TITLE

No time to die: Temporal patterns of nest predation in a multi-brooded Southern Hemisphere passerine bird

AUTHORS

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ABSTRACT

1. Nest predation is frequently the primary cause of early-life mortality in wild avian populations, generating selection for optimising the timing of reproduction to reduce predation risk. Investigating temporal patterns of nest predation is therefore necessary for understanding the intricate relationships between birds and their predators.
2. In this study, we considered the role of temporal variation in nest predation in a wild population of cooperatively breeding superb fairy-wrens *Malurus cyaneus* in southeastern Australia, using data collected from nearly 4000 nests over a 27-year period (1994 to 2020). In this species, more than half of all nest attempts end in failure, mostly due to nest predation, with females sometimes initiating as many as ten clutches over their long breeding season.
3. We analysed temporal variation in daily nest predation risk over three temporal scales in relation to: (i) the age of the young within the nest; (ii) the timing of nesting within the breeding season; and (iii) differences between years. For each of these temporal scales, we considered predation during the overall nesting period and for three specific stages of development: (i) the incubation stage (1 to 13 days from the onset of incubation); (ii) the early nestling stage (1 to 5 days post-hatching); and (iii) the late nestling stage (6 to 11 days post-hatching).
4. We found that the average daily risk of predation was lowest during the incubation stage (0.016 ± 0.124 SD), intermediate during the early nesting stage (0.025 ± 0.158 SD) and highest during the late nestling stage (0.066 ± 0.248 SD). Predation increased with the age of the clutch during the incubation stage and with the age of the brood during the early nestling stage, but there was no further increase during the late nestling stage.
5. Throughout the breeding season, daily nest predation rates varied quadratically, with a peak approximately mid-season. There was no evidence that these within-season trends differed between years, and we also found little evidence of any longer-term directional change in daily nest predation rates over the study period. Neither within

nor between-year variation in nest predation was related to changes in nest density (i.e., the proportion of active nests at a given time). Instead, within-season patterns closely mirrored the breeding behaviour of pied currawongs *Strepera graculina*, a large corvid-like passerine that is a common predator of superb fairy-wren eggs and nestlings in our study area.

6. In addition to the temporal variation, we found higher daily rates of nest predation for females assisted by fewer helpers, for younger females, and for nests built at lower heights. However, the significance and magnitude of these effects varied across the different development stages. Furthermore, we found mixed effects of clutch and brood size. Our results therefore indicate a close association between temporal patterns of nest predation in superb fairy-wrens and this seemingly important avian nest predator.

Keywords: ‘nest predation’, ‘multi-brooded’, ‘temporal variation’, ‘’, ‘passerines’, ‘Southern Hemisphere’, ‘superb fairy-wren’, ‘Malurus cyaneus’

INTRODUCTION

Nest predation – the loss to predation of eggs and nestlings in nests – is the primary determinant of nesting failure in most avian species. It is common for nest predation to occur in more than 50% of all nesting attempts (Jara et al., 2020; Martin, 1993a; Ricklefs, 1969; Robinson et al., 2000). Consequently, the effects of nest predation play an important role in shaping avian life histories (Ibáñez-Álamo et al., 2015; Lima, 2009; Lima & Dill, 1990). Recent evidence suggests that global nest predation rates have increased in recent decades (Kubelka et al., 2018; Matysioková & Remeš, 2022; Remeš et al., 2012a, 2012b). In some extreme cases, this trend has been associated with regional population declines and even species extinctions (Blackburn et al., 2004). Understanding and predicting patterns of nest predation is therefore central to understanding the impact of changes in predation risk on the demography and viability of many avian populations, and for developing effective conservation management strategies for imperilled species.

Whilst numerous studies have focused on assessing nest predation, the factors that make a nest more or less likely to be depredated are still poorly understood (Lahti, 2009). It is widely accepted that nests that are easily found and accessed by predators should experience higher predation rates. Therefore, the selection of nest-sites surrounded by dense and complex vegetation is expected to be advantageous. These vegetation characteristics are thought to reduce sensory cues to predators and act as a physical barrier, impeding predators and reducing their ability to search for nests efficiently (Davis, 2005; Filliater et al., 1994; Magrath et al., 2010; Martin, 1993a, 1993b; Martin & Roper, 1988). However, there is limited evidence supporting the idea that nests located in such areas have reduced predation rates. Most studies to date have found no or even positive associations between vegetation density and complexity and rates of nest predation (Borgmann & Conway, 2015; Götmark et al., 1995; Holway, 1991; Jara et al., 2020; Remeš, 2005; Turner et al., 2023). Effects of other nest-site characteristics such as nest height, the proximity to habitat edges, or the degree of habitat fragmentation have similarly yielded equivocal findings (Boulton & Clarke, 2003; Caro, 2005; Chalfoun et al., 2002; Colombelli-Négrel & Kleindorfer, 2009; Cox et al., 2012a; Fulton, 2018; Guan et al., 2018; Lahti, 2001; Matysioková & Remeš, 2023; Morrison & Bolger, 2002; Paton, 1994; Vetter et al., 2013). Collectively, these studies suggest that many spatial factors may influence nest-site selection and the risk of predation, but that few consistent patterns exist.

The risk of nest predation can also vary temporally depending on the age and developmental stage of the young in the nest, different times within the breeding season, and from year to year (Borgmann et al., 2013; Burhans et al., 2002; Cox et al., 2012b; Dinsmore et al., 2022; Grant et al., 2005; Husby & Hoset, 2018; Polak, 2016; Smith & Wilson, 2010; Wilson et al., 2007). For example, nest predation is often higher during the nestling stage, after the eggs have hatched. This increased risk may be associated with increased parental activity and increased vocalisations of nestlings, which can attract predators to the nest's location (Haff & Magrath, 2011; Haskell, 1994, 2002; Husby, 2019; Magrath et al., 2010; Martin et al., 2000; Muchai & du Plessis, 2005; Skutch, 1949). However, temporal variation in nest predation can also be influenced by factors such as the dietary preferences of dominant predators, changes in predator diversity and abundance over time, or shifts in predator behaviour in response to changes in nest density or the availability of alternative prey (Bêty et al., 2001; Borgmann et al., 2013; Kurki et al., 1997; Nams, 1997).

Despite extensive research on spatial patterns of nest predation, there has been less attention given to assessing detailed temporal patterns. This limited focus can be attributed, in part, to several fundamental research biases. One such bias is the predominant use of the Mayfield method, a commonly employed methodology for estimating nest predation, but which assumes a constant predation risk over time (Mayfield, 1961, 1975). However, in recent decades, new methods have been developed that allow for the analysis of variation in nest predation patterns over time, and studies that have used these approaches have shown that predation rates are rarely constant (Dinsmore et al., 2002; Rotella et al., 2004; Shaffer, 2004). Second, existing research has a geographical bias towards cold temperate regions of northern Europe and North America, with a disproportionate focus on passerine species in these regions. These species typically have short breeding seasons during which only one or few nesting attempts are possible (Wyndham, 1986). In such systems, the age or development stage of the young in the nest can therefore be confounded with the time of the year, making it challenging to determine the direction and magnitude of different temporal-related effects in analyses. Furthermore, it remains uncertain whether the findings from these studies can be applied to tropical, subtropical, and Southern Hemisphere species, where species often have longer lifespans, more complex life histories, and longer breeding seasons than their Northern Hemisphere counterparts (Johnson et al., 1997; Martin, 1996, Martin et al., 2000; Russell, 2000; Russell et al., 2004). Third, the majority of extensive and long-term studies have either focused on nest-box populations of hole-nesting species or used artificial or inactive nests to estimate predation rates (Kaliński et al., 2014; Major & Kendal, 1996; McCleery et al., 1996; Vetter et al., 2013). However, these nest types often yield unrealistically low rates of nest predation when compared to naturally occurring, real, and active nests, and therefore may be limited in the insights they provide into temporal variation in nest predation (Kuitunen & Aleknonis, 1992; Nilsson, 1984; Thompson III & Burhans, 2004; Zanette, 2002). Nest-boxes may also influence other life history traits related to breeding performance (Sudyka et al., 2022).

In this study, we investigate the temporal patterns of nest predation in a wild population of superb fairy-wrens *Malurus cyaneus* over a 27-year period (1994 to 2020) in southeastern Australia. Superb fairy-wrens are small passerines (*c.* 10 g, Dunning Jr, 2007) that exhibit facultative cooperative breeding. Individuals live on year-round territories in groups composed of a dominant breeding pair. Although the pair may breed alone, they can be assisted by up to five male helpers that are typically offspring reared on the territory in previous breeding seasons (Cockburn et al., 2016; Hajduk et al., 2021). Females are solely responsible for nest-building and incubation, but all group members defend and provision the brood (Cockburn et al., 2008). Superb fairy-wrens breed from approximately September to March, with a peak in activity often between November and December (Lv et al., 2019). During this period, females can initiate as many as ten clutches and successfully rear up to four broods. Nests are dome-shaped and often built close to the ground in small shrubs or thick grass tussocks (Colombelli-Négrel & Kleindorfer, 2009; Nias, 1986; Turner et al., 2023). A new nest is usually built between each breeding attempt; only very rarely are nests reused, although sometimes nest material is reused (Turner et al., 2022).

Our superb fairy-wren study population experienced a long-term decline in population size of more than 50% over the years considered in this study (Backhouse et al., 2023; Lv et al., 2023). While various factors may have contributed to this decline, we focused here on investigating the potential impact of nest predation. Nest predation accounts for approximately 90% of nesting failure, and more than half of all nests end in predation (Turner et al., 2023). Superb fairy-wrens have many nest predators throughout southeastern Australia (including, e.g., snakes, lizards, birds, and both native and introduced mammal species; Colombelli-Négrel & Kleindorfer, 2009; Nias, 1986; Rowley & Russell, 1997). In our study area, the pied currawong *Strepera graculina*, a large corvid-like passerine (*c*. 300 g, Cockburn et al., 2016; Dunning Jr, 2007; Prawiradilaga, 1996; Yasukawa & Cockburn, 2009), is a common and seemingly important nest predator for superb fairy-wrens. This is evident through the frequent discovery of colour-bands from nestling superb fairy-wrens found in the regurgitated pellets of pied currawongs (Prawiradilaga, 1996). Additionally, by utilising motion-sensing trail cameras in two recent years (2019 and 2020), we have obtained direct evidence of superb fairy-wren nest predation by pied currawongs, as well as by eastern brown snakes *Pseudonaja textilis* and, during one-year, red foxes *Vulpes vulpes* (refer to Table S1, although we emphasise the small sample sizes associated with these data).

Previous studies of superb fairy-wrens have investigated the impact of various nest-site characteristics on nest-site selection and nest predation (Backhouse et al., 2023; Colombelli-Négrel & Kleindorfer, 2009; Nias, 1986; Turner et al., 2023). However, the temporal nest predation patterns for this species, specifically throughout the nesting period and across the breeding season, remain less understood. Therefore, the aim of our study was to specifically investigate the temporal variability of daily nest predation risk in superb fairy-wrens, in relation to: (i) the age of the young within the nest; (ii) the timing within the breeding season; and (iii) variation between years. For each of these temporal scales, we considered daily nest predation risk during the overall nesting period (i.e., the total duration of a nest from incubation to completion) and for three specific stages of development: the incubation stage, the early nestling stage, and the late nestling stage (details below). We assessed temporal changes in risk of predation of superb fairy-wren nests by quantifying as follows:

1. Differences in daily nest predation rates between different developmental stages. We anticipated higher predation of nestlings than of eggs due to their greater nutritional value of nestlings. Additionally, during the nestling stage, there is an increased presence of visual and acoustic cues that may be utilised by predators, such as pied currawongs, to locate nests (Dunn & Cockburn, 1996; Macgregor & Cockburn, 2002).
2. If older nestlings face a higher risk of daily predation compared to younger nestlings, based on previous evidence showing positive associations between the amplitude of superb fairy-wren nestling begging calls and age (Macgregor & Cockburn, 2002).
3. Changes in rates of daily nest predation across the superb fairy-wren breeding season, and whether within-season trends differed between years. We aimed to consider in particular if changes in predation risk closely corresponded to the relatively short period of time when pied currawongs raise their own young, and thus food demand may be increased (Prawiradilaga, 1996).
4. If daily nest predation rates have increased over the duration of our study, with the aim of determining whether changes in predation pressure could explain the observed decline in population size of superb fairy-wrens in our study area (Lv et al. 2023).

MATERIALS AND METHODS

Study area and data collection

Our analyses were based on data from a long-term study of superb fairy-wrens in and adjacent to the Australian National Botanic Gardens, Canberra, Australian Capital Territory, Australia (35°16'30.0"S, 149°06'28.8"E). We have studied the population continuously since 1988, although because the study was progressively expanded until 1993, we report here data from 1994 to 2020. Almost all individuals in the study population were uniquely colour-banded during the study period, either as nestlings if they were born in the study area or as juveniles or adults if they dispersed into the study area, thus allowing for individual recognition.

Throughout each breeding season, we surveyed all nests belonging to each superb fairy-wren breeding pair in the study population. Nests were located by observing females with nesting material or by tracking them to the nest during egg laying or incubation. We monitored the progress of each nest every second day throughout the nesting period. To minimise disturbance, we observed nests from a distance with binoculars and only approached them: (i) around the expected dates of laying, incubation, and hatching; (ii) when colour-banding nestlings; or (iii) when group members were no longer attending the nest. While most nests were found during nest building or egg laying stages, some nests were not. In these rare cases, we estimated the incubation and hatch dates as follows: (i) if a nest was found during the incubation stage and the eggs hatched, we estimated the incubation date by subtracting 13 days (i.e., the average incubation period; Rowley & Russell, 1997) from the hatching date; (ii) if a nest was found during the incubation stage but was depredated before nestlings were observed, we estimated the average incubation date from the earliest and latest possible incubation dates, based on information relating to either the number of days the nest was observed during incubation or the time taken for the female to renest after a nest failure. After a nest failure, females immediately initiate new nests, and typically lay the first egg of the new clutch 7 to 8 days later (Cockburn et al., 2016; Double & Cockburn, 2000; Turner et al., 2022); and (iii) if a nest was found during the nestling stage, we estimated the hatch date based on the physical appearance of the nestlings.

Measuring daily nest predation rates

A nest was considered active on a given day if it was attended to by at least one group member. Depredation was assumed when all eggs or nestlings disappeared before the expected fledging date (*c.* 24 days from the onset of incubation). Because we do not survey nests every day, we estimated the date of predation as the midpoint between observations, considering the time required for the female to renest (as described above). A nest was considered successful if we observed fledging, heard fledgling begging calls, or saw at least one fledgling. For our analyses, nests that failed due to reasons other than predation such as heavy rainfall and flooding of the nest site, inadvertent human activity such as pruning by gardeners, the death of the breeding female, or rare cases of brood parasitism by Australian cuckoos (Turner et al., 2022) were excluded (n = 176). The final dataset used in this study therefore comprised observations from a total of 3997 nests (n = 76489 nest-days across 27 years) from 787 females. The timing of nest initiation and the final fate of these 3997 nests in relation to their initiation date are summarised in Figure 1. From these data, we estimated daily nest predation rates for each nest during the following four distinct stages, with nests assigned a binary score of 1 if they were depredated on a given nest-day within each stage (otherwise, 0):

1. O*verall nesting period*: 1 to 24 days from the onset of incubation.
2. I*ncubation stage*: 1 to 13 days from the onset of incubation.
3. E*arly nestling stage:* 1 to 5 days post-hatching.
4. L*ate nestling stage*: 6 to 11 days post-hatching.

We chose a brood age of 6 days as the threshold to distinguish between the early nestling stage and the late nestling stage, as it represents approximately half the average duration of the full nestling stage observed in successful nests.

Statistical analysis

Analyses were conducted using a Bayesian framework implemented in the package 'brms' (v.2.15.0; Bürkner, 2017) in R (v.4.0.5; R Core Team, 2021). We constructed Bayesian hierarchical generalised linear regression models for the overall nesting period and for each of the three stages of development (as described above). The models were fitted with a Bernoulli-error distribution and a logit link function. All explanatory parameters were mean standardised for analysis (Harrison et al., 2018; Schielzeth, 2010). We assessed correlations between covariates and all values were <0.58, indicating no concerns regarding multicollinearity (Dormann et al., 2013, Zuur et al., 2009). Unless stated otherwise, each model contained the following six fixed effects related to time:

1. *Development stage:* Fitted as a three-level factor: incubation stage, early nestling stage, and late nestling stage. Note that the development stage was modelled only in the overall nesting period model.
2. *Age of young*: Fitted as a covariate, corresponding to the clutch age during the incubation stage and the brood age during the two nestling stages (i.e., post-hatching). Note age was not included in the overall nesting period model. For 154 nests (0.04% of the total), predation occurred after day 13 of incubation, but hatching of eggs had not been confirmed. In these cases, we included daily nest predation data in the incubation stage model only to reduce any biasing of results.
3. *Fortnight*: Fitted as a covariate with a quadratic effect. We divided the breeding season into 15 fortnight-long intervals to analyse the within-season trends in daily nest predation (following, e.g., Hajduk et al., 2020). The first fortnight (fortnight 1) of each breeding season began on 1 September and ended on 14 September, and included the earliest active nest observed during the study period. The last fortnight (fortnight 15) began on 16 March and ended on 29 March, and included the latest active nest during the study period. Out of the total 3977 nests considered in this study, a total of 109 nests were active in fortnights 1 or 2 (mean ± SD: 6.81 ± 5.97 nests per year) and a total of 496 nests were active in fortnight 11 or later (mean ± SD: 19.84 ± 10.98 nests per year; Figure S1). For these rarer cases, we grouped nests that appeared very early into a single category (i.e., ≤fortnight 2), and nests that appeared very late into another single category (i.e., fortnight 11+; Figure S1).
4. *Year:* Fitted as a covariate ranging from 1994 to 2020.
5. *Relative daily nest density*: To model variation in nest density (i.e., the number of nests in the study area at a specific time during the breeding season), we determined the proportion of active nests at that particular time. This was calculated by dividing the number of nests active on a given day by the total number of nests in that year. The resulting proportion was fitted as a covariate ranging from 0.005 to 0.373.

6. *Total seasonal nest density*: To model variation in nest density between years, we estimated the total number of nests in a given year. This was fitted as a covariate ranging from 66 to 224.

In addition to the above temporal fixed effects, our models also included four other fixed effects that may affect daily nest predation rates:

1. *Clutch/brood size*: The number of eggs in a nest during incubation and the number of nestlings in a nest post-hatching, accounting for changes in size due to unhatched eggs or, very rarely, partially depredated nests during the incubation stage. Fitted as a covariate ranging from 1 to 5 (with a strong mode of 3; Cockburn et al., 2016).
2. *Number of helpers*: Fitted as a three-level factor: 0, 1, and 2+, where the '2+' level consisted mainly of 2 helpers (following, e.g., Hajduk et al. 2021).
3. *Female age*: Fitted as a two-level factor: 1 year old, and 2+ year old (following, e.g., Kruuk et al., 2015; Hajduk et al., 2018). We opted for this categorisation, rather than treating female age as a continuous covariate based on findings from previous studies of our population, which have revealed no significant change in female breeding performance (i.e., the number of independent offspring produced in a given breeding season) subsequent to an initial increase observed from 1 year old to 2 years old (Cockburn et al., 2008; Cooper et al., 2021).
4. *Nest height*: Measured as the distance from the ground to the base of the nest entrance. For the purpose of this study, we fitted nest height as a 2-level factor: ≤50 cm, and >50 cm. This categorisation was necessitated, in part, by different methodologies over the years. Specifically, between 1994 to 2012, nest height was recorded as a multi-level categorical variable (0–25 cm, 26–50 cm, 51–100 cm, 101–200 cm, and >200 cm); whereas, from 2013, nest height was recorded to the nearest centimetre, with nests ranging from 5 to 600 cm off the ground (mean ± SD: 69.05 ± 66.25 cm; n = 1298 nests). Note, the nest height categories used in our analyses closely correspond with the ≤60 cm

and >60 cm categories used in a previous study of superb fairy-wren nest predation by Colombelli-Négrel & Kleindorfer (2009).

Each model also included three random effects, which were treated as multi-level factors:

1. *Year*: To account for multiple measurements within each breeding season.
2. *Female ID:* To account for repeated measurements of individual females during the during study period.
3. *Nest ID:* To account for repeated measurements of the same nest.

We considered two-way interactions between all fixed effects. However, non-significant interaction effects in all analyses were discarded from final models (and are not presented here). To assess whether the within-season patterns in daily nest predation rates varied across years, we fitted two additional random effects terms separately into each model. The first term included a linear effect of fortnight nested within each year, which modelled the variation of daily nest predation rates across different fortnights for each year separately. The second term incorporated a quadratic effect of fortnight (fortnight + fortnight^2) nested within each year, and thus allowed for a curved or non-linear relationship between the fortnight and daily nest predation rates within each year.

We used the Bayesian expected log predictive density leave-one-out (ELPD $_{\text{LOO}}$) method to determine the random effects structure that best explained our data. This method, which was implemented using the *loo* function in the package 'loo' (v.2.4.1; Vehtari et al., 2020), calculates the log likelihood of posterior predictions by fitting each model multiple times, while excluding one data point in each iteration (Vehtari et al., 2017). The resulting log likelihoods are then averaged across all data points to derive the final ELPD $_{\text{LOO}}$ value. Similar to other commonly used information criteria such as the Akaike Information Criterion (AIC; Akaike, 1974) or the Widely Applicable Information Criterion (WAIC; Watanabe, 2013, 2021;

Watanabe & Opper, 2010), ELPD $_{LOO}$ values reflect the predictive performance of different models, albeit on a different scale (Gelman et al., 2014). Models with higher ELPD $_{LOO}$ values are considered to have better predictive performance. Typically, models are considered to be distinct if the difference in ELPD $_{LOO}$ between them (ΔELPD $_{LOO}$) is greater than 4 (Bürkner et al., 2020; Sivula et al., 2020; Vehtari et al., 2017).

We fitted all models on 4 independent Markov Chain Monte Carlo (MCMC) chains for a total of 10000 iterations per chain. To reduce autocorrelation between samples, we used a thinning interval of 6. The warm-up period on each MCMC chain was set to 4000 iterations, resulting in 4000 posterior samples overall. We specified weakly informative priors with a normal-error distribution for each parameter, with the mean (μ) set to 0 and the variance (σ^2) set to 1 (Gelman et al., 2015). To assess the convergence of the MCMC chains, we examined the potential scale reduction ($\hat{R}$) factors for all parameters. The $\hat{R}$ values for all parameters were <1.05, indicating convergence (Gelman et al., 2013; Vehtari et al., 2021). We present the model parameter estimates as the posterior means along with their standard deviations (± SD) and 95% credible intervals (CI). We considered there to be statistical support for specific parameters when the 95% CI did not span zero.

RESULTS

From our analyses of 3997 superb fairy-wren nests (n = 76489 nest-days across 27 years), a total of 2177 nests were depredated (54.47%; which includes 154 nests depredated after day 13 of incubation, but where hatching was not confirmed); the remaining 1820 nests (45.53%) successfully fledged at least one young. Figure 1 shows the timing of nest initiation across the breeding season, and the relative proportion of the different fates that a nest could experience, in relation to its initiation date. From these data, we then considered the causes of variation in rates of predation on a daily basis.

Development stage

Daily nest predation rates increased across the different stages of development (Figure 2; Table 1). During the incubation stage, the daily nest predation rate averaged 0.016 ± 0.124 SD (n = 47728 nest-days), resulting in 18.50% of nests (n = 740 nests) being depredated before their expected hatch date. During the early nestling stage (1 to 5 days post-hatching), the mean daily nest predation rate increased to 0.025 ± 0.158 SD (n = 15014 nest-days), with 12.30% of nests (n = 382 nests) being depredated out of the 3103 nests known to have hatched. Daily nest predation rates peaked during the late nestling stage (6 to 11 days old post-hatching) at 0.066 ± 0.248 SD (n = 13747 nest-days). Of the 2721 nests that reached the late nestling stage, a total of 901 (33.11%) were depredated before their expected fledging date.

Age of young within each development stage

Within the incubation and early nestling stages, the risk of predation increased with the age of young, though the rate of increase was much greater for the early nestling stage. The high predation risk in the late nestling stage remained constant as the brood aged (Figure 2; Table 1).

Within-season trends in nest predation

Overall, daily nest predation rates increased from the beginning of the breeding season until approximately fortnight 6 (10 November to 23 November), at which point predation plateaued then declined from approximately fortnight 8 (8 December to 21 December) onwards until the end of the breeding season (Figure 3; Table 1). This pattern, characterised by the timing and duration of predation peaks during each developmental stage in a given year, was captured by a quadratic effect of fortnight in each analysis (Figure 3; Table 1).

Comparisons of models with different random effects structures indicated no evidence that within-season trends of daily nest predation differed between years. In all analyses, there was no evidence for difference in support for models containing a random intercept of year versus random regressions with either a linear or quadratic effect of fortnight nested within year

(ΔELPD $_{\mathrm{LOO}}$ ≤4; Table S2). Note, the estimates presented in Table 1 are derived from the model with the more complex random effects structure. This choice was made in order to report the $\sqrt{\text{Variance}}$ estimates for these terms.

Long-term trends in nest predation

There was no statistical support for directional change in daily nest predation rates over the study during the incubation stage, early nestling stage, or the overall nesting period (Figure 4a–c; Table 1). Daily nest predation rates during the late nestling stage decreased over time (Figure 4d, Table 1). However, this association was strongly affected by exceptionally low rates of nest predation in 2020, without which the decline was non-significant (posterior mean ± SD: -0.08 ± 0.05 [95% CI: -0.19, 0.02]).

Nest density

There was no evidence of an any association of nest density with daily nest predation rates during the overall nesting period nor during any specific stage of development. Nests were no more likely to be depredated during periods of higher nest density, either within a given day each year (i.e., relative daily nest density) or between years (i.e., total seasonal nest density) (Table 1).

Clutch/brood size

There was very little variation in clutch/brood size, as most clutches comprised of 3 eggs (n = 2756 nests; 69.30% of the total) or 4 eggs (n = 996 nests; 24.92% of the total). Only in extremely rare cases were there clutch sizes of 1 egg (n = 21 nests), 2 eggs (n = 221 nests) or 5 eggs (n = 3 nests). Nevertheless, we found contrasting effects of clutch/brood size during the different development stages. Larger clutch sizes had reduced daily nest predation rates in the incubation stage (Table 1). In contrast, daily nest predation rates of younger nestlings increased with brood size, but there was no further increase during the late nestling stage

(Table 1). Consistent with these findings, we found an interaction effect between clutch/brood size and development stage in our analysis of the overall nesting period (Table 1).

Number of helpers

The presence of helpers was partially associated with reduced predation, with daily nest predation rates averaging 0.028 ± 0.164 SD (n = 45865 nest-days) for nests without helpers, 0.025 ± 0.156 SD (n = 19654 nest-days) for nests with one helper, and 0.025 ± 0.155 SD (n = 10970 nest-days) for nests with two or more helpers. However, while the overall nesting period model indicated a statistically significant reduction in predation rates among nests with helpers, there was little evidence that having two or more helpers, as opposed to just one, enhanced this effect (Table 1). Moreover, the influence of helpers on daily nest predation rates during each developmental stage was marginal; only during the incubation stage did we observe a statistically significant effect of helpers, with the presence of two or more helpers being associated with reduced predation of eggs (Table 1).

Female age

Older females were associated with reduced daily nest predation rates, although effects were non-significant during the incubation stage and late nestling stage (Table 1). During the early nestling stage, the daily predation rate of nests of one-year-old females was on average 0.033 ± 0.177 SD (n = 4155 nest-days) compared to 0.023 ± 0.149 SD (n = 10859 nest-days) for nests of older mothers.

Nest height

Overall, 65.68% of the 2723 nests built within 50 cm of the ground were depredated, compared with only 41.92% of the 1274 nests built higher than 50 cm above ground. During the overall nesting period and all stages of development, nests built closer to the ground were more likely to be depredated (Table 1). We found no evidence of an interaction effect between nest height and development stage (which we do not present here) indicating that the observed decrease in daily nest predation with nest height occurred at a similar rate across the incubation stage, early nestling stage, and late nestling stage.

DISCUSSION

We present here an analysis of nest predation in a wild population of superb fairy-wrens, a multi-brooded passerine bird endemic to southeastern Australia (Cockburn et al., 2016; Rowley & Russell, 1997), using repeat survey data spanning nearly three decades from almost 4000 naturally occurring nests. Our analyses revealed variation in overall and development stage-specific daily nest predation rates at three temporal scales related to the age of the young in the nests, the timing within the breeding season, and differences between years. However, we found no evidence that within-season trends differed between years. Furthermore, we found no indication that temporal variation in nest density influenced nest predation rates, with nests being equally vulnerable to predation during periods of higher nest density, both within the breeding season and between different years, than periods of lower nest density. In addition, we found that females with fewer helpers, younger females, and nests built at lower heights all experienced higher overall daily nest predation rates. However, the magnitude and significance of these effects varied between different development stages. Furthermore, we found mixed effects of clutch and brood size. We discuss the implications of these findings below, in particular focusing on the role of pied currawongs as a nest predator.

Changes in predation with the age of the young in the nest

Our findings indicate a significant increase in the vulnerability of superb fairy-wren nests to predation as the young age and develop. Previous studies of superb fairy-wrens have shown that as nestlings grow older, parents and helpers collectively – but mothers especially – increase their provisioning rates, indicating an active effort to meet the increasing demands of the nestlings (Dunn & Cockburn, 1996). Additionally, Macgregor and Cockburn (2002) found that the begging behaviour of superb fairy-wren nestlings intensifies with age, peaking at 8 days post-hatching. These findings, along with our results, support hypotheses suggesting that increased parental activity and vocalisations of the nestlings may inadvertently expose the nest's location to visually and auditorily oriented predators, such as pied currawongs, thereby increasing the risk of nestling predation (Haff & Magrath, 2011; Haskell, 1994, 2002; Husby, 2019; Muchai & du Plessis, 2005). Interestingly, we did not find any evidence that the age of the brood influenced predation risk during the late nestling stage. This suggests that there may be a plateau in predation risk during this stage, possibly due to the levelling off of nestling begging intensity and, presumably, of parental activity.

Our study did not investigate the impact of surrounding vegetation structure on nest predation. However, two previous studies conducted on our study population observed increased nest predation rates with higher vegetation density, despite superb fairy-wrens preferentially choosing to nest in such vegetation (Backhouse et al., 2023; Turner et al., 2023). These findings suggest that the vegetation structure of nest-sites preferred by superb fairy-wrens may not sufficiently reduce the transmission of sensory cues to predators. Nevertheless, further research is needed to explore whether variation in vegetation surrounding individual nests is associated with variation in predation rates, particularly among older nestlings.

Seasonal-related patterns in nest predation and the role of pied currawongs

Like previous studies (Borgmann et al., 2013; Grant et al., 2005; Husby & Hoset, 2018; Smith & Wilson, 2010; Wilson et al., 2007), we identified variable within-season patterns of nest predation. Specifically, in all analyses, we observed lower rates of nest predation during the early and late stages of the breeding season, while higher rates of nest predation occurred approximately mid-season. These patterns closely correspond to the pied currawongs' breeding ecology (Prawiradilaga, 1996).

Although pied currawongs primarily consume fruits and seeds during winter, their diet shifts during spring and summer when they feed on arthropods. To sustain their growing young during their own breeding season, which spans from approximately September to December, they rely heavily on the eggs and, particularly, the nestlings of other bird species (Prawiradilaga, 1996; Wood, 1998, 2000). Notably, during this period, pied currawongs are often implicated as the dominant nest predator of most small passerines that occupy their range (Bayly & Blumstein, 2001; Fulton, 2019; Fulton & Ford, 2001). While superb fairy-wrens are vulnerable to a number of nest predators (Rowley & Russell, 1997; see Table S1), it is likely that only pied currawongs can explain our mid-season peaks in nest predation. Among the other predators in our study area, for which we have direct evidence of them depredating superb fairy-wren nests (Table S1), red foxes are likely to pose a constant risk throughout the year, whereas eastern brown snakes are maximally active at intermediate temperatures, and so would be expected to demonstrate an inverse seasonal trend to our observations. Consequently, this finding strongly suggests that pied currawongs are the dominant predator of superb fairy-wren nests in our study area, and that they have consistently maintained their dominance throughout each year of our study.

Despite substantial variation in the timing of breeding and the abundance of breeding pairs between years (Lv et al., 2019), we did not observe any significant differences in these within-season trends between years. We also found no direct effects of relative daily nest density (i.e., within-season patterns of nest density) or total seasonal nest density (i.e., between-year patterns of nest density) as predictors of nest predation. Several factors may explain this lack of an association of nest density. First, it is possible that the density of superb fairy-wren nests, even during the peak of the breeding season, is insufficient to detect density dependence. The highest relative daily nest density recorded during our study period was 0.373, which corresponded to a total of 40 active nests on a given day (out of a seasonal total of 118 nests in 2002). This equates to less than 1 nest per hectare across our study area. Additionally, the highest total seasonal nest density observed was 224 nests in 1995, equivalent to 3.446 nests per hectare throughout the entire breeding season. Second, although pied currawongs are common predators of superb fairy-wren nests, the latter species is not their sole focus of predation. A previous study by Prawiradilaga (1996) has shown that the diet of nestling pied currawongs includes not only superb fairy-wren eggs and nestlings, but also other prey items, including from up to fifteen other bird species. Therefore, the lack of an association between superb fairy-wren nest density and nest predation in our study may be attributed to the presence of alternative prey, which may offer higher nutritional value or be more easily detectable. Consequently, the observed seasonal patterns of superb fairy-wren nest predation may not be determined by nest density, but rather influenced by the dynamic availability of alternative prey resources during the pied currawong breeding season.

We found limited evidence of a long-term directional change in predation. While we did observe a decrease in nest predation during the late nestling stage over time, this trend was driven by unusually low rates in a single year, 2020. When excluding this outlier, the observed decline lost statistical significance. These findings partly contrast with our previous research on the same population, which showed decreased nest predation rates over the years (Backhouse et al., 2023; Turner et al., 2023). However, there are notable differences between our study and these two earlier ones, particularly regarding the time period and spatial scales considered when assessing nest predation. In this study, we specifically focused on individual daily nest-level observations, whereas the two previous studies examined nest predation rates at larger habitat-level scales over the entire breeding season. These differences could potentially account for the contrasting results observed. Nevertheless, across these three studies, there is clearly no evidence of any increase in predation over the study, and hence no indication that the observed population decline (Backhouse et al., 2023; Lv et al., 2023) may be driven by increased predation.

Previously, pied currawongs were seasonal migrants, breeding in highland montane areas during spring and summer and congregating in lowland areas during autumn and winter (Lenz, 1990; Prawiradilaga, 1996; Redshaw, 1968). In recent decades, they have established breeding populations near human settlements in lowland areas, and these populations have increased in size over the years (Fulton & Ford, 2001; Menkhorst et al., 2017), including in our study area (A. Cockburn, unpublished data; Prawiradilaga, 1996). The lack of an increase in superb fairy-wren nest predation between years, despite an increase in the pied currawong population size over the same period, is therefore unclear (A. Cockburn, unpublished data). This is particularly puzzling as the within-season trends, as discussed above, suggest that pied currawongs are consistently the dominant superb fairy-wren nest predator. However, notably, previous studies focusing on the impact of nest predation by pied currawongs have similarly failed to demonstrate any population decline in the observed prey species (Prawiradilaga, 1996; Wood, 1995, 1998). One possible explanation is that the increased numbers of pied currawongs may not necessarily correlate with a rise in the numbers of their breeding pairs or nestlings. It is these nestlings that are the primary meat consumers in this species (Prawiradilaga, 1996).

Other predictors of superb fairy-wren nest predation

We demonstrate that several additional factors have a significant influence on the predation risk of superb fairy-wren nests. Specifically, we found complex associations between clutch or brood size and daily nest predation rates. Larger clutches during the incubation stage were associated with lower rates of predation, whilst larger broods during the early nestling stage were associated with higher rates of predation, possibly due to more frequent and louder begging calls and higher provisioning rates that could attract predators. However, we did not observe any significant change in predation rates during the late nestling stage with varying brood size. Thus, the underlying mechanisms driving these patterns remains unclear, but we suggest that there may be a levelling-off effect, whereby older nestlings may be loud enough to be heard easily regardless of brood size. Although previous studies have documented seasonal peaks or seasonal declines in clutch size and subsequently brood size in some species (Borgmann et al., 2013; Crick et al., 1993; Decker et al., 2012), our daily nest-level analyses revealed only a weak positive effect (Pearson correlation coefficient = 0.03) and no discernible effect (Pearson correlation coefficient = 0.00) between clutch/brood size and fortnight, or a quadratic effect of fortnight, respectively. Importantly, because we accounted for these fine-scale time periods in our analyses, the associations we observed between clutch/brood size and daily predation risk cannot be solely explained by seasonality.

In addition, our findings show that nests belonging to older females and those attended by a higher number of helpers had reduced rates of daily nest predation throughout the overall nesting period. Although these trends remained generally consistent across different stages of development, the statistical significance of these effects varied. However, our study does not establish a causal relationship between these factors and nest predation rates. In the superb fairy-wren system, the number of helpers within a group is likely correlated with aspects of territory quality (Cockburn et al., 2008). Male helpers are philopatric, and generally live and die on either their natal territory or an immediate neighbouring territory (Mulder, 1995). Thus, territories must demonstrate lower nest predation rates in previous years in order for helpers to accumulate (Cockburn et al., 2008). Moreover, older females are more likely to inhabit territories containing helpers (Backhouse et al., 2023). Future studies are therefore still needed in order to disentangle the effects of the social environment (e.g., number of helpers and female age) from the physical characteristics of the territory on rates of nest predation in superb fairy-wrens (but see, Backhouse et al., 2023; Taylor, 2021).

Finally, nests situated higher above the ground experienced comparatively lower predation rates. This pattern was consistent across all development stages, and also supports findings from a previous study on another population of superb fairy-wrens (Colombelli-Négrel & Kleindorfer, 2009) and more generally among open-nesting forest passerines (Matysioková & Remeš, 2023). The association between nest height and predation risk cannot be solely attributed to any seasonal-related variation in nest height (Guan et al., 2018; Hatchwell et al., 1999) as we accounted for fortnight (and a quadratic effect of fortnight) in our analyses. Rather, the lower predation rates for higher nests may be attributed to the pied currawongs' ability to target nests from any height (Haff & Magrath, 2011) and the fact that other known predators in our study area, such as the red fox and the eastern brown snake are both grounddwelling, although the latter species is capable of climbing small trees and shrubs (Sleeth et al., 2021). Thus, higher nests may be afforded a certain level of protection against these specific predators. However, we did observe all three of these predators preying on nests at both height intervals considered in this study (Table S1), and thus, the lower predation rates for higher nests cannot be solely attributed to a predator exclusion effect.

CONCLUSION

Our study provides fine-scale insights into the temporal patterns of nest predation in a wild population of superb fairy-wrens in southeastern Australia. By examining these dynamics, we shed light on the role of pied currawongs as an important nest predator in our study system. Our findings contribute to a greater understanding of the factors influencing nest predation in a cooperatively breeding and multi-brooded passerine bird in the Southern Hemisphere, whilst also addressing the methodological and geographical research biases of previous studies on nest predation.

ACKNOWLEDGEMENTS

We wish to thank the many field assistants who have contributed to the long-term study over the years. We are grateful to the Australian National Botanic Gardens for permission to work at the study site (Permit Number: 2013/14-1) and for logistical support, and to the Australian Research Council for long-term funding of the project, of which the most recent grant was DP190100424 to Loeske E. B. Kruuk, Andrew Cockburn, and Martijn van de Pol. Richard S. Turner was supported through an Australian National University HDR Scholarship, and through funding by the Ecological Society of Australia's Holsworth Wildlife Research Endowment Fund. Ethics approval was granted by the Australian National University Animal Experimentation Ethics Committee (Protocol Number: A2019/23). We thank Sue Lewis, Anne Peters, and Bradley Law for useful comments on an earlier draft of the manuscript. We acknowledge the Ngunnawal people, the traditional custodians of the land upon which our study was undertaken, and we pay our respects to their elders, past, present, and emerging.

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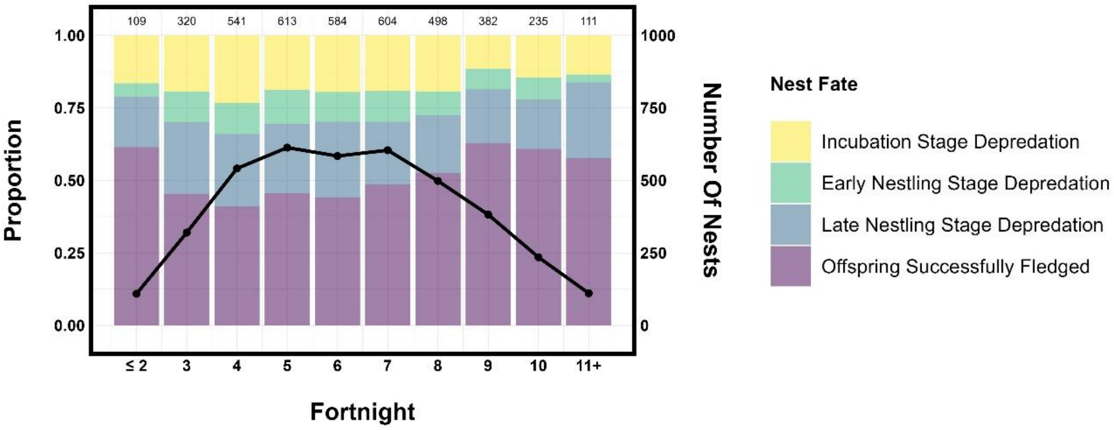

Figure 1: *Summary of superb fairy-wren nesting data, showing the ultimate fate of nests in relation to the fortnight in which they were initiated. The first fortnight (fortnight 1) extends from 1 September to 14 September. The black line illustrates the total number of nests (right-hand Y axis) initiated within each fortnight throughout the study period (1994–2020), with corresponding sample sizes given at the top of the plot. The coloured bars represent the variation in nest fate, showing the proportion (left-hand Y axis) of nests initiated in that fortnight that were ultimately subject to predation at the incubation (yellow), early nestling (green) or late nestling (blue) stage, or that successfully fledged at least one offspring (purple). Note, the values presented here reflect the fate of a nest based on its initiation date, but the actual completion of the nest may be several weeks after the initiation date. Nests that failed for reasons other than predation were excluded from the analyses and are not depicted here (see main text for further details).*

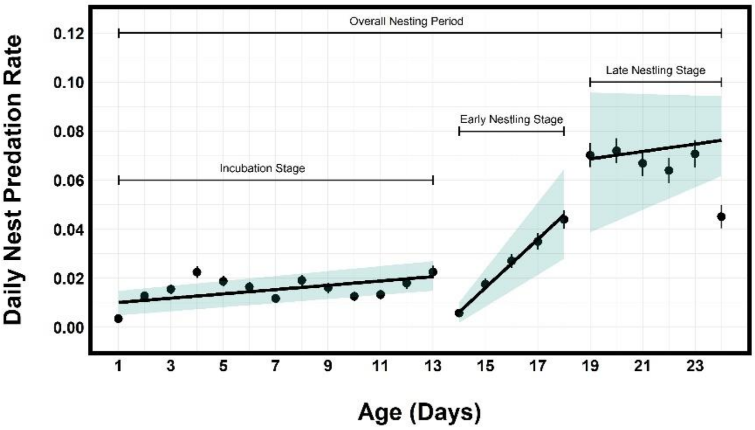

Figure 2: *Changes in daily nest predation rates in relation to the age of the young in the nest within each stage of development. Regression lines show model estimated marginal means (± 95% CI), after correcting for fixed effect parameters, as described in Methods. The points show the mean (± SE) of the raw data for each age. Model estimates and sample sizes are provided in Table 1.*

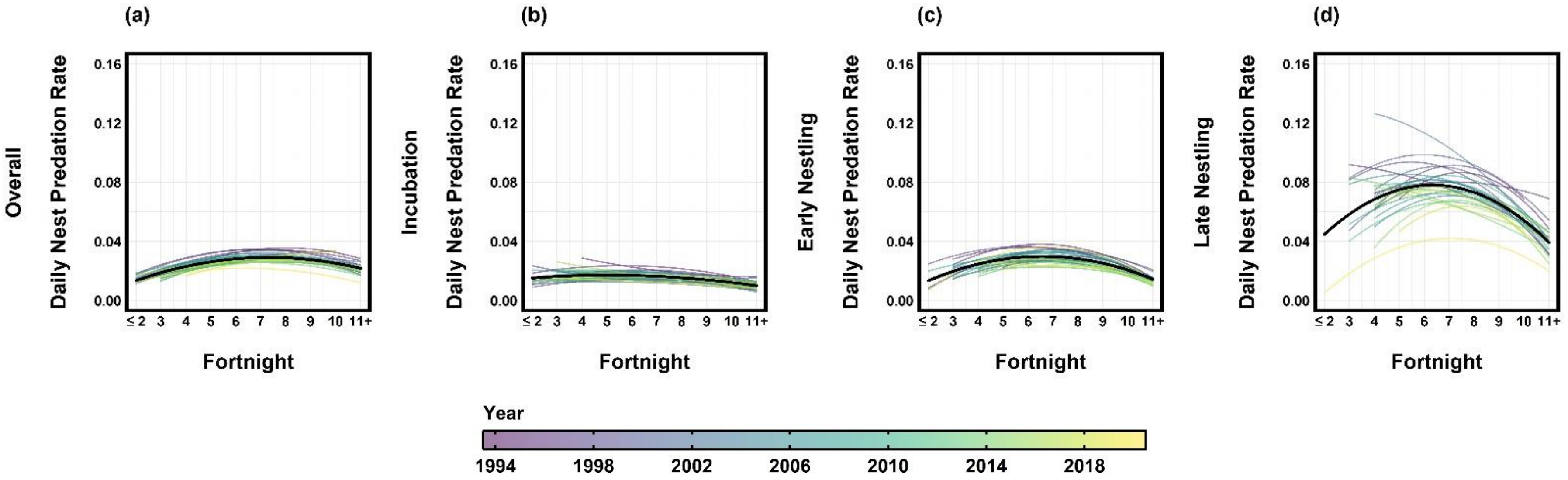

Figure 3: *Within-season trends in daily nest predation rate for each of the 27 years of the study (1994 to 2020) during the (a) overall nesting period; (b) incubation stage; (c) early nestling stage; and (d) late nestling stage. Regression lines show the predicted reaction norms for each year. The black line shows the mean predicted reaction norm across all years.*

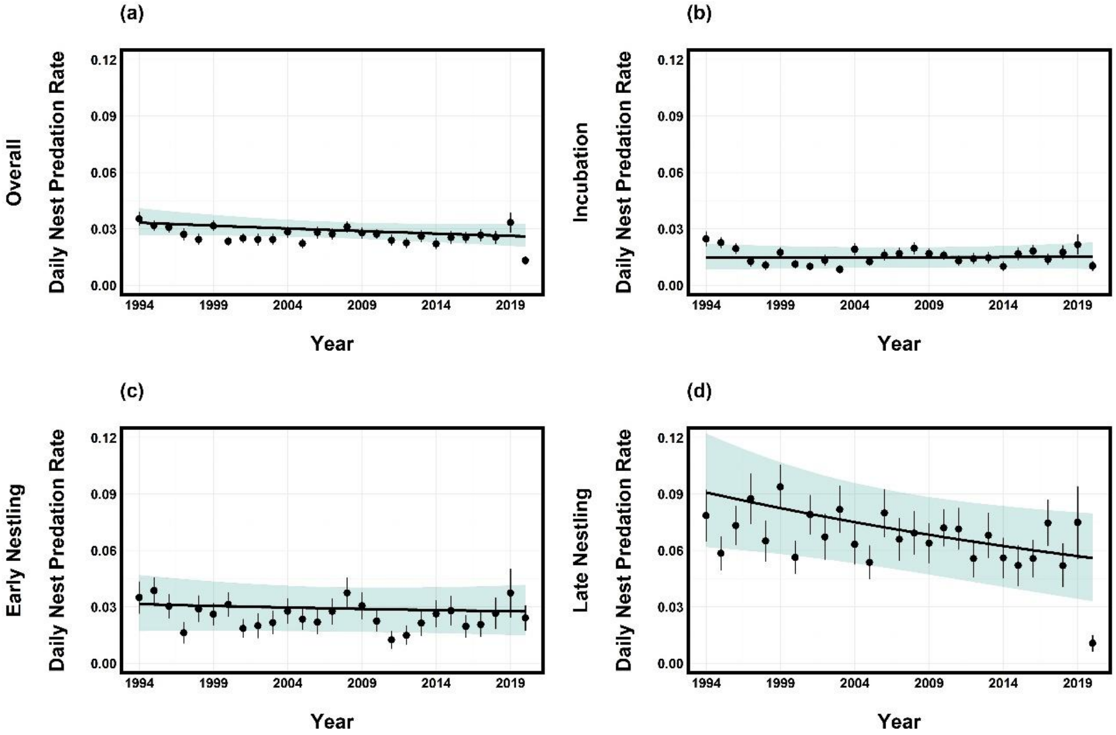

Figure 4: *Changes in daily nest predation rate over the study period (1994 to 2020) during the (a) overall nesting period; (b) incubation stage; (c) early nestling stage; and (d) late nestling stage. Regression lines show the model estimated marginal means (± 95% CI), after correcting for fixed effect parameters, as described in Methods. The points show the mean (± SE) of the raw data for each year. Model estimates are provided in Table 1.*

Table 1: *Summaries of the Bayesian hierarchical generalised linear regression models of daily nest predation rates during the overall nesting period, and then its three components of the incubation stage, the early nestling stage, and the late nestling stage. All explanatory parameters were mean standardised for analysis. Parameter estimates are presented as posterior means ± standard deviation (SD) and 95% credible intervals (CI) and are on the logit link scale. Fixed effect estimates for which the 95% CI do not overlap zero are highlighted in bold.*

Parameters	**Overall**	**Incubation**	**Early Nestling**	**Late Nestling**
Fixed Effects	Estimate ± SD (95% CI)	Estimate ± SD (95% CI)	Estimate ± SD (95% CI)	Estimate ± SD (95% CI)
Intercept	**-3.821 ± 0.074 (-3.970, -3.682)**	**-4.084 ± 0.187 (-4.499, -3.773)**	**-3.083 ± 0.124 (-3.331, -2.844)**	**-2.343 ± 0.111 (-2.564, -2.133)**
Age of Young		**0.226 ± 0.064 (0.123, 0.383)**	**0.600 ± 0.068 (0.476, 0.746)**	0.046 ± 0.104 (-0.107, 0.275)
Fortnight	**-0.136 ± 0.030 (-0.197, -0.077)**	**-0.132 ± 0.053 (-0.237, -0.032)**	**-0.198 ± 0.079 (-0.358, -0.047)**	**-0.212 ± 0.072 (-0.359, 0.075)**
Fortnight^2	**-0.123 ± 0.035 (-0.191, -0.053)**	**-0.116 ± 0.058 (-0.232, -0.001)**	**-0.178 ± 0.082 (-0.343, -0.016)**	**-0.140 ± 0.066 (-0.275, -0.016)**
Year	-0.075 ± 0.053 (-0.180, 0.028)	0.008 ± 0.086 (-0.164, 0.175)	-0.040 ± 0.080 (-0.197, 0.119)	**-0.155 ± 0.079 (-0.328, -0.009)**
Relative Daily Nest Density	-0.029 ± 0.037 (-0.100, 0.045)	-0.049 ± 0.063 (-0.173, 0.077)	-0.098 ± 0.088 (-0.271, 0.082)	0.008 ± 0.067 (-0.125, 0.140)
Total Seasonal Nest Density	0.011 ± 0.054 (-0.102, 0.117)	0.094 ± 0.084 (-0.070, 0.259)	0.010 ± 0.085 (-0.161, 0.174)	-0.035 ± 0.077 (-0.189, 0.116)
Clutch/Brood Size	**-0.203 ± 0.043 (-0.286, -0.119)**	**-0.207 ± 0.044 (-0.294, -0.122)**	**0.164 ± 0.068 (0.047, 0.282)**	0.050 ± 0.046 (-0.037, 0.147)
Number of Helpers (Relative to 0 Helpers)				
1 Helper	**-0.123 ± 0.058 (-0.237, -0.013)**	-0.113 ± 0.101 (-0.312, 0.081)	-0.081 ± 0.133 (-0.339, 0.178)	-0.173 ± 0.105 (-0.386, 0.023)
2+ Helpers	**-0.168 ± 0.076 (-0.315, -0.021)**	**-0.362 ± 0.138 (-0.640, -0.094)**	0.002 ± 0.164 (-0.313, 0.316)	-0.093 ± 0.127 (-0.351, 0.156)
Female Age (Relative to 1 Year Old)				
2+ Years Old	**-0.172 ± 0.055 (-0.279, -0.061)**	-0.099 ± 0.097 (-0.284, 0.094)	**-0.401 ± 0.123 (-0.642, -0.164)**	-0.186 ± 0.100 (-0.386, 0.002)
Nest Height (Relative to <50 cm)				
>50 cm	**-0.394 ± 0.057 (-0.509, -0.279)**	**-0.454 ± 0.105 (-0.663, -0.248)**	**-0.513 ± 0.135 (-0.784, -0.256)**	**-0.337 ± 0.106 (-0.567, -0.148)**
Development Stage (Relative to Incubation)				
Early Nestling	**0.575 ± 0.066 (0.442, 0.702)**			
Late Nestling	**1.649 ± 0.060 (1.536, 1.768)**			
Clutch/Brood Size x Early Nestling †	**0.337 ± 0.062 (0.215, 0.459)**			
Clutch/Brood Size x Late Nestling †	**0.234 ± 0.051 (0.136, 0.331)**			
Random Effects	$\sqrt{\text{Variance}}$ ± SD (95% CI)	$\sqrt{\text{Variance}}$ ± SD (95% CI)	$\sqrt{\text{Variance}}$ ± SD (95% CI)	$\sqrt{\text{Variance}}$ ± SD (95% CI)
Year	0.172 ± 0.052 (0.078, 0.285)	0.252 ± 0.089 (0.081, 0.437)	0.165 ± 0.107 (0.008, 0.405)	0.172 ± 0.097 (0.014, 0.385)
	(n = 27)	(n = 27)	(n = 27)	(n = 27)
Fortnight | Year	0.047 ± 0.034 (0.002, 0.124)	0.088 ± 0.063 (0.004, 0.238)	0.156 ± 0.091 (0.008, 0.351)	0.121 ± 0.075 (0.007, 0.287)
Fortnight^2 | Year	0.043 ± 0.032 (0.002, 0.116)	0.076 ± 0.054 (0.004, 0.203)	0.099 ± 0.071 (0.004, 0.258)	0.119 ± 0.075 (0.007, 0.275)
Female ID	0.283 ± 0.046 (0.187, 0.368)	0.519 ± 0.084 (0.355, 0.691)	0.199 ± 0.128 (0.011, 0.468)	0.240 ± 0.118 (0.023, 0.467)
	(n = 787)	(n = 787)	(n = 753)	(n = 730)
Nest ID	0.162 ± 0.113 (0.007, 0.423)	0.585 ± 0.360 (0.030, 1.309)	0.493 ± 0.349 (0.021, 1.266)	0.858 ± 0.449 (0.054, 1.692)
	(n = 3997)	(n = 3997)	(n = 3103)	(n = 2721)

SUPPLEMENTARY INFORMATION

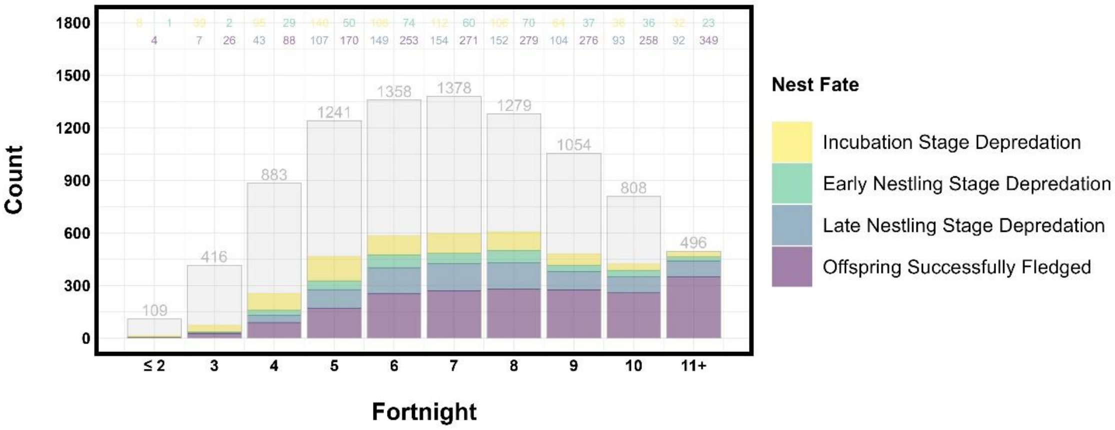

***Figure S1**: Variation in nest activity and nest fate across the breeding season. The first fortnight (fortnight 1) extends from 1 September to 14 September. The grey bars depict the overall count of active nests observed within each fortnight throughout the study period (1994–2020), with corresponding sample sizes given at the top of each bar. The coloured bars indicate the fate of nests within the respective fortnight in which offspring either successfully fledged (purple) or were depredated at the incubation (yellow), early nestling (green) or late nestling (blue) stage. The number of nests for each group is given at the top of the plot. Note, due to the 24-day duration of a successful nest attempt, an active nest can span across multiple fortnights.*

Table S1: *Records of predation of superb fairy-wren nests in the study area, as captured using motion-sensing trail cameras, in 2019 and 2020.*

Species	**Class**	**Year**	**Nest Contents**	**Nest Height (cm)** Range (Mean ± SD)	**Sample Size**
Pied currawong	Avian	2019	Eggs	29	1
Strepera graculina		2019	Nestlings	51–71 (61.00 ± 14.14)	2
		2020	Eggs	20	1
		2020	Nestlings	14–64 (32.67 ± 27.30)	3
Red fox	Mammalian	2019	Eggs	35–53 (43.50 ± 7.42)	4
Vulpes vulpes		2019	Nestlings	27–117 (61.00 ± 35.36)	7
		2020	Eggs	-	-
		2020	Nestlings	-	-
Eastern brown snake	Reptilian	2019	Eggs	-	-
Pseudonaja textilis		2019	Nestlings	29	1
		2020	Eggs	73	1
		2020	Nestlings	-	-

In an attempt to identify nest predators in our study area, a total of 38 nests were monitored using Bushnell 119877 motion-sensing trail cameras (Bushnell Outdoor Products, 2015) during the two most recent years of our study (2019: n = 27 nests; 2020: n = 11 nests). In each year, the nest predator was unidentifiable for two of the nests that ended in depredation.

Table S2: *Comparisons of the four Bayesian hierarchical generalised linear regression models of daily nest predation when fit with different random effects structures.*

Overall

Random Effects Structure †	ELPD LOO (± SE)	ΔELPD LOO (± SE)	LOO IC (± SE)
(1 | Year)	-8816.466 (152.421)		17632.932 (304.841)
(1 + Fortnight | Year)	-8817.500 (152.451)	-1.035 (0.682)	17635.001 (304.901)
(1 + Fortnight + Fortnight^2 | Year)	-8818.620 (152.462)	-2.154 (1.047)	17637.240 (304.923)

Incubation

Random Effects Structure †	ELPD LOO (± SE)	ΔELPD LOO (± SE)	LOO IC (± SE)
(1 | Year)	-3754.811 (110.280)		7509.622 (220.560)
(1 + Fortnight | Year)	-3754.973 (110.275)	-0.162 (0.926)	7509.946 (220.549)
(1 + Fortnight + Fortnight^2 | Year)	-3755.698 (110.302)	-0.886 (1.255)	7511.395 (220.603)

Early Nestling

Random Effects Structure †	ELPD LOO (± SE)	ΔELPD LOO (± SE)	LOO IC (± SE)
(1 + Fortnight | Year)	-1706.986 (67.796)		3413.973 (135.592)
(1 + Fortnight + Fortnight^2 | Year)	-1707.189 (67.754)	-0.202 (1.416)	3414.377 (135.507)
(1 | Year)	-1707.852 (67.814)	-0.866 (0.654)	3415.704 (135.628)

Late Nestling

Random Effects Structure †	ELPD LOO (± SE)	ΔELPD LOO (± SE)	LOO IC (± SE)
(1 + Fortnight + Fortnight^2 | Year)	-3286.938 (76.546)		6573.876 (153.093)
(1 + Fortnight | Year)	-3287.363 (76.551)	-0.425 (1.517)	6574.726 (153.102)
(1 | Year)	-3288.029 (76.535)	-1.091 (1.989)	6576.058 (153.069)

† Additional random effects of Mother ID and Nest ID were included in all models. ELPD $_{LOO}$: A Bayesian leave-one-out (LOO) estimate of out-of-sample predictive performance, the Expected Log Pointwise Predictive Density (ELPD) provides a measure of expected predictive accuracy (Vehtari et al., 2017). ΔELPD $_{LOO}$: The difference in ELPD $_{LOO}$ between the best fitting model and the focal model. When ΔELPD $_{LOO}$ is less than 4, the difference between models is negligible. LOO $_{IC}$: -2 x ELPD $_{LOO}$ (i.e., ELPD $_{LOO}$ on the deviance scale, Vehtari et al., 2017). SE: Standard errors of each measurement. Model comparisons were implemented using the loo function in the package 'loo' (v.2.4.1; Vehtari et al., 2020) in R (v.4.0.5; R Core Team, 2021).

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