in summer and autumn exceeded the long-term mean by 150 to 240%,
with below average winter rainfall and average spring rainfall (Table 1). From 2004 to 2010, rainfall was above average for spring and summer and below average in autumn and winter (Table 1). Rainfall from September 2008 (spring) to January 2009 (summer) was three times above the long-term mean for those months (317 mm vs 102 mm), with rainfall in June and July 2009 (winter) also exceeding the long-term mean (92 mm vs 57 mm).

Table 1. Percent of long-term (1897-2010) seasonal rainfall at Norseman for the years 1999-2003 and 2004-2010.

<table>
<thead>
<tr>
<th>SEASON</th>
<th>YEARS</th>
<th>SUMMER</th>
<th>AUTUMN</th>
<th>WINTER</th>
<th>SPRING</th>
</tr>
</thead>
<tbody>
<tr>
<td>99/03</td>
<td>236</td>
<td>151</td>
<td>78</td>
<td>97</td>
<td></td>
</tr>
<tr>
<td>04/10</td>
<td>108</td>
<td>87</td>
<td>77</td>
<td>110</td>
<td></td>
</tr>
</tbody>
</table>

Methods

We studied woodland birds at Norseman in 2003, 2005 to 2008, and 2010. Our visits were timed to coincide with the spring breeding season, but differed between years. In 2003 (September 20-27) and 2005 (September 13-21), we worked exclusively west of Norseman along the Hyden Road. In 2006 (September 9-22), 2007 (September 16-26, October 10-21), 2008 (September 30 - October 13), and 2010 (September 11 - October 2), we alternated between the plots west of Norseman and those north.

Bird Census Procedures

We applied two different counting procedures in the census of birds. Following Recher and Davis (2002), on each visit to the plots west of Norseman the number of individuals of each species heard or seen by HFR was recorded. The duration of these counts ranged from 2 to 6 hours, with few species or individuals added after the first two hours. Counts commenced when we arrived on a plot, but all plots had counts beginning shortly after sunrise and others during the afternoon. Abundant species (e.g., honeyeaters, lorikeets) were recorded in orders of magnitude (i.e., 1-10, 10-100, 100-1000, and >1000 individuals).

For the plots north of Norseman where we compared burnt with unburnt plots (see Recher and Davis 2013 for details), birds were censused using a modified version of Loyne's (1986) 'area search'. Loyne's procedure holds the time of a count to 20 minutes and the area searched to about 3 ha, but in semi-arid Western Australian woodlands areas of a few hectares hold few birds and detecting changes in abundance requires more counts than was feasible in the time we had available. We therefore standardized counts on plots north of Norseman at 20 minutes, but recorded all individuals seen or heard within a 250 m radius (~20 ha). Plots were spaced a minimum of 500 m apart to minimize duplicate counting.

We selected a different starting plot for each day of censusing and began the first count as soon after sunrise as allowed by light. The last census commenced before 0900 h to avoid high temperatures and increasing wind. Censuses were not conducted on windy days or during rain. Two observers searched simultaneously, each on a different half of the plot, and compared results at the end of each count, with the counts combined while avoiding duplication. Observers alternated the half of the plot they searched on successive counts. One observer (WED) was hearing impaired and relied primarily on visual sightings. The second observer (HFR) recorded all birds seen and heard; WED was unable to participate in censuses in 2008 and HFR searched the entire plot each count in 2008.

Breeding Observations

HFR recorded all instances of breeding activity encountered during studies of foraging behaviour and bird censuses, including those detected by WED. This included courtship (e.g., males feeding females, displays/song), copulation, nest site exploration and nest building (whether the nest was found or not), nests (including inactive nests of the year), and feeding nestlings and fledglings. All work was done during the peak of the breeding season and it is unlikely that differences in the timing of visits affected the number of breeding attempts recorded annually.

Foraging Behaviour

Foraging behaviour was recorded for all birds encountered; this was the primary purpose of the research. For each individual, we recorded up to five consecutive foraging manoeuvres following the procedures of Recher and Davis (1998, 2002). We recorded the species of bird, the substrate and height of the prey, and the manoeuvre used by the bird (‘prey-attack’ behaviour).

Nectar

We did not quantify the abundance of blossom available to nectar-feeding birds. As an indicator of nectar abundance, we use figures provided by Ray Marcon, a local apiarist, on honey production in the vicinity of Norseman.

Data analysis

This paper combines data from two independent studies. The longer term study, Norseman West, ran from 2003 to 2010, excluding 2004 and 2009. Its aim was to describe the foraging ecology of woodland birds. The birds and estimates of their numbers were recorded on each visit to a different site to provide an index of the kinds and relative abundances of bird species on the sites where foraging data were collected. There was no objective to obtain a precise census of bird numbers. The shorter term study, Norseman North, ran from 2006 to 2010. Its aim was to document post-fire recovery of birds on an area of woodland burnt in an intense wildfire in December 1995 (Recher and Davis 2013). Hence, we used a standardized census procedure so that the burnt plots could be compared statistically to a set of unburnt plots. Because of the different ways in which bird numbers were obtained in the two studies, it is not possible to analyze and present them similarly. Despite this, the data from both sites can be used to assess trends in abundance over time in relation rainfall patterns.

Species richness and abundance

Each plot north of Norseman was censused twice, with one count early in the morning and one later. To obtain an estimate of the numbers of individuals and species using a plot, the two counts were combined and the numbers
added. We did not estimate densities and the objective was solely to compare changes in abundance and species richness between years. Each plot was treated as a sample and the mean and standard deviation calculated for the 2006 and 2007 plots separately. Only the 16 unburnt plots are considered in this paper.

To obtain a single (annual) count of the birds for each plot west of Norseman the number of individuals was taken as the greatest number of individuals recorded for each species for any count regardless of the count’s duration, day, time of day, or the number of counts completed on a plot. A calculation of the number of species and individuals accumulated with successive counts indicated that one or two counts was sufficient to record most species and their abundances on the plots, bearing in mind that most counts were two or more hours in duration and all counts were completed within a few weeks of each other.

For species that were recorded in orders of magnitude, the mid-point of estimates between 10 and 1000 was taken as the number of individuals (i.e., 50, 500). Numbers greater than 1000 were taken as 1000. As the intent is only to compare changes in abundance between years and not express an estimate of density, we consider that this method of estimating abundances is adequate to detect differences in abundance between years.

As a gauge of changes in species richness over time for the plots west of Norseman, we compared the total number of species for each individual plot recorded during annual counts from 2003 to 2007 with those from 2008 and/or 2010. The time periods chosen for comparison were selected to contrast those years with or following above average rainfall to years with low rainfall and where the woodlands were obviously drier (e.g., dry litter, lack of ephemeral vegetation, shrub death). Within each of those periods, we used the count for each plot that had highest number of species recorded, irrespective of year, taking any difference in species number as indicating an increase or decrease in species richness between periods. As an estimate of changes in abundance over time, we compared the total number of individuals (all species combined) recorded each year for each plot censused from 2003 to 2010 using linear regression in the PAST statistical package.

Only a few species were sufficiently abundant for a comparison of numbers between years. To obtain an estimate of changes in the abundance of birds within different foraging guilds of insectivores on both the Norseman West and Norseman North plots, we combined the counts for all species within a guild from each plot censused for each year. We placed species in the guilds identified by Recher and Davis (1998, 2002, 2010, 2011, and unpub. data) for woodland birds in Western Australia. Changes in abundance over time were then compared using linear regression analysis. The same procedure was used to compare changes in abundance of individual species of insectivores.

We also compared counts of insectivores and nectarivores on the Norseman West plots between years for individual plots noting whether numbers in the respective guilds on consecutive counts increased or decreased regardless of the magnitude of change. We then tested the number of increases and decreases over time for significance using a signs test and/or Chi square available in the PAST statistical package (Hammer et al. 2001).

For raptors and cuckoos on the Norseman West plots, we calculated the mean maximum number of individuals for all plots censused for each year. Regression analysis was used to test for changes in abundance between years. Numbers of raptors and cuckoos on the Norseman North plots were insufficient for analysis.

**Foraging behaviour**

We tested for differences in foraging behaviour and foraging substrates between years using Chi-square. Regression analysis was used to test for trends in foraging height between years.

**Nectar-feeding**

As an estimate of differences between years in the amount of nectar-feeding, and hence of the amount of blossom, we used the number of foraging observations/person day that were of birds feeding on nectar and compared these using linear regression. To allow for differences between years in the number of person hours of observation, we also compared the percent of foraging observations that were nectar-feeding between years. As there was only a single observer in 2008 (HFR), differences between years in the percentage of nectar-feeding were calculated both including and excluding the data from 2008. This was justified as bird numbers in 2008 were low and high temperatures and strong winds restricted avian foraging on most days to a few hours immediately after dawn when nectar was most abundant. As a result, HFR spent proportionally more time observing nectar-feeders than he would have had conditions been more favourable.

**Breeding records**

All breeding records for a given year for each species were combined regardless of the plots where they were observed, with data from Norseman West and North combined. Preliminary analysis found there was no correlation between the number of days spent in the field and the number of nests or other breeding activity recorded. That is, for a given year, about the same number of new breeding attempts was recorded per day regardless of the number of days of fieldwork. This was almost certainly the result of visiting different plots on successive days. Numbers were therefore adjusted for the differing number of days of fieldwork between years by calculating the mean number of breeding records recorded per person day. We consider this procedure adequate, as it is intended only as an estimate of changes in the amount of breeding activity between years.

**Results**

**Species richness and abundances**

Changes in species richness and abundances are presented first for the Norseman North plots, then for Norseman West.

**Norseman North**

There was little difference in the mean number of species recorded on the plots north of Norseman between 2006
and 2010. On the plots established in 2006, species richness was greatest in 2007 and least in 2008. Species richness on the plots established in 2007 was also greatest in 2007, with no difference between 2008 and 2010 (Table 2).

Table 2. Mean number of species per plot recorded during two 20 min counts on plots north of Norseman. Standard deviation in parenthesis. The number of plots was increased from 8 to 16 in 2007. There were no counts in 2009.

<table>
<thead>
<tr>
<th>YEAR</th>
<th>PLOTS</th>
<th>2006</th>
<th>2007</th>
<th>2008</th>
<th>2010</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006 Plots</td>
<td>8.4 (2.7)</td>
<td>9.6 (3.3)</td>
<td>8 (2.1)</td>
<td>8.2 (1.9)</td>
<td></td>
</tr>
<tr>
<td>2007 Plots</td>
<td>N/A</td>
<td>9.5 (3.2)</td>
<td>9.3 (3)</td>
<td>9.3 (2.3)</td>
<td></td>
</tr>
</tbody>
</table>

The mean number of individuals on the plots north of Norseman declined from 2006 to 2010 (Table 3). Numbers per plot were greatest in 2006 for the 2006 plots and in 2008 for the 2007 plots (Table 3). Combining the plots, numbers declined from 2007 to 2010, but increased in 2010 for the 2006 plots (Table 3). High standard deviations are associated with large numbers of nectar-feeders on plots with flowering eucalypts and their relative absence from plots without a nectar source. Differences in the abundances of nectar-feeders account for most of the differences between years in the numbers of individuals (see below).

Table 3. Mean number of individuals recorded during two 20 minute counts on plots north of Norseman. Standard deviation in parenthesis. The number of plots was increased from 8 to 16 in 2007. There were no counts in 2009.

<table>
<thead>
<tr>
<th>YEAR</th>
<th>PLOTS</th>
<th>2006</th>
<th>2007</th>
<th>2008</th>
<th>2010</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006 Plots</td>
<td>24.4 (14.7)</td>
<td>23.6 (17.9)</td>
<td>15.8 (5.7)</td>
<td>18.8 (6.5)</td>
<td></td>
</tr>
<tr>
<td>2007 Plots</td>
<td>N/A</td>
<td>32.6 (17.6)</td>
<td>39.4 (29.6)</td>
<td>23.8 (13.5)</td>
<td></td>
</tr>
<tr>
<td>ALL</td>
<td>N/A</td>
<td>28.1</td>
<td>27.6</td>
<td>21.3</td>
<td></td>
</tr>
</tbody>
</table>

On the 2006 plots, ground-foraging insectivores declined from 2006 to 2008 then increased in 2010 (Figure 4). The pattern differed on the 2007 plots, with ground-foraging insectivores increasing each year from 2007. In neither case was the trend significant (R² = 0.37; p = 0.4; R² = 0.99; p = 0.06, respectively). The trend for the 2006 plots with the 2010 count deleted was negative, but not significant (R² = 0.98; p = 0.08). On both sets of plots, there was a significant decline in abundance of foliage-foraging insectivores from 2006 to 2010 (R² = 0.94; p = 0.02; R² = 0.99; p = 0.02, respectively for the 2006 and 2007 plots) (Figure 4).

Norseman West

Changes in species richness between years on the Norseman West plots is confounded by the different number of counts between years and the fact that not all plots were censused in every year. However, for the plots where species richness can be compared between 2003/2007 and 2008/2010, the maximum number of species recorded on a plot was greater for seven plots in 2003/2007 than in 2008/2010. For one plot there was no difference and for another more species were recorded in 2008/10 than in 2003/2007.

The number of individuals for all species combined increased significantly between 2003 and 2005. From 2005 to 2010, there was a significant decrease in numbers (R² = 0.93; p < 0.005). When considered separately, abundances also decreased from 2003/7 to 2008/10 for ground and foliage foraging guilds (Table 4), but neither decrease was significant. There was no difference, or only marginal significance, between the two guilds in changes in abundance between the two time periods (χ² = 6; p = 0.05). Combining all species within these two guilds, there was a significant decrease in abundance between 2003/7 and 2008/10 (Sign: R = 10, p = 0.002).

Table 4. Changes in the abundance of insectivorous ground, shrub, and canopy foragers in woodlands west of Norseman, Western Australia between 2003/2007, and 2008/2010. Changes are based on differences in the combined number of individuals of all species within the guild recorded during counts on the same plots during the two different time periods regardless of magnitude.

<table>
<thead>
<tr>
<th>ABUNDANCE</th>
<th>GUILD</th>
<th>COUNTS</th>
<th>INCREASE</th>
<th>DECREASE</th>
<th>SAME</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foliage-foragers</td>
<td>32</td>
<td>5</td>
<td>18</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Ground-foragers</td>
<td>35</td>
<td>2</td>
<td>24</td>
<td>9</td>
<td></td>
</tr>
</tbody>
</table>

The mean number of raptors recorded during counts on the Norseman West plots remained high throughout 2006 (Figure 5). Numbers then decreased to 2008, increasing in 2010. The decrease from 2003 to 2010 was significant (R² = 0.74; p = 0.03).

Changes in the abundance of cuckoos (Black-eared...
Figure 5. Mean number of raptors recorded for all plots west of Norseman combined. All species are combined and the mean is based on the maximum number of individuals recorded on each plot censused during that year.

Chestnut-rumped Thornbills increased in abundance in 2003, remaining high until 2008 when this species became scarce and could not be found on most of the plots where it previously occurred. Chestnut-rumped Thornbills increased in abundance in 2010 (Figure 6). Redthroats increased in abundance from 2003 to 2006 becoming one of the most common insectivorous birds on the plots. It then declined precipitously to 2008, with a recovery in 2010 (Figure 6). The mean number of cuckoos increased from 2003 to 2007, lagging behind those of the Redthroat, then decreasing in 2008 as host numbers fell, and increasing in 2010 as host numbers recovered (Figure 6).

Nectar-feeders

Eucalypts were the principal source of nectar for nectar-feeders at Norseman, with most nectar from Gimlet, Merrit, Red Morrel, Redwood, Sand Mallee, Square-fruited Mallee, and other mallee species (Recher and Davis unpubl.). There were year to year differences among eucalypts in the timing and amount of blossom (Recher and Davis unpubl.). Honey production by Ray Marcon commenced in 2006 north of Norseman. Approximately 300 kg of honey were consigned to market in March and April 2006 and 600 kg in May and November. Similar quantities (300-600 kg) were produced in summer and autumn of 2007, with production ceasing in the spring of 2007 and not resumed due to a lack of blossom (Ray Marcon, in litt., October 2010). Less blossom also meant less nectar-feeding and fewer nectar-feeders.

West of Norseman the number of observations/person day of nectar-feeding declined from 2003 to 2010 ($R^2 = 0.92; p = 0.002$) (Figure 7). Excluding observations from 2008 (see above for a justification), the proportion of foraging observations, as distinct from the number of observations, that was nectar-feeding declined from 2003 to 2010 ($R^2 = 0.82; p = 0.04$). If 2008 is included in the analysis, the decline from 2003 to 2010 is not significant ($R^2 = 0.19; p = 0.4$).

Figure 7. Mean number of nectar-feeding observations/person day recorded at Norseman West from 2003 to 2010 shown as a solid black line.

On the plots north of Norseman, the proportion of nectar-feeding observations was greater in 2006/2007 than 2008/2010, with a peak in 2007 due to large numbers of Purple-crowned Lorikeets Glossopsitta porphyrocephala and a bloom of Merrit and Red Morrel. However, the difference is not significant ($R^2 = 0.22; p = 0.5$). If only honeyeaters are considered, the decline in nectar-feeding after 2006/2007 is greater, but remains insignificant ($R^2 = 0.75; p = 0.13$).

Abundance

Comparing successive counts of species on the same plots between 2003 and 2007, there were more increases in the abundance of nectar-feeders (44% of counts) west of Norseman than decreases (22%) (Table 5). On counts between 2007 and 2010, decreases (53%) outnumbered increases (27%) (Table 5). The difference between the two time periods is significant ($\chi^2 = 122.15; p$
< 0.0001). The pattern is the same for all nectar-feeders and for the nectar-dependent long-billed honeyeaters (Brown Honeyeater *Lichmera indigsta*, Red Wattlebird *Anthochaera carunculata*, Spiny-cheeked Honeyeater *Acanthagenys nufogularis*, and White-fronted Honeyeater *Pamella albifrons*) ($\chi^2 = 94.667; p < 0.0001$).

Table 5. Changes in the abundance of nectar-feeders (Meliphagid honeyeaters and Purple-crowned Lorikeet) on plots west of Norseman between 2003 and 2010. The abundances of individual species were compared between successive years of counts on the same plots from 2003 to 2007, and from 2007 to 2010. That is, 2003 counts were compared to counts in 2005, 2006, and 2007, and so on. Any difference in abundance, regardless of magnitude, was accepted as an increase (INC) or decrease (DEC).

<table>
<thead>
<tr>
<th>COUNTS</th>
<th>% INC</th>
<th>% DEC</th>
<th>% SAME</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALL NECTAR-FEEDERS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2003/7</td>
<td>110</td>
<td>44</td>
<td>22</td>
</tr>
<tr>
<td>2007/10</td>
<td>60</td>
<td>27</td>
<td>53</td>
</tr>
<tr>
<td>LONG-BILLED HONEYEATERS</td>
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<td></td>
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<tr>
<td>2003/7</td>
<td>66</td>
<td>46</td>
<td>12</td>
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<tr>
<td>2007/10</td>
<td>36</td>
<td>25</td>
<td>50</td>
</tr>
</tbody>
</table>

On the plots north of Norseman, from 2007 to 2010 nectar-feeders were more abundant on the 2007 than 2006 plots (Figure 8). On the 2006 plots, numbers increased from 2006 to 2007 with an influx of Purple-crowned Lorikeet and Brown-headed Honeyeater *Melithreptus brevirostris*, decreased in 2008 as these birds departed, and increased in 2010 with an influx of Red Wattlebird. On the 2007 plots, numbers increased between 2007 and 2008 then decreased in 2010 (Figure 8). The increase in 2007 was due to the movement on to the plots of large numbers of nomadic Yellow-plumed Honeyeaters *Lichenostomus orinatrix* (Recher and Davis unpubl.). The sharp decline in 2010 followed the departure of nomadic Yellow-plumed Honeyeaters and reduced numbers of Purple-crowned Lorikeets.

Breeding

Breeding for all species combined declined from 2003 to 2008 ($R^2 = 0.99, p = 0.0003$), as did nectar-feeders ($R^2 = 0.94, p = 0.006$), shrub/canopy-foragers ($R^2 = 0.92, p = 0.009$), and canopy insectivores ($R^2 = 0.92, p = 0.013$). When these guilds were considered separately, breeding activity for all groupings increased in 2010 (Figure 9), although the declines from 2003 remained significant (p's $\leq 0.02$). There was no obvious trend in the breeding activity of ground-foragers, with the greatest breeding activity recorded in 2007 and the least in 2010 (Figure 9).

For most species there were too few breeding records for separate analysis. However, there were 24 to 44 records of breeding activity for four species, Yellow-plumed Honeyeater, Inland Thornbill *Acanthiza apicalis*, Striated Pardalote *Pardalotus striatus*, and Weebill *Smicrornis brevirostris*, permitting a comparison between years. Breeding activity for Yellow-plumed Honeyeaters was similar (7 - 10 observations) in all years bar 2008 when there were only two records. Inland Thornbill had similar levels of breeding activity (2-4 observations) in all years bar 2007 when there were nine records. There were 31 breeding observations for Striated Pardalotes, with 16 in 2006, none in 2008, one in 2010, and 4-6 in other years. Weebill was the only species to show a significant trend between years, with the number of breeding observations declining from eight in 2003 to none in 2008 ($R^2 = 0.93, p = 0.009$), and increasing to nine in 2010.

Although overall breeding activity declined from 2003 to 2010, individuals continued to nest and raise young. This included pairs of Dusky Woodswallow *Artamus cyanopterus*, Inland Thornbill, Rufous Treecreeper *Climacteris rufa*, and Western Yellow Robin *Eopsaltria australis*.

Foraging behaviour

There were no differences in foraging behaviour between years, either in foraging substrates or foraging manoeuvres. However, a few species appeared to forage higher in the vegetation as habitats became drier. On the plots west of Norseman, Inland Thornbills, a shrub and lower canopy forager, increased their mean foraging height from 0.52, p = 0.11. There were insufficient data for analysis for Port Lincoln Parrot on the Norseman North plots. Striated Pardalote and Weebill tended to forage higher in the canopy on the plots north of Norseman between 2006 and 2010. The difference was significant for pardalotes ($R^2 = 0.98, p = 0.02$), but not for Weebill ($R^2 = 0.67, p = 0.18$). There was no difference in the mean foraging heights of Striated Pardalote and Weebill on the plots west of Norseman between 2003 and 2010, foraging higher in some years and lower in others.

3. Note that the species comprising the guild 'canopy insectivores' are also included within 'shrub/canopy foragers'.

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**Figure 8.** Abundance of nectar-feeders (honeyeaters and Purple-crowned Lorikeet) on plots north of Norseman from 2006 to 2010. There were no counts in 2009. Abundance is the sum of individuals for two 20 minute counts across all plots. Plots established in 2006 (solid line) and those established in 2007 (broken) are shown separately.
Discussion

Despite the variability of rainfall in Australia, there are few studies of the effects of differences in seasonal or annual rainfall on terrestrial birds. In an early paper, Barnard (1917) commented on the decline of bird populations and reduced breeding associated with severe drought in central Queensland, while other observers recorded arid and semiarid zone birds congregating in areas where rain had fallen to take advantage of increased food resources and breed (e.g., Serventy and Whittell 1962; Keast 1968). It is only recently that more detailed studies of the effects of drought on birds have been published. Mac Nally et al. (2009) reported that prolonged drought (12 years) in northern Victoria resulted in all categories (guilds based on foraging, nesting habits, relative mobility, habitat, and distribution or range) of woodland birds declining in abundance. This was attributed to the reduced abundance of arthropods and nectar as a consequence of the lack of rain. Burbidge and Fuller (2007) recorded declines in the abundance and species richness of birds on plots in the Gibson Desert with increasing drought. Abundances and the number of species increased following heavy rain, with dispersive granivores, nectarivores, and insectivores joining resident birds, which were primarily insectivorous. Breeding was strongly associated with rain. In the Tanami Desert, the abundance and species richness of birds fluctuated with rainfall (Paltridge and Southgate 2001). Saunders and Doley (2013) correlated species’ abundances with rainfall in an agricultural district north of Perth, Western Australia, which they also attributed to differences in food abundance between dry and wet years. Stevens and Watson (2013) and Ellis and Taylor (2014) reported variable responses among woodland bird species to drought and rainfall in semi-arid woodlands in eastern Australia (New South Wales). Ellis and Taylor (2014) traced population sizes of birds in fragmented habitat during drought and after drought breaking rains. They reported ‘limited and uneven responses’ among species and guilds to rain, with only a small proportion of species
increasing. Stevens and Watson (2013) working in an extensive area of unbroken native vegetation found that rainfall predicted the subsequent abundance of 13 of the 25 most common species. They concluded that food shortages during drought were responsible for species declines, and that food abundance and type affected species composition.

In Australia, reduced rainfall and drought results in the reduced breeding of terrestrial bird species (Keast 1981, Rowley and Russell 1993, Stevens and Watson 2006, MacNally et al. 2009). Smith (1982) made similar observations during drought in North America, with declines in species’ abundances and changes in community composition. Insectivores and nectarivores decreased in abundance, while granivorous species increased, which Smith (1982) also attributed to changes in the abundance and kinds of food available to birds. Bolger et al. (2005) found significantly higher nesting rates and breeding success among four species of passerines during a year with ‘average’ rainfall compared with a year of ‘below average’ rainfall.

We documented declines in species’ abundances and reduced breeding among birds at Norseman in the GWW as conditions became drier from 2003 to 2008. As with other observers, we attribute this to reduced abundances of arthropods and nectar, as well as reductions in prey for raptors and hosts for cuckoos. However, unlike the majority of preceding studies that emphasized drought, technically the Norseman region was not drought affected. Nonetheless, our first response to the changes we observed at Norseman was that the woodlands and their avifauna were becoming drought affected, that is, there was a prolonged period of ‘acute water shortage’ caused by low rainfall (see http://www.bom.gov.au/climate/glossary/drought.shtml for a definition of drought).

As the amount of annual rainfall declined at Norseman following a period of high summer and autumn rainfall, the soil, litter, and ground vegetation dried first, with shrubs and trees not showing visually obvious drought effects (e.g., shrub deaths, limited flowering) until 2008. These changes were accompanied by declines in the abundances of birds and breeding activity.

We recognize the limitations of our data and accept that we cannot confirm all our observations quantitatively. Nonetheless, the balance of evidence and the consistency of trends in abundances, nectar-feeding, and breeding effort points to woodland birds being adversely affected by reduced rainfall and responding rapidly to increased rainfall. In these semi-arid woodlands, drought is not necessary for reduced breeding effort and a decline in numbers; average rainfall may be insufficient to maintain population numbers and prevent local extinction. Moreover, there is a pattern of response to reduced rainfall that is determined by where birds forage and the kinds of food resources they require. Although not demonstrated by the data, our impression was that ground-foragers were affected first, with declining numbers and fewer attempts to nest. As habitats continued to become drier, nectar-feeders, herbivores, food nomads, migrants, and canopy-foragers failed to breed and declined in abundance, either through increased mortality or dispersal, with migrants and nomads not returning to habitats previously occupied.

Yellow-plumed Honeyeaters, for example, deserted habitats that were presumably marginal and which had been colonized only as recently as 2005 when conditions were wetter (Recher and Davis, unpubl.). As the numbers of smaller birds declined, so did the numbers of raptors and cuckoos.

All species were adversely affected by the drying conditions, but some, such as Inland Thornbill and Rufous Treecreeper, remained abundant, although in reduced numbers, and bred successfully in all years. Even among species, such as Dusky Woodswallow, which were much less abundant as habitats became drier, a few pairs bred successfully.

Rainfall and birds

The extensive tall-woodlands of the GWW with 25-30 m canopy heights contrast with other woodlands receiving less than 300 mm average annual rainfall where shrubs and small trees dominate the vegetation (Prober et al. 2011). The reasons for this anomaly are not clear as eucalypts appear to have no significant advantage over other plants with respect to efficiency of water use and the groundwater in the GWW can be saline and acidic, so that its use by trees may not be possible (Prober et al. 2011). For an area receiving less than 300 mm annual rainfall, the woodlands of the GWW, with its species rich biota, appear luxurious, but productivity is not high. Even under favourable conditions and aggregations of nectar-feeders on flowering eucalypts, birds are not abundant.

Our census procedures do not allow precise estimates of population densities, but the data from standardized 20 minute/20 ha counts suggest densities of fewer than 2 birds/ha, including nectar-feeders, which is comparable to Bell et al.’s (2013) estimate of 1.01 bird/ha for woodlands along the Mulga-Eucalypt Line with a similar rainfall to Norseman. This is substantially less than the densities of 15 to 24 individuals/ha recorded by Recher and Holmes (1985; Table 2, p. 83) during summer (December) for woodlands and forest in southeastern Australia where rainfall exceeded 800 mm/y. It is also less than the densities of birds of 3-4 birds/ha recorded in Wandoo (Eucalyptus wandoo) woodlands by Arnold (1988; Table 2, p. 501) northeast of Perth, WA, with an average annual rainfall of 580 mm (Arnold et al. 1987). It is likely that bird species abundances (densities) are (at least partially) determined by annual and seasonal rainfall similar to canopy arthropods (Recher et al. 1996a, b) and small mammals (Recher et al. 2009) in eucalypt forests.

Food abundance for birds is a function of habitat productivity. Recher et al. (1996a, b) found that canopy arthropod abundances in eucalypt forests and woodlands differed between seasons, years, and regions according to rainfall and foliar nutrients. Abundances were greatest during winter and spring when temperatures were moderate and moisture levels high, and on plots with high foliar and soil nutrient levels. Canopy arthropod abundances decline with drought (Bell 1985), as do soil and litter invertebrates (Taylor 2008). Canopy arthropods include sap-sucking insects that produce lerp and honeydew, which are the principal foods for pardalotes, some thornbills (Acanthiza), Weebill, and short-billed honeyeaters (Lichenostomus,
Melithreptus) in the GWW (Recher 1989; Recher and Davis unpubl.). As illustrated by the collapse of commercial honey production at Norseman in 2007, nectar production is also a function of rainfall, with eucalypts failing to flower in drier years or flowering less regularly (Porter 1978; Law and Chidel 2009; Mac Nally et al. 2009).

The cascade of declining numbers and reduced breeding appearing to begin with ground-foraging birds and continuing through canopy-foragers, nectar-feeders, raptors, cuckoos, migrants, and food nomads was undoubtedly driven by reductions in the amount and kinds of food available to birds. As soil and litter dried, and ephemeral ground vegetation failed to grow, food availability for ground-foragers would have been affected first. Stevens and Watson (2013) reported significant declines of ground-foraging woodland birds with drought in eastern Australia. At Norseman, birds dependent on resources (arthropods, nectar, lerp, honeydew, buds, foliage and flowers, fruit, and seeds) provided by shrubs and trees were probably buffered by the ability of these plants to access moisture deeper in the ground or use water, energy, and nutrient reserves stored in trunks and a roots thereby sustaining food resources longer after rainfall returned to long-term means. Stevens and Watson (2013) also found significant declines in shrub and canopy insectivores, but only after removing lerp-specialists, Weebill and Spotted Pardalote P. punctatus, from the analysis. Both lerp-specialists increased in abundance during drought, which Stevens and Watson (2013) attributed to an increase in psyllid populations as trees became water stressed. Increases in psyllid populations may also explain the increased breeding of Striated Pardalotes we recorded at Norseman in 2006, but there was no similar response on our sites by Weebills.

Despite any changes in food abundance, we did not find any consistent differences in foraging behaviour. On some plots, some species foraged higher in the canopy as habitats became drier, but most woodland birds forage over a broad height range (Recher and Davis unpubl.) and foraging heights often differ significantly between locations regardless of rainfall. A change in foraging heights may therefore only indicate local variation in the height distribution of food resources and bear no relation to drying conditions. Although we have no data from the GWW, our observations in mulga (Acacia aneura) shrublands during drought indicated significant shifts in the types of food used by birds. Thornbills (Acanthiza spp.), for example, foraged exclusively on scale insects and their exudates during drought, while taking a much wider range of arthropods when water was more abundant (Recher and Davis unpubl.). Shifts in foraging behaviour and food resources with variation in rainfall is a subject requiring further study.

Although we did not measure food abundance or availability, we have surrogates for nectar-feeders and raptors. As shown by the decline and eventual collapse of commercial honey production, the amount of nectar available to nectar-feeders fell as summer and autumn rainfall returned to ‘average’ or ‘near average’ levels. With less nectar, there were fewer nectar-feeders. Nectar-feeders are probably a primary food resource for raptors in the GWW and as the numbers of nectar-feeders fell, so did the numbers of raptors. Cuckoo numbers also declined as the number of host nests declined.

It was not until we looked closely at rainfall figures that we realized that, while the woodlands were affected by a shortage of water, it was not a drought as defined by the Bureau of Meteorology. The two decades (1983-1992 and 1993-2002) before we began our studies at Norseman were wetter than the long-term mean, with high bird species abundances and breeding from 2003 to 2007. From 2003 to 2010, annual rainfall approximated the long-term mean, but was associated with declining bird species abundances, reduced breeding and nectar production, and less plant growth suggesting that above average rainfall was required for the ecosystem to function at full productivity. Moreover, the pattern of seasonal rainfall indicated that, at least during the time of our study, the system was driven by high rainfall in summer and autumn.

It could be argued that reduced winter rainfall adversely affected spring plant growth and hence the food available to birds. However, as average winter rainfall was similar in both time periods (1999-2003, 2004-2010), the primary difference between the periods was in the amount of summer and autumn rain. Above average rainfall during spring and summer 2008/2009 and winter 2009 also appears to have led to increased numbers of birds and increased breeding during 2010. However, neither plant growth (e.g., ephemeral ground vegetation, amount of eucalypt blossom) nor the breeding of birds equalled that we observed from 2003 to 2007 following exceptionally high summer and autumn rain. Allowing for differences in the numbers of nomads, this pattern of response to episodic rainfall events is common in arid and semi-arid Australian environments (Burbidge and Fuller 2007; Morton et al. 2010; Wardle et al. 2013).

Conservation and climate change

Our observations in the GWW show that woodland birds are sensitive to annual differences in the pattern of rainfall. The heavy summer and autumn rains from 1999 to 2003 had several significant effects on woodland bird communities; there were more migrants and food nomads, a wider range of habitats were occupied, and populations of resident species increased. As conditions returned to normal and habitats became drier there was an equally pronounced and rapid decline in numbers, with marginal habitats abandoned. With climate change, changes in species abundances are likely to become greater as the intervals between high rainfall events increase in duration. Not only will this affect resident species, but migrants and food nomads will find fewer locations where food is abundant. Ensuring that the woodland avifauna can survive between high rainfall events requires management on regional, if not continental scales. Fragmenting habitats, such as the GWW, into a system of conservation reserves cannot provide the resources birds will require as the climate becomes hotter and there is less rain. Less rain leads to declines in abundance and reduced reproduction. Longer intervals between high rainfall events will require as the climate becomes hotter and there is less rain. Less rain leads to declines in abundance and reduced reproduction.
events mean fewer opportunities for population expansion and recolonization. The more habitats are fragmented and isolated, as in a system of conservation reserves, the more likely populations will be smaller and prone to local extinction, and the less likely recolonization can occur. These risks occur even within small areas where patches the size of individual pair territories may differ significantly in quality. During dry periods, only what we perceived as the highest quality, most productive patches allowed birds, such as Dusky Woodswallow and Rufous Treecreeper, to reproduce. It may be that these ‘micro-refuges’ allow species to persist within a region, but current conservation management does not embrace protocols at a scale that recognizes and protects such small areas. If the worst effects of climate change are to be mitigated, a new approach to the conservation of Australia’s biota is required; one which accepts the imperative of habitat connectivity (Soule et al. 2004; Wyborn 2011), while simultaneously conserving patch dynamics.

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Response of birds to episodic summer rainfall

Harry Recher enjoying a coffee break west of Norseman, W.A. Photo by W. E. Davis, Jr.
Open Red Morrel woodland with an open, tall shrub layer of *Melaleuca uncinata* and Broom Bush *Eremophila scoparia* on the Old Hyden Road north of Norseman. Photo by H.F. Recher.

Red Morrel woodland north of Norseman with tall (3-3.5 m) *Melaleuca uncinata* and Native Cherry *Exocarpos aphyllus* (on left, to the side). The dark areas of bare ground are biocrust. Photo by H.F. Recher.

Gimlet woodland along the Hyden-Norseman Road approaching Lake Johnstone west of Norseman. This likely to be even-aged post-fire regeneration. The shrubs are Daisy Bush *Olearia* sp. and Broom Bush *Eremophila scoparia*. Photo by H.F. Recher.
Response of birds to episodic summer rainfall

Salmon Gum with mallee eucalypts and *Melaleuca uncinata* north of Norseman. Photo by H. F. Recher

Dundas Blackbutt west of Norseman. This is probably an even-aged stand regenerated after burning (est.) 100-150+ years ago. Such stands are typically dominated by Yellow-plumed Honeyeaters, with Rufous Treecreeper and Dusky Woodswallow. Photo by H. F. Recher

Redwood woodland on Old Hyden Road north of Norseman. Photo by H. F. Recher
Even aged (est. 100-150y) postfire regeneration of Red Morrel north of Norseman. This was a stand with very few birds. Photo by H. F. Recher

Open woodland with Red Morrel, Gimlet, and Salmon Gum along the Hyden-Norseman Road west of Norseman. There is a tall shrub layer of Melaleuca uncinata, with a species rich lower layer dominated by Eremophila scoparia. Photo by H. F. Recher

Ted Davis in a Dundas Blackbutt woodland west of Norseman, W.A. inspecting a tree felled some years earlier and opened up to take nestling parrots. Apparently this was a common practice during the early 20th Century. Photo by H. F. Recher
Salmon Gum woodland north of Norseman with a Bluebush Maireana sp. shrub layer. In the background is an understorey of mallee eucalypts. Photo by H. F. Recher.

Whiptail fire regeneration of Redwood and Red Morrel west of Norseman. Trees are estimated to be 20-40y post fire. The understory is Melaleuca uncinata, with wattles (Acacia spp.).

Gimlet woodland with Salmon Gum and Red Morrel to the rear. The shrubs are Bluebush Maireana sp., with Geebung or Snottygobble Persoonia sp., Native Cherry Exocarpos aphyllus, and Broom Bush Eremophila scoparia in the foreground. Photo by H. F. Recher.
This was an especially rich site north of Norseman for birds in 2006. The trees are Gimlet and Goldfields Blackbutt. The shrub layer was mostly Bluebush, with stands of tall Melaleuca uncinata, sapling eucalypts, and Broom Bush Eremophila scoparia. Photo by H. F. Recher

Salmon Gum woodland with tall Melaleuca uncinata along the Old Hyden Road north of Norseman. Photo by H. F. Recher

Salmon Gum woodland, with an understorey of mallee eucalypts, Snottygobble Persoonia sp., and Melaleuca uncinata on the Old Hyden Road north of Norseman. Photo by H. F. Recher