Population decline reduces cooperative breeding in a spatially heterogenous population of superb fairy-wrens

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Abstract

1. Reproductive performance in birds can be affected by both social environment and small-scale environmental heterogeneity via food abundance, availability of nesting sites, and predation risk. However, to date, the best studies of effects of microhabitat variation on avian populations have been on northern hemisphere passerines using nestboxes, where birds have limited control over nest sites and have a comparatively simple social structure.
2. Here we utilise a multi-decade dataset on the superb fairy-wren, *Malurus cyaneus*, a southern hemisphere passerine with facultative cooperative breeding. We monitored territory characteristics, nest locations and breeding success, and used GIS to relate these to social organisation and a survey of vegetation characteristics throughout the study area.
3. There was a long-term nearly two-fold decline in population density over the study period (1994-2015). This was associated with a corresponding decline in the mean number of helpers per group, and hence in the extent of cooperative breeding: in the first four years of the study (1994-1997), 56% of groups had at least one helper, but in the final four years (2012-2015), this was reduced to 28%. Mean territory size also increased (from 0.74ha in the first four years to 1ha in the final four years) such that on average, years with lower numbers of helpers per territory had larger territory sizes. However, helper number was positively correlated with territory size within years.

4. Reproductive performance was related to microhabitat heterogeneity: fledgling production was lower and nest predation higher in territories with dense midstorey vegetation, possibly because avian predators using visual information to detect nests can conceal themselves from nesting birds. Predation during the nesting phase decreased over time, indicating that the population decline was not driven by increased predation.
5. The causes of overall population decline remain to be determined, however our analyses have uncovered both microspatial patterns in nesting behaviour of birds, and temporal changes in population density and social group dynamics. From a methodological perspective, the study demonstrates the utility of GIS methods for investigating fine-scale habitat dynamics over time.

Key words

Reproductive success, population decline, cooperative breeding, spatial ecology, nest predation, long-term study

Introduction

Understanding the effects of the environment on the reproductive performance of individuals in wild populations is an intrinsic component of ecology, the importance of which has grown given the impact of accelerating anthropogenic climate change. These effects can vary substantially both spatially and temporally, and at both local and global scales, and may be driven by a variety of factors including effects of resource availability, climatic conditions, competition, predation, and availability of suitable breeding habitat (Fuller 2012). However while there has been extensive work documenting the impact of extrinsic ecological factors on reproductive performance, studies rarely assess their importance relative to the variation in a species' social environment and interactions with conspecifics.

The availability of resources can affect the performance of an organism within a particular area or habitat type, although it may be difficult to assess accurately. In studies of insectivorous bird species, measures of vegetation type are often used as a proxy for food, as vegetation composition can be more readily scored than the availability of arthopod prey (Blondel et al. 1991, Amininasab et al. 2016). Climatic conditions such as precipitation and temperature may also have an impact on insect abundance, which in turn may influence avian reproductive parameters (Eeva et al. 2000, Nooker et al. 2005, Kruuk et al. 2015).

In addition to resource availability, predation can also have a significant impact on survival and reproductive success, with approximately 80% of nest losses in birds estimated to be due to predation (Martin 1993). Larger territories may lower predation rates by increasing the distance between nests, thereby decreasing the chance of detection (Brooker and Rowley 1995). Through the same mechanism, a higher density of birds or nests may attract predators, thereby increasing predation rate (Martin 1988, Sofaer et al. 2014). Predation may also be impacted by the vegetation composition of an area. Dense vegetation cover around the nest can block visual and auditory cues from reaching predators, and indeed has been shown to reduce predation in some birds (Martin 1993, Remeš 2005, Rangel-Salazar et al. 2008, Colombelli-Négrel and Kleindorfer 2009). However, this is not universal, as other studies have shown little or no effect of nest concealment (Stutchbury and Howlett 1996, Willson and Gende 2000). Dense vegetation may also limit visibility from the nest, and so some species may prefer less well hidden nest sites that afford them a view of nearby predators (Götmark et al. 1995).

For cooperatively breeding species, these ecological processes have the potential to shape group structure, in particular the number of helpers, or 'supernumeraries', with consequential effects for reproductive success. Cooperative breeding occurs when more than two individuals combine to rear a single brood of young (Cockburn 2006, Hatchwell 2009). While the presence of helpers does not always increase the reproductive success of a breeding pair (Cockburn 1998), helpers can have a substantial positive impact on the productivity of a group or territory, and it has been argued that the benefits of cooperative breeding will be greatest in poor quality habitat (Emlen 1982, Magrath 2001). The presence of supernumeraries may reduce nest predation through increased vigilance, or may increase the lifetime reproductive success of a female through load lightening, allowing her to re-nest sooner (in multi-brooded species), or have a higher probability of survival (Cockburn 1998, Cockburn et al. 2008b, Langmore et al. 2016).

Long-term, individual-based studies of wild animal populations can provide an excellent opportunity to study relationships between survival or reproductive success and environmental heterogeneity (e.g. Brooker and Rowley 1995, Brouwer et al. 2006, Wilkin et al. 2007). Monitoring populations over an extended period can reveal relationships with changing weather conditions, such as rainfall and temperature (Kruuk et al. 2015). Long-term studies can also reveal whether habitat use has changed over time, and can distinguish between short-term, unusual changes and long-term trends (Enemar et al. 2004, Fuller 2012). However, one problem in studying effects of environmental heterogeneity is the potential complexity of information. Studies of habitat use often involve data over large spatial scales that are both difficult and time-consuming to collect (Dettmers and Bart 1999). Habitat features are often diverse and expressed at differing scales, increasing the size and complexity of datasets (Store and Jokimäki 2003). Given these challenges, many spatial ecologists have taken to using Geographic Information Systems (GIS) to collect and interpret such spatial data, allowing them to combine and assess multiple layers of spatial data of quite different scales and classes (Brooker and Rowley 1995, Dettmers and Bart 1999, Store and Jokimäki 2003).

Despite the importance of understanding effects of environmental heterogeneity on wild animal populations, there are still significant gaps in the research. Most of the avian studies mentioned here were conducted in the northern hemisphere, where clutch sizes are generally larger and there are fewer instances of cooperative breeding than in the southern hemisphere or tropics (Russell 2000, Ghalambor and Martin 2001, Russell et al. 2004). In addition, many studies on woodland passerines such as blue or great tits are conducted using nest-boxes (e.g. Wilkin et al. 2006, Amininasab et al. 2016). This confounds the ability of the birds to choose their own territories and nest locations, and reduces or even eliminates the risk of nest predation. Finally, the use of GIS has not often been paired with long-term, individual-based studies to explore relationships with small-scale environmental heterogeneity, although see Wilkin et al. (2006) for the application of GIS to analyses of reproductive performance in a wild bird population.

Here we use a combination of GIS and traditional field methods to explore the role of environmental heterogeneity and social environment on a population of superb fairy-wrens

(*Malurus cyaneus*) that has been intensively monitored since 1993. Superb fairy-wrens are cooperatively-breeding passerines that live on year-round territories. Males are highly philopatric, typically spending their whole lives on their natal territory, where they help care for young. Females on the other hand always disperse prior to their first breeding season in order to gain a breeding vacancy (Cockburn et al. 2003). A breeding pair may therefore be assisted by up to four (or very occasionally five) male helpers, the majority of whom are offspring of the breeding female from previous reproductive events (Hajduk et al. 2021) – or they may breed without helpers. The breeding season of superb fairy-wrens can begin in late August and end as late as March (Lv et al. 2020). Females can successfully raise up to three or occasionally four broods in a single season, each containing two to four young (Cockburn et al. 2008b). However, nest predation rates are high, and as a result females may initiate up to nine nests in a single breeding season due to repeated predation events (R. Turner, unpublished data).

In this study we first assessed the demographic changes over time apparent in the long-term data on the superb fairy-wren study population, Secondly, we quantified the effects of a range of vegetation and habitat characteristics and the social structure of each group on several measures of performance, reproductive success, and risk of predation.

Methods

Study site

This study uses data collected on superb fairy-wrens in the Australian National Botanic Gardens (ANBG) and surrounding area. The ANBG is situated in the Australian Capital Territory (35°16’S, 149°6’E) and encompasses 40 ha of Australian native plantation (Double and Cockburn 2000, Kruuk et al. 2015, Australian National Botanic Gardens 2016). The area used in the study also includes 20 ha of natural woodland on Black Mountain Nature Reserve, and the western side of the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Black Mountain site. Hereafter we refer to the study site as the ANBG.

The native vegetation in this area is characterized by open grassy woodland with an understorey of grass tussocks and shrubs, many of which are defended by spines. The ANBG houses a very diverse collection of Australian native species, and contains a wide array of habitat types and vegetation structures, including open lawns, a rainforest gully, and unmaintained natural woodland. The area between the gardens and CSIRO contains small gullies in which water can collect and *Rubus* brambles grow, and includes thickets of the native shrub *Bursaria spinosa*.

The mean annual rainfall in Canberra during the study period (1994 – 2015) was 635 mm (data from the ANBG: Bureau of Meteorology 2016). Mean minimum and maximum daily temperatures ranged from 0.1C to 12.2C in July, to 13.8C to 29.1C in January (data from Canberra airport: Bureau of Meteorology 2016), with an increasing trend over the study period (Kruuk et al. 2015). The area has experienced considerable variation in rainfall during the period in which the superb fairy-wren population has been monitored. There has been a tendency for rainfall to decline (Kruuk et al. 2015) with a severe drought from 2003 to mid-2009, which was broken by some of the highest rainfall on record in 2010 (from data from the Bureau of Meteorology).

The vegetation grown in the ANBG has experienced some structural changes during the study period, but these changes are relatively small compared to the larger-scale distinction between the plantations and the surrounding natural woodland within the study area. Changes in rainfall and watering regimes are likely to have altered some of the vegetation characteristics, but the overall structure of the study area, including distinctions between habitat types and the species grown in each area, has been relatively constant. Major changes in land use are also not likely to be important, as they typically involved a change from one unusable habitat type to another. In addition to this, a map of all nest sites since 1994 shows substantial structure in the placement of nests, with some areas in the gardens never containing a nest, and other areas used for nesting virtually every year (Fig. 1a). This indicates that any changes over time have not altered whether an area is fundamentally suitable or unsuitable for nesting.

Superb fairy-wren field data

Demographic and spatial data have been collected from the study population since 1988. However here we only used data from the 1994-5 breeding season, from when precise details of nest sites were consistently recorded, until the 2015-6 breeding season. All birds in the data base have been ringed (either as chicks or as immigrating adults), and so are individually recognisable. The entire population is censused at least once a week and all social relationships noted. Detailed census methods are documented in Cockburn et al. 2003, but in brief, territory boundaries are determined by observation of aggressive territorial behaviour and are mapped to ±3m accuracy. All nest-building attempts throughout each breeding season are recorded, noting the location, success or failure, and cause of failure of each nest. Throughout, we refer to a given breeding season by the calendar year in which it started.

For each territory in a given year, we considered the following measures as response variables:

- *territory size*: measured in hectares,
- *helper number*: the number of adult male supernumeraries on the territory (from 0 – 5; helpers are almost always males in this species),
- *nest count*: the total number of nests built in each territory throughout a breeding season,
- *nest predation rate*: the proportion of nests in each territory lost to predation at any stage between laying eggs and fledging young,

- *fledgling count*: the total number of fledglings produced in each territory throughout a breeding season.

We also considered the following demographic variables in simple statistical models:

- *population density*: measured as the total number of adult birds (one year or older) alive at the time the territories were mapped over the total area covered by territories in that year,
- *proportion of territories with helpers*: the total number of territories with at least one helper over the total number of territories in a given year.

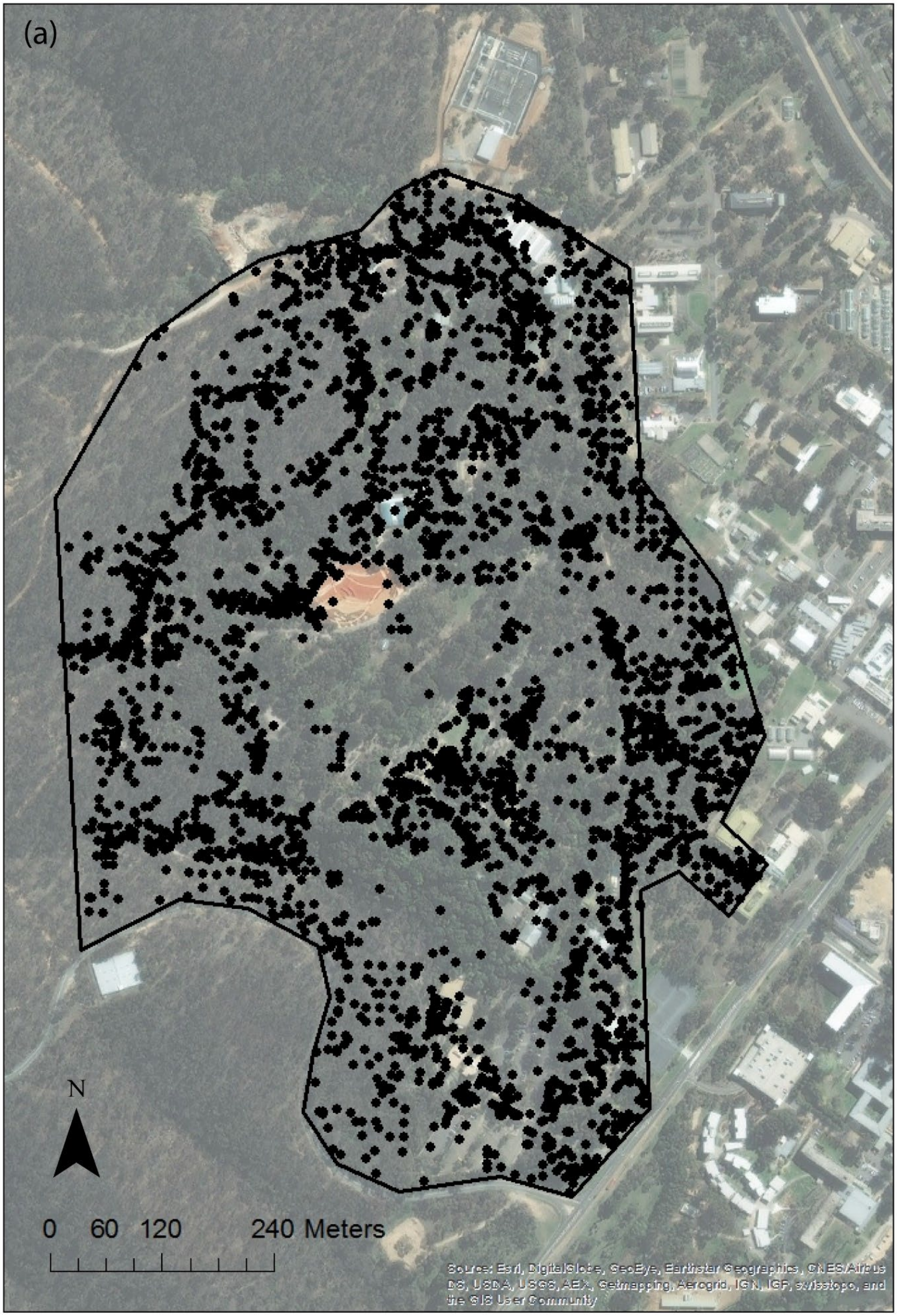
Previous work has shown that a female's age and the number of helpers in her group are positively associated with reproductive success, and that these differences are most apparent between one-year-old and older females, and between no helpers, one helper, and two or more helpers (Cockburn et al. 2008b). To investigate the importance of these individual-level variables we included the following fixed effects in our models:

- *female age*: defined as a two-level factor (one year or older),
- *dominant male age*: defined as a two-level factor (one year or older),
- *helper number*: distinct from the number of helpers as a response variable, defined as a three-level factor (no helpers, one helper, at least two helpers).

Map digitising

We used the GIS program ArcMap version 10.3.1 (Environmental Systems Research Institute Inc. 2015) to digitise and analyse spatial information on superb fairy-wren territories from the 1994-2015 breeding seasons (inclusive; n = 22 breeding seasons). Territory boundaries had been drawn on a map of the ANBG several times each year throughout the study. Maps from the closest possible date to 15 November of each year, when group structure and territory boundaries have usually been established for the breeding season (Cockburn et al. 2003), were scanned and imported into ArcMap, then georeferenced to a geographically accurate digital map of the ANBG by linking four or five recognisable reference points between the maps. The average of the root mean square error from digitising the maps, a measure of consistency between points, was 2.98 ± 1.07 m (measures for each year are presented in Supporting Information Table S1).

We created polygons for each territory by tracing the boundaries drawn on the paper maps (Fig. 1b). Each of the resulting 1599 polygons (from the 22 years) was assigned a *territory name* based on its location in sub-areas of the study population (e.g. 'blkmtn13' represents the thirteenth territory in north-east section ot the study area; Supporting Information Fig. S1). Often there was very little change in territory boundaries from one year to the next, and in this case territories in the same location in consecutive years were given the same name. In other years where there was more instability, new territory names were created for territories that did not match the previous year. This resulted in a total of 282 territory names across all years, of which 153 persisted for more than one year (see Supporting Information Fig. S2). We also created a *year-specific territory ID* for each of the unique 1599 territories consisting of the territory name and breeding season (e.g. '2000blkmtn13', '2006blkmtn13'), which was linked to the birds present on that territory on 15 November of the corresponding year. We then used algorithms in ArcMap to calculate the area and centroids of each year-specific territory ID (see Supporting Information Table S2 for details), and added the nest coordinates from the long-term census records to the appropriate territory in each year.


(a)
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Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 1: Examples of spatial data. (a) Sites of all superb fairy-wren nests since 1994 contained within the study area; and (b) the territory boundaries in 2007. The line in (a) indicates the boundary of the study area; territories that fell completely outside this boundary were excluded. The unoccupied areas in (b) are a lawn and a gully with dense rainforest plantation, neither of which are used by fairy-wrens for nesting.

Habitat and environmental data

We assessed the effect of spatial variation in territory quality by a ground survey of habitat characteristics conducted in June 2016. This was done by surveying 30 m x 30 m cells in a grid laid over the study site. The grid started at X = 691290, Y = 6093780 in the Geocentric Datum of Australia (GDA) Map Grid of Australia (MGA94) section 55 coordinate system produced by Geoscience Australia. We used the Global Positioning System (GPS) application 'GPS Calculator' (Kitya 2016) to determine our position on the map, accurate to approximately 3m. We limited data collection to an area that had been sampled consistently over the study period (605 cells in total; see Fig. 1a), to avoid bias from including under-sampled areas. As per the discussion above, we assume that this survey of vegetation characteristics is representative of the habitat over the time-span of the study.

For our ground survey, each cell in the grid was sampled using four observations, one from each of the corners of the cell, facing towards the centre. For each cell we determined:

- *Vegetation cover, in the form of ground, midstorey and canopy cover*: Ground cover included all vegetation below approximately 70 cm such as grass tussocks and low growing shrubs, as well as natural structures such as fallen branches that could provide cover. The midstorey included shrubs and hedges from approximately 70 cm to 2.5 m in height. Canopy cover was scored as the percentage of sky covered by vegetation above 2.5 m. All three variables were scored using visual estimations on a scale of 1-5 based on increments of percent coverage (0-20%, 20-40%, etc.). These data were collected by one person (FB) to ensure consistent measurements.

- *Habitat type*: We classified vegetation in the study area into four major habitat types: plantation, natural woodland, Bursaria thicket and unusable habit (see Supporting Information Table S3 for definitions).
- *Features*: We also considered the presence of various features that may be important for bird breeding performance, such as the presence of water (e.g. pond or stream) or certain species of plant (Supporting Information Table S3).

These observations were averaged or summarised across the four observations for each cell, and then imported into ArcMap to link with the territories. Territory-level characteristics were then estimated by summarising the cell-level variables across the territory, such that territories had an average score for each level of vegetation cover, the proportion by area of each vegetation type, and the presence or absence of each feature (detailed methods can be found in the Supporting Information Sections S1 - S2).

We also calculated estimates of total spring (August to November) rainfall, which has been shown to affect aspects of superb fairy-wren reproduction (Dalziell and Cockburn 2008, Kruuk et al. 2015). Rainfall data for the ANBG were obtained from the Ecosystem Modelling and Scaling Infrastructure (eMAST), using the software package ANUClimate 1.0 developed by Michael Hutchinson (Australian National University). This package estimates temperature and rainfall variables across a 0.01° grid based on factors such as topography and proximity to the coast (Hutchison and Xu 2015).

Statistical methods

We examined the trajectories of population density, territory size, the proportion of territories containing helpers, and the number of helpers on each territory. We then analysed the territory-level data with linear mixed models in `R` version 3.2.0 (R Core Team 2015) using the packages ‘lme4’ (Bates et al. 2014) and ‘lmerTest’ (Kuznetsova et al. 2016).

Response variables: We fitted a series of mixed models with response variables of *territory size*, *helper number*, *nest count*, *fledgling count*, and *nest predation rate* (see definitions above) for a given territory within a given year.

Fixed effects: The explanatory variables were the *vegetation cover* scores and *proportions of habitat type* calculated for each territory, *year* as a continuous covariate (to test for any temporal trends), *total spring rainfall*, and the *ages* of both the breeding female and the dominant male. *Territory size* and the presence of *special features* were also included in all models except the model in which territory size was the response variable itself. The *number of helpers* on each territory was included as a fixed effect in the models on nest count, predation rate, and fledgling count. In the model with helper number as a response variable, we combined vegetation types of lawn, rainforest and carpark into a single ‘unusable habitat’ (Supporting Information Table S3).

Random effects: In all models, we fitted four random effects to account for repeated measures across and between years: the identities of the dominant male and of the dominant female, the territory name (common across years), and year as a multi-level factor.

Model construction: All models were fitted with maximum likelihood, with a Gaussian error distribution unless otherwise specified. Helper number was analysed as a Poisson distributed variable using a generalised linear mixed model (GLMM) with a logarithmic link function. Nest count was transformed by taking the natural logarithm (note that all territories contained at least one nest). Predation rate was analysed as a binomial variable (with the number of nests that suffered predation as numerator and total number of nests in the territory that year as denominator) using a GLMM and logit link. Fledgling count provided a difficulty in that the distribution showed a large peak at zero and a second peak at three, reflecting the high proportion of nests containing three eggs. We transformed fledgling count using a square-root transformation, which generated an approximately normal distribution with a large spike of zeros. Year as a fixed effect (covariate) was scaled by dividing by 1000. We reduced all models using backward deletion until only significant variables remained in the model. Because we were including a large number of explanatory variables, we used $p < 0.01$ as the criterion for significance.

During preliminary analysis of the data, we found that larger territories tended to have more helpers, but years with a larger mean territory size had a lower mean number of helpers. To investigate this relationship we ran a model on helper number as before, and instead of the individual territory sizes, we fitted two covariates: the annual mean territory size, and the deviation of each individual territory size from the annual mean that year. This approach is equivalent to van de Pol and Wright's (2009) mean-centring approach for describing plasticity by separating responses into within- versus between-individual effects, but in this case separating within- versus between-year effects.

Results

Population-level trends

The mean total population density was 3.03 ± 0.52 SD adult birds per hectare. This density declined over the study period, with 4.1 birds per hectare in 1994, to 2.2 birds per hectare in

2015 (Fig. 2a). Territory sizes in the study area varied by more than two orders of magnitude, from 0.01 ha (Cambia19, in 2001) to 3.73 ha (South7, in 2009), with a mean of 0.86 ± 0.41 SD ha. As expected from the population decline, the number of territories decreased and the mean size of territories increased over the study period (Fig. 2b).

Across the whole study period, the proportion of territories with helpers was on average 43%. The proportion of territories containing helpers and the mean number of helpers on each territory declined substantially over the study period (Fig. 2c-d). There were particularly sharp demographic changes during the period 2002-2006: the population size dropped in 2002 and the mean territory size increased dramatically, but the population then recovered in 2005-2006 before declining again.

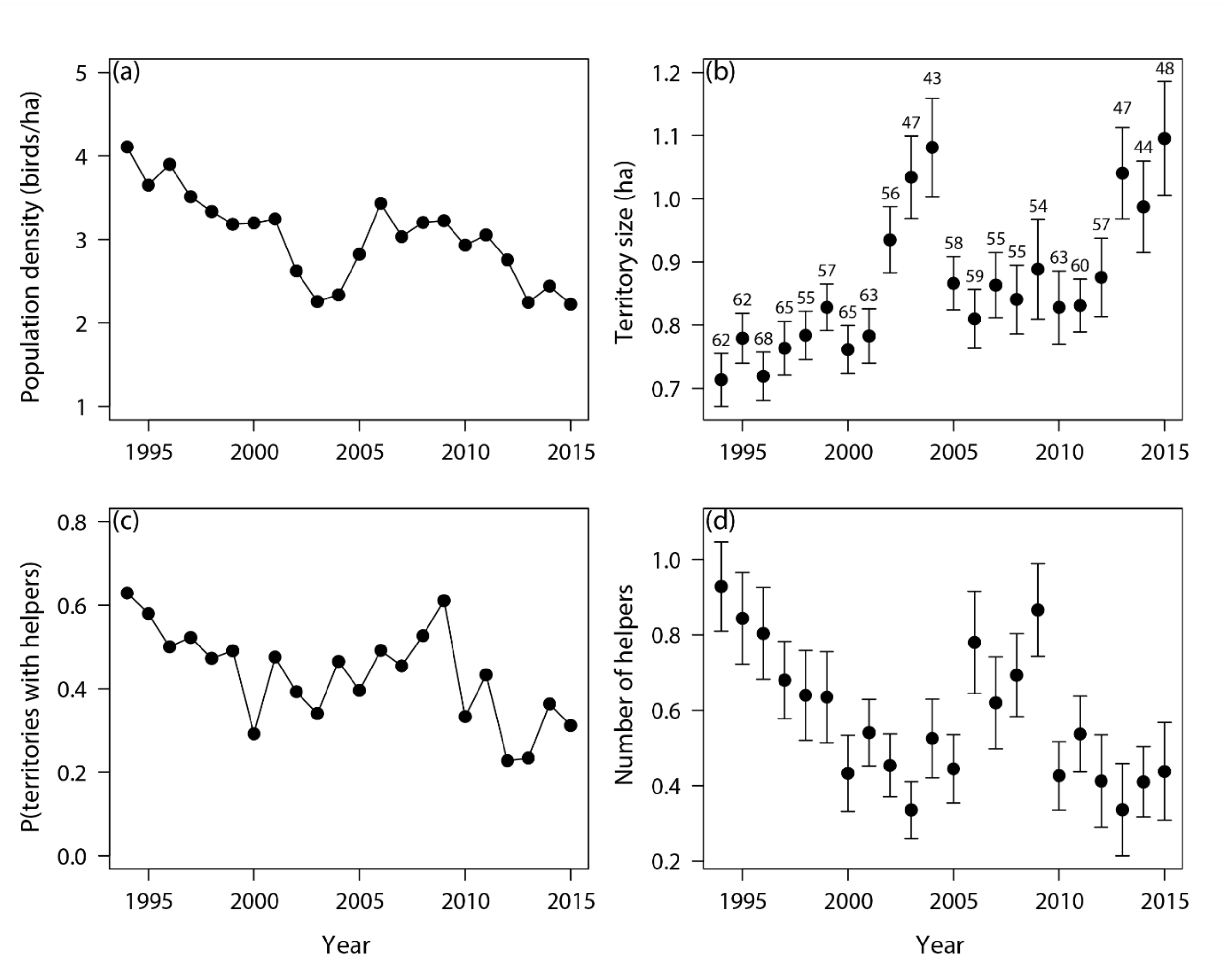

Figure 2: Changes over time in (a) population density (adult birds/ha), (b) mean territory size (ha), (c) the proportion of territories containing at least one helper, and (d) the mean number of helpers per territory. Error bars in plots (b) and (d) show standard errors; sample sizes for (b-d) (number of territories) are given in (b).

Territory-scale analysis

As suggested by the trends in Fig. 2b, the model of *territory size* confirmed that territories increased in size over time (Table 1). Territory size also increased with the age of the dominant male. Smaller territories were more likely to have a higher proportion of the bursaria habitat (Table 1).

The *number of helpers* was higher in larger territories, and both older females and older dominant males tended to have more helpers. Territories containing a larger proportion of unusable habitat (lawn, rainforest and carpark) had fewer helpers, and helper number was also negatively associated with the presence of retaining walls beside roads (Table 1).

Interestingly, while the number of helpers was higher in larger territories, years that had a larger mean territory size had fewer helpers. Within years, helper number and territory size were positively correlated (Fig. 3a; Table 1), whereas between years, the two were negatively correlated (Fig. 3b). A generalised linear mixed model containing both the mean territory size in each year and the size of each territory relative to the mean that year confirmed these two relationships (mean territory size: slope = -1.59 ± 0.53 SE, z = -3.03, p = 0.002; relative territory size: slope = 0.68 ± 0.12 SE, z = 5.60, p < 0.001).

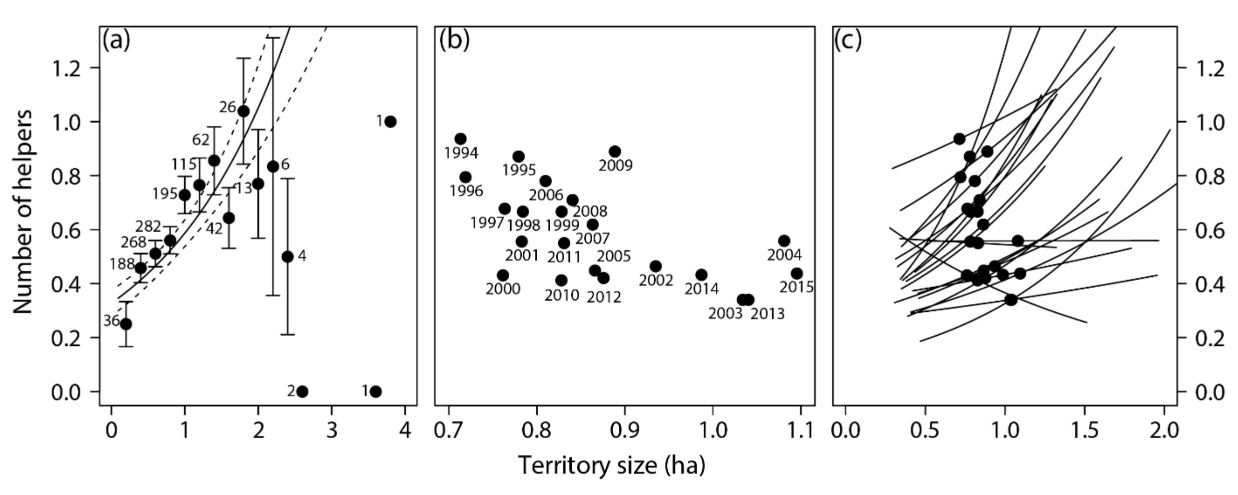

Figure 3: The relationship between territory size and the number of helpers. (a) The mean number of helpers for different categories (bins of 0.2 ha) of territory size. Error bars are standard errors. (b) The mean helper number in each year plotted against the mean territory size in each year. (c) Yearly means with the slope of the relationship between helper number and territory size for each year, determined by models identical to the final model on helper number, run on data subset by year. Lines in (c) range from the lower and upper 95th percentile of the territory sizes

in each year. Note that the points in (c) are the same as those in (b), but that the range of the x-axis differs between the two.

The number of both *nests* and *fledglings* in a territory increased with the age of the dominant female (Fig. 4a vs Fig. 4b), the number of helpers, and spring rainfall (Table 1). Territories with denser midstorey cover produced fewer fledglings (Fig. 4), but territories containing ponds had higher fledgling productivity. *Nest predation* was higher in territories with dense midstorey cover (Fig. 5a), and lower in territories containing two or more helpers than in territories without helpers (Fig. 5b; Table 1). The proportion of nests lost to predation declined over the study period (Fig. 5b; Table 1).

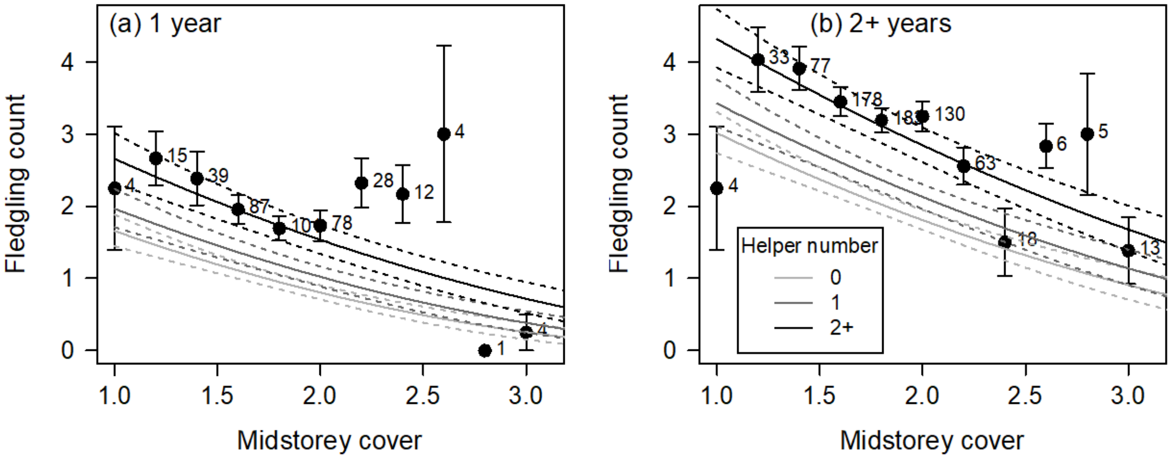

Figure 4: The effect of midstorey cover on the number of fledglings on each territory when the mother is (a) one year and (b) two years or older. Relationships shown are between fledgling count and midstorey cover, female age, and helper number. Solid lines are predictions from the final model when considering different numbers of helpers: none, one, or at least two, coloured as light grey, mid grey and black respectively. Broken lines represent the standard errors of these predictions. Fledgling counts are mean counts for different categories (bins of 0.2) of midstorey cover. Error bars show standard error. Sample sizes are the number of territories with a female of the respective age in each level of midstorey cover.

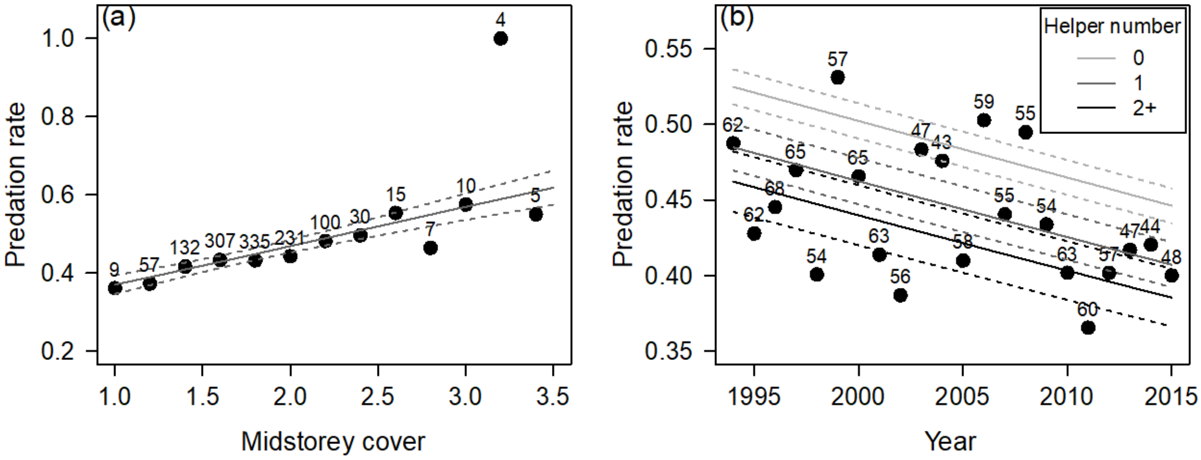

Figure 5: Nest predation rate in relation to (a) midstorey cover, and (b) time (years). Lines in (b) also show the relationship between helper number and predation rate. Solid lines are predictions from the final model; in (b) these consider different numbers of helpers. Broken lines represent the standard errors of these predictions. Scores of midstorey cover in (a) were allocated to categories separated by 0.2 for presentation.

Table 1: Summary of the effects of different environmental characteristics and social attributes of each territory. Slope estimates (and standard errors) and significance for relationships in the models marginally significant at $p < 0.05$ and significant at $p < 0.01$. † $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Cells are empty where the relationship was not significant. Parameter estimates should not be compared between models as some variables have been transformed and different types of link functions were used (see Methods). Parameter estimates for the different habitat types are proportions of the total territory. Full model outputs are presented in the Supporting Information Tables S4-S8.

	Response variables				
Fixed effects	**Territory Size**	**Helper number**	**Nest count**	**Predation[1]**	**Fledgling count**
Female age (2+ relative to 1)	0.031 (0.019)	0.240 (0.097) †	**0.104 (0.021) *****	<0.001 (0.077)	**0.437 (0.057) *****
Male age (2+ relative to 1)	**0.122 (0.029) *****	**0.986 (0.205) *****	-	0.024 (0.120)	-
Helpers (relative to none)					
1	-	**-**	**0.071 (0.024) ****	-0.168 (0.084) †	0.120(0.063)
2+	-	-	0.075 (0.030) †	-0.256 (0.101) †	**0.351 (0.078) *****
Year	**14.26 (3.398) *****	-22.80 (10.252) †	4.900 (5.226)	-14.69 (6.989) †	5.121 (5.673)
Rainfall	<0.001 (0.018)	-0.101 (0.053)	0.092 (0.032) †	-0.075 (0.039)	**0.181 (0.033) *****
Territory size	-	**0.518 (0.129) *****	0.060 (0.031)	-0.052 (0.102)	0.073 (0.081)
Bursaria thicket	-0.564 (0.262) †	-	-0.014 (0.207)	0.352 (0.699)	-0.820 (0.557)
Unusable habitat	-	**-3.242 (0.999) ****	-	-	-
Midstorey cover	0.045 (0.052)	-0.044 (0.189)	0.011 (0.041)	**0.360 (0.139) ****	**-0.361 (0.110) ****
Ponds	-	0.092 (0.113)	0.006 (0.025)	-0.127 (0.081)	0.164 (0.067) †
Wall	-	**-0.496 (0.148) *****	-0.033 (0.032)	-0.022 (0.108)	0.198 (0.088) †
Random effects (variance component, and number of levels in parentheses)					
Year (factor)	0.004 (n=20)	$6.9x10^{-3}$ (n=20)	0.014 (n=20)	$7.1x10^{-8}$ (n=20)	0.004 (n=20)
Territory name	0.048 (n=188)	$5.9x10^{-5}$ (n=188)	0.000 (n=188)	$7.6x10^{-8}$ (n=188)	0.021 (n=188)
Female ID	0.010 (n=497)	$5.7x10^{-7}$ (n=497)	0.010 (n=497)	$9.2x10^{-8}$ (n=497)	0.033 (n=497)
Male ID	0.017 (n=436)	$3.8x10^{-1}$ (n=436)	0.004 (n=437)	$3.3x10^{-2}$ (n=436)	0.000 (n=437)
Residual	0.061		0.092		0.708

[1] Note that positive parameter estimates for predation imply higher rates of predation, so effects on superb fairy-wren success are in the opposite direction than for the other variables.

Discussion

Here we report spatial, temporal, and social patterns in the performance of the cooperatively-breeding superb fairy-wren during a multi-decade study. Although the overall space occupied has remained constant, there has been a decline in the number of territories, and also in the prevalence of male supernumerary helpers (and hence the mean group size) on those territories. Our detailed records of nest location and performance suggest that microspatial heterogeneity in nesting behaviour and performance may be important for understanding population and social dynamics. They also reveal that the decline in population size has occurred despite a reduction in nest predation.

Population decline

Although the study area was consistently occupied by contiguous territories, the density of superb fairy-wrens in the study area almost halved over twenty years (Fig. 2). The decline was largely monotonic, though there was a temporary population resurgence in 2004-2006. Reasons for the population decline are not entirely clear, although recent analyses indicate that warming temperatures in both summer and winter have contributed to a substantial increase in over-winter adult mortality over the study period, and thus suggest that the decline may be associated with the current climate warming (Lv et al. 2023). The number of breeding females holding territories declined, with a concomitant increase in territory size. The mean number of helpers on territories also declined, and was closely linked to the increase in territory sizes; there were fewer helpers per territory in years where the number of breeding territories was low and territory sizes were larger (Figs 2-3).

Interestingly, within a given year, larger territories had more helpers (Fig. 3). A similar positive association between territory size and group size has been noted in the sister species of *M. cyaneus*, the splendid fairy-wren (*Malurus splendens*, Brooker and Rowley 1995). There are several possible reasons for this within-year association. Firstly, territories may be larger because helpers enable the breeding pair to expand or defend territory boundaries (Hunter 1985, Brooker and Rowley 1995). Secondly, or additionally, larger territories may have more resources, leading to increased production of young and hence recruitment of more helpers. These possibilities would require larger territories to be advantageous (Brooker and Rowley 1995).

Conversely, if larger territories occur in poor quality areas, the association between helper number and territory size may need an alternative explanation. Territory boundaries in our study population usually change through either fission into new territories or fusion of territories. Territory fission usually occurs after productive breeding seasons when a young immigrant female pairs with one of the helpers and partitions off part of the territory on which she has settled as an immigrant (Cockburn et al. 2003, Cockburn et al. 2008a). This inevitably decreases the territory sizes in the affected region, and as one helper becomes a dominant and the number of helpers is reduced, the mean number of helpers per territory also decreases. Territory fusion occurs when female mortality is high: the loss of a breeding female causes two territories to fuse, relegating all males but the oldest dominant bird to a helping position, and inevitably increasing the mean number of helpers on territories. In this way, productive years will have smaller territory sizes with a high population density, while small individual territories are likely to have fewer helpers. This system may also explain the relationship between territory size and age of the dominant male, as territory fission allows younger helpers to become dominant males, and territory fusion allows only the oldest males to remain dominant males.

There are very few long-term avian studies that explore the relationship between helper number and territory size (but see Brooker and Rowley 1995), yet the result we present here is likely to hold true for any territorial, cooperatively breeding species where fusions and fissions occur. Detecting this interesting relationship depends on methods that dissect both within-subject and between-subject (in this case, within- and between-year) effects (see van de Pol 2009). The effect is biologically interesting but also adds greater complexity to the difficulties in dissecting cause and effect that plague investigation of the costs and benefits of the presence of supernumeraries in cooperatively breeding birds (Dickinson and Hatchwell 2004, Rubenstein and Lovette 2007, Cockburn et al. 2008b).

Spatial heterogeneity in reproduction

Studies of microspatial effects on reproductive success in birds are unsurprisingly dominated by species provided with a surplus of nestboxes, relieving constraints imposed by the availability of suitable nest sites (Wilkin et al. 2007, Atiénzar et al. 2010, Amininasab et al. 2016). Female fairy-wrens usually construct a new nest for each clutch, and use a remarkable variety of substrates for nest construction. Despite this, there are physically adjacent areas that were either used for nesting every year of our study, or never used at all (Fig. 1a), indicating that fairy-wrens are responding strongly to spatial heterogeneity in the availability of nest sites.

The results of this study showed that female age and the presence of helpers are correlated with reproductive success regardless of spatial heterogeneity in habitat, consistent with previous studies (Cockburn et al. 2008b, Cooper et al. 2021). Helpers in this species may provide a benefit through increased longevity of the dominant female (Cockburn et al. 2008b), and through increased nestling mass, which increases fledgling survival (Hajduk et al. 2020). Territories with helpers will therefore increase the production of fledglings, which in turn leads to the accumulation of more helpers.

The analysis in this study confirms that spring rainfall is important for reproductive success (Dalziell and Cockburn 2008, Kruuk et al. 2015), even when spatial factors are taken into consideration. Additionally, Canberra has been drying during the study period (Kruuk et al. 2015), and deviations from the trend of population decline match periods of unusual rainfall. This implies a close link between superb fairy-wren success and water availability, and suggests that the drying of Australia under climate change (Collins et al. 2013) has had and may continue to have a role in the decline of the population, although increases in rainfall since 2020 may have prompted a revival in population size. Areas where nests are concentrated include gullies formed by streams with intermittent water flow, small retaining walls along roads, and artificial ponds within the study area (Table 1). Further, our analyses also showed that territories with a pond had higher fledgling productivity. Higher moisture affords more vigorous growth of vegetation, which improves the possibility of nest concealment from predators.

Predation of nestlings is the principal cause of nest failure in fairy-wrens. Fledging success was highest in areas with low midstorey cover, with nest predation increasing almost linearly with the amount of midstorey cover (Fig. 5a). This result is somewhat unexpected given that increased cover around the nest reduces nest predation in many bird species (Flaspohler et al. 2000, Rangel-Salazar et al. 2008), and nest concealment reduced predation in superb fairy-wrens at another site (Colombelli-Négrel and Kleindorfer 2009). Recent analyses on the same population using remotely sensed measures of vegetation density showed that a high vegetation density in the ground-storey, where most nests are located, also increases rates of nest predation (Turner et al. 2022, preprint). In other species, dense vegetation can increase predation by concealing predators from the birds guarding the nest (Götmark et al. 1995). Fairy-wrens in our study site have a number of common predators, including introduced mammals (*Rattus rattus, Vulpes vulpes*), native mammals (*Trichosurus vulpecula*) and brown snakes (*Pseudonaja textilis*), all of which can forage at night and are likely to locate nests using scent or heat during the day or night. Pied currawongs (*Strepera graculina*) are the chief diurnal nest predators of fairy-wrens, and the principal predator of bird nests throughout south-eastern Australia (Fulton 2019). Currawongs are attracted to fairy-wren nests when adult fairy-wrens (particularly the brightly-coloured males) visit the nest; they can also be observed sitting quietly listening for the begging calls of chicks (Yasukawa and Cockburn 2009). This suggests that dense midstorey cover may not impede the currawong's ability to detect the nest, and may instead allow them to locate nests without alerting the provisioning adults. Once the nest is located, there is no evidence that fairy-wrens can deter the currawongs (Yasukawa and Cockburn 2009).

Currawongs underwent a massive population increase and range expansion in the 1960s, and during the course of our study the number of currawongs in the study site increased rapidly from about 5 pairs in the 1990s to a maximum 35 pairs (A. Cockburn, pers. obs.). However, the results we present here show that predation at the nest has declined over time. It is possible that despite the increasing numbers of predators, superb fairy-wrens are learning to cope with the increased predation pressure. Many species use behavioural strategies to conceal the nest, such as distraction displays to lure predators away from the nest, or avoiding flying to and from the nest when predators are nearby (Götmark et al. 1995, Remeš 2005, Yasukawa and Cockburn 2009). Some species have adapted to the introduction of exotic predators through changing their nest-site choice and increasing anti-predator behaviour (Wiebe 2004, Massaro et al. 2008, Vanderwerf 2012). In addition, superb fairy-wrens adjust nest vigilance in the presence of cuckoos, and there is evidence that this behaviour can be learnt socially (Feeney and Langmore 2013, Langmore and Feeney 2015). It is possible then that superb fairy-wrens have either learnt or evolved to be more vigilant or to better conceal their nests in the presence of a relatively novel predator.

Conclusions

The use of spatial tools in GIS software can provide valuable insight into proximate correlations of breeding success in wild populations. We have applied these techniques to valuable long-term data on a declining population. Understanding the ultimate effects of environmental heterogeneity, such as why certain conditions are chosen for nesting or result in better reproductive performance, remains complicated. However, it is clear that spatial and temporal heterogeneity of the environment have profound impacts on reproductive success and social organisation in superb fairy-wrens, highlighting the need for further work to understand the use of space in this species. Addtionally, these analyses have provided a different result from what might have arisen from analysing the fate of individual nests, and illustrate the value of investigating patterns of reproductive success in wild populations with a long-term, population-wide approach.

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Conflict of interest

None to report.

Author's contributions

L.E.B.K. and A.C. designed the study. A.C., H.L.O. and F.B. collected the data. F.B. performed the analysis with assistance from J.S. and B.D. F.B. led the writing of the manuscript. All authors contributed to drafts and gave final approval for publication.

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Supporting information for: "Population decline reduces cooperative breeding in a spatially heterogenous population of superb fairy-wrens"

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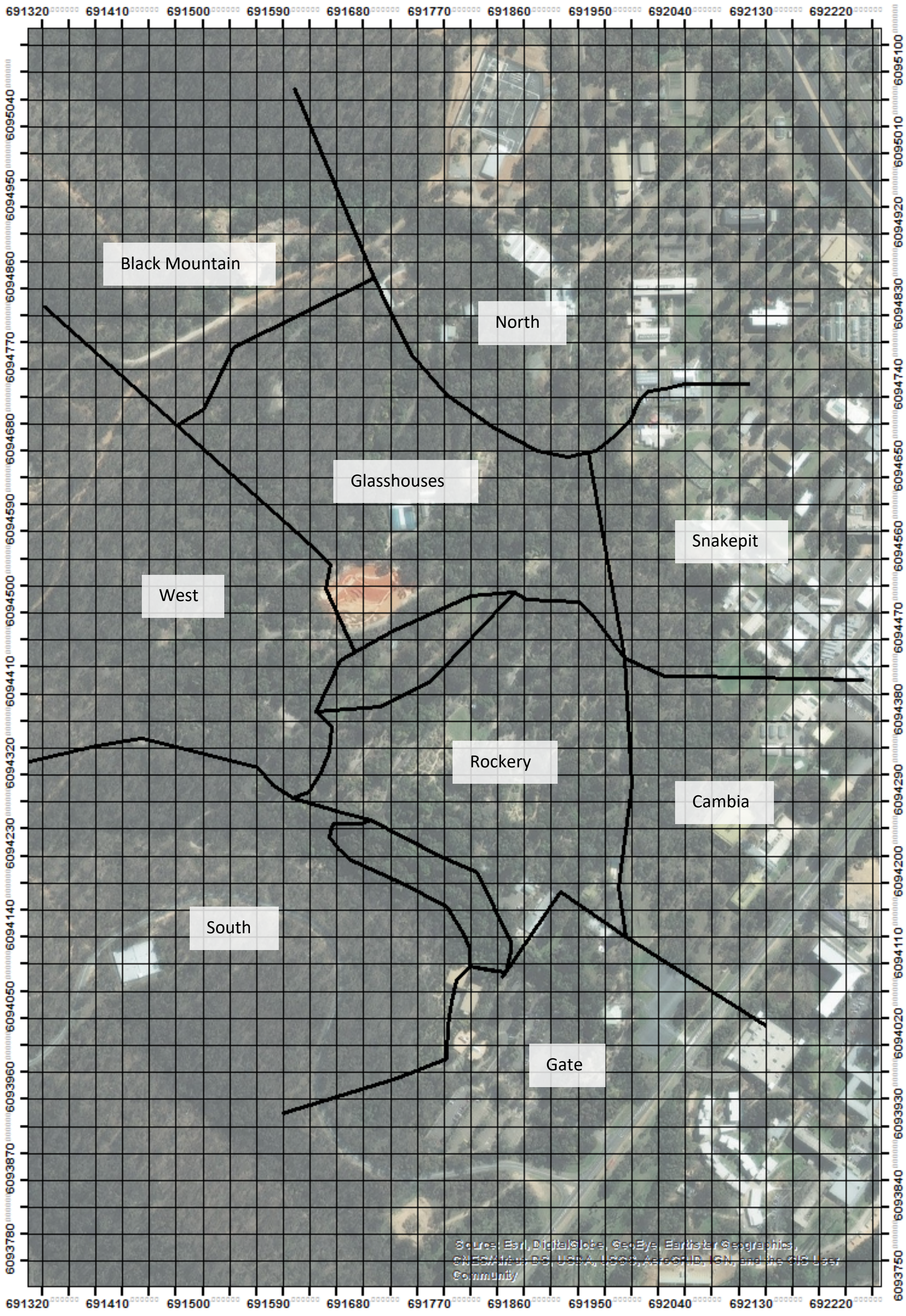
Table S1: Root mean square (RMS) errors for the georeferencing of each territory map. RMS indicates the consistency between the changes made to each point ("Links") used to georeference the paper territory map to the geographically accurate map of the Australian National Botanic Gardens. RMS errors should be as close to zero as possible (Esri, 2016).

Map	**Links**	**Total RMS Error (m)**
November 1994	5	2.78
November 1995	5	4.56
October 1996	4	2.58
November 1997	5	4.12
October 1998	6	2.69
November 1999	4	2.83
November-December 2000	5	3.31
October-November 2001	5	3.25
November 2002	5	3.24
November 2003	4	1.84
November 2004	4	1.97
November 2005	4	1.97
November 2006	5	3.68
October 2007	5	4.09
October 2008	4	1.87
November 2009	5	5.43
November 2010	5	3.78
November 2011	5	4.22
November 2012	4	1.04
November 2013	4	2.54
December 2014	4	1.94
November 2015	4	1.90



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure S1: The nine sub-areas used to name the territories, and the grid used to sample vegetation. The grid starts at X=691290, Y=6093780 in the GDA 94 MGA 55 coordinate system. Cell size is 30 x 30 m.

Figure S2: Digitised territory boundaries comparing consecutive years, showing years with (a) very little change from year to year, 2008 (grey) and 2009 (black); and (b) greater change from year to year, 2004 (black) and 2005 (grey). Where territories were largely consistent between years, they were given the same name. New territories that did not obviously align to a territory in the previous year were given new names.

Table S2: ArcMap procedures for creating territory layers and calculating territory attributes.

Procedure	Details
Georeferencing	We linked 4-5 recognisable points on each paper territory map to the appropriate points on a digital map of the ANBG. These points were spread evenly around the map.
Polygon construction	We started each territory layer by drawing a polygon around a single territory using the ‘Draw’ toolbar. We then started a new layer based on this first polygon, and traced the rest of the territories using the ‘Edit’ toolbar.
Area and centroid calculation	We used the ‘Calculate Geometry’ tool to calculate the area and centroid (centre coordinates) for each territory. We used the ‘centroid_inside’ function to calculate the central coordinates of each territory, as there were at least two that were of such a shape that the centroid otherwise fell outside the territory boundaries. In all other territories the method of calculating the centroids made no difference.

Table S3: The habitat variables for each of the 605 $30m^2$ cells. For 'Habitat type', n is the number of cells in which that habitat was predominant across all years. For 'Features', n is the number of cells containing at least one of the features. Cells can contain several features, but can only be one habitat type.

Variable	**Description**	**n**
Habitat type		
Plantation	Within ANBG or areas outside the gardens which were originally artificially planted (with native Australian species) and where watering/maintenance occurred	339
Natural woodland	Surrounding the plantation, characterised by grass tussocks, sparse shrubs and *Eucalyptus* spp.	174
Bursaria thicket	An often weedy area outside the ANBG, between the gardens and CSIRO, characterised by the presence of *Bursaria spinosa*	57
Unusable habitat		
a. Lawn	Open areas of mown grass	18
b. Rainforest	Characterised by plants such as tree ferns (e.g. *Dicksonia antarctica*) and dense canopy cover	9
c. Road/carpark	Classified as such if asphalt covered most or all of the cell	8
Features		
Graminoids	A dense patch of tussock form including a range of genera such as *Lomandra* (Asparagaceae), *Gahnia* (Cyperaceae) or *Dianella* (Asphodelaceae)	120
Vines	A diverse range of genera, counted as present if dense enough to conceal a nest	86
Procumbent shrub	Dense, low-growing shrub, usually horticultural variants of Australian native plant species	108
Prickly shrub	Taller, dense shrubs including hedges, often Proteaceae	229
Brambles	*Rubus* spp., counted as present if dense enough to conceal a nest	18
Ponds	Permanent water features such as ponds	46
Wall	Small wall on uphill side of road in native vegetation	25
Gully	Direction noted (8 possible directions: N, NE, E etc.) – some directions may catch more light for vegetation growth	112

Section S1: Summarising habitat characteristics for each cell

The habitat characteristics of each cell in the grid were sampled using observations from each corner of the grid. We measured the following variables:

- *Levels of ground, midstorey and canopy cover*: All three variables were scored on a scale of 1-5 based on increments of percent coverage (0-20%, 20-40%, etc.) *Ground cover* included vegetation such as grass tussocks and low growing or 'procumbent' shrubs, as well as structures such as fallen branches that could potentially provide cover. *Midstorey cover* included shrubs and hedges from approximately 70 cm to 2.5 m in height. *Canopy cover* was scored by estimating the percentage of open sky from 2.5 m
- *Habitat type*: For each cell, habitat type was classified as either plantation, native woodland, bursaria thicket, lawn, rainforest, or carpark. See Table 1 in main text for details, and the numbers of cells in which each habitat type was predominant.
- *Features:* We scored the presence of various potentially important features in each cell. These were the presence of any gully and its direction, and the presence of features that might be useful for nesting such as dense shrubs or brambles, based on known or suspected nest site choices. Table 1 in the main text contains a full list of all features.

We then used ddply from the package 'Plyr' (Wickham, 2011) in R to summarise these variables to give one value for each cell. Ground, midstorey and canopy cover were averaged over each cell, so that scores could be any multiple of 0.25 between 1 and 5. Cells were given a yes/no score for each feature.

For cells that contained more than one habitat type, habitat type was scored given the following preferences:

1. Plantation: any cell containing plantation has been tampered with through procedures such as watering and weeding, and so will not be completely natural,
2. Bursaria: this area often contained thick, weedy vegetation (e.g. brambles) and so would not be entirely native,
3. Native: this was given higher preference over the remaining categories, as it is still more valuable for superb fairy-wrens that lawn, carparks, or rainforest,
4. Lawn: lawns, while never used for nesting, are often used for feeding, and so were deemed more valuable than carparks or rainforest.

There were no cells that contained both carpark and rainforest, so there was no need to decide a hierarchy among these last two habitat types.

Section S2: Calculation of habitat characteristics for each territory

We combined the habitat variables collected for each cell into a single dataset, and calculated the coordinates of the centre of each cell (i.e. 15 m to the north and east of the coordinate used to identify the cell). We imported the data into ArcMap as XY data to create a point layer. Using the point-to-raster tool, we turned this point layer into a separate raster for each vegetation variable, to create a grid with different values for each cell. These raster layers were then converted into polygons layers for each variable with the value of each cell (e.g. ground cover = 2.25) assigned to a polygon. We combined these polygon layers into a single polygon layer using the overlay tool, so that each cell we collected data for was now a polygon with a set of variables. We then combined this polygon layer in the same way with each of the territory layers, and used ddply ('Plyr', Wickham, 2011) in R to summarise the variables as follows:

- *Levels of ground, midstorey and canopy cover*: Each territory was given an average of these, based on the total area taken up by each score (i.e. 1, 1.25, 1.5 etc) of the different layers.
- *Habitat type*: We initially explored both the total area of a territory taken up by each habitat, and the proportion of a territory’s total area that contains each habitat. We only found significant results with the proportions of habitat types, and so did not include the areas in the main text.
- *Features*: As with the cells, each territory was given a yes/no score for whether it contained a certain feature or not.

Table S4: Mixed model of territory size. The table shows the output from the full model with all variables fitted. Random effects fitted were identity of both the female and dominant male, territory name (common across years), and year (n gives the number of factor levels for that random effect). All habitat types are proportions of the total territory. Estimates for female age and dominant age are for the difference between one year and older. Special features (e.g. walls, graminoids etc.) were left out of the model as an increase in territory size will automatically increase the chance of containing a special feature. N = 1078 territories, AIC = 606.8.

Fixed effects	**Estimate**	**SE**	**t-statistic**	**P-value**
Intercept	-27.730	6.820		
Habitat type (% in territory):				
Native woodland	-0.248	0.255	-0.974	0.330
Plantation	-0.396	0.257	-1.539	0.124
Bursaria thicket	**-0.564**	**0.262**	**-2.156**	**0.032**
Rainforest	<-0.001	1.107	0.000	>0.999
Lawn	-0.225	0.334	-0.674	0.500
Vegetation cover scores				
Ground cover	-0.073	0.052	-1.416	0.157
Midstorey cover	0.045	0.052	0.863	0.388
Canopy cover	0.147	0.078	1.884	0.060
Female age	0.031	0.019	1.621	0.105
Dominant age	**0.122**	**0.029**	**4.270**	**<0.001**
Year	**14.26**	**3.398**	**4.195**	**<0.001**
Spring rainfall	<0.001	0.018	0.020	0.984
Random effects	**Variance**	**n**		
Female ID	0.010	497		
Male ID	0.017	436		
Territory name	0.048	188		
Year	0.004	20		
Residual	0.061			

Table S5: Generalised linear mixed model on the number of helpers per territory, with Poisson error distribution and log link function. The table shows the output from the full model with all variables fitted. Random effects fitted were identity of both the female and dominant male, territory name (common across years), and year. Unusable habitat is the proportion of the territory that is either lawn, rainforest or carpark. Estimates for female age and dominant age are for the difference between one year and older. Features (wall – gully) are defined as present or not within a territory. N = 1078 territories, AIC = 2146.5.

Fixed effects	**Estimate**	**SE**	**z-statistic**	**P-value**
Intercept	44.334	20.555		
Territory size	**0.518**	**0.129**	**4.034**	**<0.001**
Native woodland	0.329	0.337	0.976	0.329
Plantation	0.410	0.356	1.153	0.249
Unusable habitat	**-3.242**	**0.999**	**-3.245**	**0.001**
Ground cover	**-0.466**	**0.225**	**-2.075**	**0.038**
Midstorey cover	-0.044	0.189	-0.232	0.816
Canopy cover	-0.088	0.284	-0.310	0.757
Wall	**-0.496**	**0.148**	**-3.345**	**<0.001**
Graminoids	-0.004	0.161	-0.024	0.981
Vines	-0.166	0.140	-1.182	0.237
Water	0.092	0.113	0.826	0.415
Procumbent shrub	0.028	0.175	0.160	0.873
Prickly shrub	-0.119	0.179	-0.664	0.507
Brambles	0.135	0.167	0.805	0.421
Gully	0.223	0.123	1.815	0.069
Female age	**0.240**	**0.097**	**2.466**	**0.014**
Dominant age	**0.986**	**0.205**	**4.821**	**<0.001**
Year	**-22.800**	**10.252**	**-2.224**	**0.026**
Spring rainfall	-0.101	0.053	-1.908	0.056
Random effects	**Variance**	**n**		
Female ID	<0.001	497		
Male ID	0.384	436		
Territory name	<0.001	188		
Year	0.007	20		

Table S6: Mixed model on nest count (log transformed) at the territory level. The table shows the output from the full model with all variables fitted. Random effects fitted were identity of both the female and dominant male, territory name, and year. All habitat types are proportions of total territory. Estimate for female age is for the difference between one year and older. Features (wall – gully) are defined as present or not within a territory. N = 1083 territories, AIC = 736.6.

Fixed effect	**Estimate**	**SE**	**t-statistic**	**P-value**
Intercept	-8.796	10.47		
Territory size	0.060	0.031	1.947	0.052
Native woodland	0.008	0.199	0.040	0.968
Plantation	0.033	0.198	0.164	0.870
Bursaria thicket	-0.014	0.207	-0.067	0.947
Rainforest	1.441	0.955	1.509	0.132
Lawn	0.197	0.263	0.748	0.455
Ground cover	-0.038	0.043	-0.877	0.381
Midstorey cover	0.011	0.041	0.274	0.784
Canopy cover	0.052	0.061	0.846	0.398
Wall	-0.033	0.032	-1.029	0.304
Graminoids	0.009	0.034	0.270	0.787
Vines	-0.030	0.030	-1.006	0.315
Water	0.006	0.025	0.226	0.821
Procumbent shrub	-0.003	0.037	-0.074	0.941
Prickly shrub	-0.058	0.038	-1.531	0.126
Brambles	-0.005	0.038	-0.119	0.905
Gully	0.010	0.026	0.365	0.715
Female age	**0.104**	**0.021**	**4.866**	**<0.001**
Helpers (in relation to none)				
1	**0.071**	**0.024**	**2.974**	**0.003**
2+	**0.075**	**0.030**	**2.527**	**0.012**
Year	4.900	5.226	0.938	0.361
Spring rainfall	**0.092**	**0.033**	**2.800**	**0.013**
Random effects	**Variance**	**n**		
Female ID	0.010	497		
Male ID	0.004	437		
Territory name	0.000	188		
Year	0.014	20		
Residual	0.092			

Table S7: Generalised linear mixed model on nest predation rate at the territory level, with binomial error structure and logit link function. The table shows the output from the full model with all variables fitted. Random effects fitted were identity of both the female and dominant male, territory name (common across years), and year. All habitat types are proportions of total territory. Estimates for female age and dominant age are for the difference between one year and older. Features (wall – gully) are defined as present or not within a territory. N = 1078 territories, AIC = 2687.3.

Fixed effects	**Estimate**	**SE**	**z-statistic**	**P-value**
Intercept	28.88	14.00		
Territory size	-0.052	0.102	-0.516	0.606
Native woodland	0.084	0.672	0.124	0.901
Plantation	0.148	0.670	0.221	0.825
Bursaria thicket	0.352	0.699	0.503	0.615
Rainforest	-2.305	3.040	-0.758	0.448
Lawn	0.362	0.892	0.405	0.686
Ground cover	-0.120	0.146	-0.750	0.454
Midstorey cover	**0.360**	**0.139**	**2.589**	**0.010**
Canopy cover	0.152	0.208	0.732	0.464
Wall	-0.022	0.108	-0.202	0.840
Graminoids	0.059	0.122	0.489	0.625
Vines	-0.019	0.099	-0.191	0.849
Water	-0.127	0.081	-1.565	0.118
Procumbent shrub	0.006	0.126	0.048	0.962
Prickly shrub	-0.176	0.132	-1.331	0.183
Brambles	-0.044	0.127	-0.352	0.725
Gully	0.026	0.089	0.291	0.771
Female age	<0.001	0.077	0.009	0.993
Dominant age	0.024	0.120	0.196	0.844
Helpers (in relation to none)				
1	**-0.168**	**0.084**	**-2.012**	**0.044**
2+	**-0.256**	**0.101**	**-2.522**	**0.012**
Year	**-14.69**	**6.989**	**-2.101**	**0.036**
Spring rainfall	-0.075	0.039	-1.896	0.058
Random effects	**Variation**	**n**		
Female ID	<0.001	497		
Male ID	0.033	436		
Territory name	<0.001	188		
Year	<0.001	20		

Table S8: Mixed model on fledgling count (square root transformed) at the territory level. The table shows the output from the full model with all variables fitted. Random effects fitted were identity of both the female and dominant male, territory name (common across years), and year. All habitat types are proportions of total territory. Estimate for female age is for the difference between one year and older. Features (wall – gully) are defined as present or not within a territory. N = 1083 territories, AIC = 2805.2.

Fixed effects	**Estimate**	**SE**	**t-statistic**	**P-value**
Intercept	-8.616	11.373		
Territory size	0.073	0.081	0.899	0.369
Native woodland	-0.678	0.536	-1.266	0.207
Plantation	-0.633	0.535	-1.184	0.237
Bursaria thicket	-0.820	0.557	-1.471	0.142
Rainforest	-2.032	2.583	-0.787	0.432
Lawn	-1.057	0.710	-1.489	0.138
Ground cover	0.130	0.116	1.124	0.262
Midstorey cover	**-0.361**	**0.110**	**-3.271**	**0.001**
Canopy cover	-0.083	0.166	-0.497	0.619
Wall	**0.198**	**0.088**	**2.259**	**0.025**
Graminoids	-0.073	0.092	-0.789	0.431
Vines	0.127	0.081	1.557	0.121
Water	**0.164**	**0.067**	**2.465**	**0.015**
Procumbent shrub	0.014	0.099	0.146	0.884
Prickly shrub	-0.091	0.103	-0.882	0.378
Brambles	0.060	0.104	0.576	0.565
Gully	0.041	0.071	0.577	0.564
Female age	**0.437**	**0.057**	**7.682**	**<0.001**
Helpers (in relation to none)				
1	0.120	0.063	1.892	0.059
2+	**0.351**	**0.078**	**4.515**	**<0.001**
Year	5.121	5.673	0.903	0.377
Spring rainfall	**0.181**	**0.033**	**5.446**	**<0.001**
Random effects	**Variance**	**n**		
Female ID	0.033	497		
Male ID	0.000	437		
Territory name	0.021	188		
Year	0.004	20		
Residual	0.708			

Section S3: Discussion

Here we discuss results that are relevant to this study population of superb fairy-wrens, and may be a useful reference for other studies on similar species or at the same study site. The most novel results, that will be applicable to a range of other species, are presented in the main text.

Habitat structure

The area including and surrounding the Australian National Botanic Gardens contains several distinct habitat types that provide potential for heterogeneous habitat use. We already suspected that superb-fairy wrens never nest in the rainforest gully and in lawns, though in winter they often use lawns for feeding (Schlotfeldt & Kleindorfer, 2006; A. Cockburn, pers. comm.). This idea was confirmed by the lower helper numbers, indicating low productivity, in territories containing large proportions of rainforest, lawn, and carpark.

We detected no difference in productivity between native vegetation and the garden plantations. The bursaria habitat was the only other type to show a relationship with any of our variables: territories tended to be smaller in this habitat type. A map of all nest locations across the study period suggests that nest placement is more random within the bursaria thicket than it is within the plantation and parts of the native woodland. The bursaria habitat type is characterised by dense vegetation that may provide a high abundance of potential nest sites. Superb fairy-wrens may perceive this area as good habitat, resulting in higher occurrences of territory fission.

The special features we measured were largely unimportant when considered at the territory scale. Potential nesting sites in the study area are common, so most territories will include at least one feature. This may be all that is required for a territory to be productive: we have observed some birds using the same nest site for multiple attempts.

The number of fledglings in a territory was higher if the territory contained a pond or other water source. Predation was also marginally lower in these territories ($p < 0.05$ when it was dropped from the model). Rather than the presence of water being advantageous, the plants surrounding ponds, often graminoids, may provide important cover from predators, or useful lookout points to detect approaching predators.

Interestingly, while we expected the small walls in the native vegetation to boost productivity due to the clustering of nests along these walls, helper number was lower in territories containing walls. This may be a by-product of the vegetation in these areas. We only measured the presence of walls within the natural woodland, as this is where the pattern in nest sites was apparent. The native vegetation in this area is largely open woodland characterised by grass tussocks. Superb fairy-wrens often nest in grass tussocks, but these nests suffer the highest predation rate of known nest site types (unpublished data). The low number of helpers in territories containing walls may be a result of low productivity in the areas of natural woodland.

Bird-related effects

Female age, the number of helpers, and spring rainfall were all positively correlated with reproductive success through both nest count and fledgling count. This is in accordance with a previous study on the same population, where the effects were on the number of independent young (Cockburn, Sims, et al., 2008). The explanatory variables were primarily added to the model to control for associations that have previously been shown to be important (Cockburn, Sims, et al., 2008; Kruuk et al., 2015), but it is also valuable to confirm that the associations still stand with habitat variables added to the models.

Older males and females tended to have more helpers. The dominant male is invariably the oldest male in the group (Cockburn, Osmond, et al., 2008): therefore the older he is, the more time he has had to accumulate helpers. Similarly, older females will have had more time to accumulate sons as helpers. One year old females are likely to start their reproductive period in a territory with no or fewer helpers than older females, from creating their own territory with a single male through territory fission (Cockburn, Osmond, et al., 2008; Cockburn et al., 2003).

While helper number appeared to have a negative influence on predation, care must be taken interpreting this result. Helpers are accumulated through the production of young: if an area is prone to predation, then fairy-wrens may not be able to produce enough young to sustain helpers. This association is then more likely due to predation reducing the production of fledglings, which in turn keeps the helper number low.

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