2023-05-29:
A revised version of this manuscript is now published at: https://doi.or/10.1002/rse2.342

TITLE

Use of Airborne Laser Scanning to assess effects of understorey vegetation structure on nest-site selection and breeding performance in an Australian passerine bird

AUTHORS

Richard S. Turner [1,2 *], Ophélie J. D. Lasne [1], Kara N. Youngentob [1,3], Shukhrat Shokirov [1,3], Helen L. Osmond [1], & Loeske E. B. Kruuk [1,2]

AFFILIATIONS

[1] Division of Ecology & Evolution, Research School of Biology, Australian National University, Canberra, ACT 2601, Australia

[2] Institute of Ecology and Evolution, School of Biological Sciences, University of Edinburgh, Edinburgh EH9 3FL, United Kingdom

[3] The Fenner School of Environment & Society, Australian National University, Canberra, ACT 2601, Australia

[*] Corresponding author. Email: richard.turner@anu.edu.au

ABSTRACT

In wild bird populations, the structure of vegetation around nest-sites can influence the risk of predation of dependent offspring, generating selection for nest-sites with vegetation characteristics associated with lower predation rates. However, vegetation structure can be difficult to quantify objectively in the field, which might explain why there remains a general lack of understanding of which characteristics are most important in determining predation rates. Airborne Laser Scanning (ALS) offers a powerful means of measuring vegetation structure at unprecedented resolution. Here, we combined ALS with 11 years of breeding data from a wild population of superb fairy-wrens *Malurus cyaneus* in southeastern Australia, a species which nests relatively close to the ground and has high rates of nest and fledgling predation. We derived structural measurements of understorey (0-8 m) vegetation from a contiguous grid of 30 x 30 m resolution cells across our *c.* 65 hectare study area. We found that cells with nests (nest-cells) differed in their understorey vegetation structure characteristics compared to unused cells, primarily in having denser vegetation in the lowest layer of the understorey (0-2 m; the 'groundstorey' layer). The average height of understorey vegetation was also lower in cells with nests than in those without nests. However, relationships between understorey vegetation structure characteristics and breeding performance were mixed. Nest success rates decreased with higher volumes of groundstorey vegetation, as did fledgling survival rates, though only in nest-cells with lower height vegetation. Our results indicate that ALS can identify vegetation characteristics relevant for superb fairy-wren nest-site selection, but that nesting preferences are not beneficial under current predation pressures. The study illustrates the potential for using ALS to investigate how ecological conditions affect behaviour and life-histories in wild animal populations.

Keywords: "Airborne Laser Scanning", "LiDAR", "Vegetation Structure", "Avian Breeding Performance", "Nest Predation", "Nest-Site Selection"

INTRODUCTION

Dependent offspring of many wild animal populations are frequently vulnerable to predation. The importance of dependent offspring predation for the evolution and plasticity of adult breeding behaviours is increasingly recognised in evolutionary and behavioural ecology (Ibáñez-Álamo et al., 2015; Lima, 2009; Lima & Dill, 1990). Studies of birds provide an excellent system to explore the determinants and consequences of dependent offspring predation. The loss to predation of eggs and

nestlings in nests (nest predation) is often the primary determinant of avian breeding failure (Martin, 1993; Ricklefs, 1969), and globally, rates of nest predation may have increased in recent decades (Kubelka et al., 2018; Matysioková & Remeš, 2022; Remeš et al., 2012a, 2012b). Even after leaving the nest, fledglings can suffer high mortality, mostly due to predation (Naef-Daenzer & Grüebler, 2016; Naef-Daenzer et al., 2001). Understanding nest and fledgling predation is therefore central to understanding the ecological pressures that shape bird breeding behaviours and life-histories, and for informing conservation and management strategies for imperilled species.

The density and complexity of vegetation surrounding a nest can determine the predation of both the nest and fledglings. Denser and more complex vegetation is thought to reduce visual and auditory cues to predators, and to create a physical barrier that impedes predators or reduces their searching efficiency (Bowman & Harris, 1980; Filliater et al., 1994; Magrath et al., 2010; Martin, 1993; Martin & Roper, 1988; Mouton & Martin, 2019). However, although natural selection should therefore favour sites with denser and more complex vegetation, especially when primary predators are visually or auditorily-oriented, there is limited evidence to date that nest-sites with such structural vegetation characteristics have reduced predation rates (Borgmann & Conway, 2015; Lahti, 2009). This may be because predators are not hindered in the way we expect. However, another possibility is that previous studies have not been able to measure vegetation structure characteristics with sufficient resolution. In part due to the high cost and labour intensive nature of manually collecting accurate and precise data, previous studies have often relied on structural vegetation data that were visually-estimated and taken from a subset of available locations, but evidence suggests that such data may be researcher-biased and not representative of the broader landscape (Block et al., 1987; Gotfryd & Hansell, 1985).

Active remote sensing such as Light Detection and Ranging (LiDAR) can provide an effective method for accurately and reliably assessing vegetation structure due to its ability to provide high-resolution and spatially contiguous data in a standardised and comparable way (Lefsky et al., 2002; Moudrý et al., 2023; Vierling et al., 2008). Airborne Laser Scanning (ALS) (i.e., a LiDAR sensor mounted on an aircraft) is the most common method for collecting LiDAR data and uses laser pulses to measure the coordinates (x, y, z) of reflective surface objects (Wehr & Lohr, 1999). As the timing and position of the sensor on the aircraft are known, the distance to each object can be calculated precisely and a three-dimensional “point cloud” can be derived (Lefsky et al., 2002; Vierling et al., 2008). Additional

attributes can be specified for each point during processing that can be used to calculate structural vegetation characteristics (Bakx et al., 2019; Davies & Asner, 2014). While some studies have used ALS data to investigate questions in evolutionary and behavioural ecology, they have generally focused on species abundance, richness, and distribution modelling in relation to vegetation structure (Ciuti et al., 2017; Davies & Asner, 2014; de Vries et al., 2021; Moudrý et al., 2023; Shokirov et al., 2023). However, with the increasing availability of ALS data (Moudrý et al., 2023), recent research has shown the potential of combining such data with detailed behavioural and life-history data of single animal populations (Davies et al., 2016, 2019; Hill & Hinsley, 2015; Hill et al., 2004; Klein et al., 2020). For example, Klein et al. (2020) used ALS data spanning 8300 hectares in an analysis of the breeding success of Siberian jays *Perisoreus infaustus* and found a positive association between increased understorey vegetation density and breeding success for birds in territories close to human settlements, which are an indicator of the occurrence of their main nest predator, the Eurasian jay *Garrulus glandarius*. The broad spatial coverage of the ALS data used in their study enabled the identification of relationships that would have been difficult to discover using traditional methods.

In this study, we used 11 years of detailed, individual-based breeding data to investigate the associations between vegetation structure and nest and fledgling predation in a population of superb fairy-wrens *Malurus cyaneus* in southeastern Australia. Although superb fairy-wrens mostly forage in open grassy areas (Schlotfeldt & Kleindorfer, 2006), they build their nests close to the ground in dense vegetation, such as grass tussocks or small shrubs, which are subject to high levels of nest and fledgling predation (Cockburn et al., 2016; Colombelli-Négrel & Kleindorfer, 2009; Rowley & Russell, 1997). Superb fairy-wrens have many nest and fledgling predators (Rowley & Russell, 1997), with their dominant predator being the pied currawong *Strepera graculina* in areas where the two species' ranges overlap (Prawiradilaga, 1996; Yasukawa & Cockburn, 2009). Indeed, pied currawongs have been implicated as an important predator of most small passerines throughout eastern and southeastern Australia (Bayly & Blumstein, 2001; Fulton & Ford, 2001; Fulton, 2019).

Pied currawongs are large, corvid-like, passerine birds that use visual and auditory cues to detect prey (Wood, 2000; Yasukawa & Cockburn, 2009). Given this searching method, we hypothesise, firstly, that superb fairy-wrens should favour nest-sites with denser and more complex vegetation, and secondly, that such nest-sites would experience lower rates of nest and fledgling predation. The first hypothesis

has not previously been tested for superb fairy-wrens. Contrary to the expectations of the second hypothesis, two previous studies of superb fairy-wrens have shown that increased vegetation density is associated with higher rates of nest predation and lower numbers of fledglings, when vegetation was measured in the immediate vicinity of the nest (Colombelli-Négrel & Kleindorfer, 2009) and at the broader territory-level (Backhouse et al., 2023), with the latter study conducted on the same population as this study. It is worth noting, however, that both these studies used visually-estimated measures of vegetation collected from a subset of locations, which were then summarised into relatively course metrics. Moreover, neither study examined whether the same characteristics were important for nest-site selection by comparing nest-sites with non-nesting sites.

The aim of this study was to test these two hypotheses regarding superb fairy-wrens and their breeding behaviour, using structural vegetation data derived from ALS. Because superb fairy-wrens nest close to the ground, we expected that the structure of the understorey vegetation, which we define here as 0 – 8 m above ground, would be most important in determining nest-site selection and breeding performance in this species (Cockburn et al., 2016; Rowley & Russell, 1997). We therefore focused on three characteristics related to understorey vegetation height, complexity, and density, using a contiguous grid of 30 x 30 m resolution cells spanning our study area. We tested: (i) whether these understorey vegetation characteristics influenced nest-site selection; and (ii) whether nest-site selection was adaptive to in relation to predation pressures, by assessing associations of understorey vegetation characteristics with rates of nest success and fledgling survival.

MATERIALS AND METHODS

Study area

Our study area is located in Canberra, Australian Capital Territory, Australia (Figure 1) and encompasses an area of *c.* 65 hectares that includes a *managed* area in the Australian National Botanic Gardens (ANBG; *c.* 43 hectares) and an *unmanaged* area in the adjacent Black Mountain Nature Reserve (*c.* 22 hectares). The study area consists of broadly of mature open sclerophyll forest, with evergreen *Eucalyptus macrorhyncha* and *Eucalyptus rossii* as the primary tree species, and *Acacia* spp.*, Callistemon* spp.*, Notodanthonia* spp., *Rytidosperma palladium*, *Triodia scariosa,* and *Lomandra longifolia* as the dominant understorey shrubs and grasses. The *managed* area also includes a diverse collection of native vegetation established in dense plantings, and three semi-artificial habitats

(specifically, a 'rainforest' area, a 'desert' area, and a grass lawn). Along the eastern perimeter of the *unmanaged* area, there is a small patch of gullies that flood with rainwater that is dominated by *Bursaria spinosa*, and non-native species including *Rubus fruticosus* (Fraser & Purdie, 2020).

Superb fairy-wren study population and data collection

Superb fairy-wrens are facultative cooperative-breeders that live on year-round territories in groups composed of a dominant breeding pair and up to five male helpers (Cockburn et al., 2016; Rowley & Russell, 1997). Females are solely responsible for nest-building and incubation, but all group members defend and provision the brood. They have a long breeding season that runs between September and March (Lv et al., 2019). Hereafter, we refer to a given breeding season by the calendar year in which it commenced. The species is multi-brooded: high rates of nest predation mean a female superb fairy-wren may initiate as many as nine or ten clutches per breeding season, but often only one brood (if any) successfully reaches independence. Clutch sizes can range from one to five eggs but clutches with three eggs are most common (Cockburn et al., 2016; Rowley & Russell, 1997). Further details regarding the breeding behaviour of superb fairy-wrens in our study area are provided as Figure S1 – S4.

Two hailstorms damaged the study area on 27 February 2007 and 19 January 2020 respectively. In this study, we therefore constrained our analyses to data from 11 breeding seasons (from 2009 –2019; up until the hailstorm on 19 January 2020); this interval is centred around 2015 when the ALS data were collected (details below). The weather conditions were consistent during this time (Figure S5) and the structure of the vegetation remained unchanged. Thus, we did not expect any time difference between the superb fairy-wren breeding data in a given year and the ALS data to affect our ability to detect any relationships (Hill & Hinsley, 2015; Vierling et al., 2014). For completeness, we also repeated all analyses using data from 1994 – 2019 (the full duration during which breeding data have been collected across the full extent of our study area). We present these results separately as Table S1.

Between 2009 – 2019, the study area supported 34 – 79 superb fairy-wren territories each year, with an average territory size of 1.09 ± 0.71 hectares (mean ± SD, n = 686 territory-years). Unique colour-banding of individuals in the study population allowed for individual recognition. To locate nests, we observed the dominant female on each territory during nest-building or incubation. The location of each nest was initially recorded using a Garmin eTrex Global Positioning System (GPS) (Garmin Co., Olathe,

Kansas, USA) or a GPS application on a mobile phone (Handy GPS, BinaryEarth, Australia), within a reported accuracy of ± 5 m for all devices. We then used a 30 m grid map of the study area to confirm nest locations to one decimal point fraction (i.e., within a 9 m^2 grid cell) based on recognisable physical landmarks in the study area (e.g., paths, buildings, and specific landscaping features). Thus, final nest locations were accurate to ± 3 m. Coordinates were collected in spatial reference Geocentric Datum of Australia 1994, Map Grid of Australia Zone 55 (Collier & Steed, 2001). All analyses presented here were subsequently conducted using this projection. We monitored the progress of each nest every second day for the duration of the nesting period (*c.* 24 days from the onset of incubation) to determine *nest fate*. Nests that fledged at least one offspring were considered *successful*. Nest predation was assumed when all eggs or nestlings disappeared prior to their expected fledging date. Because our interest was in whether nest-site selection influenced breeding performance via predation risk, we excluded 172 nests (9.35% of the total) that failed due to reasons other than predation (Figure S3). When nests were successful, we closely monitored individual fledglings to determine their survival to independence, defined as four weeks (28 days) post-fledging. Although most offspring were still being provisioned at this age, five-weeks post-fledging is the earliest known age of dispersal in our study area; this cut-off point therefore avoids any chance of dispersal being confused with mortality (Hajduk et al., 2018, 2020). Causes of fledgling mortality were generally unknown, but the recovery of colour-bands of fledglings from pellets of pied currawongs suggests that predation is an important source of mortality (Prawiradilaga, 1996). In this study, we used all fledgling mortality as a measure of fledgling predation.

Using the grid map of our study area as reference, we derived measurements of understorey vegetation structure at a 30 x 30 m resolution spanning the extent of our study area (n = 768 cells; further details are provided below; see also Backhouse et al., 2023). Because superb fairy-wren territories were on average 1.09 hectares in size, each 30 x 30 m resolution cell therefore encompassed *c.* 10% of the average territory. Each nest was then assigned to a cell based on its location. We excluded breeding data from 25 cells (3.3% of the total) that encompassed the three semi-artificial habitats in the study area (described above), as superb fairy-wrens do not inhabit these regions of our study area because they contain vegetation that is very different from their native range. Breeding data from a further two cells were later excluded as they contained no understorey vegetation structure data (details below).

The superb fairy-wren breeding dataset used in this study therefore comprised of observations from a total of 1431 nests (from 318 females), encompassing 741 cells over 11 years (n = 8151 cell-years). For analysis of nest-site selection, cell-years were subsequently designated as nest-cell-years (cell-years with a nest, n = 1094 cell-years) or unused-cell-years (cell-years without a nest, 7057 cell-years). For each nest-cell-year we estimated two measures of breeding performance: (i) *nest success rate* and (ii) *fledgling survival rate*, both of which are defined in Table 1. In rare cases, more than one female occupied a given nest-cell-year – for example, in cases where cells overlapped territory boundaries, or the death of a female resulted in her being replaced by a different female. In these cases, observations were treated as independent for each female (female-nest-cell-year).

The number of nest-cells declined significantly over the course of the study (Figure S6a), a finding that is consistent with the observation of a 72.16% population decline of females during the period considered here (Figure S6b), and with a general decline across the entire study period (Backhouse et al., 2023; Lv et al., 2023). This decline in population size may be linked to increased rates of adult winter mortality associated with climate change (Lv et al., 2023). For the purpose of this study, and because we are focusing on a shorter time-scale, we do not consider this decline in detail.

Airborne Laser Scanning data

ALS data were collected between 21 May 2015 and 5 April 2016 by the Australian Capital Territory Government's Environment, Planning and Sustainable Development Directorate (www.planning.act.gov.au), using an AX60 scanner mounted to an aircraft (with a Riegl LMS-Q780 sensor and Trimble AP50 GPS). Details of the ALS survey were as follows: flight elevation above ground level: 450 m; point density: 8 pulses/m^2; footprint size: 0.12 m; swath width: 539 m; overlap: 25%; vertical precision: ± 0.30 m; horizontal precision: ± 0.80 m. Further details including the flight speed, laser wavelength, scan frequency, and pulse frequency were not provided with the dataset (www.planning.act.gov.au). The data were pre-processed by the vendor and came with a classification of *ground*, *building*, *water*, *vegetation*, and *noise* points, and were distributed in LAS v.1.4 format projected in spatial reference Geocentric Datum of Australia 1994, Map Grid of Australia Zone 55 (Collier & Steed, 2001).

We separated the ALS data into each of our 30 x 30 m resolution cells using LAStools (rapidlasso GmbH; van Rees, 2013). Using the package 'lidR' (v.3.1.3; Roussel et al., 2020) in R (v.4.0.5; R Core Team, 2021), we further processed the data to derive vegetation structure characteristics for each cell as follows: First, point cloud data were normalised by subtracting the height of ground points from the height of non-ground points (following e.g., Ciuti et al., 2017; Koma et al., 2021; Shokirov, 2021; Shokirov et al., 2023). Second, points classified as *ground*, *building*, *water*, and *noise* were removed, resulting in only points classified as *vegetation* being retained. A total of two cells were found to contain no *vegetation* points, and so were excluded from further processing. Third, *vegetation* points were categorised into two layers: *understorey layer* (0 – 8 m), and *canopy layer* (> 8 m). We used 8 m as the threshold distinguishing these two vegetation layers based on the distribution of the normalised *z* coordinates (height values) of the point cloud (Figure S7) and knowledge of the primary *Eucalyptus* spp. in the study area (Fraser & Purdie, 2020). We then removed *canopy vegetation* points from the point cloud data as we expected the structure of the understorey vegetation to be most relevant for superb fairy-wrens based on their nesting behaviour (Figure S1 – S2). Fourth, from the *understorey vegetation* points, we calculated the following three vegetation structure characteristics: (i) *mean height* of the understorey vegetation, (ii) *variation in height* of the understorey vegetation (as measured by the standard deviation, SD) and (iii) *volume* of the understorey vegetation. We initially calculated *volume* within four specific height thresholds (0 – 2 m, 2 – 4 m, 4 – 6 m, 6 – 8 m) but because the nests of superb fairy-wrens are generally <2 m above the ground, in our analyses we considered *volume* at the lowest height threshold only (hereafter referred to as '*groundstorey volume*'). Definitions of each of the three understorey vegetation structure characteristics are provided in Table 2. The final ALS point cloud dataset used in this study comprised a total of 1,686,744 understorey vegetation points, with a mean ± SD of 2270.18 ± 1994.04 points/cell.

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). Prior to analysis, explanatory parameters were mean standardised to allow for effect size comparisons (Harrison et al., 2018; Schielzeth, 2010), and potential multicollinearity (Dormann et al., 2013, Zuur et al., 2009) and spatial autocorrelation (Ciuti et al., 2017; Dormann et al., 2007) were assessed. Potential spatial autocorrelation was accounted for by including

a spatial conditional autoregressive (CAR) structure in our models (Bürkner, 2017; Dormann et al., 2007). Further details are provided as Appendix S1, Figure S8 – S9, and Table S2 – S3.

We constructed Bayesian spatial hierarchical generalised linear regression models for each of our three response variables of nest presence, nest success rate, and fledgling survival rate (Table 2). Each model included fixed effects of year (as a continuous covariate) plus the three understorey vegetation structure parameters. To account for repeated measurements of non-independent data, we included cell ID and year (as multi-level factors) as random effects. Female ID was additionally included as a random effect in the two models of breeding performance to account for multiple observations of the same female.

We initially also considered: non-linear effects of all understorey vegetation structure parameters; the two regions of the study area (as a two-level factor: managed, unmanaged); and two-way interactions between all explanatory parameters. Where these effects were non-significant, we discarded them from our final models (and do not present them here). Previous studies of superb fairy-wrens have shown positive associations between a female's age, the number of helpers, and different breeding performance metrics (e.g., Cockburn *et al.,* 2008; Hajduk et al., 2020, 2021). We therefore included as fixed effects female age (as a two-level factor: 1 year old, 2+ year old, following e.g., Kruuk et al., 2015; Hajduk et al., 2018) and number of helpers (as a two-level factor: 0 helpers, 1+ helpers, following e.g., Cooper et al., 2020; Taylor & Langmore, 2020) in our two models of breeding performance to control for their effects, but we do not focus on these effects in detail.

We ran all models on 4 independent MCMC chains for 8000 iterations, with a thinning interval of 10 and a warm-up period of 3000 iterations (resulting in 2000 posterior samples), specifying weakly informative priors with a normal error distribution (μ: 0; σ^2: 1; Gelman et al., 2015). Effective sample sizes for specific parameters varied owing to autocorrelation, but they were always above 400 (a minimum effective sample size of 100 per chain; Vehtari et al., 2021). Model convergence was confirmed by ensuring that potential scale reduction factors were < 1.01 (Gelman et al., 2013; Vehtari et al., 2021). For each model, we assessed the goodness-of-fit using the posterior predictive check, *pp_check*, function in the package 'bayesplot' (v.1.8.1; Gabry & Mahr, 2021). Unless stated otherwise, summary statistics are presented as means (± SE). Model parameter estimates are presented as posterior means

(± SD) and 95% credible intervals. We considered there to be statistical support for specific parameters when the 95% credible intervals do not span zero.

RESULTS

Understorey vegetation structure parameters

The mean (± SD) of the three understorey vegetation structure parameters were as follows: mean height: 3.3 ± 1.0 m (Figure 2c); SD height: 2.2 ±0.4 m (Figure 2d); groundstorey volume: 378.4 ± 267.8 m^3 (Figure 2e). There was a positive correlation between mean height and SD height (Pearson correlation coefficient = 0.30), and negative correlations between mean height and groundstorey volume (Pearson correlation coefficient = -0.42) and between SD height and groundstorey volume (Pearson correlation coefficient = -0.25; Table S3).

Nest-site selection

Of the 741 cells, 39.41% (n = 292 cells) never had a nest during the 11 years of our study, while 23.35% (n = 173 cells) had a nest in only one year (Figure 1, Figure S10). The maximum number of years a cell had a nest was nine (two cells; Figure 1).

Nest presence in a cell decreased with increasing mean height (nest-cell-years: 3.01 ± 0.03 m; unused-cell-years: 3.33 ± 0.01 m; Table 3, Figure 3a – b), and increased with increasing groundstorey volume (nest-cell-years: 477.20 ± 8.53 m^3; unused-cell-years: 363.09 ± 3.12 m^3; Table 3, Figure 3c – d). Note, because a cell encompassed *c.* 10% of the average superb fairy-wren territory, random nest-site selection within a territory would mean an average probability of 0.10 of nest presence. Therefore, rates of nest presence >0.10 indicate non-random site selection for particular cells (Figure 3b, d). We found no significant effect of SD height on nest presence (Table 3). However, this was possibly due to a lack of power in the 11 year subset of data (2009 – 2019) used in this analysis. Our analysis of the full dataset (1994 – 2019) did find statistical support for the positive association between SD height and nest presence, due to relatively smaller error around the parameter estimate (Table S1).

Nest success rate

Nest success rate was on average 0.44 ± 0.01 (n = 1138 female-nest-cell-years) and varied between years. Nest success rate was highest in 2012 (0.51 ± 0.04; n = 123 female-nest-cell-years) and lowest in

2019 (0.36 ± 0.07; n = 50 female-nest-cell-years). We found no significant change in nest success rate over time (Table 3). However, our analysis of the full dataset (1994 – 2019) did find evidence of a longer-term increase in nest success rate. Most often cells contained only one nest from one female in a given year (80.84% female-nest-cell-years; range 1 – 4). As such, nest success rates were generally either 0.00 (51.41%; n = 585 female-nest-cell-years) or 1.00 (39.81%; n = 453 female-nest-cell-years).

We found no effect of mean height on nest success rate (female-nest-cell-years in which nest success rate > 0.00: 3.00 ± 0.04 m; female-nest-cell-years in which nest success rate was 0.00: 3.02 ± 0.03 m; Table 3, Figure 4a–b). Similarly, we found no effect of SD height on nest success rate (Table 3). However, there was a significant decline in nest success rate with increasing groundstorey volume (female-nest-cell-years in which nest success rate > 0.00: 463.96 ± 11.39 m^3; female-nest-cell-years in which nest success rate was equal to 0.00: 490.16 ± 12.07; Table 3, Figure 4c–d).

Fledgling survival rate

Fledgling survival rate was on average 0.61 ± 0.02 (n = 556 female-nest-cell-years). Fledgling survival rate was highest in 2016 (0.76 ± 0.04; n = 53 female-nest-cell-years) and lowest in 2013 (0.50 ± 0.05; n = 57 female-nest-cell-years). The average number of fledglings produced across all female-nest-cell-years was 2.96 ± 0.05 (range: 1 - 9).

None of the understorey vegetation structure parameters were significant as main effects for fledgling survival rate (Table 3). However, we did find a significant interaction between mean height and groundstorey volume: fledgling survival rates decreased with groundstorey volume when female-nest-cell-years contained smaller understorey vegetation (when mean height was lower than the population-level average, n = 268 female-nest-cell-years; Table 3, Figure 5).

DISCUSSION

Our study combined ALS-derived measures of understorey vegetation structure with breeding data from a long-term study of a population of superb fairy-wrens. We found differences in the characteristics of understorey vegetation structure in sites chosen for nesting, but no evidence that this selection reduced rates of nest or fledgling predation. We discuss the outcomes of these results below,

and the implications for the use of ALS in studies of the evolutionary and behavioural ecology of wild animal populations.

Understorey vegetation structure characteristics and nest-site selection

Our results show that female superb fairy-wrens select nest-sites based on aspects of the understorey vegetation. Nest presence increased with decreasing mean height of the understorey vegetation and with groundstorey volume, which is indicative of an area containing more grass tussocks and small shrubs, substrates preferentially used in our study area by superb fairy-wrens for nesting (Figure S2). We found no statistical significance of SD height affecting the probability of nest presence in our main analysis, using data from 2009 – 2019. However, there was statistical support for the positive association between SD height and nest presence in our analysis of the full dataset (1994 – 2019), suggesting that there is a potential role for vegetation complexity in nest-site selection in superb fairy-wrens. Denser and more complex vegetation is expected to be favoured in response to visually and auditorily-oriented predators (Bowman & Harris, 1980; Martin, 1993; Martin & Roper, 1988; Filliater et al., 1994). Our results are therefore consistent with the expectation that superb fairy-wrens' choice of nest-site is shaped by predation pressures.

Understorey vegetation structure characteristics and breeding performance

Despite the observation of preference for nest-sites with denser vegetation, our study using ALS data confirmed previous, somewhat counterintuitive, findings that nest success and fledgling survival rates of superb fairy-wrens decrease with increasing vegetation density (Backhouse et al., 2023; Colombelli-Négrel & Kleindorfer, 2009) at a height relevant to this species. These findings contradict the expectation that dense vegetation should be adaptive against visually and auditorily-oriented predators, such as pied currawongs. We suggest several possible explanations for this paradox.

Although pied currawongs were previously identified as the dominant predator of superb fairy-wren nests and fledglings in our study population (Prawiradilaga, 1996), they were not present in our study area until the 1970s (Taylor, 1992). Thus, superb fairy-wren nest-site selection likely evolved in response to historical selection pressures from different predatory species (Chalfoun & Schmidt, 2012). It is therefore possible that current nest-site preferences are insufficient at impeding the pied currawong's ability to detect and access the nests and fledglings of superb fairy-wrens. Alternatively, superb fairy-

wren nest-site selection might be adaptive against pied currawongs, but the current importance of pied currawongs as a predator may have been overestimated or have changed in recent years, since Prawiradilaga (1996). There is some support for this notion in the fact that despite an increase in the number of pied currawongs in our study area (A. Cockburn, unpublished data), long-term rates of superb fairy-wren nest predation have decreased (Table S1; Backhouse et al., 2023).

It is also possible that nesting in areas with increased groundstorey volume may make superb fairy-wren nests and fledglings more vulnerable to other predators (Filliater et al., 1994), such as red foxes *Vulpes vulpes*, which are common predators of superb fairy-wren nests and fledglings in our study area (R.S. Turner, unpublished data). Red foxes have been linked to the extinction of native species and population declines elsewhere throughout Australia because of their generalist diet and ability to thrive in various habitats (Woinarski et al. 2019, 2022). Moreover, they often locate their prey using olfactory cues, which may not be reduced by structural vegetation characteristics (Colombelli-Négrel & Kleindorfer, 2009). We do not have sufficient observations of predation events to determine if the importance of understorey vegetation structure impacts superb fairy-wren breeding performance differently depending on the predator, but our results illustrate the need to understand the potential importance of other predators.

Potential use and limitations of ALS in evolutionary and behavioural ecology

Studies have demonstrated the effectiveness of using ALS-derived measurements to assess relationships between vegetation structure and the abundance, richness, and distribution of different species (Ciuti et al., 2017; Davies & Asner, 2014; de Vries et al., 2021; Moudrý et al., 2023; Shokirov et al., 2023). More recently, some studies have also shown that ALS can be used to assess how structural vegetation characteristics affect breeding behaviours and life-histories of single populations or species (Davies et al., 2016, 2019; Hill et al., 2004; Hill & Hinsley, 2015; Klein et al., 2020). However, to date these studies have been largely limited to specific regions – in particular, North America and Europe – and taxonomic groups (Davies & Asner, 2014). With the increasing accessibility of national and regional ALS datasets (Kissling et al., 2022; Lefsky et al. 2002; Moudrý et al., 2023; Vierling et al. 2008) global studies for entire taxonomic groups and ecosystems are now possible, and with them the potential to significantly improve our understanding of animal-habitat relationships.

Compared to traditional manual methods of measuring vegetation structure (Block et al., 1987; Gotfryd & Hansell, 1985; MacArthur & MacArthur, 1961) ALS is overall less costly, less labour intensive, and less subjective. ALS also allows for data collection in remote or inaccessible areas, and over larger spatial extents, and can produce high-resolution measures of vegetation structure that are more representative of the broader landscape (though previous studies have found positive associations between structural vegetation characteristics derived from ALS and those measured in the field; Hyde et al., 2005, 2006). Additionally, ALS allows for more complex measures of vegetation structure to be calculated (Bakx et al., 2019), which can be updated as our understanding improves.

Despite its potential, ALS has some limitations. First, data can be computationally demanding and require a significant amount of memory (Kissling et al., 2022; Vo et al., 2016). The unprocessed ALS data for our comparatively small study area was *c.* 10 GB in size and initially consisted of *c.* 250 million data points. Additionally, processing, and analysing ALS data requires a certain level of specialisation. However, there has been considerable development in the field of available software that has made processing and analysing ALS data more accessible (Kissling et al., 2022; Roussel et al., 2020; van Rees, 2013). Second, ALS surveys are often conducted in winter, during leaf-off conditions for deciduous species, as their primary function is generally to provide accurate mapping of the ground terrain (Reutebuch et al., 2005). Future studies are needed to understand the effect of seasonality on the ability of ALS to capture structural data, particularly in landscapes with abundant deciduous species. In our study area, the vegetation is predominantly evergreen (Fraser & Purdie, 2020). Third, ALS may be less effective at capturing structural characteristics of understory vegetation in landscapes with dense canopy coverage (Bakx et al., 2019), particularly when point clouds are of a low density. However, a recent study by Shokirov et al. (2023) showed that ALS can effectively capture understorey vegetation in similar landscapes to our study area, which has an open canopy, when compared to higher-resolution Terrestrial Laser Scanning (TLS) data. Moreover, several other studies have shown that estimating vegetation structure at coarser resolution of 20 – 25 m can be sufficient at reducing potential errors in sampling due to low point cloud density (Ruiz et al., 2014; Treitz et al., 2012; Wilkes et al., 2015).

CONCLUSION

Our study used ALS to investigate breeding behaviour in a wild superb fairy-wren population and found that aspects of understorey vegetation structure played a role in nest-site selection. However,

relationships between understorey vegetation structure and breeding performance were complex and our findings highlighted the need for future research to consider the importance of specific predators. The increasing availability of ALS data offers potential for obtaining more complex, and less subjective, measures of vegetation structure for use in furthering our understanding the ecological pressures that shape breeding behaviours and life-histories of wild animals.

ACKNOWLEDGEMENTS

We thank Andrew Cockburn for the superb fairy-wren breeding dataset and for discussion and comments on the manuscript. We also thank Fiona Backhouse for useful discussion during the conceptualisation of this project, and to the many field assistants who have contributed to the long-term study over the years. We thank 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 which the latest grant for data used in this study was DP190100424 to Loeske E. B. Kruuk, Andrew Cockburn, and Martijn van de Pol. We also thank two anonymous reviewers for helpful comments on the manuscript. Richard S. Turner was funded through an Australian National University Research Scholarship (7382018) and HDR Fee Merit Scholarship (3202015) and Loeske E. B. Kruuk was funded by an Australian Research Council Laureate Fellowship (FL200100068) and a Royal Society Research Professorship. Ethics approval was granted by the Australian National University Animal Experimentation Ethics Committee (Protocol Number: A2019/23). We wish to acknowledge the Ngunnawal people, the traditional custodians of the land upon which our study was undertaken. We pay our respects to their Elders, past, present, and emerging.

CONFLICT OF INTEREST

The authors declare no conflict(s) of interest.

AUTHOR CONTRIBUTIONS

Project conceptualisation: RST, OJDL, KNY, SS, LEBK; Airborne Laser Scanning data processing: RST, OJDL, KNY, SS; Superb fairy-wren data collection and management: HLO; Statistical analysis: RST; Original draft of manuscript: RST; Editing and review of manuscript: RST, KNY, LEBK. All authors gave approval of final manuscript.

DATA SHARING

Data needed to evaluate the conclusions presented in this study have been deposited at https://doi.org/10.6084/m9.figshare.21743402 and will be publicly available following peer-review.

REFERENCES

Backhouse, F., Osmond, H.L., Doran, B., Stein, J., Kruuk, L.E.B., & Cockburn, A. (2023). Population decline reduces cooperative breeding in a spatially heterogenous population of superb fairy-wrens. *EcoEvoRxiv*, https://doi.org/10.32942/X2FG6R.

Bakx, T.R.M., Koma, Z., Seijmonsbergen, A.C., & Kissling, W.D. (2019). Use and categorisation of light detection and ranging vegetation metrics in avian diversity and species distribution research. *Diversity and Distributions*, *25*, 1045–1059.

Bayly, K.L., & Blumstein, D.T. (2001). Pied currawongs and the decline of native birds. *Emu, 101,* 199–204.

Béland, M., Baldocchi, D.D., Widlowski, J.L., Fournier, R.A., & Verstraete, M.M. (2014). On seeing the wood from the leaves and the role of voxel size in determining leaf area distribution of forests with terrestrial LiDAR. *Agricultural and Forest Meteorology*, *184*, 82–97.

Block, W.M., With, K.A., & Morrison, M.L. (1987). On measuring bird habitat: Influence of observer variability and sample size. *The Condor*, 89, 241–251.

Borgmann, K.L., & Conway, C.J. (2015). The nest-concealment hypothesis: New insights from a comparative analysis. *The Wilson Journal of Ornithology*, *127*, 646–660.

Bowman, G.B., & Harris, L.D. (1980). Effect of spatial heterogeneity on ground-nest depredation. *The Journal of Wildlife Management*, *44*, 806–813.

Bürkner, P.C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software* 80, 1–28.

Chalfoun, A.D., & Schmidt, K.A. (2012). Adaptive breeding-habitat selection: Is it for the birds? *The Auk*, *129*, 589–599.

Ciuti, S., Tripke, H., Antkowiak, P., Gonzalez, R.S., Dormann, C.F., & Heurich, M. (2017). An efficient method to exploit LiDAR data in animal ecology. *Methods in Ecology and Evolution*, *9*, 893–904.

Cockburn, A., Brouwer, L., Margraf, N., Osmond, H.L. & van de Pol, M. (2016). Superb fairy-wrens: Making the worst of a good job. In: Koenig, W.D. & Dickinson, J.L. (Eds). Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behaviour, pp. 133–149. Cambridge University Press, Cambridge, UK.

Cockburn, A., Sims, R.A., Osmond, H.L., Green, D.J., Double, M.C., & Mulder, R.A. (2008). Can we measure the benefits of help in cooperatively breeding birds: The case of superb fairy-wrens *Malurus cyaneus*? *Journal of Animal Ecology*, *77*, 430–438.

Collier, P., & Steed, J. (2001). Australia's national GDA94 transformation grids. In *42nd Australian Surveyors Congress, Brisbane, Australia*.

Colombelli-Négrel, D., & Kleindorfer, S. (2009). Nest height, nest concealment, and predator type predict nest predation in superb fairy-wrens (*Malurus cyaneus*). *Ecological Research*, *24*, 921–928.

Cooper, E.B., Bonnet, T., Osmond, H.L., Cockburn, A., & Kruuk, L.E.B. (2020). Do the ages of parents or helpers affect offspring fitness in a cooperatively breeding bird? *Journal of Evolutionary Biology*, *33*, 1735–1748.

Davies, A.B., & Asner, G.P. (2014). Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends in Ecology & Evolution*, *29*, 681–691.

Davies, A.B., Marneweck, D.G., Druce, D.J., & Asner, G.P. (2016). Den site selection, pack composition, and reproductive success in endangered African wild dogs. *Behavioural Ecology*, *27*, 1869–1879.

Davies, A.B., Oram, F., Ancrenaz, M., & Asner, G.P. (2019). Combining behavioural and LiDAR data to reveal relationships between canopy structure and orangutan nest site selection in disturbed forests. *Biological Conservation*, *232*, 97–107.

de Vries, J.P.R., Koma, Z., de Vries, M.F.W., & Kissling, W.D. (2021). Identifying fine-scale habitat preferences of threatened butterflies using airborne laser scanning. *Diversity and Distributions*, *27*, 1251–1264.

513 Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B.,
514 Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B.,
515 Skidmore, A.K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it
516 and a simulation study evaluating their performance. *Ecography*, *36*, 27–46.

517 Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel,
518 A., Jetz, Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr,
519 F.M., & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species
520 distributional data: A review. *Ecography*, *30*, 609–628.

521 Filliater, T.S., Breitwisch, R., & Nealen, P.M. (1994). Predation on northern cardinal nests: Does choice
522 of nest site matter? *The Condor*, *96*, 761–768.

523 Fulton, G.R. (2019). Meta-analyses of nest predation in temperate Australian forests and woodlands.
524 *Austral Ecology*, *44*, 389–396.

525 Fulton, G.R., & Ford, H.A. (2001). The pied currawong's role in avian nest predation: A predator
526 removal experiment. *Pacific Conservation Biology*, *7*, 154–160.

527 Fraser, I., & Purdie, R. (2020). Black Mountain: A natural history of a Canberra icon. Friends of Black
528 Mountain, Canberra, Australia.

529 Gabry, J., & Mahr, T. (2021). bayesplot: Plotting for Bayesian models. R package version 1.8.1. Available
530 from: https://mc-stan.org/bayesplot.

531 Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., & Rubin, D.B. (2013). Bayesian data
532 analysis (3rd edition). Chapman & Hall/CRC Press, London, UK.

533 Gelman, A., Lee, D. & Guo, J. (2015). Stan: A probabilistic programming language for Bayesian
534 inference and optimization. *Journal of Educational and Behavioural Statistics, 40,* 530–543.

535 Gotfryd, A., & Hansell, R.I.C. (1985). The impact of observer bias on multivariate analyses of vegetation
536 structure. *Oikos, 45*, 223–234.

537 Hajduk, G.K., Cockburn, A., Margraf, N., Osmond, H.L., Walling, C.A., & Kruuk, L.E.B. (2018).
538 Inbreeding, inbreeding depression, and infidelity in a cooperatively breeding bird. *Evolution*, *72*, 1500–
539 1514.

Hajduk, G.K., Walling, C.A., Cockburn, A., & Kruuk, L.E.B. (2020). The 'algebra of evolution': The Robertson-Price identity and viability selection for body mass in a wild bird population. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 375, 20190359.

Hajduk, G.K., Cockburn, A., Osmond, H.L. & Kruuk, L.E.B. (2021). Complex effects of helper relatedness on female extrapair reproduction in a cooperative breeder. *Behavioural Ecology*, *32*, 386–394.

Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D., Robinson, B.S., Hodgson, D.J., & Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *Peer J, 6,* 1–32.

Hill, R.A., & Hinsley, S.A. (2015). Airborne LiDAR for woodland habitat quality monitoring: Exploring the significance of LiDAR data characteristics when modelling organism-habitat relationships. *Remote Sensing*, *7*, 3446–3466.

Hill, R.A., Hinsley, S.A., Gaveau, D.L.A., & Bellamy, P.E. (2004). Cover: Predicting habitat quality for great tits (*Parus major*) with airborne laser scanning data. *International Journal of Remote Sensing*, *25*, 4851–4855.

Hyde, P., Dubayah, R., Peterson, B., Blair, J.B., Hofton, M., Hunsaker, C., & Walker, W. (2005). Mapping forest structure for wildlife habitat analysis using waveform LiDAR: Validation of montane ecosystems. *Remote sensing of Environment*, *96*, 427–437.

Hyde, P., Dubayah, R., Walker, W., Blair, J.B., Hofton, M., & Hunsaker, C. (2006). Mapping forest structure for wildlife habitat analysis using multi-sensor (LiDAR, SAR/InSAR, ETM+, Quickbird) synergy. *Remote Sensing of Environment*, *102*, 63–73.

Ibáñez-Álamo, J.D., Magrath, R.D., Oteyza, J.C., Chalfoun, A.D., Haff, T.M., Schmidt, K.A., Thomson, R.L., & Martin, T.E. (2015). Nest predation research: Recent findings and future perspectives. *Journal of Ornithology*, *156*, 247–262.

Klein, J., Haverkamp, P.J., Lindberg, E., Griesser, M., & Eggers, S. (2020). Remotely sensed forest understory density and nest predator occurrence interact to predict suitable breeding habitat and the occurrence of a resident boreal bird species. *Ecology and Evolution*, *10*, 2238–2252.

567 Koma, Z., Grootes, M.W., Meijer, C.W., Nattino, F., Seijmonsbergen, A.C., Sierdsema, H., Foppen, R.,
568 & Kissling, W.D. (2021). Niche separation of wetland birds revealed from airborne laser scanning.
569 *Ecography*, *44*, 907–918.

570 Kruuk, L.E.B., Osmond, H.L., & Cockburn, A. (2015). Contrasting effects of climate on juvenile body
571 size in a Southern Hemisphere passerine bird. *Global Change Biology,* 21, 2929–2941.

572 Kubelka, V., Šálek, M., Tomkovich, P., Végvári, Z., Freckleton, R.P., & Székely, T. (2018). Global pattern
573 of nest predation is disrupted by climate change in shorebirds. *Science*, *362*, 680–683.

574 Lahti, D.C. (2009). Why we have been unable to generalise about bird nest predation. *Animal*
575 *Conservation*, *12*, 279–281.

576 Lefsky, M.A., Cohen, W.B., Parker, G.G., & Harding, D.J. (2002). LiDAR remote sensing for ecosystem
577 studies: LiDAR, an emerging remote sensing technology that directly measures the three-dimensional
578 distribution of plant canopies, can accurately estimate vegetation structural attributes and should be of
579 particular interest to forest, landscape, and global ecologists. *BioScience*, *52*, 19–30.

580 Lima, S.L. (2009). Predators and the breeding bird: Behavioural and reproductive flexibility under the
581 risk of predation. *Biological Reviews*, *84*, 485–513.

582 Lima, S.L., & Dill, L.M. (1990). Behavioural decisions made under the risk of predation: A review and
583 prospectus. *Canadian Journal of Zoology*, *68*, 619–640.

584 Lv, L., Yang L., Osmond, H.L., Cockburn, A. & Kruuk, L.E.B. (2019). When to start and when to stop:
585 Effects of climate on breeding in a multi-brooded songbird. *Global Change Biology, 26*, 443–457.

586 Lv, L., van de Pol, M., Osmond, H.L., Liu, Y., Cockburn, A., & Kruuk, L.E.B. (2023). Winter mortality of
587 a passerine bird increases following hotter summers and during winters with higher maximum
588 temperatures. *Science Advances*, *9*, eabm019.

589 MacArthur, R.H., & MacArthur, J.W. (1961). On bird species diversity. *Ecology*, *42*, 594–598.

590 Magrath, R.D., Haff, T.M., Horn, A.G., & Leonard, M.L. (2010). Calling in the face of danger: Predation
591 risk and acoustic communication by parent birds and their offspring. In: Brockmann, H. J., Roper, T.
592 J., Naguib, M., Wynne-Edwards, K. E., Mitani, J. C., & Simmons, L. W. (Eds.), Advances in the Study of
593 Behaviour, pp. 187–253. Academic Press, London, UK.

Martin, T.E. (1993). Nest predation and nest sites. *BioScience*, *43*, 523–532.

Martin, T.E., & Roper, J.J. (1988). Nest predation and nest-site selection of a western population of the hermit thrush. *The Condor*, *90*, 51–57.

Matysioková, B., & Remeš, V. (2022). Stronger negative species interactions in the tropics supported by a global analysis of nest predation in songbirds. *Journal of Biogeography*, *49*, 511–522.

Moudrý, V., Cord, A.F., Gábor, L., Laurin, G.V., Barták, V., Gdulová, K., Malavasi, M., Rocchini, D., Stereńczak, K., Prošek, J., & Wild, J. (2023). Vegetation structure derived from airborne laser scanning to assess species distribution and habitat suitability: The way forward. *Diversity and Distributions*, *29*, 39–50.

Mouton, J.C., & Martin, T.E. (2019). Nest structure affects auditory and visual detectability, but not predation risk, in a tropical songbird community. *Functional Ecology*, *33*, 1973–1981.

Naef-Daenzer, B., & Grüebler, M.U. (2016). Post-fledging survival of altricial birds: Ecological determinants and adaptation. *Journal of Field Ornithology*, *87*, 227–250.

Naef-Daenzer, B., Widmer, F., & Nuber, M. (2001). Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal ecology*, *70*, 730–738.

Prawiradilaga, D. M. (1996). Foraging ecology of pied currawongs *Strepera graculina* in recently colonised areas of their range [PhD Thesis]. Australian National University.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Remeš, V., Matysioková, B., & Cockburn, A. (2012a). Long-term and large-scale analyses of nest predation patterns in Australian songbirds and a global comparison of nest predation rates. *Journal of Avian Biology*, *43*, 435–444.

Remeš, V., Matysioková, B., & Cockburn, A. (2012b). Nest predation in New Zealand songbirds: Exotic predators, introduced prey and long-term changes in predation risk. *Biological Conservation*, *148*, 54–60.

Reutebuch, S.E., Andersen, H.E., & McGaughey, R.J. (2005). Light detection and ranging (LIDAR): An emerging tool for multiple resource inventory. *Journal of Forestry*, *103*, 286–292.

Ricklefs R.E. (1969). An analysis of nesting mortality in birds. *Contributions to Zoology*, *9*, 1–48.

Roussel, J.R., Auty, D., Coops, N.C., Tompalski, P., Goodbody, T.R.H., Sánchez Meador, A., Bourdon, J.F., De Boissieu, F. & Achim, A. (2020). lidR: An R package for analysis of Airborne Laser Scanning (ALS) data. *Remote Sensing of Environment, 251*, 112061.

Rowley, I. & Russell, E.M. (1997). Fairy-wrens and grasswrens: Maluridae. Oxford University Press, Oxford, UK.

Ruiz, L.A., Hermosilla, T., Mauro, F., & Godino, M. (2014). Analysis of the influence of plot size and LiDAR density on forest structure attribute estimates. *Forests*, 5, 936–951.

Sasaki, T., Imanishi, J., Fukui, W., & Morimoto, Y. (2016). Fine-scale characterization of bird habitat using airborne LiDAR in an urban park in Japan. *Urban Forestry and Urban Greening*, *17*, 16–22.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution, 1*, 103–113.

Schlotfeldt, B., & Kleindorfer, S. (2006). Adaptive divergence in the superb fairy-wren (*Malurus cyaneus*): A mainland versus island comparison of foraging behaviour, morphology, and vegetation. *Emu-Austral Ornithology*, 106, 309–319.

Shokirov, S. (2021). Using multi-platform LiDAR to assess vegetation structure for woodland forest fauna [PhD Thesis]. Australian National University.

Shokirov, S., Jucker, T., Levick, S.R., Manning, A.D., Bonnet, T., Yebra, M., & Youngentob, K.N. (2023). Habitat highs and lows: Using terrestrial and UAV LiDAR for modelling avian species richness and abundance in a restored woodland. *Remote Sensing of Environment*, *285*, 113326.

Stoker, J. (2009). Visualization of multiple-return LiDAR data: Using voxels. *Photogrammetric Engineering and Remote Sensing*, *75*, 109–112.

Taylor, C.J., & Langmore, N.E. (2020). How do brood-parasitic cuckoos reconcile conflicting environmental and host selection pressures on egg size investment? *Animal Behaviour*, *168*, 89–96.

Taylor, M. (1992). Birds of the Australian Capital Territory: An Atlas. Canberra Ornithologists Group and National Capital Planning Authority, Canberra, Australia.

Treitz, P., Lim, K., Woods, M., Pitt, D., Nesbitt, D., & Etheridge, D. (2012). LiDAR sampling density for forest resource inventories in Ontario, Canada. *Remote Sensing*, 4, 830–848.

van Rees, E. (2013). Rapidlasso: Efficient tools for LiDAR processing. *GeoInformatics, 16,* 14–16.

Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., & Bürkner, P.C. (2021). Rank-normalization, folding, and localisation: An improved R-hat for assessing convergence of MCMC (with discussion). *Bayesian Analysis*, *16*, 667–718.

Vierling, K.T., Swift, C.E., Hudak, A.T., Vogeler, J.C., & Vierling, L.A. (2014). How much does the time lag between wildlife field-data collection and LiDAR-data acquisition matter for studies of animal distributions? A case study using bird communities. *Remote sensing letters*, *5*, 185-193.

Vierling, K.T., Vierling, L.A., Gould, W.A., Martinuzzi, S., & Clawges, R.M. (2008). Lidar: Shedding new light on habitat characterization and modelling. *Frontiers in Ecology and the Environment*, *6*, 90–98.

Vo, A.V., Laefer, D.F., & Bertolotto, M. (2016). Airborne laser scanning data storage and indexing: State-of-the-art review. *International Journal of Remote Sensing*, 37, 6187–6204.

Wilkes, P., Jones, S. D., Suarez, L., Haywood, A., Woodgate, W., Soto-Berelov, M., Mellor, A., & Skidmore, A.K. (2015). Understanding the effects of ALS pulse density for metric retrieval across diverse forest types. *Photogrammetric Engineering & Remote Sensing*, 81, 625–635.

Woinarski, J.C., Braby, M.F., Burbidge, A.A., Coates, D., Garnett, S.T., Fensham, R.J., Legge, S.M., McKenzie, N.L., Silcock, J.L., & Murphy, B. P. (2019). Reading the black book: The number, timing, distribution and causes of listed extinctions in Australia. *Biological Conservation*, *239*, 108261.

Woinarski, J.C., Stobo-Wilson, A.M., Crawford, H.M., Dawson, S.J., Dickman, C.R., Doherty, T.S., Fleming, P.A., Garnett, S.T., Gentle, M.N., Legge, S.M., Newsome, T.M., Palmer, R., Rees, M.W., Ritchie, E.G., Speed, J., Stuart, J.M., Thompson, E., Turpin, J., & Murphy, B.P. (2022). Compounding and complementary carnivores: Australian bird species eaten by the introduced European red fox *Vulpes vulpes* and domestic cat *Felis catus*. *Bird Conservation International*, *32*, 506–522.

Wood, K.A. (2000). Notes on the feeding habits of the pied currawong *Strepera graculina* at Wollongong, New South Wales. *Australian Bird Watcher, 18,* 259–266.

673 Yasukawa, K., & Cockburn, A. (2009). Antipredator vigilance in cooperatively breeding superb fairy-
674 wrens (*Malurus cyaneus*). *The Auk*, *126*, 147–154.

675 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., & Smith, G.M. (2009). Mixed effects models and
676 extensions in ecology with R. Springer, New York, USA.

677

678 **SUPPORTING INFORMATION**

679 Additional supporting information may be found in the published version online in the Supporting
680 Information section at the end of the article.

681 **Video S1**. Animation of height-normalized LiDAR point cloud data used in this study. Appendix S1.
682 Supplementary methods. Assessing spatial autocorrelation of different understorey vegetation
683 structure parameters.

684 **Figure S1**. The height (cm) at which superb fairy-wrens build their nests in the study area.

685 **Figure S2**. The percentage of superb fairy-wren nests built in different vegetation substrates in the
686 study area (A) between 2009–2019; (B) between 1994–2019.

687 **Figure S3**. The fate of superb fairy-wren nests in the study area (A) between 2009–2019; (B) between
688 19942019.

689 **Figure S4**. Mean (SE) daily mortality rate of superb fairy-wren fledglings until independence (A)
690 between 2009–2019; (B) between 1994–2019.

691 **Figure S5**. Mean (SE) daily maximum) and minimum temperature, and total rainfall for each year
692 of the study between 2009–2019.

693 **Figure S6**. The change in (A) nest presence; (B) the number of breeding females in the study area over
694 time.

695 **Figure S7**. Mean (SE) number of LiDAR vegetation points in each cell at 2 m height increments.

696 **Figure S8**. Density plots of Monte-Carlo simulated Moran's I statistics (n = 2000 simulations) for (A)
697 mean height; (B) SD height; and (C) groundstorey volume in each dataset.

698 **Figure S9**. Visualisation of the spatial weights matrix used in each of our three Bayesian spatial
699 hierarchical generalised linear models.

700 **Figure S10**. Spatiotemporal distribution of superb fairywren nest-sites in the study area between
701 2009–2019.

702 **Table S1**. Summaries of Bayesian spatial hierarchical generalised linear regression models using the
703 full breeding dataset from 1994–2019.

704 **Table S2**. Checking for multicollinearity among model parameters.

705 **Table S3**. Pearson coefficients indicating the level of relationship between main effect parameters in
706 each of the three Bayesian spatial hierarchical regression models: (A) nest presence; (B) nest success
707 rate; (C) fledgling survival rate.

708 **Table S4**. Checking for spatial autocorrelation among understorey vegetation structure parameters.

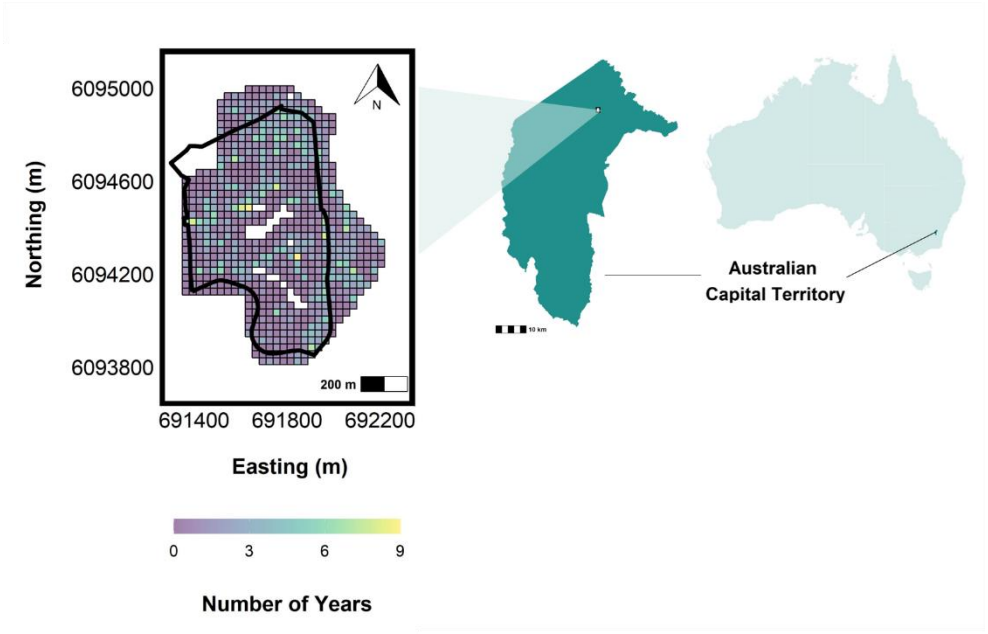

Figure 1: *Location of the study area in Canberra, Australian Capital Territory, Australia. The study area encompasses an area of c. 65 hectares that includes a managed area (c. 43 hectares) in the Australian National Botanic Gardens (ANBG; the perimeter of which is shown in black) and an unmanaged area (c. 22 hectares), which is part of the adjacent Black Mountain Nature Reserve. We established a 30 x 30 m resolution grid (n = 768 cells) over the extent of the study area, for which superb fairy-wren breeding data and ALS-derived vegetation structure parameters were extracted. Data for 27 of the 768 cells were excluded from analyses (shown in white), leaving a total of 741 cells (see main text for further details). The left-hand panel shows the spatial distribution of the 741 cells across the study area, with cells shaded based on the number of years they contained a nest-site; the middle panel shows the location of the study area within the Australian Capital Territory; and the right-hand panel shows the latter's location in Australia.*

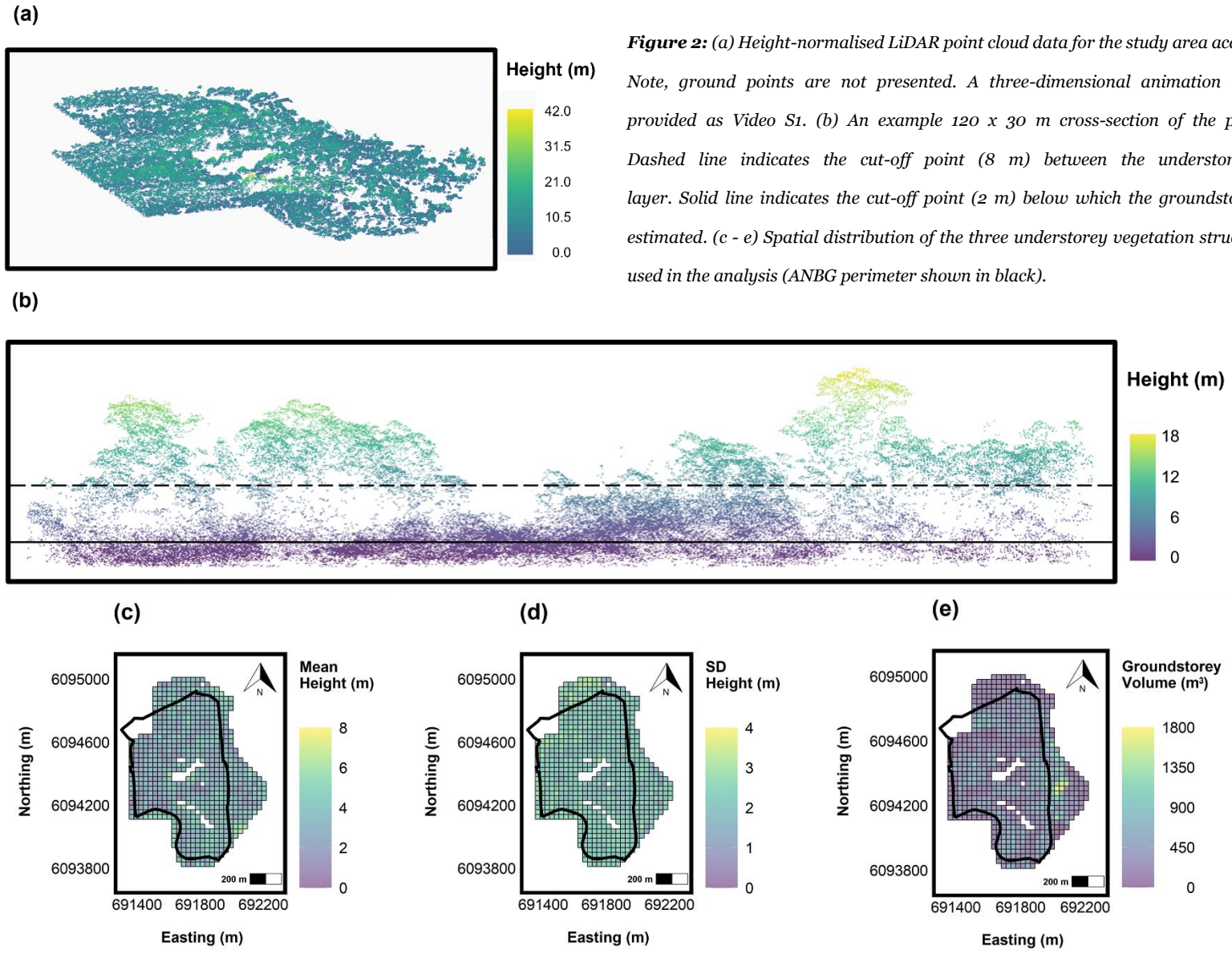

Figure 2: *(a) Height-normalised LiDAR point cloud data for the study area acquired using ALS. Note, ground points are not presented. A three-dimensional animation of these data is provided as Video S1. (b) An example 120 x 30 m cross-section of the point cloud data. Dashed line indicates the cut-off point (8 m) between the understorey and canopy layer. Solid line indicates the cut-off point (2 m) below which the groundstorey volume was estimated. (c - e) Spatial distribution of the three understorey vegetation structure parameters used in the analysis (ANBG perimeter shown in black).*

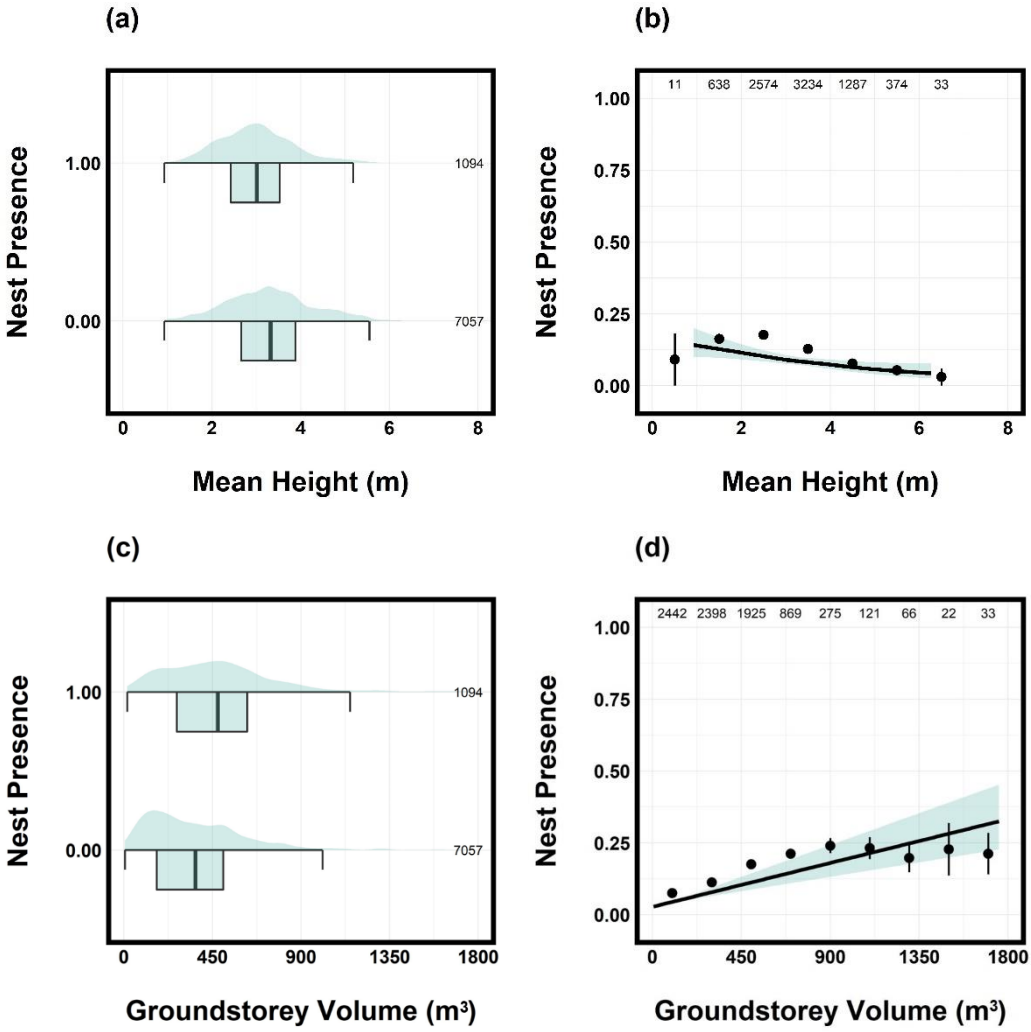

Figure 3: *Nest presence in relation to (a – b) mean height and (c – d) groundstorey volume. Panels (a) and (c) show the distribution of the raw data. The box and whiskers show the mean, plus upper and lower quartiles, and the interquartile range of the raw data for each group. Panels (b) and (d) show the model estimated marginal means (± 95% confidence intervals), after correcting for main effect parameters, as described in Methods. For visualisation purposes, the raw data were grouped into bins (each bin represents an interval of 1 m in (b) and an interval of 200 m³ in (d)) with points showing the group mean ± SE. In all panels, the number of observations (cell-years) in each group is given. Model estimates are provided in Table 3.*

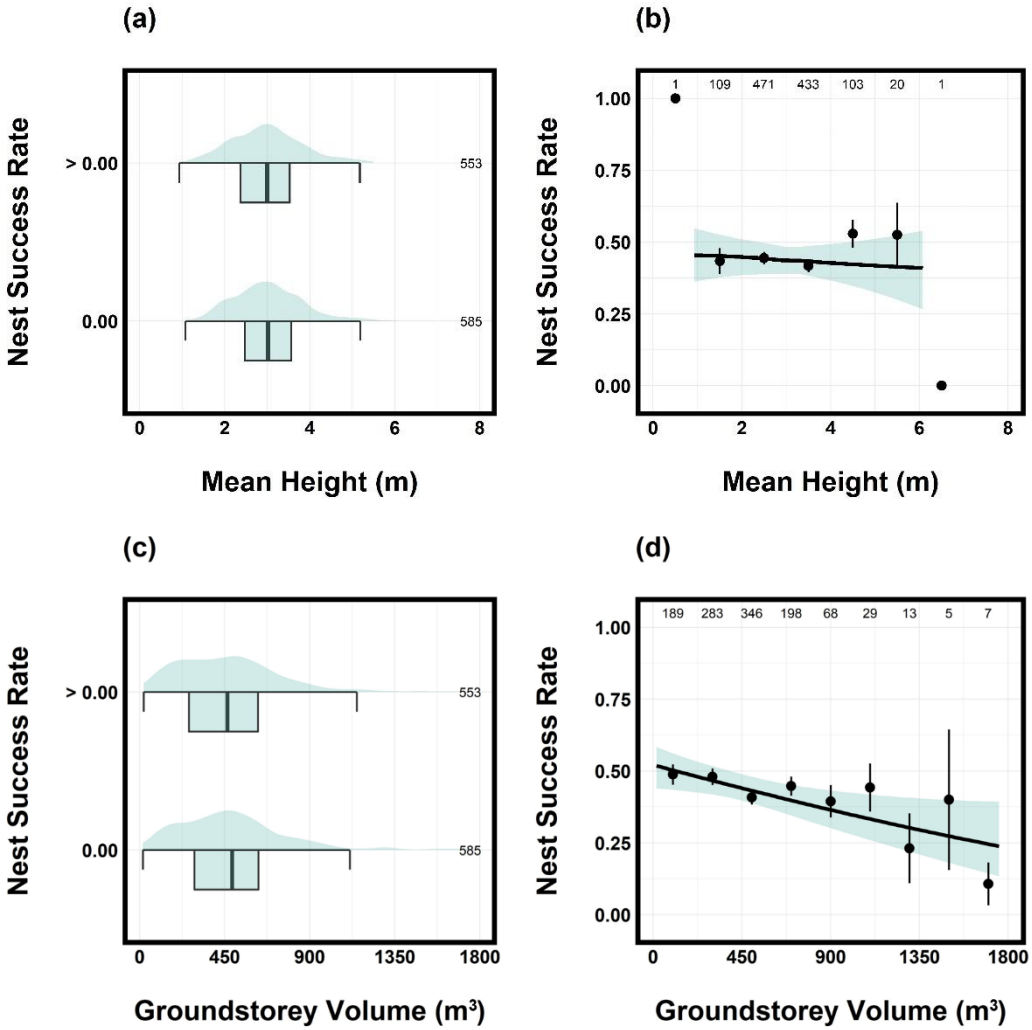

Figure 4: *Nest success rate in relation to (a – b) mean height and (c – d) groundstorey volume. Panels (a) and (c) show the distribution of the raw data. For visualisation purposes, the raw data were grouped into two bins: 0.00 and > 0.00. The box and whiskers show the mean, plus upper and lower quartiles, and the interquartile range of the raw data for each group. Panels (b) and (d) show the model estimated marginal means (± 95% confidence intervals), after correcting for main effect parameters, as described in Methods. For visualisation purposes, the raw data were grouped into bins (each bin represents an interval of 1 m in (b) and an interval of 200 m³ in (d)) with points showing the group mean ± SE. In all panels, the number of observations (female-nest-cell-years) in each group is given. Model estimates are provided in Table 3.*

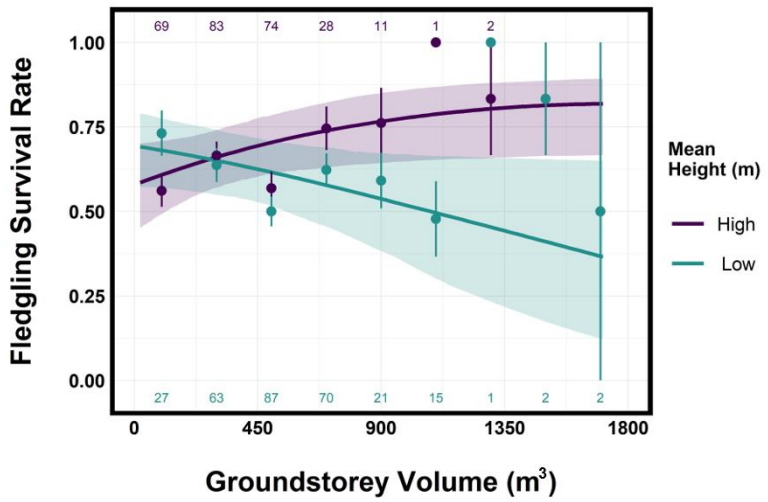

Figure 5: *Fledgling survival rate in relation to groundstorey volume when vegetation is low (green; mean height is less than the population-level average) or high (purple; mean height is greater than the population-level average). Regression lines show the model estimated marginal means (± 95% confidence intervals), after correcting for main effect parameters, as described in Methods. For visualisation purposes, the raw data were grouped into bins (each bin represents an interval of 200 m³) with points showing the group mean ± SE. The number of observations (female-nest-cell-years) in each group is given. Model estimates are provided in Table 3.*

2023-05-29:
A revised version of this manuscript is now published at: https://doi.or/10.1002/rse2.342

Table 1: *Definition of terms and overview of the superb fairy-wren breeding parameters used in this study.*

Breeding Parameter	**Observation Level**	**Number of Observations**	**Description**	**Model Structure**
Nest Presence	A 30 x 30 m resolution cell in a given year (cell-year)	8151 cell-years (741 cells; 11 years)	Cells that contained a nest in a given year were assigned a binary score of 1 (nest-cell-year) otherwise 0 (unused cell-year)	Bernoulli error distribution (and logit-link function)
Nest Success Rate	A nest-cell for a given female in a given year (female-nest-cell-year)	1138 female-nest-cell-years	The number of successful nests relative to the total number of nest attempts for each female in a nest-cell in a given year	Binomial error distribution (and logit-link function). The denominator (the total number of nest attempts for each female-nest-cell-year) was equal to 1 in 80.8% of observations
Fledgling Survival Rate	A nest-cell for a given female in a given year (female-nest-cell-year)	556 female-nest-cell-years. Only female-nest-cell-years that contained one or more fledgling were included in this model	The number of fledglings to survive to independence relative to the total number of nestlings that successfully fledged for each female in a nest-cell in a given year	Binomial error distribution (and logit-link function). In total, 22.1% of observations were zeros. Therefore, to account for excess zeros in the Binomial error distribution, we included a zero-inflated parameter in this model (Bürkner, 2017)

Table 2: *Overview of the understorey vegetation structure parameters derived from ALS for each 30 x 30 m resolution cell. z = normalised height value of LiDAR point; Voxel = A value of volume represented in three-dimensional (x, y, z) space.*

Parameter	**Parameter Abbreviation**	**Height Threshold**	**Description**	**Ecological Interpretation**
Mean height of the understorey vegetation (measured in metres)	Mean Height	0 – 8 m	Mean value of *z* within each 30 x 30 m resolution cell	A high mean height value indicates that a cell contains more tall shrubs and small trees, and fewer grass tussocks. A low mean height value indicates that a cell contains more grass tussocks and small shrubs. The spatial distribution of mean height across the study area is shown in Figure 2c.
Standard deviation of the height of the understorey vegetation (measured in metres)	SD Height	0 – 8 m	SD of *z* values within each 30 x 30 m resolution cell	SD height describes the variation in the vegetation height. A high SD height value indicates that a cell contains a more heterogenous, or complex, vegetation height distribution. The spatial distribution of SD height across the study area is shown in Figure 2d.
Volume of the vegetation in the lowest layer of the understorey (measured in cubic metres).	Groundstorey Volume	0 – 2 m	The number of 1 x 1 x 1 m voxels† between 0–2 m containing one or more vegetation point within each 30 x 30 m resolution cell. Maximum potential groundstorey volume is 1800 m^3 (30 x 30 x 2 m).	The density of vegetation in the lowest understorey layer. The spatial distribution of groundstorey volume across the study area is shown in Figure 2e.

† *Note: ALS point cloud data were converted to 1 x 1 x 1 m voxels using the voxelize_points function in the package 'lidR' (v.3.1.3; Rousel et al., 2020) in in R (v.4.0.5; R Core Team, 2021). The method of using voxels to estimate vegetation density followed e.g., Béland et al. (2014); Sasaki et al. (2016); Shokirov (2021), Shokirov et al. (2023); Stoker (2009).*

2023-05-29:
A revised version of this manuscript is now published at: https://doi.or/10.1002/rse2.342

Table 3: *Summaries of Bayesian spatial hierarchical generalised linear regression models. The parameter estimates are presented as posterior means ± standard deviation (SD) and 95% credible intervals (CI). All explanatory parameters were mean standardised for analysis. Main effect parameters for which the 95% CI do not overlap zero are highlighted in bold.*

Parameters	**Nest Presence** Estimate ± SD [95% CI]	**Nest Success Rate** Estimate ± SD [95% CI]	**Fledgling Survival Rate** Estimate ± SD [95% CI]
Intercept	**-2.37 ± 0.09 [-2.54 – -2.19]**	**-0.38 ± 0.13 [-0.63 – -0.12]**	**1.17 ± 0.24 [0.70 – 1.64]**
Year	**-0.28 ± 0.07 [-0.43 – -0.13]**	0.04 ± 0.09 [-0.13 – 0.20]	0.05 ± 0.16 [-0.27 – 0.37]
Mean Height	**-0.24 ± 0.09 [-0.41 – -0.08]**	-0.04 ± 0.09 [-0.21 – 0.13]	0.24 ± 0.15 [-0.06 – 0.54]
SD Height	0.10 ± 0.07 [-0.04 – 0.25]	-0.04 ± 0.07 [-0.18 – 0.10]	-0.19 ± 0.13 [-0.44 – 0.05]
Groundstorey Volume	**0.42 ± 0.08 [0.26 – 0.57]**	**-0.20 ± 0.07 [-0.33 – -0.06]**	0.07 ± 0.12 [-0.17 – 0.31]
Groundstorey Volume: Mean Height	0.07 ± 0.07 [-0.06 – 0.20]	0.02 ± 0.07 [-0.11 – 0.16]	**0.34 ± 0.13 [0.10 – 0.59]**
Female Age (Relative to 1 Year Old)			
2+ Years Old		-0.02 ± 0.14 [-0.28 – 0.24]	-0.08 ± 0.21 [-0.50 – 0.33]
Number of Helpers (Relative to 0)			
1+ Helpers		0.26 ± 0.13 [-0.01 – 0.51]	-0.07 ± 0.20 [-0.46 – 0.32]
Random Effects	$\sqrt{\text{Variance}}$ ± SD [95% CI]	$\sqrt{\text{Variance}}$ ± SD [95% CI]	$\sqrt{\text{Variance}}$ ± SD [95% CI]
Cell ID	0.35 ± 0.19 [0.03 – 0.71]	0.19 ± 0.13 [0.01 – 0.49]	0.90 ± 0.18 [0.54 – 1.27]
	(*n = 741*)	(*n = 448*)	(*n = 301*)
Female ID		0.52 ± 0.11 [0.28 – 0.74]	0.81 ± 0.22 [0.33 – 1.24]
		(*n = 317*)	(*n = 250*)
Year	0.19 ± 0.08 [0.06 – 0.37]	0.13 ± 0.10 [0.01 – 0.36]	0.37 ± 0.17 [0.08 – 0.75]
	(*n = 11*)	(*n = 11*)	(*n = 11*)
Spatial Correlation	2.21 ± 0.23 [1.71 – 2.62]	0.17 ± 0.09 [0.01 – 0.39]	0.14 ± 0.11 [0.00 – 0.41]
Zero Inflation Parameter			0.13 ± 0.02 [0.09 – 0.17]
	n = 8151 cell-years	*n = 1138 female-nest-cell-years*	*n = 556 female-nest-cell-years*