

# The influence of ENSO and rainfall on the numbers of breeding pairs in a woodland bird community from south-eastern Australia

R. Marchant<sup>A,D</sup>, S. Guppy<sup>B</sup> and M. Guppy<sup>C</sup>

<sup>A</sup>Museum Victoria, GPO Box 666, Melbourne, Vic. 3001, Australia.

<sup>B</sup>1708 Maulbrooks Road, Moruya, NSW 2537, Australia.

<sup>C</sup>Division of Evolution, Ecology and Genetics, Research School of Biology, ANU College of Medicine, Biology & Environment, Canberra, ACT 0200, Australia.

<sup>D</sup>Corresponding author. Email: [rmarch@museum.vic.gov.au](mailto:rmarch@museum.vic.gov.au)

**Abstract.** Climate and rainfall in southern Australia are strongly influenced by the El Niño–Southern Oscillation (ENSO) phenomenon. If breeding of forest birds is related to rainfall, then ENSO may influence fluctuations in breeding activity. We recorded the numbers of breeding pairs of 17 species over 17 years on a 10 ha forest plot near Moruya, NSW, in order to evaluate the influence of ENSO (as measured by the Southern Oscillation Index, SOI) and rainfall on yearly changes in breeding activity. The mean SOI for the months April–July immediately before the breeding season (August–January) was strongly correlated with the change in number of breeding pairs (D) from year to year:  $r = 0.82$ ,  $P < 0.001$ . D was also strongly correlated with rainfall (August to December) during breeding:  $r = 0.84$ ,  $P < 0.001$ . A positive SOI resulted in >300 mm rainfall during breeding and a positive D value; a negative SOI resulted in <300 mm of rain and a negative D value. SOI was a better predictor because it was less subject to the extreme variation shown by rainfall. This is the first time an association between breeding and SOI has been shown for forest birds in temperate Australia.

**Additional keywords:** change in numbers of breeding pairs, rainfall during breeding, SOI.

Received 31 August 2015, accepted 25 December 2015, published online 18 February 2016

## Introduction

Long-term studies of the breeding and abundance of a bird community can reveal much about the many factors influencing population change. For instance, a 37 year study of 15 bird species in a northern hardwood forest in the United States (US) (Holmes 2007) demonstrated that both local (density-dependent fecundity, food limitation) and regional factors (weather effects) limited and regulated the abundance of species within the community. The persistence and predictability of these factors varied markedly with time and it was apparent that only a long-term study could accurately reveal them. Nott *et al.*'s (2002) study of 34 bird species (over 9 years at 33 forested sites in the Pacific north-west of the US) also demonstrated the influence of weather on breeding productivity, in particular the influence of global climatic phenomena such as the El Niño–Southern Oscillation (ENSO) of the Pacific Ocean and the North Atlantic Oscillation (NAO) of the Atlantic Ocean.

Breeding observations on bird communities in Australia have yet to be related to global phenomena such as ENSO, but have commonly been associated with local climate variables, most often rainfall (Serventy and Whittell 1962; MacNally *et al.* 2009; Recher and Davis 2014). However, breeding data for a single genus, the Australian Fairy-wrens (*Malurus* sp.), have been

related to large scale climatic indices (van de Pol *et al.* 2013) such as the Indian Ocean Dipolar Mode Index (DMI) and the Southern Oscillation Index (SOI), which is a measure of ENSO activity, as well as to local rainfall. Data on annual reproductive success were available for 16 populations of 7 species (widely spread across Australia), most of which had been monitored for 3–13 years (two populations for 24 and 38 years). Breeding success varied widely in its correlation with DMI or rainfall. Van de Pol *et al.* (2013) concluded that global climate indices must be well related to local weather variables if they are to be useful predictors of breeding.

In this paper we are concerned with the influence of the SOI climatic index and rainfall on the breeding of woodland birds in an Australian coastal forest. The study covers two periods of observation on a 10 ha forested site near Moruya, New South Wales (NSW) in Australia. Stephen Marchant (SM; Marchant 1992) began his work in 1975 and monitored the number of breeding pairs of 17 species, over 10 years (1975–1984). The study site remained undisturbed after 1984, and a second period of observations began in the 2007 breeding season. We have data for 7 breeding seasons (Michael and Sarah Guppy (MSG), 2007–13) for the same 17 species. There are no other studies in southern Australia that have recorded the breeding of woodland

bird species over similarly long periods. There has, however, been a long-term study (21 years) of the abundance of 25 species in 9 ha of woodland (situated in continuous forest, as is our site) in the Warrumbungle Mountains of northern NSW (Stevens and Watson 2013). This study used indices of bird abundance to determine whether species were increasing or decreasing during the period 1990–2010. They concluded that prolonged drought produced food shortages that resulted in declines of certain species. They showed that the abundances of 13 species were either positively (10 species) or negatively (3 species) correlated with rainfall, with time lags of 0.75–1.75 years. In contrast, the climatic features of this region that influence bird breeding are generally unknown. Local rainfall may well be influential, because the primary productivity of these southern forests (Woinarski and Cullen 1984; Bell 1985) is dependent on rainfall and the abundance and biomass of forest arthropods (the likely food of breeding birds) is dependent on such productivity. For example, the biomass of arthropods on eucalypt leaves increased as the concentration of foliar nutrients (an index of plant production) increased (Recher *et al.* 1996b).

During our study the prevailing climate varied from very dry to very wet. The notoriously variable rainfall of southern and eastern Australia is associated with oscillations in the wind patterns in the tropical and subtropical Pacific Ocean, namely the ENSO phenomenon (Nicholls 1991; Lake 2011). As ENSO fluctuates so too will rainfall and potentially the breeding success of forest birds. Thus our study is concerned with two questions. First, is breeding activity of the bird community related to SOI? Second, if it is related to SOI, is it also related to rainfall? Breeding activity may be positively related to SOI, because periods with high positive values of SOI usually result in high rainfall in eastern Australia (Nicholls 1991).

## Methods

### *The site*

The study site (35°52'S, 150°03'E) is a 10 ha woodland (~200 m 500 m; 100 m above sea level) 6 km north-west of Moruya, NSW, Australia. It is divided into a grid of 50 m squares by paths. The site is on the west side of a ridge and gently slopes to an intermittent small creek in the west, but rises steeply near the eastern ridgetop. Vegetation comprises a mixture of open woodland (Blackbutt (*Eucalyptus pilularis*), White and Yellow Stringybarks (*E. globoidea* and *E. muelleriana*), Spotted Gum (*Corymbia maculata*), and lesser content of Grey Ironbark (*E. paniculata*) and Rough-barked Apple (*Angophora floribunda*)), thickets of Burrawang (*Macrozamia communisa*), Black Sheoak (*Allocasuarina littoralis*) and Tick Bush (*Kunzea ambigua*), a power-line clearing 30 m wide running the length of the site comprising Tick Bush, Bracken (*Pteridium esculentum*) and open grassland, and a hectare of Swamp Paperbark (*Melaleuca ericifolia*). In addition, there are several small dams containing Cumbungi (*Typha orientalis*), Spikerush (*Eleocharis spp*) and Common Reed (*Phragmites australis*), and near the creek a variety of riparian shrubs (Water Gum (*Tristania laurina*), Grey Myrtle (*Backhousia myrifolia*), *Melaleuca spp*, *Callistemon spp*, and River Sheoak (*Casuarina cunninghamiana*)).

This type of woodland is widespread immediately inland of the coast between Ulladulla and Bermagui, NSW (Austin 1978).

Our site adjoins state forest and is situated in a mixed landscape of forest and cleared grazing land, with forest as the dominant component. Aerial photos of the nearby state forest (pers. comm., Forestry Corporation of NSW, Southern Region) show that few and only small changes to the area of forested land have occurred since 1949.

Rainfall and daily maximum and minimum temperatures (a combination of max/min thermometers and a Hobo data logger in a Stevenson Screen) were recorded at the south-east corner of the site. Mean annual rainfall (18 years of records) was 1054 mm (range 511–1885 mm) and was higher during 1975–84 (1213 mm) than during 2007–13 (855 mm), but the difference was barely significant ( $F=3.6$ ,  $P=0.075$ ). Some very high rainfall years (1975 and 1976 had almost twice the average) account for the difference. Mean rainfall (350 mm) during the breeding season (August–December inclusive) did not vary between the two phases of the study (381 mm [SM] vs 311 mm [MSG];  $F=0.58$ ,  $P=0.46$ ). Air temperatures varied from a mean minimum of 6–7°C to a mean maximum of 29–30°C. Annual rainfall was strongly correlated ( $r^2=0.9$ ,  $P<0.001$ ) with that measured at an Australian Bureau of Meteorology (BOM) weather station (station number 069018; mean annual rainfall 954 mm) ~9 km to the south-east. These data suggest rainfall at our site was representative of that in the surrounding district.

Monthly SOI values were available for all years of the study from the BOM (Bureau of Meteorology 2015). Other large scale climatic patterns may influence rainfall in southern Australia (van de Pol *et al.* 2013), but SOI was the only climatic index considered in this study.

### *Field work*

During both phases of the study the same procedure was used to quantify the number of breeding pairs of each species: nests were searched for, individual birds associated with each nest were identified, and nests were monitored until fledglings left or the nest was destroyed (usually by predators). Colour-banding was used to distinguish different breeding pairs. Birds were colour-banded either at the nest, or by systematically netting the entire site. Observations took place while walking the grid on most (80–90%) days during the breeding season (August–January inclusive), with a daily average of 2.9 h (MSG's study) to 3.4 h (SM's study). Walks covered 1.5–2.5 km and were constantly varied in direction.

### *Breeding pairs*

In both phases of the study, breeding was defined as the progression of a nest to at least one egg. Fifty species were known to have bred on the site at least once. Numbers of breeding pairs were only estimated for 17 species (Table 1). The other 33 species were excluded (Appendix 1) because: (a) 18 bred during only one phase; (b) three species built nests that were too difficult, or too time consuming, to find and observe and (c) 12 species bred irregularly and in very low numbers.

The species for which numbers of breeding pairs were recorded can be divided into two groups (Table 1). For group 1 (10 species), the majority of pairs contained at least one colour-banded bird. Thus all pairs were identifiable and the numbers of breeding pairs were known exactly. Group 2 species (7 species)

**Table 1. The range in numbers of breeding pairs for each of the 17 species in groups 1 and 2, during the two phases of the study**

	1975– 1984	2007– 2013
Group 1		
White-throated Treecreeper ( <i>Cormobates leucophaea</i> )	2	0–1
Superb Fairy-wren ( <i>Malurus cyaneus</i> )	1–8	5–11
Variagated Fairy-wren ( <i>Malurus lamberti</i> )	0–3	1–3
White-browed Scrubwren ( <i>Sericornis frontalis</i> )	1–4	0–4
Brown Thornbill ( <i>Acanthiza pusilla</i> )	1–10	6–14
Lewin's Honeyeater ( <i>Meliphaga lewinii</i> )	0–1	0–2
Yellow-faced Honeyeater ( <i>Lichenostomus chrysops</i> )	0–10	9–24
Eastern Yellow Robin ( <i>Eopsaltria australis</i> )	3–6	3–8
Golden Whistler ( <i>Pachycephala pectoralis</i> )	1–2	1–2
Rufous Whistler ( <i>Pachycephala rufiventris</i> )	1–4	1–5
Group 2		
Sacred Kingfisher ( <i>Todiramphus sanctus</i> )	0–1	0–1
Noisy Friarbird ( <i>Philemon corniculatus</i> )	0–1	0–4
Black-faced Cuckoo-shrike ( <i>Coracina novaehollandiae</i> )	0–1	0–1
Wonga Pigeon ( <i>Leucosarcia picata</i> )	0–1	0–1
Grey Fantail ( <i>Rhipidura albiscapa</i> )	1–3	2–5
Eastern Spinebill ( <i>Acanthorhynchus tenuirostris</i> )	0–3	1–7
Spotted Pardalote ( <i>Pardalotus punctatus</i> )	0–9	1–5

were either not colour banded or not comprehensively colour banded. For six of these species the numbers of breeding pairs were accurately known because the nests or the activity of the breeding pairs were obvious and there were few individuals on the site. Thus we always knew the number of concurrent nests. The only species for which there was some doubt was the Eastern Spinebill (*Acanthorhynchus tenuirostris*) where we may have underestimated the number of breeding pairs by one nest in some years. These two groups accounted for ~70% of the individuals on the site.

#### Identification of patterns in breeding activity

We were primarily concerned with the breeding dynamics of the community as a whole rather than with the breeding of individual species. Thus we concentrated our analysis on total numbers of breeding pairs.

Untransformed numbers of breeding pairs (ranges for each species are given in Table 1) were analysed because probability plots indicated that these data were normally distributed. However, the total number of pairs in one year was likely to be correlated with the number in the previous year (and the previous several years) because the same individuals (if not the same pairs) bred each year over several years; in other words the data on the total number of pairs breeding each year were unlikely to be independent. Analysis of temporal autocorrelation indicated that the total number of pairs in one year was related to that in the previous year ( $r=0.80$ ,  $P<0.001$ ). There were still significant correlations for lags of 2 and 3 years ( $r=0.65$ – $0.75$ ,  $P<0.05$ ) but a lag of 4 years was not significant ( $r=0.37$ ,  $P=0.33$ ). Thus the total numbers breeding in one year were related to some extent to those breeding up to 3 years previously, but the greatest influence came from the numbers breeding in the previous year.

To remove autocorrelation so that temporal trends could be examined, the differences in the total number of breeding pairs between successive years (D) were calculated. This was done separately for the two phases of the study. D showed no temporal autocorrelation and was normally distributed (according to probability plots). Calculation of such differences is a standard technique for dealing with such temporally autocorrelated measurements (Legendre and Legendre 1998). A further index of population change was also calculated:  $\ln(T_{x+1}/T_x)$  where  $T_x$  is the total number of pairs in year  $x$  (Pearce-Higgins *et al.* 2015). It also showed no temporal autocorrelation and was strongly related to D ( $r=0.92$ ,  $P<0.001$ ). Analyses were carried out mostly with D, but repeated with  $\ln(T_{x+1}/T_x)$  in some cases.

To examine how SOI influenced breeding we identified the months over which SOI gave the strongest correlation with D. SOI is given as mean monthly values by BOM (Bureau of Meteorology 2015). We calculated the mean SOI for overlapping two- (Jan–Feb to Nov–Dec), three- (Jan–Mar to Oct–Dec) and four-month (Jan–Apr to Sep–Dec) intervals for each year (1976–1984; 2008–2013). These mean values, none of which showed any temporal autocorrelation, were then correlated with D. Cross correlation (between the time series of D and SOI) was used to identify any time delays in the correlations. It was important to show that significant correlation occurred only when mean SOI and D were measured in the same year. Time lags of one or more years were not considered biologically interpretable. Rainfall during the breeding season (R; this showed no temporal autocorrelation) was also correlated with D and with mean SOI.

D was also calculated individually for the four species with the highest numbers of pairs: Brown Thornbill (*Acanthiza pusilla*), Eastern Yellow Robin (*Eopsaltria australis*), Yellow-faced Honeyeater (*Lichenostomus chrysops*) and Superb Fairy-wren (*Malurus cyaneus*). These data were correlated with mean SOI and R to determine whether patterns at the community level were repeated for individual species.

Time series analyses and other statistical tests were carried out using SYSTAT version 13.0.

## Results

The total number of breeding pairs varied substantially (Fig. 1) during both phases of the study. During the SM phase (Fig. 1a) numbers declined by ~50% over 10 years from 50 pairs in 1975 to 23 in 1984. Drought in 1980 accompanied by a bushfire at the beginning of the breeding season and low rainfall in 1982 undoubtedly contributed to this decline. The opposite occurred during the MSG phase (Fig. 1b) with numbers not quite doubling between 2007 and 2013 (from 44 to 77 pairs) largely as a result of increases in the numbers of Yellow Faced Honeyeaters, Brown Thornbills and Eastern Spinebills. Numbers between 2007 and 2009 were much the same as those recorded by SM during the first few years of his study. After 2009 numbers increased, perhaps as a response to the ending of the decade long drought in NSW.

Differences in the total numbers of D showed a strong correlation with mean SOI for the months immediately preceding the beginning of the breeding season (August) for the year in which the difference was calculated (Fig. 2). The mean SOI was calculated for intervals of two, three or four months, and in all

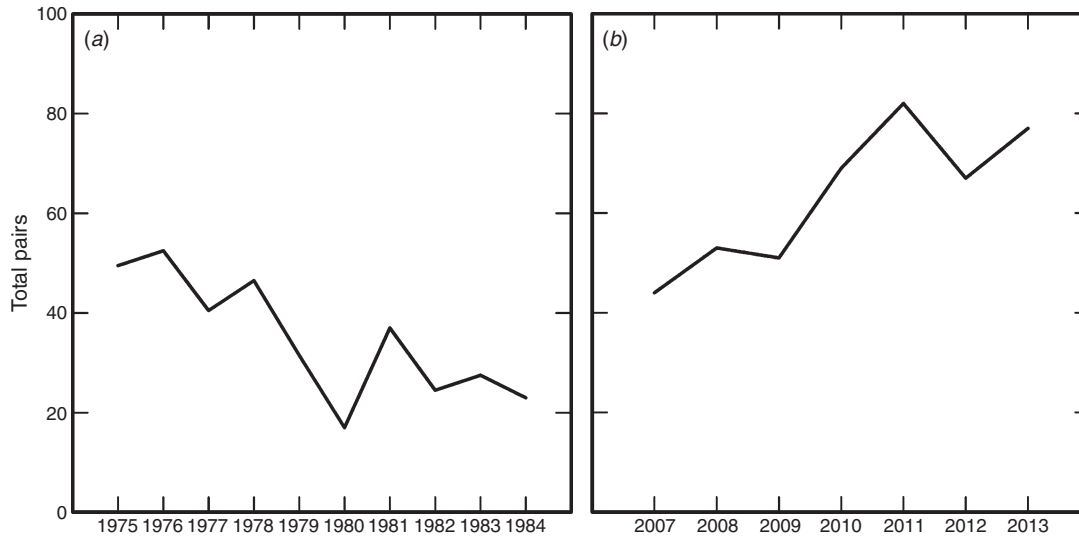


Fig. 1. The total number of breeding pairs recorded each year during the first (a) and second (b) phases of the study.

cases the correlation coefficient rose rapidly from January–April and reached a maximum in June–July (Fig. 2a;  $r=0.78$ ,  $P=0.001$ ), May–July (Fig. 2b;  $r=0.78$ ,  $P=0.001$ ) or April–July (Fig. 2c;  $r=0.82$ ,  $P<0.001$ ). From August to the end of the year such correlations decreased somewhat, but still remained higher than at the beginning of the year. This suggests the breeding community was influenced by the SOI index in the 3–4 months leading up to the breeding season and that after breeding had begun this influence declined but was not entirely absent.  $\ln(T_{x+1}/T_x)$  showed a similar pattern, but maximum correlation coefficients were somewhat lower:  $r=0.69$  for June–July ( $P=0.004$ );  $r=0.70$  for May–July ( $P=0.004$ ) and  $r=0.69$  for April–July ( $P=0.005$ ).

Cross correlation of D with mean SOI (only for months with the maximum  $r$  values shown above) revealed no lag effects: correlation was always highest and only significant for values of D and SOI recorded in the same year. A plot of D (Fig. 3) vs mean SOI (April–July; the interval with the highest correlation) showed that a positive SOI index usually resulted in a positive value for D and a negative SOI resulted in a negative value. The years 1976, 1983 and 2009 were exceptions to this pattern, but in these cases the values for D were the lowest recorded (2–3).

Rain fall during the breeding season (R) was generally positively correlated with D (Fig. 4), although two years (1976, 1983) were obvious exceptions to this pattern. When these two years were omitted R was strongly correlated with D ( $r=0.84$ ,  $P<0.001$ ) and with mean SOI (April–July) ( $r=0.80$ ,  $P=0.001$ ); R was also correlated with  $\ln(T_{x+1}/T_x)$  ( $r=0.77$ ,  $P=0.002$ ). Of the two outlying years 1976 was clearly exceptional: 642 mm of rain fell in October, more than half the annual rainfall, and about 10 times the mean for this month; rainfall during the other months of this breeding season was not unusually high or low. If this amount is subtracted from R (and the average for October [57 mm] substituted) then the adjusted rainfall would have been 410 mm for 1976. Similarly, if the high October rainfall (207 mm) in 1983 is subtracted from R (and the average substituted), the adjusted rainfall for 1983 is 415 mm. R values of 410–415 mm would

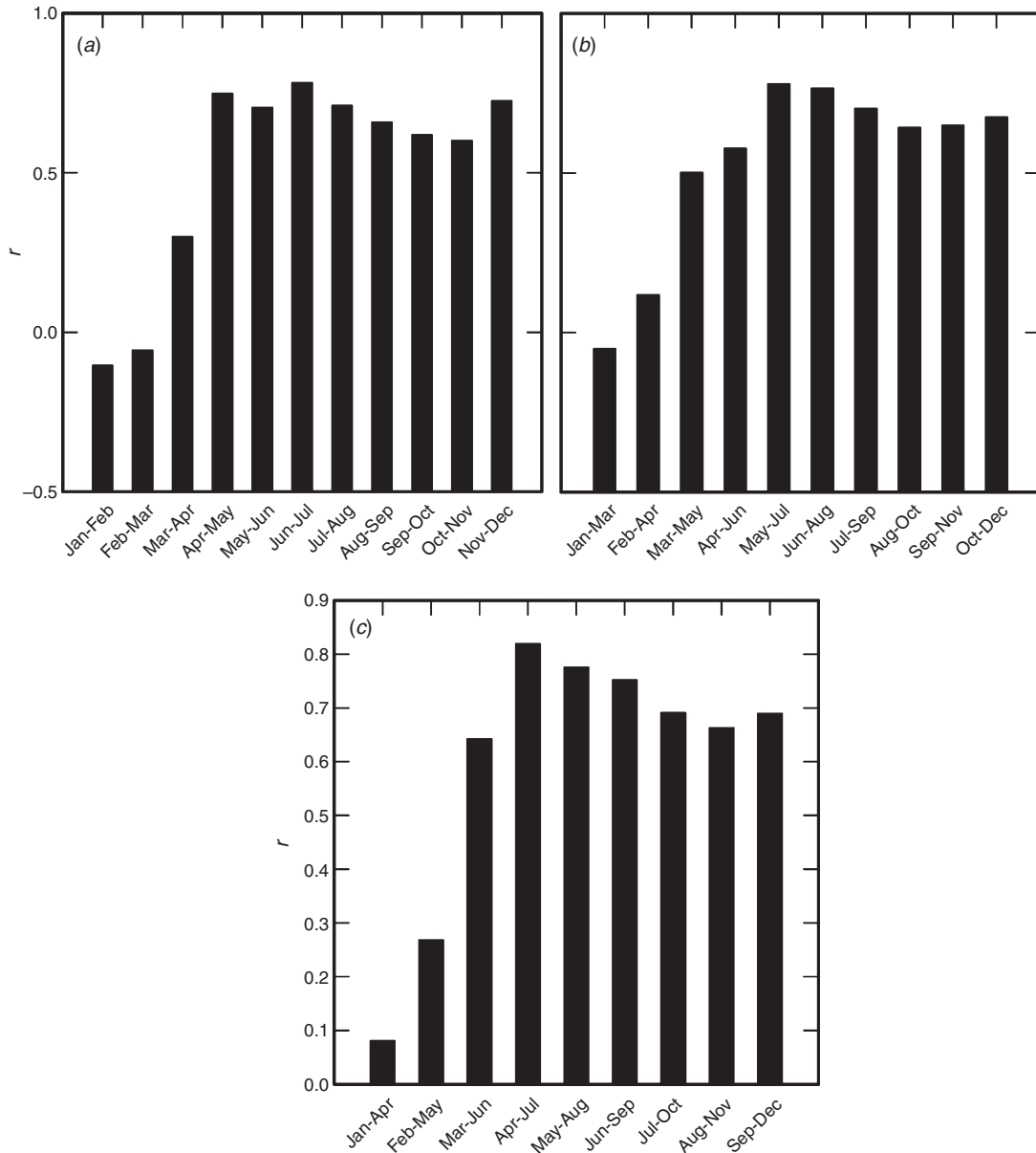
result in both years becoming part of the same linear trend displayed by the remaining years (Fig. 4).

There was no correlation between annual rainfall and D ( $r=0.33$ ,  $P=0.23$ ; without 1976 and 1983,  $r=0.37$ ,  $P=0.22$ ). Mean monthly rainfalls (for months taken two, three or four at a time) between January and July were also unrelated to D ( $r=-0.26$  to  $0.39$ ), indicating there was no connection between D and rainfall immediately preceding breeding.

Correlations between mean SOI (April–July) and values of D for each of the four most abundant species were weak and non-significant ( $r=0.12$ – $0.47$ ,  $P=0.08$ – $0.67$ ). If, however, the numbers of breeding pairs of these four species were summed and D recalculated then the correlation with mean SOI was stronger and significant ( $r=0.66$ ,  $P=0.008$ ), but not as strong as the correlation for data from all 17 species ( $r=0.82$ ). An almost identical pattern occurred for correlations with R:  $r=0.12$ – $0.46$  ( $P=0.10$ – $0.69$ ) for individual species and  $r=0.70$  ( $P=0.006$ ) for the combined data. The different strengths of these correlations undoubtedly reflect the lack of reliability of such analysis when numbers are low. This is what we suspected while assembling the data and why our interest lay in the dynamics of the community as a whole.

## Discussion

The mechanism behind the relationship between D and SOI appears to be that a positive SOI (April–July), which was evident for years 1978, 1981, 2008, 2010, 2011, 2013, resulted in  $>300$  mm rainfall during the breeding season (Fig. 4); and this lead to an increase in the number of pairs between years i.e. positive D value. When SOI (April–July) was negative (years 1977, 1979, 1980, 1982, 2012), rainfall was  $<300$  mm, and D was negative. Four years had SOIs close to zero, and in each year D was also close to zero, despite either low (1984, 2009) or high rainfall (1976, 1983; Fig. 4). This suggests that mean SOI (April–July) was a better predictor of D than rainfall during the breeding season. In this situation mean SOI (April to July) may

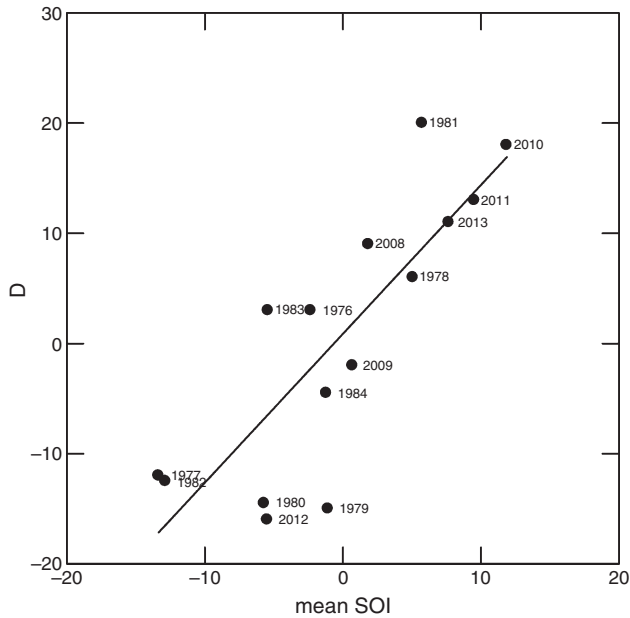


**Fig. 2.** The correlation coefficients between the differences (D) in the total numbers of breeding pairs in successive years and the mean Southern Oscillation Index (SOI) of months taken two (a), three (b) and four (c) at a time.

represent, better than any single local variable, a variety of climate features that affect breeding. Stenseth *et al.* (2003) in their review of the ecological effects of large-scale climatic indices strongly endorse this view.

Both measures of change in the breeding population [ $D$  and  $\ln(T_{x+1}/T_x)$ ] were strongly positively correlated with mean SOI (April–July) and with rainfall during the breeding season, thus answering the questions initially posed. It is well established that positive values of SOI are associated with increased rainfall and negative values with drought in southern Australia (Nicholls 1991; Lake 2011). Thus an association between SOI and some measure of breeding might be expected, and our study demonstrates this for a community of forest birds in temperate Australia.

We only considered one large scale climatic factor (ENSO) known to influence the climate in south-eastern Australia. Van de Pol *et al.* (2013) related another factor (DMI) to the breeding success of Fairy-wrens in southern Australia, but noted that DMI and ENSO were strongly correlated, especially during spring. In fact, they found breeding success showed the highest correlations with the mean DMI for March–January or the mean SOI for May. For both indices some or all of the autumn or winter months were included in these intervals. Our findings were similar with numbers of breeding pairs maximally correlated with SOI averaged over late autumn and early winter (April–July). In the Pacific North-west Nott *et al.* (2002) showed that breeding productivity of 34 species between May–August was most strongly correlated

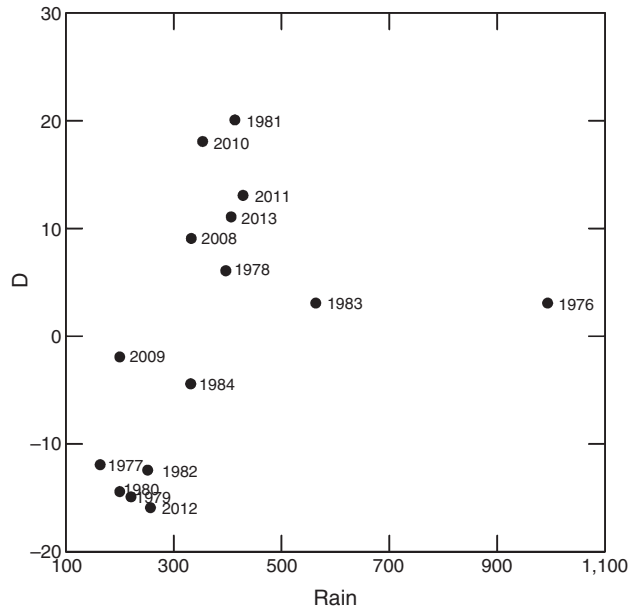


**Fig. 3.** Differences in number of breeding pairs between successive years (D) plotted against the mean Southern Oscillation Index (SOI) during April to July for the stated year. The regression line was highly significant ( $P < 0.001$ );  $r^2 = 0.67$ .

with mean monthly indices for ENSO or NAO measured between March–May. Thus large scale climatic factors do influence breeding, but it is the values these factors take immediately before the breeding season which appear to be the best predictors, not the annual mean values (correlation of mean annual SOI with D:  $r = 0.67$ ,  $P = 0.006$ ). The months immediately before breeding could be described as critical periods because of the marked influence their mean SOI or DMI values have on the subsequent breeding season.

In Australia, at least, local rainfall is also clearly related to breeding of forest birds (e.g. Recher and Davis 2014). We found a strong correlation between rainfall during the breeding season (August–December) and change in the number of breeding pairs (D). Van de Pol *et al.* (2013) found highest correlations with total rainfall from April–December. In our case we cannot readily separate the influence of rainfall and the SOI on D as these two variables were strongly correlated ( $r = 0.8$ ). However, when the SOI was approximately zero, D did not appear to respond to variations in rainfall, (Fig. 4). As noted previously, SOI may be a better predictor of D because it is less subject to the extreme variation shown by rainfall.

Increased rainfall during the breeding season probably increases the primary production of the surrounding forest and thus the abundance of forest insects. Woinarski and Cullen (1984) showed that the greatest numbers of foliage arthropods at 16 sites in Victorian forests occurred in spring, and lowest numbers occurred in winter, although the decline was not pronounced. The authors had few data on yearly changes in abundance, except at one site where drought caused large reductions in density in the second year of observations. Recher *et al.* (1996a) found similar fluctuations in arthropod numbers on two species of eucalypt in eastern NSW. Bell (1985) conducted a three year study at a single



**Fig. 4.** Rainfall during the breeding season (August–December inclusive; mm) versus differences between years in the total number of breeding pairs (D). A clear linear trend between these variables is evident except for two years (1976, 1983), which are outliers. Rainfall in October of these years (642, 207 mm) greatly exceeded the long-term mean for this month (57 mm). The linear trend was highly significant ( $P < 0.001$ );  $r^2 = 0.71$ .

forested site in northern NSW and sampled both the foliage and the ground layer for arthropods. The last two years of this study spanned a drought. Arthropod biomass was lowest in winter, but increased in spring and summer, and was well correlated with the monthly primary production of the forest, but not with monthly rainfall. Primary production was reduced during drought, which resulted in reductions in abundance for most arthropod groups.

If breeding birds in these southern forests rely on insects to feed their young, then they may assess insect productivity of their forest habitat before nesting begins. It is unknown whether birds have this capacity. But the fact that a climatic index prevailing during autumn and winter is an excellent predictor of annual change in numbers of breeding pairs suggests that environmental factors present before breeding provide important clues about the quality of the subsequent breeding season.

We believe strong relationships with climate were revealed by our study because it was based on accurate data accumulated over 17 years. Long-term studies in North America (Nott *et al.* 2002; Holmes 2007) were also based on accurate measures of breeding and showed strong relationships between breeding and ENSO or NAO ( $r = 0.69$  to  $0.73$ ). On the other hand, van de Pol *et al.* (2013), used data on breeding success for 16 populations of Fairy-wrens across southern Australia, but had only three populations that had been monitored for a decade or more. Breeding success for these was weakly related ( $r = -0.22$  to  $-0.60$ ) to DMI. Breeding success in another four showed high correlations ( $r = -0.81$  to  $-0.92$ ) with DMI, while rainfall was positively correlated ( $r = 0.77$ – $0.90$ ) with breeding in a further five populations. However, these high correlations all occurred with populations that had been followed for only 3–7 years and the shortness

of the record suggests that they may not be reliable. Conclusions about the influence of large scale climatic indices on bird breeding should be based on data gathered over at least a decade because ENSO cycles in southern Australia repeat approximately every 5–7 years (Nicholls 1991).

Stevens and Watson (2013) made no allowance for cyclical changes in climate (e.g. ENSO) when concluding that 6 species of birds declined in abundance during a 21 year study in a northern NSW forest. Nor did they use any data on the breeding activity of these species to support their interpretation. In our study, a general decrease in abundance in the period 1975–1984 and an increase from 2007–2013 (Fig. 1) reveal little about the underlying dynamics of the bird community and ignore yearly changes in numbers of breeding pairs. The most salient features of our study are such yearly changes, rather than trends in abundance through time.

The fact that individual birds on our plot were identifiable in the field ensured a degree of accuracy we think is necessary before the effects of climate can be investigated. Some recent studies rely on short (e.g. 20 min), spatially limited (e.g. a few hectares), surveys over several or many sites to acquire data on bird numbers or breeding activity (e.g. MacNally *et al.* 2009; Recher and Davis 2014; Selwood *et al.* in press). Similar techniques were tried but were shown to be inadequate at our site (see Marchant 1992). More importantly, data from short surveys will be inherently noisy compared with numbers of breeding pairs, which in our case were derived from 4–5 months of continuous observations each breeding season. Noisy data will undoubtedly make analysis of the relationships of birds with climate and other environmental variables less certain.

### Acknowledgements

We dedicate this paper to the late Stephen Marchant, who instigated this study and who believed that the study of breeding was a central aspect of the life history of birds. We were helped immeasurably by a group of dedicated bird banders led by Anthony Overs, operating under banding licence numbers 2195 and 2857. We also thank the Australian Bird and Bat Banding Scheme for the supply of numbered metal bands.

### References

- Austin, M. P. (1978). Vegetation. In 'Volume 2, Biophysical Background Studies, Land Use on the South Coast of NSW' (Ed. R. H. Gunn), pp. 44–66. (CSIRO: Melbourne.)
- Bell, H. L. (1985). Seasonal variation and the effects of drought on the abundance of arthropods in savanna woodland on the Northern Tablelands of New South Wales. *Australian Journal of Ecology* **10**, 207–221. doi:10.1111/j.1442-9993.1985.tb00884.x
- Bureau of Meteorology (2015). S.O.I. (Southern Oscillation Index) Archives – 1876 to present. Available at <http://www.bom.gov.au/climate/current/soihtml.shtml> (Verified 12 August 2015).
- Holmes, R. T. (2007). Understanding population change in migratory songbirds: long-term and experimental studies of Neotropical migrants in breeding and wintering areas. *The Ibis* **149**(Suppl. 2), 2–13. doi:10.1111/j.1474-919X.2007.00685.x
- Lake, P. S. (2011). 'Drought and Aquatic Ecosystems: Effects and Responses.' (Wiley-Blackwell: UK)
- Legendre, P., and Legendre, L. (1998). 'Numerical Ecology'. 2nd edn. (Elsevier: Amsterdam.)
- MacNally, R., Bennett, A. F., Thomson, J. R., Radford, J. Q., Unmack, G., Horrocks, G., and Vesk, P. A. (2009). Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. *Diversity & Distributions* **15**, 720–730. doi:10.1111/j.1472-4642.2009.00578.x
- Marchant, S. (1992). A Bird Observatory at Moruya, NSW 1975–84. Occasional Publication No. 1. Eurobodalla Natural History Society, Moruya.
- Nicholls, N. (1991). The El Niño/Southern Oscillation and Australian vegetation. *Vegetatio* **91**, 23–36. doi:10.1007/BF00036045
- Nott, M. P., Desante, D. F., Siegel, R. B., and Pyle, P. (2002). Influences of the El Niño/Southern Oscillation and the North Atlantic Oscillation on avian productivity in forests of the Pacific Northwest of North America. *Global Ecology and Biogeography* **11**, 333–342. doi:10.1046/j.1466-822X.2002.00296.x
- Pearce-Higgins, J. W., Eglinton, S. M., Martay, B., and Chamberlain, D. E. (2015). Drivers of climate change impacts on bird communities. *Journal of Animal Ecology* **84**, 943–954. doi:10.1111/1365-2656.12364
- Recher, H. F., and Davis, W. F. (2014). Response of birds to episodic summer rainfall in the Great Western Woodlands, Western Australia. *Australian Zoologist* **37**, 206–224. doi:10.7882/AZ.2014.011
- Recher, H. F., Majer, J. D., and Ganesh, S. (1996a). Seasonality of canopy invertebrate communities in eucalypt forests of eastern and western Australia. *Australian Journal of Ecology* **21**, 64–80. doi:10.1111/j.1442-9993.1996.tb00586.x
- Recher, H. F., Majer, J. D., and Ganesh, S. (1996b). Eucalypts, arthropods and birds: on the relation between foliar nutrients and species richness. *Forest Ecology and Management* **85**, 177–195. doi:10.1016/S0378-1127(96)03758-9
- Selwood, K. E., Clarke, R. H., Cunningham, S. C., Lada, H., McGeoch, M. A., and MacNally, R. (in press). A bust but no boom: responses of floodplain bird assemblages during and after prolonged drought. *Journal of Animal Ecology*. doi:10.1111/1365-2656.12424
- Serventy, D. L., and Whittell, H. M. (1962). 'Birds of Western Australia'. (Paterson Brokensha: Perth.)
- Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K., Yoccoz, N. G., and Adlandsvick, B. (2003). Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society B: Biological Sciences* **270**, 2087–2096. doi:10.1098/rspb.2003.2415
- Stevens, H. C., and Watson, D. M. (2013). Reduced rainfall explains avian declines in an unfragmented landscape: incremental steps toward an empty forest? *Emu* **113**, 112–121. doi:10.1071/MU12063
- van de Pol, M., Brouwer, L., Brooker, L. C., Brooker, M. G., Colombelli-Negrel, D., Hall, M. L., Langmore, N., Peters, A., Pruett-Jones, S., Russell, E. M., Webster, M. S., and Cockburn, A. (2013). Problems with using large-scale oceanic climate indices to compare climatic sensitivities across populations and species. *Ecography* **36**, 249–255. doi:10.1111/j.1600-0587.2012.00143.x
- Woinarski, J. C. Z., and Cullen, J. M. (1984). Distribution of invertebrates on foliage in forests of south-eastern Australia. *Australian Journal of Ecology* **9**, 207–232. doi:10.1111/j.1442-9993.1984.tb01359.x

**Appendix 1. The 33 species that bred at least once during either phase of the study, but were not included in the analysis of breeding pairs**

† species that bred irregularly or in very low numbers; \* species that built nests that were too time-consuming to find and observe; the remaining species bred only once

Painted Button-quail (*Turnix varius*)  
 Common Bronzewing (*Phaps chalcoptera*)  
 Brush Bronzewing (*Phaps elegans*)  
 Tawny Frogmouth (*Podargus strigoides*)  
 Topknot Pigeon (*Lopholaimus antarcticus*)  
 Brown Gerygone (*Gerygone mouki*) †  
 Yellow Thornbill (*Acanthiza nana*)  
 Striated Thornbill (*Acanthiza lineata*) \*  
 Red Wattlebird (*Anthochaera carunculata*)  
 Yellow-tufted Honeyeater (*Lichenostomus melanops*)  
 White-naped Honeyeater (*Melithreptus lunatus*) \*  
 Crescent Honeyeater (*Phylidonyris pyrrhopterus*)  
 New Holland Honeyeater (*Phylidonyris novaehollandiae*) †  
 White-cheeked Honeyeater (*Phylidonyris niger*)  
 Scarlet Honeyeater (*Myzomela sanguinolenta*) †  
 Jacky Winter (*Microeca fascinans*)  
 Eastern Whipbird (*Psophodes olivaceus*) †  
 Varied Sitella (*Daphoenositta chrysoptera*)  
 Crested Shrike-tit (*Falcunculus frontatus*) †  
 Grey Shrike-thrush (*Colluricincla harmonica*) †  
 Black-faced Monarch (*Monarcha melanopsis*)  
 Rufous Fantail (*Rhipidura rufifrons*) †  
 Leaden Flycatcher (*Myiagra rubecula*) †  
 White-bellied Cuckoo-shrike (*Coracina papuensis*)  
 Cicadabird (*Coracina tenuirostris*) †  
 Olive-backed Oriole (*Oriolus sagittatus*)  
 Dusky Woodswallow (*Artamus cyanopterus*)  
 Pied Currawong (*Strepera graculina*)  
 Satin Bowerbird (*Ptilonorhynchus violaceus*) †  
 Red-browed Finch (*Neochmia temporalis*) \*  
 Mistletoebird (*Dicaeum hirundinaceum*) †  
 Silvereye (*Zosterops lateralis*) †  
 Bassian Thrush (*Zoothera lunulata*)