Corella, 2025, 49: 44-54

Selection of nest and roost sites by Eastern Barn Owls *Tyto alba delicatula* in north-western Victoria

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Received: 5 February 2025
Accepted: 22 May 2025

Abstract. Nest-site and roost-site selection of the Eastern Barn Owl *Tyto alba delicatula* were studied by JGM in north-western Victoria during 1987–1990, in agricultural and woodland areas (*n* = 15 nests and 82 roost-only sites). Most nests were in tree hollows (93%), in those local tree species providing the largest hollows, and one in a hay shed; nests occurred in agricultural and non-agricultural land. Roost-only sites were mostly in tree hollows, but a higher proportion were in foliage in agricultural than non-agricultural land, and the reverse applied to tree hollows. The few roosts in artificial sites were in agricultural land. Stepwise (additive) logistic regression and stepwise (additive) discriminant analysis identified six variables that enabled discrimination between nest hollows and roost-only hollows with >90% accuracy: hollow wall integrity (number of splits), % foliage cover over the entrance, cavity floor area, angle of hollow entrance from vertical, hollow wall thickness at floor level and tree height (log-transformed). In agricultural land, hollow availability was greatest in patches of woodland (one hollow per 1.4 ha), less in shelterbelts (one per 5.5 ha) and least in roadside verges (one per 9.9 ha), translating to one hollow per 4.9 km. of linear verge. Hollow availability may be limiting for Barn Owls in the Victorian Mallee and, given rural tree decline and the loss of hollows from farmland, will require appropriate management for conservation of this species in agricultural landscapes.

Keywords: Barn Owl, *Tyto alba*, nest hollows, roost sites, agriculture, conservation, Victoria

INTRODUCTION

The quantified nest-site and roost-site characteristics of the Eastern Barn Owl *Tyto alba delicatula* (hereafter Barn Owl) in Australia, to the extent then known, were summarised by Higgins (1999), based largely on an unpublished thesis by McLaughlin (1994). In Australia, Barn Owls roost in a variety of sites from tree hollows and foliage to caves, sheltered sites on the ground and artificial structures including old buildings. However, in Australia they typically nest in tree hollows and sometimes in other sites such as caves, rock clefts, mine shafts and even under tussocks or shrubs on the ground, but rarely nest in buildings (Higgins 1999, Olsen 2011). It is unclear why Barn Owls do not nest routinely in buildings in Australia, in contrast with their overseas counterparts, including in nearby Indonesia (e.g. Olsen 2011). Presented here is the detail supporting the summary statements of Higgins (1999) on Barn Owl nest- and roost-sites that cited McLaughlin (1994). Some roost- and nest-hollow parameters of the Eastern Barn Owl were since described by Mawson *et al.* (2024). Barn Owl nest- and roost-site selection elsewhere in the world was described and reviewed by Taylor (1994) and Roulin (2020). Furthermore, it is apparent from these references and Meaney *et al.* (2021) that Barn Owls show site fidelity when nesting in buildings and in artificial hollows or nest boxes.

The primary purpose of this study was to investigate whether Barn Owls exhibit any selectivity in their choice of nest site and, if so, to determine the physical parameters of nests that may account for this selectivity. A secondary purpose was to obtain details of the abundance, characteristics and use of suitable tree hollows and other roost sites. This information has implications for both the long-term conservation of the Barn Owl in the Australian wheat belt, and its potential as a predator of the introduced House Mouse *Mus musculus* (a domestic and agricultural pest).

The Australian Barn Owl is currently classified by BirdLife Australia as subspecies *delicatula* of the global *Tyto alba*, although genetic studies have revealed it to be a subspecies of *T. javanica* of Asia to Australasia, distinct from *T. alba* (Europe, Middle East and Africa) and *T. furcata* (Americas) (Aliabadian *et al.* 2016, Jønsson *et al.* 2013, Uva *et al.* 2018).

STUDY AREA AND METHODS

Study area

Barn Owls were studied by JGM from July 1987 to December 1990 in the semi-arid Mallee wheat belt of north-western Victoria, at two main sites: intensively managed agricultural land (1030 ha) at the Mallee Research Station at Walpeup (35º08'S, 142º02'E), ~30 km west of Ouyen; and state forest (~1000 ha) ~7 km west of Red Cliffs, immediately north-east of Thurla (34º20'S, 142º08'E). Regionally, >50% of the original vegetation of the area has been cleared for agriculture, with <20% of the original vegetation remaining in intensively farmed areas. Land use is dryland cropping of winter cereals, mainly wheat *Triticum aestivum* with some barley *Hordeum vulgare*. Most crops are sown on long fallow, with a three year rotation of fallow, crop and pasture (consisting of mainly regenerating introduced medics *Medicago* spp. and grasses). Sheep *Ovis aries* and cattle *Bos taurus* are grazed on fallow paddocks and pastures and on the understorey of remnant woodland stands.

Mean annual rainfall is 250–400 mm and winter-dominant. Summer temperatures frequently exceed 34ºC, often 40ºC, and winter minima are often below 2ºC.

The Walpeup site consisted of 805 ha of cleared land (intensive cropping ~300 ha, pasture or fallow 500 ha, grazed by 500 sheep) and ~20 ha of retained shelterbelts and woodland patches. Native vegetation at Walpeup consisted of medium to tall (5–12 m) mallee eucalypts, most notably Oil Mallee *Eucalyptus oleosa* and White Mallee *E. gracilis* on sandy soils, and Belah *Casuarina pauper* and Slender Cypress-pine *Callitris preissii*, often with Cattlebush *Alectryon oleifolius*, on loamier soils; both had an understorey of chenopods and exotic grasses. The major function of the Research Station is the development and assessment of cropping and pasture cultivars, and in any one year approximately 100 ha of arable land is devoted to this research. Approximately 200 ha each year is devoted to commercial bulk cropping, with the remaining 500 ha under either pasture or fallow.

Official land use at the Thurla site included apiculture (not intense, with Honey Bee *Apis mellifera* hive sites well separated), and other passive activities permitted in state forest. No legal wood gathering or grazing occurred at this site during the study, although the site was occasionally visited by illegal wood collectors. Vegetation at the Thurla site consisted of a closed woodland of Grey Mallee *E. socialis*, Dumosa Mallee *E. dumosa* and Slender-leaved Mallee *E. leptophylla* with an understorey of Porcupine Grass *Triodia irritans* on sand-dune crests; and tall open mallee woodland of large (>12 m) Oil Mallee and some White Mallee and Grey Mallee with a midstorey of scattered small stands of Cattlebush, Sugarwood *Myoporum platycarpum,* Desert Cassia *Senna artemisioides*, Slender-leaved Hopbush *Dodonaea angustissima* and various *Acacia* spp. (e.g. Umbrella Wattle *A. oswaldii*) and a ground layer of chenopods and others (e.g. Ruby Saltbush *Enchylaena tomentosa*, Rosy Bluebush *Maireana erioclada* and Shrubby Twin-leaf *Zygophyllum aurantiacum*) on the heavier soils in swales.

Methods

Initially, information on the location of Barn Owl roost and nest sites was sought and obtained from members of the general public and local birdwatching and naturalist groups. Barn Owl nest and roost sites were located mainly by thorough daytime searches and visual inspection of tree hollows. On agricultural land, buildings, sheds, farm machinery and water tanks were also inspected. Access to tree hollows was either by climbing or by using an extendable aluminium ladder. Data were gathered between July 1987 and December 1990: ~10 days per month on fieldwork during July–December 1987, and subsequently 3–8 days per month, except April–May 1989 and February 1990 (no fieldwork); total >220 days in the field, including multiple inspections of each tree hollow and foliage roost sites.

During this study, Barn Owls used tree hollows, tree/shrub foliage and a variety of buildings for nesting and diurnal roosting. Data were collected from most (86.6%, $n = 84$) of these sites (see McLaughlin and Debus in press for details of search methods). Nest and roost sites located in buildings (5.2%, $n = 5$) were not measured. A general description of most foliage roost sites (60.0%, $n = 12$) was undertaken, and although they comprised 20.6% ($n = 20$) of all sites, they differed substantially in structure from sites located in tree hollows and were not subject to detailed statistical analysis. Measurements from nest trees were obtained within two weeks of all young leaving the nest and are assumed to be the same as at the time of site selection. Roost sites were measured when first located, or within 2–4 weeks.

For each tree hollow nest and roost site, initially ~30 variables were measured that detailed site location, land-use, and tree and cavity characteristics. Subsequent exploratory analysis (including the combination of some variables, and the elimination of some highly correlated variables) reduced this data set to 13 variables considered to have the potential to discriminate between sites. Variables included for further analysis, and their units of measurement, were:

(1) tree height (to highest point of tree) (m) [THEIGHT];

(2) height of lowest point of hollow opening above ground (m) [HEIGHT];

(3) width of entrance (cm) [WIDTH];

(4) internal depth of hollow, measured along the trunk (m) [DEPTH];

(5) floor area (calculated as the area of a circle with a diameter equal to the mean of two maximum right-angle measurements) (cm^2) [FLOOR];

(6) external diameter of tree at breast height (cm) [DIAMTR];

(7) hollow wall thickness at floor level (cm) [WALL];

(8) closest suitable (or apparently suitable, nest or roost) tree hollow (m) [CLOSEST];

(9) mean percentage canopy cover recorded at each of four cardinal points 2 m from the entrance [MEANCAN];

(10) percentage canopy cover directly above entrance [CANENTR];

(11) number of discontinuities >0.5 cm width in the hollow wall within 0.5 m of the hollow floor (n) [SPLITS];

(12) angle from vertical faced by the plane of the hollow opening (degrees) [ANGLE1];

(13) compass bearing (aspect) of entrance (degrees magnetic).

Percentage foliage cover was measured from the ground using a 'moose-horn' cover estimator (Mueller-Dombois and Ellenberg 1974). Measurements of tree heights were obtained by triangulation. Other linear measurements were made using either a 50-m tape measure, flexible plastic rod (marked into cm), steel rule or callipers. Aspects were obtained using a prismatic compass, and angular measurements with an inclinometer. For some trees it was difficult to obtain data on certain variables (e.g. FLOOR, WALL), and in some cases certain variables were not applicable (e.g. aspect for hollow openings that faced directly upwards). 'Missing cases' accounted for ~5% of the potential total data set.

Among intensively managed agricultural properties in the study area, the Mallee Research Station is atypical in that it possesses wide (up to 200 m) shelterbelts, and patches of old-growth woodland that are infrequently grazed by stock. To obtain a general indication of the availability of tree hollows suitable for Barn Owls within the broader study area, 150 woodland patches, roadside verges, and shelterbelts (the three most common habitats likely to provide suitable Barn Owl hollows) within cropping land throughout the study area were randomly selected (using random number tables and Australian Mapping Grid references). Each 'point location' was plotted on a 1:100,000 topographic mapsheet, and during the course of the study 123 (82%) of these sites were visited. At each 'point location' the number of apparently suitable (nest or roost) tree hollows was recorded within a 1-ha area (the shape of which depended on the habitat type) surrounding the selected point.

Data analysis

Means and their standard deviations were calculated for all variables contained in the refined data set, and separately for the groups 'nest sites' and 'roost-only sites'. Where variances differed significantly between groups (*F*-tests), data were transformed to natural logarithms before detailed statistical analysis. Variables comprising percentages were transformed using the arcsine transformation (Zar 1974). Two nest sites were located in different hollows in the same tree (presumed same breeding pair). Consequently, some measurements from these nesting attempts are identical. For the purposes of this study, these attempts are considered independent, and the common measurements entered twice.

To determine factors important in the selection of nest sites, the 'null data set' was restricted to sites utilised by Barn Owls as roost-only sites, rather than compare nest sites with randomly selected sites (e.g. Belthoff and Ritchison 1990a, Tidemann *et al.* 1992). Although this method increases the 'realness' of the test (McCallum and Gehlbach 1988), it has the disadvantage of reducing the likelihood of isolating important effects (Belthoff and Ritchison 1990a).

The identification of variables that discriminated between nest and roost-only sites was undertaken by stepwise (additive) logistic regression (Dillon and Goldstein 1984, Haberman 1978). Because logistic regression is not greatly affected by departures from normal distribution of data (Flury and Riedwyl 1988, Haberman 1978), it was likely to give more reliable results than the similar discriminant analysis, a method that assumes multivariate normality (Dillon and Goldstein 1984). However, as discriminant analysis is a robust technique that produces reasonable results despite minor violations of distributional assumptions (Dillon and Goldstein 1984, Flury and Riedwyl 1988), a stepwise (additive) discriminant analysis was also undertaken, and the results of the two techniques compared. For reasons given by Wilkinson (1988), *SYSTAT* (version 4.1) has no facility for automatically computing stepwise regressions for logistic and discriminant analyses. Consequently, these procedures were carried out manually. With the exception of nest/roost orientation (hollow aspect) data, all variables of the refined data set ($n = 12$) were available for inclusion in the logistic and discriminant analysis.

Logit ('log-odds') models investigate the relationship of a dichotomous dependent variable (in this study, nest site or roost-only site) to one or more independent variables, using a log-linear function (Haberman 1978). The model used in this study is of the form,

$$\text{logit}\,(P) = \ln\,(1 / 1 - P) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \ldots + \beta_n x_n$$

where β is estimated (see below) from the available data, x. The response variable P is constrained between 0 and 1, and can be interpreted as an index of probability of group membership (Straw *et al.* 1986).

To maximise the likelihood of the logistic function (minimise the negative of the log-likelihood), modelling of the logistic function in *SYSTAT* utilised negative log-likelihood as the loss function (Wilkinson 1988). Stepwise (additive) logistic regression was achieved by initially incorporating single variables (predictors) in a logistic function (on the basis that each predictor was the only one available for inclusion in the model) and recording the final value of the loss function. As reduction of the loss function value indicates improved accuracy of the model, the variable that produced the smallest loss function value was incorporated into the logistic model. On this basis, successive steps (involving recalculation of the logistic function) added additional variables. This process continued until no substantial improvement (minimisation) in the value of the loss function was obtained. To determine the accuracy of the model to classify the data from which it was derived, predicted case probabilities were compared with observations at the $P = 0.5$ level.

Discriminant analysis is a technique for classifying individuals or objects into mutually exclusive and exhaustive groups (i.e. nest or roost-only sites) on the basis of a set of independent variables, by maximising the between-group variance relative to the within-group variance (Dillon and Goldstein 1984). Stepwise (additive) discriminant analysis was undertaken by initially calculating univariate *F*-values for each variable, on the basis that each variable was the only one available for inclusion in the discriminant function. The predictor with the largest univariate *F*-value was then chosen to enter the discriminant function. Successive steps added new variables on the basis of their covariance-controlled partial *F*-value, a figure derived by conditioning on those predictors already made part of the discriminant function. Variables selected at an adjusted (multivariate) significance level of $P = 0.01$ were included in the discriminant function.

Entrance orientation data were considered separately because they required circular statistical procedures. Overall and group mean entrance aspect, circular standard deviation (s) and associated angular dispersion (r) were calculated using Rayleigh's test, and between-group difference in mean direction calculated using the non-parametric Watson's U test (Zar 1974).

A caveat on the statistical treatments is that JGM's raw data or notes were not retrievable. Hence, it is not possible to describe the process used to eliminate highly correlated variables; nor quantify the extent of multicollinearity in the predictors used in the logistic regression model with a variance inflation factor (Spearman correlation matrix does not detect multicollinearity beyond pairwise relationships); nor say how missing data were handled. Thus, reproducibility is limited. It was also not possible to explore an Akaike Information Criterion-based model selection, which, rather than reliance on statistical significance for variable selection, balances goodness of fit with complexity.

RESULTS

Land use

Fourteen active nests were located: 13 (92.8%) in tree hollows and one (7.2%) in a hayshed (see also McLaughlin and Debus in press). An additional tree hollow used in courtship by a pair of owls, but abandoned before egg-laying (apparently related to human disturbance: the site was immediately adjacent to a trail-bike track), took the total to 15 nest sites. Nine (60.0%) were in intensively managed agricultural areas and six (40.0%) in primarily non-agricultural areas, i.e. state forest and other remnant woodland, mainly tall open mallee. Two (13.3%) of the nests were located on the major agricultural study site at Walpeup and five (33.3%) on the primarily non-agricultural study site near Red Cliffs.

Of 82 roost-only sites, 78% were in agricultural land and 22% in non-agricultural land. Tree hollows (*n* = 58) accounted for 65.6 % and 88.9% of roosts, respectively; foliage (*n* = 20) 28.1% and 11.1%; and artificial sites (*n* = 4) were all on agricultural land (6.3%; Fig. 1).

Searching intensity was greater in agricultural areas. Nevertheless, foliage roosts in agricultural areas comprised a larger proportion of natural roost sites than in non-agricultural areas (a non-significant trend: $\chi^2_1 = 1.71$, 2×2 contingency table, $P<0.2$). Similarly, in comparison to agricultural land, tree hollows tended to comprise a larger proportion of all roost-only sites in primarily non-agricultural land ($\chi^2_1 = 2.64$, 2×2 contingency table, $P<0.1$). If the exposed foliage roosting sites adopted by some recently fledged young are excluded from the data set (*n* = 1 for agricultural land, *n* = 2 for non-agricultural land), the comparison is significant ($\chi^2_1 = 4.01$, 2×2 contingency table, $P<0.05$).

Nest and roost sites

Means, standard deviations and ranges for variables comprising the refined data set, for all tree hollows (roosts and nests) known to be used by Barn Owls during this study, are given in Table 1. The mean entrance orientation for all sites was 349° ($s = 119°$, $r = 0.112$), but no significant directionality was indicated (Rayleigh's test, $z_{69} = 0.871$, $P>0.05$).

Two tree species accounted for all Barn Owl tree hollows: Oil Mallee (*n* = 60) and Belah (*n* = 12). Irrespective of habitat or land use, tree hollows used by Barn Owls (either nest or roost hollows) were situated no more than 10 m from either cleared land or a clearing >800 m^2.

Variable means, standard deviations and ranges for all tree-hollow nest sites located during the study are given in Table 2. Mean entrance orientation for nest sites alone was 107° ($s = 90°$, $r = 0.292$), with no significant directionality (Rayleigh's test, $z_{14} = 1.195$, $P>0.05$; Fig. 2). All nest hollows located (*n* = 14) were in Oil Mallee.

Variable means, standard deviations and ranges for tree hollow roost-only sites located during the study are given in Table 3. The mean entrance orientation for roost-only sites was 328° ($s = 105°$, $r = 0.188$), with no significant directionality (Rayleigh's test, $z_{55} = 1.936$, $P>0.05$) (Fig. 3). Roost-only tree hollows were located in Oil Mallee (*n* = 46) and Belah (*n* = 12).

Barn Owls roosted in the foliage of mallee eucalypts (Oil Mallee *n* = 6 [including three instances of recently fledged young roosting in exposed positions]; White Mallee *n* = 6; Red Mallee *Eucalyptus calycogona n* = 3), Belah (*n* = 1), Cattlebush (*n* = 2), African Boxthorn *Lycium ferocissimum* (*n* = 1) and Peppercorn *Schinus areira* (*n* = 1). Roosts in densely treed shelterbelts or roadside verges were located immediately

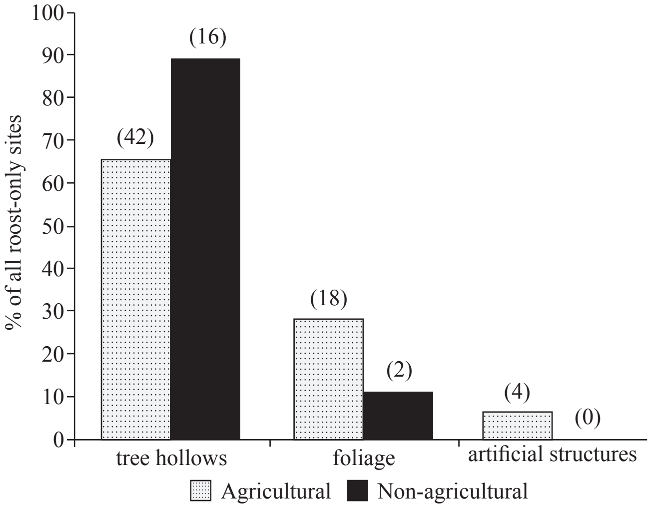

Figure 1. *Comparison of roost-only sites located in intensively managed agricultural and primarily non-agricultural land. Numbers in parenthesis indicate sample size.*

Table 1

Variable means, sample sizes, standard deviations and ranges for all tree-hollow sites (roosts and nests) utilised by Barn Owls in north-western Victoria.

Variable (unit of measurement)	(*n*)	Missing cases	Mean	Standard deviation	Range
THEIGHT (m)	71	1	10.2	3	3.4–18.4
HEIGHT (m)	72	0	3.9	0.9	2.2–6.8
WIDTH (cm)	71	1	18.4	4.1	9.0–28.0
DEPTH (m)	68	4	1.9	1.2	0.2–6.5
FLOOR (cm^2)	59	13	537	294	132–1452
DIAMTR (cm)	70	2	38.6	9.4	22–60
WALL (cm)	60	12	4.3	1.6	0.8–8.5
CLOSEST (m)	71	1	55	44	1–150
MEANCAN (%)	68	4	28	14	0–53
CANENTR (%)	70	2	19	20	0–67
SPLITS (n)	72	0	5.3	2.8	0–9
ANGLE1 (degrees)	69	3	45	25	5–123

Table 2

Variable means, sample sizes, standard deviations and ranges for all Barn Owl tree-hollow nest sites located in north-western Victoria.

Variable (unit of measurement)	(*n*)	Missing cases	Mean	Standard deviation	Range
THEIGHT (m)	14	0	11.5	1.5	9.2–14.1
HEIGHT (m)	14	0	4.2	0.7	3.4–5.7
WIDTH (cm)	14	0	18.8	5.3	14.5–28.0
DEPTH (m)	14	0	1.5	0.6	0.5–2.7
FLOOR (cm^2)	13	1	839	318	433–1452
DIAMTR (cm)	14	0	43.3	5.9	31–56
WALL (cm)	13	1	5.4	1.1	4.0–8.5
CLOSEST (m)	14	0	42	34	2–100
MEANCAN (%)	14	0	38	6	27–48
CANENTR (%)	14	0	43	16	0–67
SPLITS (n)	14	0	1.7	1.5	0–3
ANGLE1 (degrees)	14	0	65	18	30–90

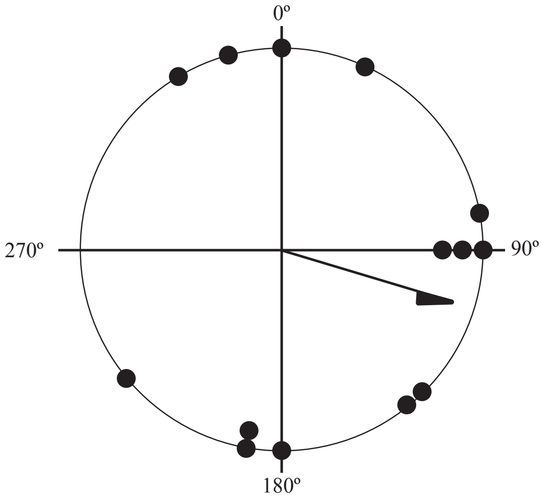

Figure 2. *Scatter diagram illustrating tree hollow entrance orientation for nest sites (*n *= 14). Arrow indicates mean direction.*

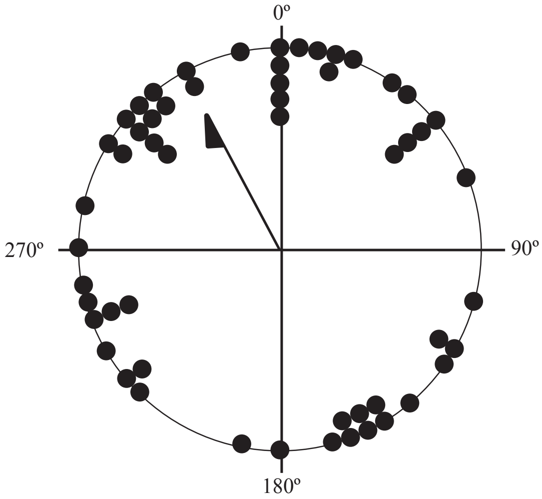

Figure 3. *Scatter diagram illustrating entrance orientation for all tree hollow roost-only sites (*n *= 55). Arrow indicates mean direction.*

Table 3

Variable means, sample sizes, standard deviations and ranges for all Barn Owl roost-only tree-hollow sites located in north-western Victoria.

Variable (unit of measurement)	(*n*)	Missing cases	Mean	Standard deviation	Range
THEIGHT (m)	57	1	9.8	3.2	3.4–18.4
HEIGHT (m)	58	0	3.9	1	2.2–6.8
WIDTH (cm)	57	1	18.4	3.9	9.0–26.0
DEPTH (m)	54	4	2	1.3	0.2–6.5
FLOOR (cm2)	46	12	452	225	132–1075
DIAMTR (cm)	56	2	37.5	9.8	22–60
WALL (cm)	47	11	4	1.7	0.8–8.0
CLOSEST (m)	57	1	58	46	1–150
MEANCAN (%)	54	3	25	15	0–53
CANENTR (%)	56	1	13	16	0–63
SPLITS (n)	58	0	6.2	2.3	0–9
ANGLE1 (degrees)	55	3	40	24	5–123

Table 4

Variable means, sample sizes, standard deviations and ranges of Barn Owl foliage roost sites in mallee eucalypts, north-western Victoria. (°) indicates mean of two maximum right-angle dimensions; (#) indicates canopy cover directly above roosting position; (*) indicates mean of canopy cover measured at four cardinal points 2 m from roosting position.

Variable (unit of measurement)	(*n*)	Missing cases	Mean	Standard deviation	Range
Tree height (m)	12	0	4.2	0.8	3.1–5.4
Roosting height (m)	10	2	2.4	0.5	1.8–3.1
Canopy width (m)°	12	0	8.3	1.8	5.6–12.5
Canopy (above) (%)#	10	2	64	8	53–80
Canopy (at 2 m) (%)*	12	0	30	6	23–45

Table 5

Land use and number of apparently suitable Barn Owl hollow-bearing trees present (within 1-ha area) at point locations visited during the study in north-western Victoria.

Land use	*N* locations visited (%)	*N* with 1–3 suitable hollows (%)	*N* with >3 suitable hollows (%)
Roadside verge	69 (56.1)	6 (8.7)	0 (0.0)
Woodland patch	21 (17.1)	5 (23.8)	1 (9.5)
Shelterbelt	33 (26.8)	2 (6.1)	1 (3.0)
Totals	123 (100)	13 (10.6)	2 (1.6)

adjacent to open fields, irrespective of the width of the treed area. In woodland patches, and open-structured shelterbelts and roadside verges, roosts were adjacent to fields or clearings adjoining fields. In comparison to tree-hollow roosts, suitable foliage roost sites appeared common. Some characteristics of mallee eucalypt foliage roost sites are given in Table 4. These data do not include instances of roosting by recently fledged young in exposed positions.

Potential hollows in farmland

The land use and occurrence of apparently suitable tree hollows associated with each of the point locations is given in Table 5. Of 123 locations visited, 15 (12.2%) had at least one hollow located within a 1-ha area centred on the point location (shape of 1-ha area dependent on land use). Based on area surveyed (123 ha) and total number of hollows identified (n = 28), the overall occurrence of suitable hollows was one per 4.4 ha. Occurrence of suitable hollows was greatest in patches of woodland (one hollow per 1.4 ha), less in shelterbelts (one per 5.5 ha) and least in roadside verges (one per 9.9 ha). As roadside verges in the study area are typically ~20 m wide (i.e. 1 chain), the equivalent mean linear distance per hollow was 4.9 km.

Use of nest and roost sites

Different hollows were used for each breeding attempt. For consecutive nesting attempts by two presumed pairs of Barn Owls, different hollows were selected for each attempt, although in one case a hollow in the same tree was used. In addition, hollows used as nest sites were never known to be used for roosting that was unrelated to breeding events. This observation includes data derived from areas where Barn Owls remained resident following a breeding attempt (see McLaughlin and Debus in press).

In general, roost sites were used on a temporary basis. Of 58 tree-hollow roost-only sites located, 38% (*n* = 22) were known only because they contained fresh recently deposited Barn Owl pellets (Barn Owls were not seen using these hollows). Barn Owls were flushed from 18 sites (31%) once only. At least half these hollows contained pellet material indicating previous use. For some of these sites Barn Owl use was more frequent than flushings indicated, because pellets or feathers were deposited between inspections. Owls were flushed from 18 sites (31%) on two or more occasions. At the Mallee Research Station, there were two hollows where Barn Owls were present more often than they were absent. At one site over a period of 13 months (from first to last known use), a single Barn Owl was flushed on seven of 11 occasions (64%) when the hollow was examined. Over a similar period at the other site, a Barn Owl was present at six of 10 hollow inspections (60%).

With one exception, foliage roost sites were used once only, and in all cases the quantity of pellet material below roosts was insufficient to indicate tenure greater than a few days. A Barn Owl was flushed from a Cattlebush roost twice in five days. Owls were flushed from foliage roosts more often in spring–summer (*n* = 16) than in autumn–winter (*n* = 4). This result was not significantly different, but suggests greater use of foliage roosts during warmer weather ($\chi^2_1 = 2.45$, $P<0.2$).

Use of hollows by other species

Use of tree hollows that were ‘owned’ by Barn Owls by vertebrates other than Barn Owls was infrequent. Two such mammal and two bird species were recorded. On two occasions Feral Cats *Felis catus* were flushed from hollows, and on one occasion a Common Brushtail Possum *Trichosurus vulpecula* was found denning in a Barn Owl’s hollow. Southern Boobooks *Ninox boobook* nested in a Barn Owl’s roost hollow (this hollow was also used by nesting Galahs *Eolophus roseicapilla*), and on one other occasion a Southern Boobook roosted in a Barn Owl’s roost hollow. Although Southern Boobooks require tree hollows for nesting, they were most often encountered roosting in tree foliage.

The potential for tree-hollow competition was greatest between Barn Owls and Galahs. At Walpeup, Galahs nested in four Barn Owl roost hollows, and deposited large quantities of fresh *Eucalyptus* leaves in at least five other Barn Owl hollows, including one Barn Owl nest site. On one occasion a Barn Owl was flushed from a hollow roost at ~1300 h; three hours later a Galah was seen carrying eucalypt leaves into the hollow. In a separate incident, a Barn Owl that was flushed from a hollow sought refuge in a hollow that was occupied by one adult and two nestling Galahs. The Barn Owl left the hollow following ~30 seconds of vigorous vocal interaction. The physical characteristics of Galah nests were not recorded; however, in comparison to Barn Owl hollows, Galahs exhibited a clear preference for narrow hollow openings. Belah, rather than mallee eucalypts, appeared to be favoured by Galahs. During July–September 1988, 17 of 23 Galah nests (74%) located on the Mallee Research Station were in Belahs. In comparison, Belahs accounted for 11 of 35 Barn Owl hollows (31%) from the same area (roost and nest sites combined).

Invertebrates using Barn Owl tree hollows were generally not recorded. However, by the end of the study period colonies of feral Honey Bees were established in two Barn Owl hollows, including one nest site.

Discrimination of tree hollow nest and roost-only sites

The relationship between variables included in the refined data set are given in Appendix 1. Although some variables appear significantly correlated, it was found that removal of one or more of the correlated variables diminished the resolving power of the logistic and/or discriminant functions.

Stepwise (additive) logistic regression identified four variables that best discriminated between tree-hollow nest and roost-only sites. These variables and the associated loss function value (at the point of inclusion of each variable in the model) are given in Appendix 2.

The final logistic function, giving the probability (*P*) that a given site was likely to be a roost-only site (P_r) was:

$$P_r = \frac{e^{12.56 + 2.15\beta_1 - 0.02\beta_2 - 0.11\beta_3 - 0.08\beta_4}}{1 + e^{12.56 + 2.15\beta_1 - 0.02\beta_2 - 0.11\beta_3 - 0.08\beta_4}}$$

or a nest site (P_n) was:

$$P_n = 1 - P_r$$

where SPLITS (i.e. cavity wall integrity) was the most important variable (Appendix 3).

For nesting purposes, Barn Owls selected hollows with fewer splits or breaks in the hollow wall, larger floor areas, and greater foliage cover directly above the hollow entrance. An additional factor in the selection of nest sites was an increase in the angle from vertical of the plane of the hollow opening (for terminally positioned openings, effectively the slope from vertical of the branch containing the hollow).

The mean probability predicted by the logistic function for the ‘classification’ of nest sites was 0.905 (s.d. 0.237, range 0.176–1.000). The probability (P_n) calculated for one nest site was 0.176, indicating that it was more similar to roost-only sites than other nest sites (P_r= 0.824). For one other nest site, the probability (P_n) was 0.669. Otherwise, the probability values assigned to all other nests was not less than 0.954. Insufficient data were obtained to compare breeding success with nest-site characteristics. However, the two nests with low (P_n) values were the only breeding attempts where eggs were laid but which failed to fledge any young.

The calculated mean probability for roost-only sites was 0.971 (s.d. 0.105, range 0.382–1.000). Only one roost-only site was classified as a nest site, with a probability value (P_r) of 0.382 (P_n = 0.618). The corresponding P_r value for all other roost-only sites exceeded 0.780. Therefore, the ability of the logistic function to discriminate between site types was high; at a discriminative level of $P = 0.5$, 92% of nest sites and 98% of roost-only sites were classified correctly.

Six variables discriminated between tree-hollow nest and roost-only sites. These variables, in order of inclusion, are given in Appendix 4. When these variables were included in the discriminant function, nest sites were classified as such 100% of the time, and roost-only sites 95% of the time. The progressive ability of the variable set to classify the data from which the discriminant function was derived, is given in Appendix 5.

The group classification coefficients and constants (comprising the Fisher discriminant functions) are provided in Appendix 6. These coefficients and constants may be applied in a linear function to new data, where each case is assigned to the group ('nest site' or 'roost-only site') with the largest function value for that case (Wilkinson 1988).

The four primary predictors of group separation identified by stepwise discriminant analysis did not differ from those selected by logistic regression. However, the order in which they were selected differed slightly. Two additional variables identified by discriminant analysis were wall thickness and log of tree height, although the latter did not enhance the discriminative ability of the function (Appendix 5). All nest sites were correctly classified with a mean probability (calculated by the program from the Mahalanobis distances) of 0.908 (s.d. 0.152, range 0.505–1.000). Group membership probability for correctly classified roost-only sites was 0.970 (s.d. 0.065, range 0.702–1.000). For the two roost-only sites classified as nests, the probability of Group 1 (nest site) membership was 0.803 and 0.541. The best single predictor of group membership was the variable SPLITS. When used alone in the discriminant function, this predictor correctly classified all nests and 81% of roost-only sites.

Nest sites and roost-only sites did not differ significantly in entrance orientation (Watson's test $U^2_{14,55} = 0.119$, $P > 0.05$). As neither group exhibited any significant directionality, and directionality did not differ between groups, aspect probably played little or no role in site selection.

DISCUSSION

The small sample of nest sites, and consequent disparity between nest and roost-site sample sizes, is a limitation on how general the findings may be. Consequently, some of the analyses may be skewed by overfitting. Nevertheless, the following conclusions are likely to be reasonable.

Selection of tree hollows

Barn Owls selected nesting hollows from those available on the basis of at least four physical characteristics: integrity of hollow wall, floor area, foliage cover above entrance and angle from vertical faced by the hollow entrance. Although occupation and use does not necessarily indicate preference (Nilsson 1984), extrinsic factors that may have resulted in the use of non-preferred nest sites, such as intraspecific competition (McCallum and Gehlbach 1988, Nilsson 1984, Rendell and Robertson 1989, Saunders *et al.* 1982), were unlikely to have been important during the study period. Consequently, these characteristics may truly indicate Barn Owl preferences.

Few other quantitative descriptions of Australian Barn Owl breeding habitat or nest sites exist (see Higgins 1999, Mawson *et al.* 2024). Overseas, Barn Owls require enclosed shady or dark undisturbed, dry sites with easy access and large floor space and a favourable microclimate, an apparent correlation between increasing rainfall and nesting in buildings reflecting relative availability of trees and buildings (Andrusiak and Cheng 1997, Bunn *et al.* 1982, Cramp 1985, Roulin 2020, Taylor 1994).

Nest-site integrity (solid hollow wall) may reduce the amount of sunlight or rain entering the cavity, and provide greater security from disturbance and potential predators. Similarly, foliage cover above the nest entrance may provide added shelter from rain, and provide shade at the hollow entrance. Cover directly above the nest is considered important for Barn Owl nests in artificial structures (Smith *et al.* 1974). In comparison to nests with overhead cover, Barn Owl nests in exposed positions may have higher failure rates (Reese 1972).

Hollows where the entrance was orientated away from vertical were favoured by Barn Owls. A clear advantage of these sites is a reduction in the amount of precipitation able to enter the hollow and reach the nest. Most (86%, $n = 12$) nest entrances were terminal, and the branch or trunk containing the hollow inclined at a corresponding angle. In these situations, floor area would increase independently of wall thickness or trunk diameter (see Appendix 1). Barn Owls in this study did not appear to select nest sites on the basis of nest entrance orientation (aspect).

The use of apparently poor nest sites by Barn Owls may be the result of competition, the lack of good-quality sites or inexperience. Barn Owls apparently use inferior or less preferred sites when breeding at high densities (Hollands 2008, Schodde and Mason 1980). Similarly, overseas Barn Owls prefer nesting in secluded situations, but will lay in more exposed positions if secluded sites are unavailable (Bunn *et al.* 1982). The two nest sites determined to be least similar to other nest sites (i.e. low P_n values) were the only nests that failed to produce young. In one, the floor of the hollow subsided, engulfing the eggs, whereas the other failure was apparently related to a crash in the prey population (see McLaughlin and Debus in press).

Use of tree hollows

Circumstantial evidence indicates that Barn Owls actively avoided nesting or roosting in hollows that had recently been used for breeding. No evidence was obtained to indicate that Barn Owls roosted in nest hollows following the fledging of young, even where Barn Owls remained resident. Similarly, two presumed breeding pairs selected different hollows for consecutive nesting attempts. Elsewhere (in the hot, humid tropics), consecutive breeding attempts by established pairs may alternate between available sites even when young have left the natal area (Lenton 1984). During the present study it was apparent that by the late nestling stage, the accumulation of faecal material and pellets rendered nest sites odorous and probably unhygienic, as is typical of Barn Owl nests (e.g. Bunn *et al.* 1982, Fleay 1968). Alternation of breeding sites for consecutive nestings may reduce parasite accumulations, as might aeration of sites (Lenton 1984), given the negative effect of parasite loads on reproductive success and nestling growth (Møller 1989). Conversely, Taylor (2002) found high nest-site fidelity in Barn Owls nesting in buildings in a cold climate. Fidelity to artificial nest hollows and optimal nest boxes elsewhere in Australia (Mawson *et al.* 2024, Meaney *et al.* 2021) also contrasts with the use of natural nest hollows in the present study.

Use of individual roost-only hollows was generally intermittent. As observed for foliage roosts, temporary or transient use may indicate high availability of these types of sites relative to the size of the Barn Owl population. Transient use may also be indicative of a highly mobile Barn Owl population (McLaughlin 1994; McLaughlin and Debus unpubl. data). As with nest sites, Barn Owls may actively rotate the use of individual roost hollows, to avoid large accumulations of pellets within the cavity. Overseas, Taylor (1994) found differences between roost-only cavities and nest cavities (e.g. the former often being smaller), but he found rotational or regular re-use of roosts, owls roosting at nest sites in winter, and annual re-use of nest cavities (Taylor 2002).

Although many hollow-using species (primarily birds) occur within the study area (LCC 1987; JGM pers. obs.), only two species (Southern Boobook and Galah) were observed to use hollows that were also used by Barn Owls. The potential for tree-hollow competition was likely to be greatest from Galahs, whose habit of filling hollows with sprays of leaves (Rowley 1990) may extend the period of competition beyond the Galah breeding season. Transport of material by other species may also explain the claim that Barn Owls may add grass or leaves to nests (cf. Higgins 1999, Schodde and Mason 1980). Further study of other potentially competing species, as well as the impact of feral bees on hollows and native hollow-using species, is required.

Foliage roosts

Excepting three occasions when recently fledged young roosted in exposed positions, Barn Owls chose roost sites with very dense foliage cover. Roost sites of similar structure are selected by other owl species, including other tytonids (e.g. Masked Owl *Tyto novaehollandiae*, Sooty Owl *T. tenebricosa*: Higgins 1999, Hollands 2008, Kavanagh 2002). Selection of dense foliage for roosting is believed to reflect microclimate (e.g. reducing summer heat-stress, enhancing warming during winter), as a protection from inclement weather and to provide concealment (Barrows 1981, Belthoff and Ritchison 1990b, Hayward and Garton 1984). Barn Owls are harassed during the day by other birds (e.g. Higgins 1999). During this study 16 species of birds were recorded mobbing Barn Owls after they were flushed from roost sites.

Because Barn Owls tended to use foliage roosts less often during autumn–winter than spring–summer, they may avoid these roost types during colder weather. Barn Owls have a narrow thermoneutral zone, low fat stores and poor insulation (Piechocki in Bunn *et al.* 1982; Millsap and Millsap 1987, Shawyer 1987), particularly with wet plumage (Webb and King 1984). As observed for some owls elsewhere (Belthoff and Ritchison 1990a, Hayward and Garton 1984), Barn Owls used foliage roosts on a temporary basis. Continual use of foliage roosts may result in obvious accumulations of faecal material, attracting potential predators (Belthoff and Ritchison 1990b). Limited re-use of foliage sites may also reflect the abundance of sites in the study area (they did not appear limiting), or a mobile or transient Barn Owl population.

Conservation of tree hollows

Failure of discriminant functions to distinguish between used and unused sites is usually taken to indicate an abundance of suitable sites (e.g. Rendell and Robertson 1989, Tidemann *et al.* 1992). Conversely, the logistic and discriminant functions derived in this study provided a high level of separation between Barn Owl nest and roost-only sites, thus suggesting that nest-site availability may be constraining Barn Owl populations in the study area.

When searching for suitable Barn Owl hollows, JGM often located cavities (primarily within non-agricultural areas) of apparent ‘roost-only’ quality that did not show evidence of recent use by Barn Owls. Conversely, very few hollows of ‘nest site’ quality were found. It is likely therefore that the occurrence of preferred nest sites (as defined by this study) in the study area is limited. However, if Barn Owl densities had been higher, many of the ‘roost-only’ sites (potentially non-preferred nest sites) may have been used as nests.

Although Australian Barn Owls use a variety of structures for nesting (e.g. Higgins 1999), like most Australian owls they are essentially tree-hollow nesters (Higgins 1999, Olsen 2011). The primary causal factor of tree-hollow formation in Australia is attack by termites and fungi (Abensperg-Traun and Smith 1993, Mackowski 1984), and although Australia lacks primary hollow excavators, in comparison to other countries Australia has the largest number of tree-hollow users (Abensperg-Traun and Smith 1993, Saunders *et al.* 1982). The Barn Owl and other *Tyto* owls are among the few Australian birds that regularly use tree hollows for both nesting and roosting. Consequently, the continued occurrence of suitable Barn Owl tree hollows is important for the conservation of the species, although purpose-built and ‘non-target’ nest boxes or artificial hollows may be important (Mawson *et al.* 2024, Meaney *et al.* 2021).

The conservation of Strigiformes and tree hollows in Australia has focused on those species (e.g. Powerful *Ninox strenua*, Masked and Sooty Owls) inhabiting forests subject to intensive commercial timber harvesting (e.g. Kavanagh 2002). Rural tree decline and tree-hollow decline have also long been acknowledged (Abensberg-Traun and Smith 1993, Saunders *et al.* 1982, Saunders and Ingram 1987).

Two tree species, Belah and Oil Mallee, provided all records of tree hollows used by Barn Owls in the study area, where they probably provide the largest hollows. In comparison to mallee shrublands and heaths growing on sandy dunefields, both tree species grow on soils with a higher loam and clay content. Consequently, these vegetation types have been preferentially cleared for cereal cropping (Blakers and MacMillan 1988, LCC 1987). A similar loss of hollow-bearing trees has occurred elsewhere in the wheat belts of southern Australia (e.g. Saunders *et al.* 1982, Saunders and Ingram 1987).

On agricultural land in the study area, the greatest density of hollows suitable for Barn Owls appears to be provided by woodland patches, thus emphasising the importance of hollow-bearing trees in farm woodlots. Such remnants are usually left on farmland to provide shade, shelter and watering points for stock. It is apparent that Barn Owl presence may be maintained in agricultural areas despite the apparent bare minimum of hollow-bearing trees. These remnant woodlots may be as important as hollow-bearing trees in other woodland patches. Such farmland remnant woodlands, however, like many other areas where suitable hollows may otherwise occur, are subject to grazing and trampling pressure from introduced stock and Rabbits *Oryctolagus cuniculus*. Natural regeneration in these areas is minimal (LCC 1987, JGM pers. obs.). Roadside verges and shelterbelts between fields may provide a greater number of hollows overall, but fewer per unit area. These areas are subject to less grazing pressure than remnant woodland patches, although they show a similar lack of regeneration. In addition, their linear shape makes them more susceptible to wind damage.

Conservation of a declining population of Barn Owls in Britain has focused primarily on the provision of suitable nest sites (e.g. Martin 2017, Shawyer 1987, Taylor 1994). To maximise any advantages conferred by the predation on House Mice by Barn Owls within the study area (McLaughlin 1994, McLaughlin and Debus unpubl. data), adequate provision of appropriate (ideally highly preferred) nest sites must be made (e.g. Fleay 1968). Short-term solutions may be provided by the use of nest boxes, which are readily used by Barn Owls (e.g. Martin 2017, Taylor 1994). Purpose-built nest boxes in Australia support high Barn Owl breeding success and non-invasive research where they include features such as an entrance platform, high entrance hole, predator-proof pole and rear-door access (Meaney *et al.* 2021). Long-term solutions, however, are likely only to be achieved through the implementation of appropriate management strategies for remnant native vegetation (see also Lindenmayer *et al.* 1991).

ACKNOWLEDGEMENTS

This paper formed part of a Masters thesis at La Trobe University, supervised by the late Peter Rawlinson, the late Dr Richard Zann, and Dr David Baker-Gabb; the University, staff and fellow students (notably Dr Beverley Van Praagh, Bruce Quin, Martyn Summers and Evan Schmidt) are gratefully acknowledged for supporting and/or facilitating the project. The Wheat Research Committee for Victoria and the M.A. Ingram Trust provided financial assistance. Thanks go to the Department of Agriculture and Rural Affairs for access to the Mallee Research Station, and the officers and staff of Mildura Region of the Department of Conservation and Natural Resources for facilitating the study. Thanks also go to John Kiley, Gary Leamon, Chris Johns, David Whelan, Bruce Quin, Alex Peart, Tania and Zac Rajic, Terry Mazzer and Les McLaughlin for field assistance. The co-operation of the many landholders, especially Florence Beaton of 'Sunshine Farm', Carwarp, is gratefully acknowledged. This study was carried out under DCNR Research Permit numbers 88-134/140, 89-151 and 90-025. Rod Kavanagh and Nathan Yaschenko commented helpfully on a draft of this paper.

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Co-author's note: this paper originated as a collaborative effort with John McLaughlin in 2019 on the basis of his long-unpublished MSc thesis, but John was unable to review and revise draft papers arising from those chapters before contracting leukaemia and passing away on 28 January 2025. The data collection, analysis, interpretation and thesis were entirely John's, leaving only post-1994 literature review to insert in an edit of his thesis chapter.

APPENDIX 1

Triangular matrix of Spearman correlation coefficients for refined data set. Asterisk indicates level of significance (Bonferroni adjusted probabilities): *P<0.05; **P<0.01.

	THEIGHT	HEIGHT	WIDTH	DEPTH	FLOOR	DIAMTR	WALL	CLOSEST	MEANCAN	CANENTR	SPLITS	ANGLE1
THEIGHT	1.000											
HEIGHT	0.119	1.000										
WIDTH	0.166	0.013	1.000									
DEPTH	–0.169	0.107	–0.047	1.000								
FLOOR	0.330	–0.265	0.345	–0.067	1.000							
DIAMTR	0.466	0.135	0.173	–0.063	0.371	1.000						
WALL	0.346	0.225	0.056	0.083	0.187	0.453	1.000					
CLOSEST	0.048	0.049	–0.067	0.187	0.036	0.031	–0.020	1.000				
MEANCAN	0.170	0.249	–0.096	0.087	0.087	–0.009	0.003	–0.087	1.000			
CANENTR	0.154	0.089	–0.093	–0.171	0.238	0.030	0.364	–0.201	0.302	1.000		
SPLITS	*–0.477	–0.355	0.228	0.313	–0.120	–0.203	–0.291	0.132	**–0.520	**–0.588	1.000	
ANGLE1	0.107	0.062	–0.029	–0.152	0.453	0.156	–0.057	–0.226	0.342	0.157	–0.337	1.000

APPENDIX 2

Variables selected by logistic regression (in order of inclusion in model) that best discriminated between nest and roost-only sites.

Variable	Value of loss function
Constant only	35.47
+SPLITS	18.52
+SPLITS+FLOOR	9.67
+SPLITS+FLOOR+CANENTR	4.73
+SPLITS+FLOOR+CANENTR+ANGLE1	3.85

APPENDIX 3

Coefficients, standard errors and confidence limits for variables selected by logistic regression.

	Variable	Variable coefficient	Standard error	95% confidence intervals
	Constant	12.56	3.76	4.99 < > 20.12
β1	SPLITS	2.15	0.48	1.18 < > 3.12
β2	FLOOR	–0.02	0	–0.03 < >–0.01
β3	CANENTR	–0.11	0.04	–0.19 < >–0.04
β4	ANGLE1	–0.08	0.03	–0.15 < >–0.02

APPENDIX 4

Variables included in the discriminant function (in order of inclusion), final partial F-values, and multivariate level of significance.

Variable	Partial F-value	Significance level
SPLITS	40.51	P<0.0001
CANENTR	28.52	P<0.0001
FLOOR	24.53	P<0.0001
ANGLE1	12.93	P<0.001
WALL	7.94	P<0.01
THEIGHT ($\log_n$)	7.26	P<0.01

APPENDIX 5

Progressive ability of variables included in the discriminant function (in order of selection) to classify data from which the discriminant function was derived. Sample size given is maximum for each category.

Variable	Nest sites (*n*=14)		Roost-only sites (*n*=58)	
	Correct (%)	Incorrect (%)	Correct (%)	Incorrect (%)
SPLITS	100	0	81	19
+CANENTR	93	7	87.5	12.5
+FLOOR	84.6	15.4	97.7	2.3
+ANGLE1	92.3	7.7	97.6	2.4
+WALL	100	0	95.2	4.8
+THEIGHT ($\log_n$)	100	0	95.2	4.8

APPENDIX 6

Group classification coefficients and constants comprising the Fisher discriminant functions.

Variable	Coefficient	
	Group 1 ('nest-site')	Group 2 ('roost-only site')
Constant	–68.77	–66.69
SPLITS	3.67	4.9
CANENTR	0.3	0.25
FLOOR	–0.01	–0.01
ANGLE1	0.17	0.12
WALL	0.69	0.17
THEIGHT ($\log_n$)	42.87	44.87