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## ECOLOGY

# Winter mortality of a passerine bird increases following hotter summers and during winters with higher maximum temperatures

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Climate change may influence animal population dynamics through reproduction and mortality. However, attributing changes in mortality to specific climate variables is challenging because the exact time of death is usually unknown in the wild. Here, we investigated climate effects on adult mortality in Australian superb fairy-wrens (*Malurus cyaneus*). Over a 27-year period, mortality outside the breeding season nearly doubled. This nonbreeding season mortality increased with lower minimum (night-time) and higher maximum (day-time) winter temperatures and with higher summer heat wave intensity. Fine-scale analysis showed that higher mortality in a given week was associated with higher maxima 2 weeks prior and lower minima in the current fortnight, indicating costs of temperature drops. Increases in summer heat waves and in winter maximum temperatures collectively explained 62.6% of the increase in mortality over the study period. Our results suggest that warming climate in both summer and winter can adversely affect survival, with potentially substantial population consequences.

## INTRODUCTION

Anthropogenic climate change is now influencing the population dynamics of many species (1) as individual fitness is affected when organisms experience climatic conditions at the extreme ends of, or even outside, the climate niches to which they are adapted. Its impact is often mediated by effects on the local environmental conditions that determine key biological processes such as fecundity and mortality (2, 3), which will directly affect population size and, hence, population dynamics (2, 4, 5). For animals living in seasonal environments in temperate regions, individuals usually suffer most mortality over winter (6, 7), and winter mortality may therefore contribute considerably to the dynamics of wild animal populations (2). An understanding of how climate change affects winter mortality is therefore critical for providing insights into how natural populations are being affected by current climate change and, hence, for informing appropriate management and conservation strategies (8, 9).

The effects of climate and climate change on winter mortality in wild animals may be complex. First, minimum and maximum temperatures may affect individual mortality in different ways, each of which depend on species-specific thresholds (7). Lower minimum temperatures in winter usually increase energy requirements for nonhibernating endotherms because thermogenesis is necessary, and food is often scarce (10, 11), potentially resulting in starvation (12, 13): For example, a recent study of northern bobwhite (*Colinus virginianus*) found that extreme cold temperature events reduced

survival (14). As a result, milder winters with higher minimum temperatures may be associated with less winter mortality. In contrast, increases in maximum temperatures in winter and the occurrence of warm spells may cause problems in cold-acclimatized animals by resulting in loss of thermogenic capacity [e.g., if high summit metabolic rates decrease in warm spells and reduce cold tolerance, (15)]. The increased occurrence of mild spells with increased daily maximum temperatures in winter may therefore be detrimental if individuals are slow to readjust their phenotype when the weather cools again (15, 16). Rising temperatures associated with climate change may be expected to reduce the frequency of cold spells but may also increase the frequency of mid-winter warm spells (17), and thus, it is as yet unclear how warming temperatures are likely to affect winter mortality in wild animal populations.

Secondly, winter mortality may also depend on levels of precipitation and its interaction with temperature. Winter precipitation can generate direct thermoregulatory challenges (18). Indirect effects of adverse precipitation levels on food availability (e.g., heavy snow cover can reduce access to food) may also have important survival consequences. As predictions for future patterns of precipitation are highly variable (17), general predictions for the implications of precipitation for climate change are therefore currently unclear. Lastly, winter mortality may also be affected by climate at other times of year through longer-term “carry-over” effects. For example, the increasing frequency of extreme high-temperature events (i.e., heat waves) and droughts during the breeding season of previous summer may have long-term implications for survival through the winter (19).

An understanding of this complex array of potential impacts of climate and climate change on winter mortality requires identification of the relevant climate variables in the relevant time periods, including potential threshold effects and their possible interactions. Long-term studies provide a valuable means with which to disentangle the complex impact of climate on winter mortality in wild

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animal populations. However, to date, relevant studies have frequently been carried out on annual time scales, considering population-level annual average rates of mortality, and often based only on monitoring conducted during the breeding season. In these studies, the effective sample size equals the number of study years, so statistical power is necessarily limited (20). Exploratory approaches for detecting relevant climate variables of moderate to strong effect sizes require at least 20 years of data to have reasonable power to distinguish true from false-positive climate signals and avoid false negatives (21). Furthermore, even with time series that span multiple decades, it can be challenging to distinguish between the effects of climate variables that are often highly correlated, and thus, attribution to particular variables may be challenging. Last, the effects of climate on individual mortality may operate on a range of scales, from short [e.g., daily, (22)] to much longer term. Robust attribution of changes in mortality to specific climate variables can therefore be challenging for studies of wild populations. The use of mortality data collected on a very fine temporal scale potentially allows for more reliable determination of the exact climate signals and can also provide valuable insights into the mechanisms by which climate affects winter mortality. However, information on precisely when individuals die within each year is difficult to attain in the field as it requires either year-round monitoring or equipping a sufficient number of individuals with bio-loggers. To our knowledge, field studies of the effects of climate that exploit the increased explanatory power of precise mortality timing data have, to date, only involved short-term periods [e.g., a few years of radiotelemetry data in (14)].

In this study, we used 27 years of individual-based weekly census data to investigate the effects of climate on mortality of superb fairy-wrens (*Malurus cyaneus*) in southeastern Australia. Superb fairy-wrens are cooperatively breeding passerines that live on year-round territories and in groups composed of a dominant breeding pair and up to five male helpers (23). The combination of year-round censusing and a near-perfect detection rate in our long-term study allows us to pinpoint the time of death of all individuals to a given week and then to relate it to recent weather patterns within and across years.

We focused on the effects of climate on variation in the adult mortality rate outside the long fairy-wren breeding season; this “nonbreeding season” is the relatively cold 6-month period of the year when most adult mortality occurs (24), presumably as a result of starvation, predation, or loss of thermogenic capacity. Across our study period of 1993–2019, the population density in our study area declined by 42% (fig. S1A), while concurrently the climate changed substantially toward higher annual average maximum temperatures, increased frequency of heat waves, and lower annual rainfall (25). While this population decline may have been driven by multiple factors, we investigated here the effect of the changing climate on adult mortality in the nonbreeding season. Previous work on the same population reported anecdotal observations of adult males dying following abrupt transitions from unusually warm, moist conditions to nights of heavy frost in some years (24). We therefore hypothesized that lower minimum temperatures, higher maximum temperatures, and more rainfall in the nonbreeding season increased mortality rate. In addition, our previous work on the population has also shown that more heat waves and less rainfall during the breeding season reduce average body mass of nestlings that year (25), indicating adverse effects of hot

dry summer conditions. Therefore, we also hypothesized that more heat waves and less rainfall in the breeding season increased mortality rate in the following nonbreeding season through carry-over effects. Finally, we tested for effects of climate change by using a path analysis to quantify the extent to which changes in different aspects of the climate over time contributed to changes of adult mortality over the study period.

## RESULTS

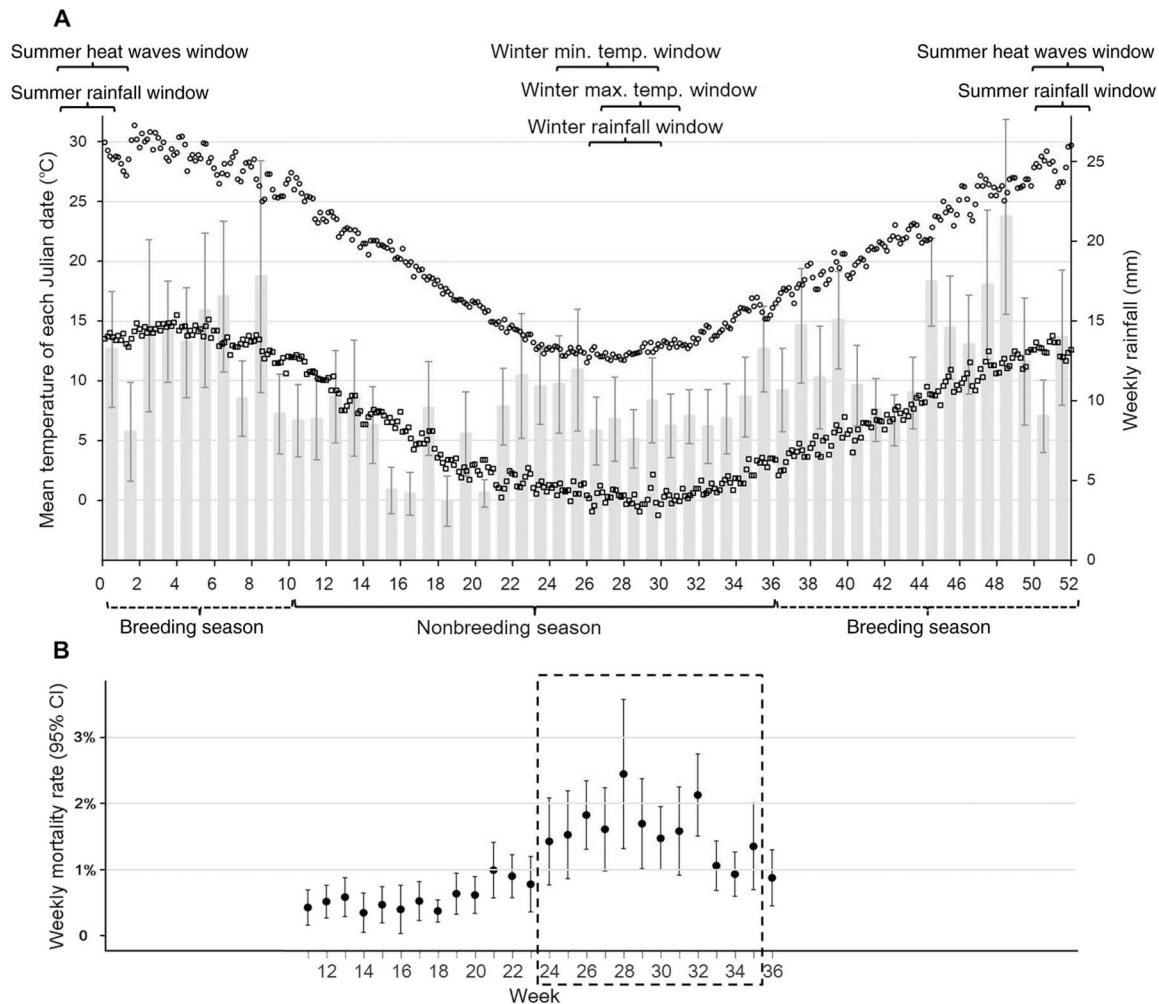
### Nonclimatic causes of variation in mortality

Our analyses of 1670 adult (aged 1 year or more) fairy-wrens across 27 years showed that 59% died in the nonbreeding season (26 weeks running from 12 March to 9 September, i.e., calendar weeks 11 to 36), 37% died in the other half of the year [the breeding season; (26)], and the remaining 4% were still alive at the end of the study period. The mortality rate in each nonbreeding season (hereafter, “seasonal mortality rate”) varied from 11.3 to 44.4%, with an average value of 23.7% ( $\pm 8.7\%$  SD;  $n = 27$  seasons). Our weekly census data also indicated considerable variability in the mortality rate in each week (hereafter, “weekly mortality rate”), ranging from 0 to 11.3% per week (mean  $\pm$  SD =  $1.1 \pm 1.4\%$ ;  $n = 702$  weeks across the 27 seasons). On average, in a given year, weekly mortality rates initially started low (in early autumn) and increased through autumn into winter, peaking in the period of weeks 24 to 35 (a 12-week winter “peak,” during which the mean  $\pm$  SD mortality rate was  $1.6 \pm 1.7\%$ ) (Fig. 1B; Fig. 1A shows the corresponding change in weather variables).

We ran a series of models to investigate the associations between climate and both annual (hereafter, “seasonal”) and weekly mortality in the nonbreeding season. To do so, we first established “baseline” Cox proportional hazards models to determine effects of nonclimatic variables on both seasonal and weekly mortality hazard rates (tables S1, S2, S3, and S4). These baseline models showed that larger group size (i.e., the number of adults and juveniles in an individual’s group, excluding juvenile females, who may disperse) was associated with lower seasonal and weekly mortality hazard rates in this cooperatively breeding species (tables S1 and S3). In addition, both seasonal and weekly mortality hazard rates showed no change with age in early life (from age one to five) but increased markedly in late life (from age six onward; seasonal mortality, table S1; weekly mortality, table S3). In establishing the baseline models for each analysis, there was no indication of any difference in mortality hazard rate between the sexes or between that of dominant breeders and male helpers (tables S2 and S4).

### Climate effects on the seasonal mortality hazard rate

We analyzed which climate variables over which period(s) had the strongest association with mortality, at both the seasonal and weekly levels, so that the consistency of results across the two time scales could be assessed. The choice of climate variables was based on previous work (see Introduction), but we had limited a priori knowledge of the time window during the year during which climate variables act most strongly. Therefore, we used a systematic “sliding window” approach (21, 27) to identify the periods of the year during which climate variables were most strongly associated with mortality, considering both interannual and intrannual variation in climatic conditions.

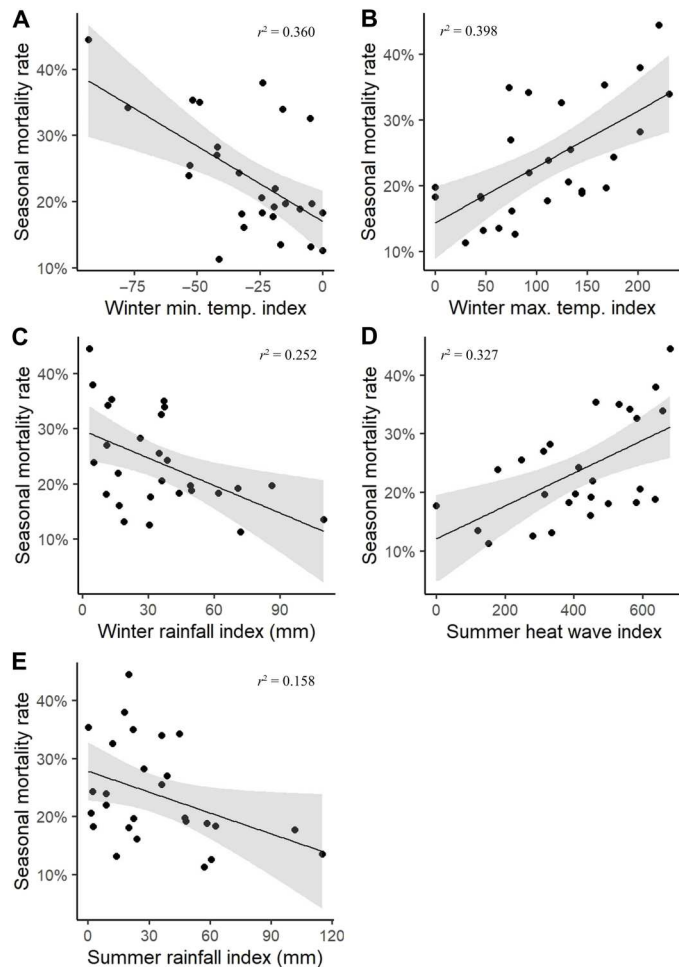


**Fig. 1. Climate and mortality rate of adult superb fairy-wrens through the year.** X axes denoting the week in the year (week 1 is from 1 to 7 January). (A) Temperatures and rainfall through the year: the mean of daily maximum temperatures (dots) and the mean of daily minimum temperatures (squares) of each date and mean weekly rainfall (gray bars with the error bars showing 95% confidence intervals) from 1993 to 2019. The dashed and solid brackets on the bottom [below the x axis in (A)] indicate the periods considered as “breeding season” and nonbreeding season (see the main text for the definitions of each period), respectively. The solid brackets at the top indicate the climate windows identified in our analyses as most relevant for the seasonal mortality hazard rate in the nonbreeding season (Table 1). (B) The average mortality rate of adult superb fairy-wrens in that week across the 27 years. Each point represents the mean mortality rate of that week with the error bars showing 95% confidence intervals. The dashed rectangle indicates the peak period of mortality in the nonbreeding season (weeks 24 to 35, from 11 June to 2 September, during which the average weekly mortality rate was ~1.6%). CI, confidence interval.

We considered effects of both temperature and precipitation, in each case, considering the sum of the respective variable within a given time window (and for temperature, also only considering values above or below certain thresholds; see Methods). For the seasonal mortality analyses, we tested whether the climate in a given period of year [i.e., in an absolute time window; (21)] was associated with mortality across that nonbreeding season, while for the weekly mortality analyses, we tested whether the mortality in a given week was associated with the climate in the recent period to that week [i.e., in a relative time window; (21)]. Our analyses found strong associations of climate with both seasonal and weekly mortality. Below, we first outline the best climate index identified for each climate variable, with reference to more detailed output in the Supplementary Materials, and then present models including all climate indices.

Considering climate in the nonbreeding season, higher seasonal mortality was associated with lower minimum temperatures (winter minimum temperature index, with a threshold of  $-4^{\circ}\text{C}$  downward; Fig. 2A), with higher maximum temperatures (winter maximum temperature index, with a threshold of  $14^{\circ}\text{C}$  upward; Fig. 2B), and with lower rainfall (winter rainfall index; Fig. 2C and Tables 1 and 2). The windows identified for each of these climate indices overlapped extensively and coincided with the same period of time in the austral winter (late June and through July, about weeks 25 to 30), just after the winter solstice (Fig. 1A, Table 1, and table S5).

There was also evidence that climate in the previous breeding season affected the mortality in the subsequent nonbreeding season. Breeding seasons with higher temperatures (summer heat wave index, where heat waves were defined as temperatures over a threshold of  $28^{\circ}\text{C}$ , i.e., higher accumulated degree days of heating;



**Fig. 2. Effects of each climate index on the seasonal mortality rate of adult superb fairy-wrens.** (A-E) Each point represents 1 year. The lines are simple linear regressions through the 27 data points, and the gray shaded areas represent 95% confidence intervals of the lines. Coefficient of determination ( $r^2$ ) values are from the linear regressions in table S9.

Fig. 2D) and lower rainfall (summer rainfall index; Fig. 2E) were associated with higher mortality rates in the subsequent nonbreeding season (Tables 1 and 2). In this case, the relevant windows surrounded the austral summer solstice (mid-December to early January, about week 51 of the previous calendar year to week 1 of the current year; Fig. 1A, Table 1, and table S6).

We then included all five climate indices identified in a final Cox proportional hazards model of seasonal mortality hazard rate (Table 2). This model again showed that lower winter minimum temperatures, higher winter maximum temperatures, and higher intensity of summer heat waves were all associated with higher seasonal mortality hazard rates. Once these three temperature indices were included, there was no evidence of any additional effects of either the winter rainfall index or the summer rainfall index (Table 2) presumably because of collinearity between the temperature and rainfall indices (e.g., there was a positive correlation between the winter minimum temperature index and the winter rainfall index; fig. S2A). Although there was no evidence of any interactions between any of the climate indices (table S7), the effect of

summer heat waves on seasonal mortality hazard rate varied with group size: Higher intensity of summer heat waves was associated with higher seasonal mortality hazard rates, especially when group size was smaller (Table 2 and table S8).

In a multiple linear regression of the association between annual average seasonal mortality rates and the different climatic variables, there was an effect of each of the three temperature indices, and they collectively explained 74.3% of the between-year variance (table S10). There was no evidence for effects of the two rainfall indices when jointly included with temperature indices, and doing so only improved the proportion of variance explained to 75.9% (table S11).

### Climate effects on the weekly mortality hazard rate

Our fine-scale weekly-level analyses using data on the exact dates of individual death similarly showed that mortality was associated with both minimum and maximum temperatures experienced in the nonbreeding season. The sum of daily minimum temperatures in the focal week and in the week previous to it influenced the mortality hazard rate in a given week, with lower minimum temperatures being associated with higher mortality hazard rate (Table 2, table S12, and fig. S3A). As with the seasonal mortality analyses, mortality was also associated with higher maximum temperatures: Specifically, there was an increase in mortality in a given week with higher daily maximum temperatures in the week approximately 2 weeks prior (Table 2, table S12, and fig. S3B). Notably, the “best” window for minimum temperature did not overlap with that for maximum temperature (Table 1). In summary, the mortality hazard rate in a given week increased both with colder minima in the current and previous weeks and with higher maxima in the week before that. To explore this further, we calculated a “temperature drop” index defined as the difference between the standardized (to zero mean, unit SD) maximum temperature index and the standardized minimum temperature index (i.e., the extent of any fall in temperature from one warm week to two cold weeks). This post hoc test showed that the mortality hazard rates were higher after individuals experienced higher temperature drops (Table 2 and fig. S3C). In addition, the model with only this temperature drop variable had similar support to that of the model that included both minimum and maximum temperature indices [Tables 2; Akaike’s information criterion corrected (AICc) values differing by 2.48].

The weekly mortality hazard rate was unlikely to be associated with rainfall as randomization analysis indicated that the best rainfall window identified by the analysis had a substantial probability of being a false-positive signal ( $P_{\Delta AICc} = 0.09$ ; table S12). Considering interactions, there was no evidence of any interaction between the minimum and maximum temperature indices or between temperature indices and nonclimatic variables (the 95% confidence interval overlapped 0).

### Temporal trends in climate indices and mortality rate

We used simple linear regressions to test for temporal trends in the climate indices that our sliding window analyses had identified as being associated with the seasonal mortality hazard rate. These indicated no evidence of changes over the study period in the winter minimum temperature index, the winter rainfall index, or the summer rainfall index (Fig. 3, A, C, and E, and table S14). However, the winter maximum temperature index increased across years (Fig. 3B and table S14), as did the summer heat wave

**Table 1. Summary of exact dates (days) and durations for climate indices identified as the best predictors for the seasonal mortality hazard rate and weekly mortality hazard rate of adult superb fairy-wrens in the nonbreeding season.**  $\Delta$ AICc is the difference in AICc values after adding a given climate index to the final baseline models (which are shown in tables S2 and S4, respectively). Temperature indices are calculated as the sum of minimum temperatures below or the sum of maximum temperatures above a given threshold (shown in “temperature threshold” column) across the specified period. Winter rainfall for the weekly mortality hazard rate was a false positive and is therefore not shown. As examples, “winter maximum temperature” for the seasonal mortality hazard rate means the sum of daily maximum temperature over 14°C from 5 July to 5 August; “winter maximum temperature” for the weekly mortality hazard rate means the sum of daily maximum temperature over 11°C from 22 days before to 17 days before the last day of a given week (i.e., maximum temperatures in the week approximately 2 weeks prior). (Samples sizes:  $n = 1670$  adults across 27 nonbreeding seasons, making 4158 adult seasons for the seasonal mortality hazard rate;  $n = 1670$  adults across 702 weeks of 27 nonbreeding seasons, making 98,098 adult season weeks for the weekly mortality hazard rate).

Climate indices:	Start date/days	End date/days	Duration (days)	Temperature thresholds (°C)	$\Delta$ AICc
<i>Seasonal mortality hazard rate</i>					
Winter minimum temperature	20 June	28 July	39	−4	−51.9
Winter maximum temperature	5 July	5 August	32	14	−65.9
Winter rainfall	1 July	28 July	28	n.a.	−37.0
Previous summer heat waves	14 December	9 January	27	28	−46.2
Previous summer rainfall	16 December	5 January	21	n.a.	−26.2
<i>Weekly mortality hazard rate</i>					
Winter minimum temperature	12 days prior	−1 days prior	14	2	−29.6
Winter maximum temperature	22 days prior	17 days prior	6	11	−23.5

index (Fig. 3D and table S14). Furthermore, the annual average mortality rate in the nonbreeding season increased substantially, nearly doubling over our 27-year study period (Fig. 3F and table S14; from 16.1 to 31.4%, equivalent to an increase of 5.9% per decade).

### Contribution of climate change to increasing mortality over time

What was the contribution of these changes in climate variables over time to the observed changes in annual average seasonal mortality rate over the study period? A path analysis showed that (i) winter maximum temperatures and the intensity of summer heat waves have increased, while average group size has decreased (fig. S1B) over time and (ii) that lower winter minimum temperatures, higher winter maximum temperatures, and higher intensity of summer heat waves were, in turn, all associated with higher seasonal mortality rates [Fig. 4A, fig. S4A (for unstandardized version), and table S15]. It showed that the increase in the seasonal mortality rate over time was mostly due to the increases in the winter maximum temperature index and in the summer heat wave index over time (Fig. 4B and fig. S4B); together, these two indices accounted for 62.6% of the total increase in the seasonal mortality rate. The indirect effects of the other pathways of the winter minimum temperature index and average group size, and the direct effect of year on the change in seasonal mortality rate over time, were very small and statistically indistinguishable from zero (Fig. 4B and fig. S4B). In addition, whether or not the average group size was included in the model gave qualitatively the same results in the path analysis.

### DISCUSSION

Our analyses of nearly three decades of weekly and annual mortality patterns showed strong associations between climate and mortality of adult superb fairy-wrens in the nonbreeding season. In line with

the proposed hypotheses, lower minimum (night-time) temperatures and higher maximum (day-time) temperatures in winter and higher intensity of heat waves in the previous summer increased nonbreeding season mortality rate. However, we found no support for the hypothesized effects of winter or summer rainfall on mortality rate in the nonbreeding season when the effects of temperatures were included. In our fine-scale weekly mortality analyses of the effects of climate in the nonbreeding season, an individual's mortality hazard rate in a given week increased with low minimum temperatures in the current and previous weeks and high maximum temperatures in a week before that. These two climate effects may have acted together, reflecting large “temperature drops” between weeks, as this alternative index received similar model support from the data. The congruence between the results of the fine-scale weekly mortality analysis and the seasonal mortality analysis suggest that the temperature variables associated with individual mortality are likely the causal drivers. Furthermore, mortality increased at older ages and decreased with group size in this cooperatively breeding species. Both the winter maximum temperature index and the summer heat wave index increased across years, and the seasonal mortality rate nearly doubled across the study period. A path analysis indicated a substantial contribution of the warming temperature trend to the increasing mortality in the study population. We discuss these points in turn below.

### Determinants of mortality rate

Both the seasonal and weekly mortality analyses showed strong associations of low winter minimum temperatures with mortality in the nonbreeding season, which suggests that, as in many other bird species (12–14), individual survival is reduced by low nighttime temperatures in winter. In particular, individuals were at risk from higher mortality hazard rates in a given week if the minimum temperatures in the current and previous weeks were low (Table 2 and fig. S3A). During a cold spell in winter, fairy-

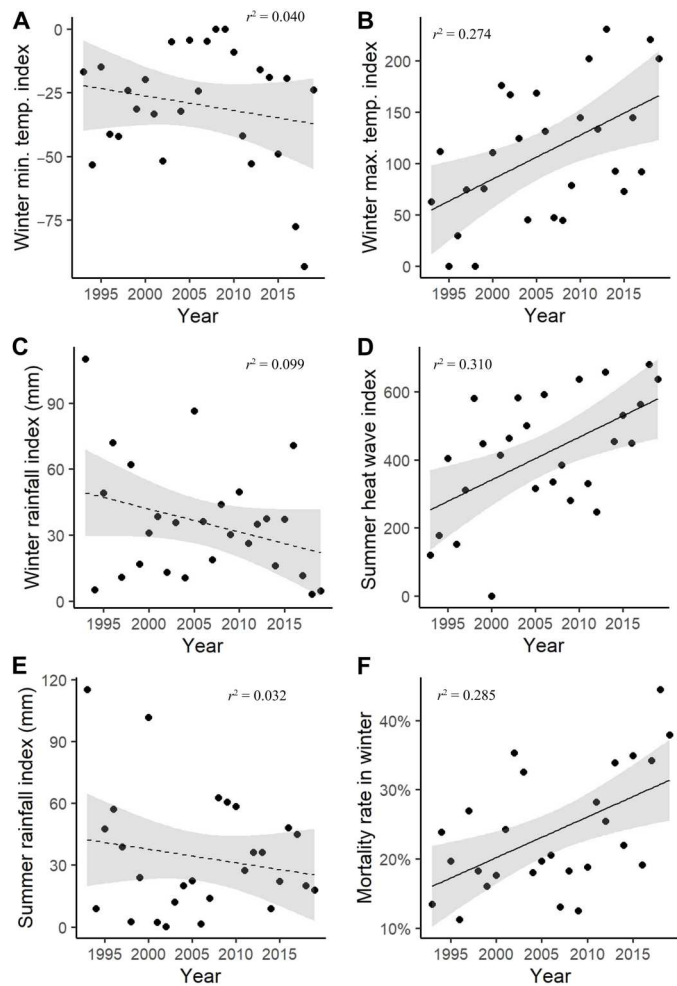
**Table 2. Summary of the final Cox proportional hazards models of determinants of the seasonal mortality hazard rate and weekly mortality hazard rate of adult superb fairy-wrens in the nonbreeding season.** “Min. temp. in the current and previous weeks” and “Max. temp. 2 weeks prior” are the climate indices of temperature identified as the best predictors for the mortality hazard rate in each week. “Temperature drop” is a measurement of the change in temperature from one warm week to following two cold weeks, which is calculated by using the standardized (to zero mean, unit SD) “Max. temp. 2 weeks prior” minus the standardized “Min. temp. in the current and previous weeks”.  $\exp(\beta)$  is the hazard ratio. “Group size” is the total number of individuals (except for juvenile females, as these are likely to disperse) in the group at the start of that nonbreeding season. “Age” is an individual’s age in years stratified by early life (from age one to five) or late life (from age six onward). “Min. Temp. in the current and previous weeks” denotes the sum of daily minimum temperature below 2°C in a period of 14 days (from 12 days before to 1 day after the last day of each week; i.e., minimum temperatures in the last 2 weeks). “Max. temp. 2 weeks prior” indicates the sum of daily maximum temperature over 11°C in a period of 6 days (from 22 days before to 17 days before the last day of each week; i.e., maximum temperatures in the week approximately 2 weeks prior). Significant effects ( $P \leq 0.05$ ) are indicated in bold. (Sample sizes:  $n = 1670$  adults across 27 nonbreeding seasons, making 4158 adult seasons for the seasonal analysis;  $n = 1670$  adults across 702 weeks of 27 nonbreeding seasons, making 98,098 adult season weeks for the weekly analysis.)

Fixed effects:	$\beta$	SE ( $\beta$ )	$\exp(\beta)$	z statistic	P value
<i>Final model of seasonal analysis</i>					
Group size	0.027	0.074	1.028	0.36	0.721
Age (covariate, from 1 to 5)	-0.056	0.070	0.945	-0.80	0.425
Age (covariate, from 6 to 9+)	0.325	0.089	1.385	3.68	< 0.001
Winter min. temp. index	$-5.7 \times 10^{-3}$	$1.6 \times 10^{-3}$	0.994	-3.59	< 0.001
Winter max. temp. index	$2.6 \times 10^{-3}$	$0.6 \times 10^{-3}$	1.003	4.62	< 0.001
Winter rainfall index	$-3.0 \times 10^{-3}$	$1.7 \times 10^{-3}$	0.997	-1.72	0.086
Summer heat wave index	$2.0 \times 10^{-3}$	$0.5 \times 10^{-3}$	1.002	3.92	< 0.001
Summer rainfall index	$-1.0 \times 10^{-4}$	$1.5 \times 10^{-3}$	0.99990	-0.07	0.945
Group size: Summer heat wave index	$-3.2 \times 10^{-4}$	$1.3 \times 10^{-4}$	0.99968	-2.52	0.012
Group size: Age (covariate, from 1 to 5)	0.027	0.018	1.027	1.47	0.142
Group size: Age (covariate, from 6 to 9+)	-0.009	0.011	0.991	-0.83	0.407
<i>Final model of weekly analysis (AICc value = 14,926.92)</i>					
Group size	-0.075	0.023	0.928	-3.26	0.001
Age (covariate, from 1 to 5)	0.023	0.027	1.023	0.84	0.402
Age (covariate, from 6 to 9+)	0.283	0.080	1.327	3.64	< 0.001
Min. temp. in the current and previous weeks	-0.015	$2.6 \times 10^{-3}$	0.986	-5.68	< 0.001
Max. temp. 2 weeks prior	$9.1 \times 10^{-3}$	$1.9 \times 10^{-3}$	1.009	4.70	< 0.001
<i>Final model of weekly analysis with temperature 'drop' (AICc value = 14,929.40)</i>					
Group size	-0.076	0.023	0.927	-3.29	0.001
Age (covariate, from 1 to 5)	0.023	0.027	1.023	0.83	0.405
Age (covariate, from 6 to 9+)	0.282	0.079	1.326	3.64	< 0.001
Temperature drop	0.213	0.029	1.237	7.52	< 0.001

wrens may have to increase their metabolic rates for thermoregulation, thus increasing their energy expenditure at the same time as when food resources for this insectivorous species may be at the lowest. Death from starvation may occur after exhaustion of energy stores (12). In addition, for fairy-wrens, the risk of predation by avian predators may also be increased during cold spells—because they need to spend more time foraging in the shorter winter days, which may prevent effective predator surveillance (28, 29). Overall, both starvation and predation may therefore lead to higher mortality rates for fairy-wrens during cold spells.

Higher mortality in the nonbreeding season was also associated with higher winter daily maximum temperatures. Specifically, individuals were more likely to die in a given nonbreeding season if the daily maximum temperature index across a near 5-week period in mid-winter was warm (Tables 1 and 2 and Fig. 2B) and more likely

to die in a given week if the maximum temperature index in the week approximately 2 weeks prior was higher (Table 2 and fig. S3B). To rule out the possibility that the latter result was due to negative effects of heat waves at the end of the previous autumn on individual mortality (Fig. 1A), we reran the weekly mortality analyses using only mortality data in the coldest period of winter, in which mortality was at its peak [i.e., weeks 24 to 35; Fig. 1B]. We found the same effects of maximum temperatures (in the same window) on individual mortality in these cold weeks (table S13). In addition, we also carried out analyses in which we used the daily temperature range (i.e., the difference between maximum and minimum temperatures on a given day) in the hope of identifying a better climate index than the maximum temperature index, but these were not informative (results not shown). Overall, our analyses indicate that the best winter climatic predictors of mortality rate in the



**Fig. 3. Temporal change in each climate index and annual average seasonal mortality rate of adult superb fairy-wrens.** (A–F) The solid lines and dashed lines represent significant and nonsignificant relationships, respectively.  $r^2$  values are from the linear regressions in table S14.

nonbreeding season were the combination of minimum and maximum temperature indices for both seasonal and weekly mortality analyses (Table 2).

Why might warmer winter temperatures be associated with higher mortality? Warm spells in winter may lead to the loss of thermogenic capacity of cold-acclimatized individuals, who then suffer increased mortality with the return of colder temperatures. Summit metabolic rate (i.e., peak oxygen consumption under cold exposure) has been confirmed as a correlate of cold endurance, with higher summit metabolic rates associated with improvements in both cold resistance (30) and survival in winter (15). A recent study of white-throated sparrows (*Zonotrichia albicollis*) suggested that within a period of 8 days, summit metabolic capacity was more rapidly lost in a warm environment than it was regained on exposure to a cold environment (16). In addition, it has been shown that small birds need around 4 weeks to adjust their summit metabolic rate when facing a sudden cold spell (31). The slow response of summit metabolic rate to low temperatures may be due to the intrinsic limitations in the rate of changes in organ size and function [e.g., pectoralis muscle; (32, 33)]. Possibly, fairy-wrens may also

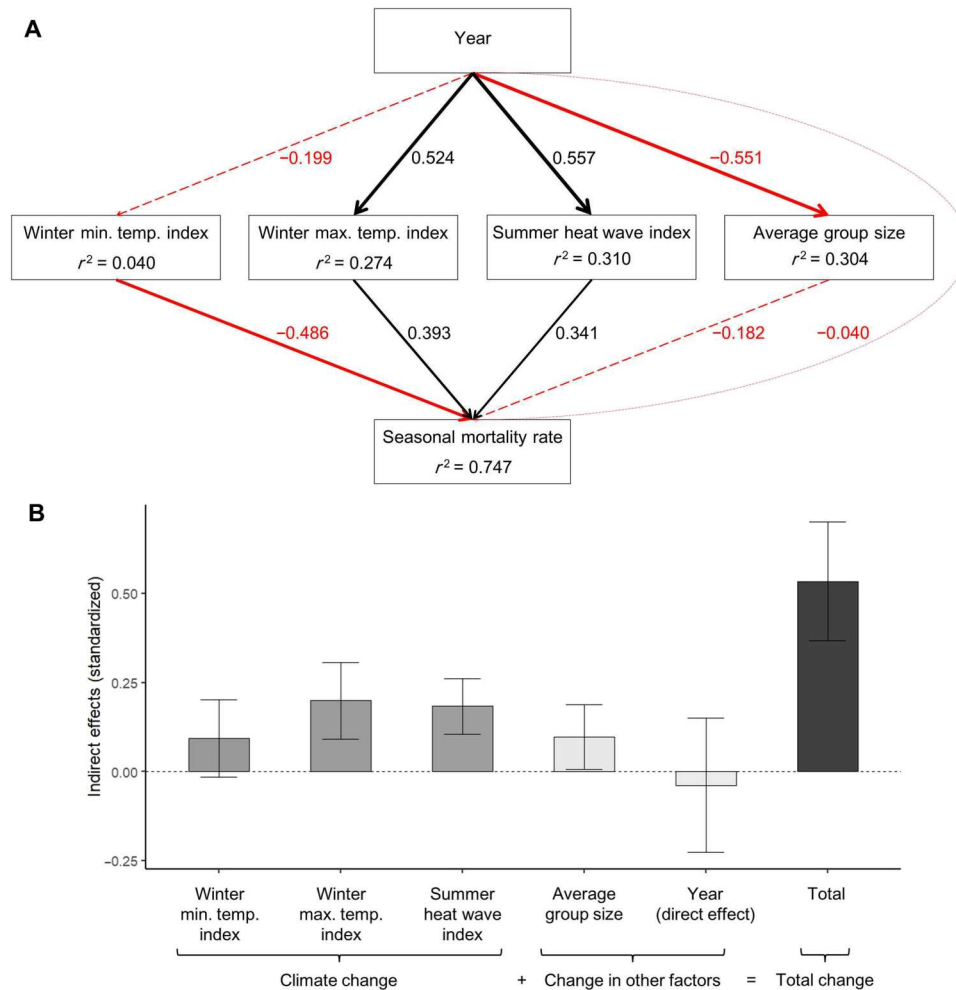
reduce their summit metabolic rate after experiencing a relatively warm spell but then have difficulty increasing it again in response to colder temperatures and, hence, not be able to produce enough heat to maintain normal body temperature in cold nights—which may increase mortality risk. This suggestion was supported by our results that individuals were more likely to die in a given week after experiencing a large temperature drop from a warm to cold spell (Table 2 and fig. S3C).

As we are lacking experimental and physiological studies on how the summit metabolic rates of individuals respond to cold spells, warm spells, or large temperature drops in this species, we are currently uncertain of the exact biological mechanisms that underlie the associations between winter temperatures and individual mortality. However, it is clear that knowing the time of death precisely (here, the week of death, due to year-round censusing) is crucial to identifying these patterns, which go unnoticed in seasonal mortality analyses. In addition, there may also be other alternative explanations for the associations of winter temperatures with mortality. For example, in relatively warm spells, fairy-wrens may become accustomed to accumulating a relatively smaller amount of reserves during the day for getting through the night. However, they may then not adjust their feeding behavior sufficiently if the temperatures drop to cooler levels, and more reserves are needed for thermoregulation. Future studies on how physiological and behavioral traits respond to extreme temperatures outside the typical climate niche of the species may provide valuable insights into the mechanism of climate-induced winter mortality in wild bird populations. In addition, comparative analyses of multiple populations or species may also provide useful insights into how birds adapt to local winter climate. Last, we note that previous studies of the effects of climate on winter mortality have usually considered only daily minimum temperature or daily mean temperature in winter and may therefore have overlooked the potential different effects of winter daily maximum temperatures (22, 34). Our analyses here indicate that winter mortality could be determined by combinations of winter minimum and maximum temperatures and also underline the difficulty of separating their different effects in seasonal mortality analyses.

Higher mortality rate in the nonbreeding season was also associated with higher intensity of heat waves in the previous summer (Table 2 and Fig. 2D). More intense heat waves in summer are usually associated with decreases in individual body mass or body condition through, for example, reduced foraging efficiency (35, 36). Therefore, individuals may enter winter in poorer condition, risking increased mortality rate in the harsh environment of sudden cold spells. This is supported by evidence in other studies that heat-exposed individuals are less likely to survive winter (37, 38). We suspect that carry-over effects of climate in the previous summer on the mortality rate in winter may be more common than currently appreciated for animals living in seasonal environments.

Neither winter rainfall nor summer rainfall affected mortality rate in the nonbreeding season if the temperature indices were also included in the model (Table 2 and table S11). In our study area in southeast Australia, the nature of the climate means that cloud cover and rainfall during both summer and winter moderate daily maxima and minima (table S16, and fig. S2, A and B). Thus, the effects of winter and summer rainfall identified in their respective univariate models may be due to their correlations with the





**Fig. 4. The standardized effect of temporal change in climate on the change of annual average seasonal mortality rate of adult superb fairy-wrens over time. (A)** Results of the path analysis model of the seasonal mortality rate in relation to three temperature indices, average group size, and year. Black and red arrows indicate positive and negative relationships, respectively, and the width of arrows is proportional to standardized path coefficients next to each arrow. The solid lines and dashed lines represent statistically significant and nonsignificant relationships, respectively.  $r^2$  values (within boxes) refer to the proportions of the variance of each response variable explained by the predictor variables in the model of that response variable. **(B)** The indirect effects of year on the seasonal mortality rate through pathways of each relevant climate index, average group size, and direct effect of year itself (accounting for effects of the other variables) in the path analysis model shown in (A). The “total change” represents the total change in the seasonal mortality rate over the study period due to both climate change (i.e., the three temperature indices) and change in other factors. Error bars are one SE. The dotted horizontal line represents the reference of 0. Statistics of goodness of fit for this model are  $\chi^2 = 2.380$ ,  $df = 6$ ,  $P = 0.882$ ; SRMR = 0.06.

winter minimum temperature index and the summer heat wave index, respectively. In addition, the weekly mortality analysis indicated that the best rainfall window identified by the models was a false-positive signal (table S12). The results therefore illustrated the difficulty of capturing the biological effects of rainfall on winter mortality, even given high-resolution mortality data due to year-round censusing.

Mortality in the nonbreeding season showed no change with age in younger birds but increased substantially with age in older birds. This result appears differently from our previous work on the same population, which reported that individual mortality rate increased linearly with individual age in both sexes (39). However, these two studies considered different periods, as the previous work focused on the mortality rate in the whole year, rather than only the nonbreeding season as considered here. There was no evidence of any

interaction between an individual’s age and the effects of the identified climate indices (table S8). This indicates that older adults who had relatively higher mortality rate in the nonbreeding season were no more sensitive to harsh climatic conditions than younger adults. Future studies are needed to reveal whether the observed age-related changes in mortality in the nonbreeding season were influenced by extrinsic factors (e.g., changes in life history or behavior) or intrinsic factors (e.g., aging).

Larger group size was associated with lower mortality rate in the nonbreeding season in both seasonal and weekly analyses (Table 2). Although a simple linear regression also indicated that larger average group size in each season was associated with lower annual average mortality rate (table S9), there was no effect of average group size on annual average mortality rate when climate indices were also included in the path analysis (Fig. 4A and table

S15; path coefficient,  $-0.182 \pm 0.117$  SE). The inconsistency between these two results may be due to collinearities between average group size and climate indices (fig. S2C and table S16). In addition, both the seasonal and weekly individual-level mortality analyses have much larger sample sizes than the path analysis and, therefore, may have more statistical power to disentangle the effects of group size and summer heat waves. We expected that group size might be relevant if individual fairy-wrens benefit from larger group sizes through huddling together to keep warm during cold nights, thereby reducing mortality rate. However, this possibility was not supported because there was no interaction between group size and winter minimum temperature index in the seasonal mortality analysis (table S8). In addition, lower mortality rates may be associated with higher territory quality (e.g., roost site, food resource, etc.) and therefore generate on average an accumulation of helper males on territories (i.e., a larger group size). Determining the mechanisms underlying the correlation between group size and mortality given the potential effects of confounding variables considered is therefore difficult, especially as mortality only occurs once for each individual. Higher nonbreeding season mortality rates were especially associated with higher intensity of heat waves in the previous summer when group size was smaller (Table 2 and table S8). This may be because group size is again an indicator of territory quality (with smaller groups on poorer territories), and individuals in poorer condition after intense summer heat waves may be more at risk of winter mortality if they are on a lower quality territory. Overall, our results indicate that social environment may be relevant for winter mortality and may also play a role in mediating the association between climate and winter mortality, but this complexity requires further study with careful analysis in the future.

### Contribution of climate change to increasing mortality over time

Our path analysis showed that increases in winter maximum temperature index and summer heat wave index over the study period made the most important contributions to an increased mortality rate in the nonbreeding season over time (Fig. 4 and table S15). Our results thereby contrast with those from a recent study, which indicated that nonclimatic effects contributed substantially to the temporal trends in avian life-history traits (40). They also contrast with other studies of climate-induced change in winter mortality, which have considered only mean temperatures in winter, and have found that warmer winters reduce winter mortality rate (5, 41, 42). We report a different pattern in birds that increases in winter maximum temperatures (and also increased intensity of heat waves in the previous summer) over time contribute to an increased mortality rate in winter. We therefore suggest that the effects of maximum and minimum temperatures on winter mortality should be tested separately in these studies.

Although our analysis revealed that climate change contributed considerably to the increase of mortality rate in the nonbreeding season, there may be other environmental changes that could also have contributed in this process. For example, although not systematically documented, the vegetation in our study area may have degraded over the study period because of the decrease in annual rainfall in this semiarid region. Degraded vegetation may lead to lower insect abundance and thereby reduce food resources for fairy-wrens, which may in turn increase mortality in harsh

winters. In addition, fairy-wrens may have difficulty hiding or escaping from avian predators in degraded vegetation. Overall, climate may affect nonbreeding season mortality directly and/or indirectly, which illustrate the difficulty of capturing the precise causal structure of this process, even given long-term data.

The congruence between the results of our weekly and seasonal mortality analyses suggest that changing climate over time could affect individual life-history traits and have demographic consequences. Recent studies have reported that climate-induced change in life-history traits may strongly affect individual fitness but still only weakly affect demographic rates [e.g., (43)]. However, for climate effects on life-history traits to contribute to population dynamics requires that the climate-induced changes in life-history traits are apparent at demographic levels (44). Our study not only shows the effects of climate on individual mortality (in weekly mortality analyses) but also illustrates the association of mortality rate in winter with climate (in seasonal mortality analyses). As the intensity of both winter warm spells and summer heat waves in our study area increased over the study period (Fig. 3, B and D) and is projected to increase further in the future (45), the adverse effects of rising maximum temperatures on winter mortality may not only contribute to historical population decline but may also constitute a substantial threat to future population persistence. To quantify the effect of maximum temperatures on population growth and predict future population dynamics, a demographic approach that considers contributions of each demographic variable to population dynamics is a logical next step (46).

## METHODS

### Study population and species

We analyzed data from a long-term study of superb fairy-wrens in the Australian National Botanic Gardens, Canberra, southeast Australia ( $35^{\circ}16'S$ ,  $149^{\circ}6'E$ ). The study site is on an inland plateau (ca. 650-m altitude) and, hence, has a highly seasonal continental climate, with the highest daily maxima of  $44^{\circ}C$  and the lowest daily minima of  $-8^{\circ}C$  during the study period. Temperature fluctuations show a clear seasonal pattern, with coldest temperatures in July and the hottest temperatures in January (Fig. 1). Daily fluctuations can exceed  $20^{\circ}C$  but are moderated by the presence of cloud cover and resultant rainfall. There is scarcely any snow, but frosts are common on dry winter mornings. Although rainfall shows a summer peak, driven by heavy summer thunderstorms, rainfall patterns are much less regular, and there have been prolonged periods of drought during the study (25).

The study area encompasses a total of  $\sim 60$  ha of plantation of Australian native shrubs and trees, which supports between 35 and 90 fairy-wren territories in a given year (23). We have studied the population continuously since 1988, although because the study area was expanded substantially in 1991/1992, we report here the data from 1993 to 2019. Almost all birds in the study population were color-banded, either as nestlings if they were born in the study area or as juveniles or adults if they had dispersed into the study area.

Superb fairy-wrens form socially monogamous pairs that live in year-round territories. During the breeding season, the dominant pair breed either alone or assisted by up to five male helpers (23). The species is multibrooded, with breeding usually starting in September, at the start of the austral spring, and the last nests fledging

around February of the subsequent calendar year (26). Females are solely responsible for nest building and incubation, but all males contribute to nest and brood defence and provisioning of nestlings and fledglings (23). Although birds forage outside their breeding territory in the nonbreeding season, territories are maintained throughout the year and are used for nighttime roosts. Female fairy-wrens always disperse to a new territory in the first year of their life, often moving over long distances. They start breeding in the first breeding season after they fledge and thereafter only rarely move more than one or two territories (47). In contrast, males are highly philopatric to their natal territories and will live and generally die on their natal territory or an immediate neighboring territory (48).

### Measuring mortality rate

We analyzed here the mortality of adult birds subsequent to their first breeding season because it is not possible to distinguish mortality from natal dispersal outside the study area in juvenile females (before the first breeding season). In addition, we focused on mortality during the nonbreeding season, which is the main period in which deaths of adults occur (24). Thus, for example, for a bird born in the 2000/01 breeding season, we would consider its potential nonbreeding season mortality from 2002 onward. For a given breeding season, the “start” was defined as the date by which 10% of females had laid their first clutch; and the “end” was defined as the date of the last nest completion for 90% of females [where nest completion is when either chicks fledged or a nest was preyed upon; following, for example, (49)]. We then used these calculations of the timing of the breeding season each year to define as an overall nonbreeding season period between the latest end of any breeding season across all years (12 March or week 11 of the calendar year, which occurred in 2011) and the earliest start of any breeding season (9 September or week 36, which occurred in both 1998 and 1999; Fig. 1A). The analyses then considered mortality in this same 6-month nonbreeding period each year.

We estimated a seasonal mortality rate as the proportion of individuals alive at the start of the nonbreeding season each year (week 11) that then died across the entire nonbreeding season that year (weeks 11 to 36; Fig. 1B). During each nonbreeding season, we aimed to observe every individual in the study population every week. If all members of a group were seen in routine weekly censuses in a given week, no further effort was devoted to that group. However, if one or more members was not seen in the weekly censuses, further attempts were made either on the same day or on subsequent days until the sighting had been achieved. Usually, this confirmation can be achieved in 2 days, but it may take longer on rare occasions. However, there have never been any cases of an individual being missing for more than 2 weeks and then being seen again. Thus, our censusing generated nearly perfect detection. Individuals were also assumed to have died if they had been replaced as the dominant on the territory by another bird. The death date of an individual was then calculated as the midpoint between the date when it was last observed and the date of the first census on which it was not observed. As our mortality data were therefore collected with weekly resolution through the nonbreeding season, we could estimate each individual’s week of death (for example, if the death date of an individual was calculated as 14 June, we estimated its death date as being week 24). From these individual death weeks, we then also calculated the weekly mortality rates in each

nonbreeding season, defined as the proportion of individuals that died in that week of that year (Fig. 1B).

### Climate data

We used data on daily weather at Canberra Airport (~8 km east of the study area) obtained from the Australian Bureau of Meteorology (<http://bom.gov.au/climate/data>). We explored the effects of minimum temperature, maximum temperature, and rainfall in our analyses.

### Mortality analyses

We fitted one set of models of individuals’ seasonal mortality rate and another of individuals’ weekly mortality rate: These models asked, respectively, whether or not an individual survived the nonbreeding season in a given year, or whether or not it survived a given week in the nonbreeding season that year. We analyzed mortality data using time-dependent Cox proportional hazards models fitted with the “coxph” function in the R package survival (50, 51). All models used a generalized estimating equation approach and specified three cluster items (i.e., grouping the correlated observations of year of observation, individual cohort, and individual ID) to control for the nonindependence of data points (52). We initially included the following fixed effects in every model:

#### Sex/breeding status

For each individual, we tested for differences in mortality hazard rate with sex and also with breeding status by fitting a factor that comprised three categories: female, dominant male, and helper male, with male status being defined from the breeding season immediately before the current nonbreeding season. Replacing “breeding status” by “sex” (i.e., just male/female) gave qualitatively the same results in the following analyses.

#### Age

We fitted an individual’s age in years and stratified the effect of age by early life (from age one to five; 90.0% of the population,  $n = 3741$  adult seasons) and late life (from age six onward; 10.0% of the population,  $n = 417$  adult seasons) with the “strata” function in the survival package because our preliminary analyses suggested that the effect of age on winter mortality was different between early life and late life [using the same method as (39)]. All analyses only considered individuals in the winters following the first breeding season they experienced, i.e., from the age of 1 year onward. Of the total of 1670 adults, there were 8 (7 males and 1 female) who reached age 10 or more. For this very small number of very old individuals, we pooled individuals aged nine or more years old into a single category and treated them all as age nine.

#### Group size

Group size is the total number of adult and juvenile individuals (except for juvenile females as these are likely to disperse) in each group at the start of the mortality period being considered (i.e., either the entire season or the respective week). This provides an index of social environment conditions.

#### Number of successful broods

The number of successful broods produced in the breeding season immediately prior to the current nonbreeding season was fitted as a four-level factor (0, 1, 2, and 3), counting the number of broods that survived to fledging. This variable was tested for any effects of previous reproductive effort on subsequent survival and was fitted for both sexes.

The two-way interactions between the four fixed effects were also tested but are not reported in detail as there was no evidence for statistical support for any of them; in particular, there was no support for any sex differences in the effects of age, group size, or number of successful broods. All continuous variables met the linearity assumption based on plotting the martingale residuals against continuous variables, and all models met the proportional hazards assumption based on plots of scaled Schoenfeld residuals (53). Collinearity among the predictor variables was assessed using the variance inflation factor (VIF) analysis. All VIF values were well below a threshold of three, indicating low collinearity among them (54). Models were compared using AICc [which balances model fit and complexity; (55, 56)] by using the “dredge” function in the R package MuMIn (57). We compared models with different combinations of fixed effects and a null model with just an intercept and identified the best models as those with the lowest AICc values.

### Identifying a baseline model

We first fitted Cox proportional hazards models for the seasonal or weekly mortality hazard rate to establish a baseline model with which to test effects of nonclimatic variables. These models had fixed effects of sex/breeding status, age, group size, and number of successful broods, as described above (see tables S1 and S3 for details of initial baseline models). For the final baseline models of both seasonal and weekly mortality hazard rates, only group size and age were included because sex/breeding status and the number of successful broods were both dropped in the model selection process (tables S2 and S4).

### Sliding window analyses

For both seasonal and weekly mortality hazard rates, we used the final baseline models to identify a single best window for each climate variable considered (temperature variables or rainfall; see below). Using a sliding window approach implemented in the R package climwin (21), we compared models fitting the sum of the climate variable within different windows varying both start and end dates (using the mean rather than the sum gave very similar results in all analyses) and identified a best window that had the model with the lowest AICc value and, hence, the greatest difference in AICc values ( $\Delta$ AICc) between it and the final baseline model with no climate variables. Given the large number of time windows being considered, we used a randomization approach to check whether this best window for a given climate variable could be a false-positive result (21): Full details are provided in the Supplementary Materials. If a false positive likely occurred, we report the window for completeness but do not consider it further. In addition, as an influence of time windows, shorter than 3 weeks on seasonal mortality seems very unlikely due to the long duration of nonbreeding season; we also required any best window to span at least 3 weeks in the analysis of the seasonal mortality hazard rate. However, we did not set any minimum length of time windows in the analyses of the weekly mortality hazard rate. Moreover, we only tested for linear effects of each climate variable because we are interested in the direction of the average effect of climate on mortality (for example, whether lower minimum temperatures in winter are associated with higher mortality) rather than more complex nonlinear relationships. We fitted slightly different climate variables for the seasonal versus weekly mortality hazard rate as follows:

### Identifying climate windows for the seasonal mortality hazard rate

For the seasonal mortality analyses, we considered absolute time windows of climate, defined by the calendar dates of the window (21). We tested for the following effects of climate in the nonbreeding season in a given year and also for the longer-term effects of climate in the previous breeding season:

For the effects of climate in the nonbreeding season, we ran sliding window analyses to identify the best window for minimum temperature, maximum temperature, or rainfall separately. Furthermore, for minimum and maximum temperatures, in addition to summing the daily temperature values within a given window, we also allowed for “threshold” effects by considering only the sum of values below (for minimum temperature) or above (for maximum temperature) a given threshold (e.g., the sum of “degree days” more than 12°C over a 30-day period). We compared models across a range of possible threshold values, and the final best model was identified as that where the climate window and (if relevant) threshold value generated the lowest AICc value. Our analyses indicate that threshold models usually gave better fits than using just the observed temperatures on each day, although results were always qualitatively similar. Full details of this process are presented in the Supplementary Materials (Supplementary Methods and table S5). As the best windows of the three climate variables all fell in austral winter (Table 1), we refer to the relevant climate windows as winter minimum temperature, winter maximum temperature, and winter rainfall.

For the longer-term (carry-over) effects of climate in the previous breeding season, we considered only maximum temperatures (and potential threshold effects; see the Supplementary Materials) and rainfall because minimum temperatures are unlikely to be limiting in the relatively warm breeding season. As the best windows of both climate variables fell in the austral summer (Table 1), we refer to the relevant climate windows as summer maximum temperature and summer rainfall. In addition, as the best window identified for summer maximum temperature had a temperature threshold of 28°C, we refer to this index as summer heat waves (Supplementary Methods and table S6).

The above analyses gave us indices for five climate variables: winter minimum temperature, winter maximum temperature, winter rainfall, summer heat waves, and summer rainfall. We tested for the effects of any interactions (i) between climate indices and (ii) between climate indices and nonclimatic variables by adding all terms plus their two-way interactions to the final baseline model of seasonal mortality hazard rate, respectively.

Last, for illustration purposes, we regressed the annual average seasonal mortality rate in each of the 27 years against each climate index in five simple linear regressions and then their combinations (see tables S10 and S11) in two multiple linear regressions. We just presented figures (with raw data) of associations between single climate index and annual average seasonal mortality rate without accounting for any other variables (Fig. 2) because they are more informative than the prediction lines of Cox proportional hazards models (e.g., fig. S3).

## Identifying climate windows for the weekly mortality hazard rate

We next used our high-resolution monitoring data from the weekly censuses to explore fine-scale effects of climate on the weekly mortality probability of individuals. As only the climate up to and including a given week can be relevant for mortality in that week of that year, we tested for the effects of climate in time windows defined by their dates relative to the focal week. Specifically, for each week, we considered the effects of climate in periods backdated from the last day of the focal week on the probability that an individual died in that week. Thus, the mortality hazard rate of each week will be related to its own window of climate (21). In this case, we only tested for recent effects of climate in the nonbreeding season, up to 30 days (i.e., a month) before and 3 days after (i.e., negative numbers in Table 1 and tables S12 and S13) the last day of the focal week. Up to 3 days after the death date were included in the analyses because the calculated death date for a given individual might be as much as 3 days earlier than the real death date. For example, if an individual died on 20 June, it would have been noted as alive in a 14 June census but not observed on 21 June, so we would calculate its death date as 17 June (i.e., the last day of week 24).

Again, using the time-dependent Cox proportional hazards models in *climwin* (21), we identified the best windows for effects of minimum temperature, maximum temperature, and rainfall on individuals' hazard rate of mortality in a given week, respectively. We also tested for the effects of interactions between these three climate indices (if identified) or between climate indices and non-climatic variables on the weekly mortality hazard rate.

## Tests for temporal trends in climate indices and mortality rate

To test whether any of the relevant climate indices or the annual average seasonal mortality rate had changed directionally during the study period, we fitted simple linear regressions. Year was fitted as a continuous effect, and the response variable was each climate index of the three winter climate variables or the two summer climate variables for the seasonal mortality hazard rate or the seasonal mortality rate (i.e., 27 years for each regression; one value per year).

## Path analysis of effect of temporal change in climate on mortality rate

Finally, we examined to what extent the change in climate over time explained the change in annual average seasonal mortality rate over the study period using path analysis in the form of structural equation models (58). We investigated the impacts of: relevant climate indices identified in the sliding window analyses of seasonal mortality rate; the average group size in the population at the start of each nonbreeding season to test for effects of the social environment; and year to control for the effects of other temporal trends not accounted for by climate or average group size (40). The path analysis was fitted with the function "sem" in the R package *lavaan* (59). We assumed that all dependent variables could be approximated by a Gaussian distribution. Furthermore, for the path analysis presented in the main text, we rescaled all variables to mean zero and SD of one such that the path analysis model outputs standardized path coefficients (Fig. 4). (For an easier interpretation of the results biologically, we also present the effects of year on the seasonal mortality rate through each pathway from the unstandardized

path coefficients in fig. S4.) We considered a model with year influencing seasonal mortality rate both directly and indirectly through effects on climate indices and average group size (Fig. 4A).

To assess whether the model fitted the observed data, we performed a chi-square test of goodness of fit and calculated the standardized root mean square residual [SRMR; (60)]. A nonsignificant chi-square test indicates that the predicted covariances among variables in the model are not distinguishable from the observed covariances, while SRMR calculates deviations between observed and predicted covariances. In addition, as there is collinearity among predictor variables in our hypothesized causal path structure (table S16 and fig. S2), we checked the bias and imprecision of estimators using numerical simulations. We generated simulated datasets with 27 observations for each variable (i.e., equal to our study sample size) based on the covariance patterns found in the case study population using the "simulateData" function in *lavaan*. For each estimator, we next calculated the mean bias [ $\hat{B} = \frac{1}{n_{\text{sim}}} \sum_{i=1}^{n_{\text{sim}}} (\hat{\theta}_i - \theta)$ ] and the average empirical standard error [ $\hat{E} = \sqrt{\frac{1}{n_{\text{sim}}-1} \sum_{i=1}^{n_{\text{sim}}} (\hat{\theta}_i - \bar{\theta})^2}$ ] of the estimate, with  $\theta$  being the parameter value used to simulate the data ("true value"),  $\hat{\theta}_i$  being the estimated parameter from the simulated  $i$ -th repetition,  $\bar{\theta}$  being the mean of the estimated parameters, and  $n_{\text{sim}} = 27$  being the number of simulated datasets (61). The simulation results indicated that our path analysis model was practically unbiased (fig. S5).

We estimated the path coefficients with a maximum likelihood method (58) and determined the significance of each with a Wald test. For each variable, we calculated the indirect effect of year on seasonal mortality rate mediated by that variable by multiplying the path coefficient of the effect of year on that variable with the path coefficient of the effect of that variable on the seasonal mortality rate (therefore, for example, the indirect effect of year on seasonal mortality rate mediated by the winter maximum temperature index was  $0.524 \times 0.393 = 0.206$ ; Fig. 4A). To obtain the SEs of these indirect effects, we bootstrapped for 10,000 samples. We defined the "total effect" of year on seasonal mortality rate as the sum of all the indirect effects plus the remaining direct effect of year. To estimate the percentage change in seasonal mortality rate over time due to a given climate pathway, we calculated the ratio of the effect for this climate pathway relative to the sum of the absolute values for all pathways [following, for example, (40)]; therefore, for example, the percentage change due to the winter maximum temperature index was  $0.206/0.633 = 32.5\%$ .

## Supplementary Materials

### This PDF file includes:

Supplementary Methods

Figs. S1 to S5

Tables S1 to S16

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## Winter mortality of a passerine bird increases following hotter summers and during winters with higher maximum temperatures

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