

An experimental approach to understanding the use of mistletoe as a nest substrate for birds: nest predation

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Abstract. Recent research has documented an unprecedented diversity of birds using mistletoes as nest-sites, and a strong preference for nesting in mistletoes has recently been demonstrated for some species. The consequences and underlying reasons for this behaviour have not been evaluated, and it is unclear whether nests in mistletoes confer advantages compared with other available substrates. Nest predation is often cited as the most important factor regulating many bird populations and is thought to influence all aspects of nest-site selection. To evaluate whether nest predation may play a role in the widespread use of mistletoe as a nest-site, we conducted an artificial nest predation experiment in a eucalypt woodland in southern New South Wales, Australia. Artificial nests were modelled on noisy friarbird (*Philemon corniculatus*: Meliphagidae) nests, baited with a single quail egg and checked after four days. We used logistic regression to model the rate of depredation between plant substrates, and demonstrate that, in this experiment, mistletoe nests experienced a lower proportion of predation than eucalypt nests (51.5% versus 63.8% respectively). This finding suggests that predation may influence the widespread use of mistletoe as a nest-site in a range of habitats and regions. In addition to clarifying priorities for further work on mistletoe nesting, this finding has implications for studies of nest-site selection generally, with researchers encouraged to supplement between-substrate comparisons with direct measurements of within-substrate variation.

Introduction

Interactions between birds and mistletoes (primarily Loranthaceae and Viscaceae, Santalales) have been described in many regions worldwide, with most research focusing exclusively on the role of birds as seed and pollen vectors for these hemiparasitic plants (Watson 2004). Many birds also use mistletoe clumps as sites for nesting and roosting but, until recently (Watson 2001), this series of interactions had attracted little attention. In a recent review of the nidification of Australian birds, 216 species of Australian bird from 28 families were reported nesting in mistletoe, representing 65% of Australian species that nest in the foliage of trees (Cooney *et al.* 2006). This review increased the total number of avian families known to exhibit this behaviour worldwide to 59, across 16 orders (Watson 2001; Cooney *et al.* 2006).

Despite the documented popularity of mistletoe as a nesting substrate, preference for mistletoe as a nest-site has only recently been demonstrated. Cooney and Watson (2005) presented data that demonstrate that diamond firetails (*Stagonopleura guttata*), in an Australian woodland, prefer nesting in mistletoe than in otherwise comparable sites. Studies of other species in North America (Reynolds *et al.* 1982; Seamans and Gutierrez 1995; Bennetts *et al.* 1996) and Australia (Oliver *et al.* 1998; Ford 1999) infer a preference by some birds for nesting in mistletoes, including endangered species. For example, the endangered regent honeyeater

(*Xanthomyza phrygia*) (Garnett and Crowley 2000) regularly nests in *Amyema* sp. mistletoes in south-eastern Australia (Oliver *et al.* 1998). Consequently, in North America, dwarf mistletoes (*Arceuthobium* spp., Viscaceae) form an integral part of habitat assessments used in the management of a range of endangered species (Hammer and Nelson 1995), including mammals that also nest and roost in the dense vegetation associated with witches' brooms (Bakker and Hastings 2002; Garnett *et al.* 2004; Lehmkuhl *et al.* 2006).

Cooney *et al.* (2006) proposed that nests in mistletoe display a suite of characteristics that enhance nest success. The rigid structural framework of a mistletoe clump and the secure nest attachment afforded by the haustorium represent a particularly strong and stable scaffold upon which to build a stick nest (Oliver *et al.* 1998). This may reduce the time and effort required to build a nest, making a nesting attempt more efficient. This same dense structure may also influence the microclimate of the nest by providing shade. Furthermore, the semi-succulent nature of mistletoe leaves and the high water content relative to host leaves (Ehleringer and Marshall 1995) may have a profound effect on microclimate by moderating diel fluctuations in ambient temperature and relative humidity (Press *et al.* 1989; Watson 2001; Press and Phoenix 2005).

Predation on the incubating parent and/or the eggs and chicks in the nest (hereafter nest predation) is a critical factor

limiting the size of many bird populations and is considered by some workers to be the most important factor regulating bird populations (Ricklefs 1969; Zarette 2001). Individuals whose nests are more vulnerable to predators are likely to produce fewer offspring that survive to maturity, and are therefore less likely to pass on heritable components of these traits to future generations (Møller 1989). Therefore, predators exert strong directional selection pressures on the nesting characteristics of their prey (Clark and Shutler 1999) and any characteristics that decrease nest predation can become fixed traits over time.

Enhanced levels of concealment, such as those afforded by the dense foliage surrounding mistletoe nest-sites, may reduce the risk of predation by hindering the development of a search image in predators (Martin 1988). Dense vegetation can also impede the movement of mammalian predators through the canopy and reduce the foraging efficiency of avian predators (Lawton and Lawton 1980). The dense thicket produced by mistletoes have similarly been observed to obstruct predation by *Accipiter* species on birds in northern Australia (J. Young, pers. comm.).

Although studying real nests may be preferable to artificial nests, finding enough real nests for meaningful analysis is often difficult (Moore and Robinson 2004). Artificial nest experiments are one way to gain further insight into nest predation and have been used to test a range of ecological and behavioural hypotheses in relation to nest-predation theory (Major and Kendal 1996; Zarette and Jenkins 2000; Moore and Robinson 2004). Such experiments allow researchers to study sufficient numbers of nests with attributes of interest to allow robust statistical analysis and interpretation (Moore and Robinson 2004). Despite this, artificial nests differ from real nests in several important ways, making them variously more or less prone to predation. Artificial nests may be 'safer' because they lack parental activity, there is no bird scent at the nest and no begging calls from chicks (Luck *et al.* 1999). Conversely, they may be

more vulnerable than real nests because they have been placed by humans rather than birds, they lack parental defence (Weidinger 2002) and predators may either see or smell the human activity around the nests (Whelan *et al.* 1994). Designed correctly, however, studies of predation on artificial nests can yield reliable estimates of the predation differences between two or more treatments (Pärt and Wretenberg 2002; Moore and Robinson 2004). This comparison can be enhanced by modelling the nesting apparatus on the appearance and location of real nests (Martin 1987).

This experiment examined a suite of factors associated with nest-site selection. By isolating mistletoe as a variable in the experiment, we test the hypothesis that mistletoe is a safer nest-site than comparable nest-sites in *Eucalyptus* canopies. We also evaluate assumptions about homogeneity of nest-sites within a nesting substrate (in this case, arboreal nests) in terms of predation. We do this by conducting a series of nest-predation experiments to evaluate three main hypotheses:

- (1) That mistletoe nests are depredated less often than otherwise comparable nests;
- (2) That mistletoe nests offer greater concealment than otherwise comparable nests; and
- (3) That levels of predation are not consistent among arboreal nest-sites and therefore vary within this general nest-site category.

Methods

Study site

The study was conducted in a patch of privately owned remnant woodland called Morgan's Ridge (147°24.0'S, 35°42.4'E), 9 km east of Holbrook in the south-west slopes region of New South Wales, Australia (Fig. 1). At ~2600 ha, Morgan's Ridge is one of the largest remnants of dry foothill forest and grassy box woodland in southern New South Wales (Cooney 2004).

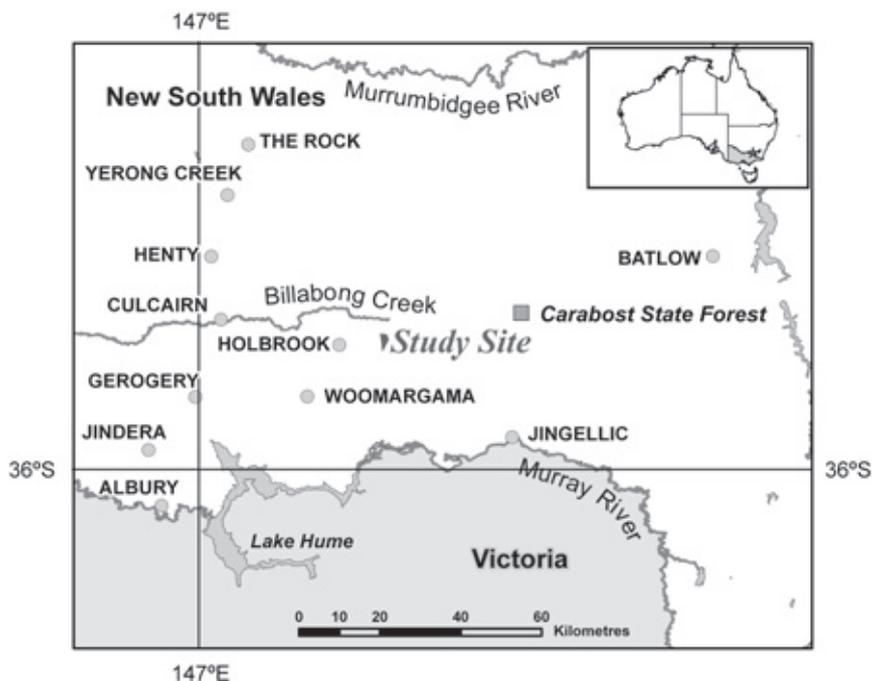


Fig. 1. Map showing the location of the study site at Morgan's Ridge, Holbrook, New South Wales, Australia, 2004.

Fieldwork was conducted in a discrete 365-ha woodland at the base of the ridge, known as Wybalena (Cooney 2004). Although this area had been grazed and used for timber production in the past, the current owner has not grazed this area since 1989 and much of the understorey and ground cover has returned to an undisturbed state (Cooney 2004). The canopy is dominated by Blakely's red gum (*Eucalyptus blakelyi*), red stringybark (*E. macrorhyncha*) and red box (*E. polyanthemus*), with stands of regrowth and dense thickets of silver wattle (*Acacia dealbata*). The understorey is open and grassy, dominated by native and introduced grasses (Cooney 2004). Two species of mistletoe occur at Morgan's Ridge, increasing in abundance towards the edges of the patch (March and Watson 2007). Box mistletoe (*Amyema miquelii*) is more abundant, parasitising *Eucalyptus* species, and it, in turn, is occasionally parasitised by fleshy mistletoe (*Amyema miraculosum*).

Methods

We conducted an experiment on artificial nests to evaluate the influence of nest-substrate on predation rate. The experiment was repeated three times in 2004: 5–11 April, 27 June–3 July and 8–24 September, which overlaps with the breeding season of the noisy friarbird (*Philemon corniculatus*: Meliphagidae) (Higgins *et al.* 2001). In all, 90 nests were deployed in each trial. In each trial half of the artificial nests were placed in the mistletoe substrate and half in the *Eucalyptus* substrate, in different locations to those used previously, to control for predator learning (Olsen and Schmidt 2004) and ensure independence.

We chose a species that regularly breeds in the study site and based the design of our artificial nests and eggs on this bird to replicate a real nesting system (Martin 1987). Noisy friarbirds are large (mean mass of 121.7 g; Higgins *et al.* 2001) honeyeaters, common in many forest and woodland assemblages in eastern Australia (Higgins *et al.* 2001). Their cup-shaped nests are built from small twigs interwoven with grass and bark, ranging from 120 to 180 mm in diameter and ~100 mm deep (Higgins *et al.* 2001), located in a wide variety of plants including *Eucalyptus* trees and mistletoe (Ford 1999). They lay 2–4 oval eggs that range in colour from reddish salmon to pale violet grey, with incubation lasting 15–19 days (Higgins *et al.* 2001).

Artificial friarbird nests were constructed by gluing sticks into the shape of a nest and moulding it in a bowl of suitable dimensions. The bowl was removed and the nests were left to dry in the open air for at least two weeks before use to minimise residual scent (Sieving 1992) and to ensure that they were fully cured. To reduce human scent that could attract predators to the nests, rubber gloves were worn at all times during nest construction, placement and egg deployment (Whelan *et al.* 1994; Luck *et al.* 1999).

We used infertile king quail (*Coturnix chinensis*) eggs sourced from a commercial quail breeder in Melbourne, Australia. These eggs resemble noisy friarbird eggs in size and shape (noisy friarbird eggs 28.4–36.6 × 21.6–23.4 mm, $n = 15$; Higgins *et al.* 2001; king quail eggs 25.1–28.4 × 18.5–20.8 mm, $n = 17$; Marchant and Higgins 1993); however, the colour of the quail eggs varied from white to dark chestnut-brown, showing broad overlap with the colours of noisy friarbird eggs. Eggs were washed after delivery, dried and stored in the refrigerator

for no more than 10 days until required (Rudnický and Hunter 1993; Luck *et al.* 1999).

Artificial nests were placed alternately in either a *Eucalyptus* tree or mistletoe clump, attached with thin black wire (Kelly 1993) and marked with flagging tape 10 m north of their location. Nests were spaced ~50 m apart, in a range of heights, aspects and levels of cover, replicating the density and location of actual noisy friarbird nests (Higgins *et al.* 2001) and minimising the likelihood of predators 'traplining' the location of nests (Buler and Hamilton 2000). After two days to imitate the nest-building phase (Sieving and Willson 1998), the nests were revisited, lined with a handful of leaf litter from the site (Rudnický and Hunter 1993; Wilson *et al.* 1998) and baited with a single quail egg. Only one egg was used in order to maximise the sample size of the experiments. Although this affected total egg mass within the nest, we felt it was unlikely to bias the results, given the variability of actual noisy friarbird clutch sizes (Higgins *et al.* 2001). Nests were checked after four days. Nests were classified as 'depredated' if the egg was damaged or missing or 'not depredated' if the egg was present and the nest intact (after Pärt and Wretenberg 2002; see Cooney 2004 for further details).

Upon completion of each predation trial, nests were retrieved and structural parameters in the immediate vicinity of the nest-site were measured (Table 1). For multistemmed trees, the largest stem was used for measurements of diameter at breast height (1.3 m), distance from trunk and support tree height. Concealment was determined using the digital photographic method of Ortega *et al.* (2002), with three photographs taken from a distance of 0.50 m, one from below the nest, one from above the nest, and one from the outside of the plant towards the centre of the plant at the height of the nest.

Statistical analysis

We used a Cochran–Mantel–Haenszel test, stratified by experimental trial, to assess differences in the proportion of nests that were depredated in the two treatments (hereafter predation rate). To model the results, all the variables were entered into an all-subsets linear regression in GENSTAT 10. Using Akaike's information criterion, we selected the variables that resulted in the best-fitting model. We then used these variables to model the predation rate in a binomial logistic regression. A significance level of $P < 0.05$ was used in all analyses.

Results

Of 130 nests in mistletoe, 51.5% were depredated within the four-day exposure period, whereas 63.8% of the 130 nests in *Eucalyptus* trees were depredated over the same period. The predation rate was significantly different between treatments ($\chi^2 = 4.023$, d.f. = 1, $P = 0.045$) (Table 2). In most cases, predation was characterised by the absence of the egg, but in some instances the egg was found damaged on the ground beneath the nest. Occasionally the nest was tipped and, although it was unclear whether this was the result of wind or attempted predation, these nests were considered depredated, since wind damage can also cause failure in real nests. Although predator identity was not systematically recorded, observations indicated a range of predators in the study area, including grey shrike-thrush (*Colluricincla harmonica*), laughing kookaburra

Table 1. Vegetation variables measured for artificial nests placed in mistletoe clumps and *Eucalyptus* trees in Morgan's Ridge, Holbrook, New South Wales, Australia, 2004

Parameter	Variable name	Methods of measurement	Reference
Nest height	NEST HEIGHT	Distance from the top of the nest to the ground (cm), measured with a tape measure	Major <i>et al.</i> 1994
Distance from trunk	DIST TRUNK	Distance from the tree trunk, or main coppice regrowth to the centre of the nest (cm), measured with a tape measure	Best and Stauffer 1980
Support tree height	TREE HEIGHT	Distance from the top of the tree to the ground (m), using a visual estimate	Major <i>et al.</i> 1994
Diameter at breast height	DBH	Distance around the tree trunk or main coppice regrowth (cm), at ~130 cm above the ground, measured with a tape measure	Major <i>et al.</i> 1994
Distance to next tree	NEXT PLANT	Distance from the centre of the nest to the outer foliage of the nearest tree (m), measured with a tape measure	Major <i>et al.</i> 1994
Distance to next artificial nest	NEXT NEST	Distance from the centre of the nest to the nearest nest (m), using DataSave 1.10™ (Magellan, USA 2000) GPS software	Major <i>et al.</i> 1994
Concealment side	SIDE %	Level of concealment provided by vegetation immediately surrounding the nest, achieved by counting the number of digital photograph pixels hidden by vegetation, expressed as a percentage of the total nest pixels, using Adobe Photoshop	Ortega <i>et al.</i> 2002
Concealment below	BELOW %	As above	
Concealment above	ABOVE %	As above	

(*Dacelo novaeguineae*), pied currawong (*Strepera graculina*) and lace monitors (*Varanus varius*).

Akaike's information criterion consistently identified PLANT as the most influential variable in the model, even when only one variable was included in the regression (Table 3). The most parsimonious model used the variables PLANT ($\beta = 0.584$, $P = 0.024$) and DBH ($\beta = 0.003$, $P = 0.089$). The model is plotted in Fig. 2 and shows that the mistletoe substrate has a reduced rate of predation compared with the *Eucalyptus* substrate ($P = 0.027$). The rate of predation appears to be correlated with the diameter of trees, with larger trees attracting more predation events (Fig. 2), although this is not a significant variable in the model that predicts the rate of predation. None of the three measures of concealment influenced the rate of nest predation using AIC. The most parsimonious model to use a concealment variable (Table 3) included CONCEALMENT ABOVE and PLANT, but the concealment variable was not a significant influence on the predation rate ($\beta = 0.584$, $P = 0.295$).

Discussion

We found support for two of the three hypotheses concerning rate of predation in different nesting substrates in this system. As predicted, we demonstrated that there can be differences within what is often considered to be a homogenous nest-site

and that nests in mistletoe were less likely to be depredated than those placed in otherwise comparable parts of the canopy. We did not find support for the third hypothesis: that mistletoe provides a greater level of concealment than otherwise comparable nests.

Having established that artificial nests in mistletoe were subject to lower predation rate, the question arises – what mechanisms underlie this pattern? It has been postulated that mistletoe provides concealment from predators due to its dense, evergreen habit (Reynolds *et al.* 1982; Bennetts *et al.* 1996; Watson 2001), and concealment is generally considered to be an important component of nest-predator avoidance (Martin and Roper 1988; Burhans and Thompson 2001; but see Götmark *et al.* 1995). Despite this expectation, concealment was not found to play a role in this experiment, having no discernible effect on nest fate. This result may be related to predator identity: predators feeding on the experimental nests may have included olfactory predators, such as reptiles and small mammals, for which visual nest concealment has little impact (Rangen *et al.* 2000; Pärt and Wretenberg 2002). Alternately, the level of variation in the concealment data may have been too high to reveal a difference, or perhaps our measure of concealment did not correspond with a predators' perception of concealment.

Inaccessibility is the second component of predator avoidance at the nest-site (Snow 1978; but see Crabtree *et al.* 1989). Again, mistletoe has been implicated in providing protection to nesting birds because its rigid structure prevents access to the nest by predators (Oliver *et al.* 1998; J. Young, pers. comm.; but see Rose 1962). We did not test this theory directly, but it is possible that the structural rigidity of mistletoes prevents large predators from preying upon associated nest contents. Future experiments should examine the importance of mistletoe as a barrier against potential nest predators by examining differences in the predator community between depredated nests in mistletoe and nests in other parts of the canopy.

Table 2. Contingency table for Cochran–Mantel–Haenszel test, stratified by TRIAL, to compare predation rate between plant substrates

Numbers represent the proportion of nests depredated. Significantly fewer artificial nests placed in mistletoe were depredated than those placed in the *Eucalyptus* substrate ($\chi^2 = 4.023$, d.f. = 1, $P = 0.045$)

Substrate	Mistletoe	<i>Eucalyptus</i>
Trial 1 (April)	21 of 45 (46.7%)	27 of 45 (60%)
Trial 2 (July)	20 of 45 (44.4%)	27 of 45 (60%)
Trial 3 (September)	26 of 45 (57.8%)	29 of 45 (64.4%)
Total	67 of 130 (51.5%)	83 of 130 (63.8%)

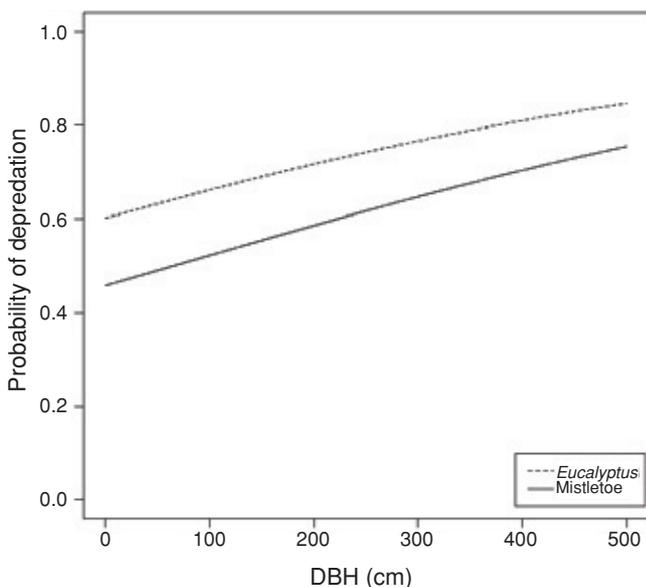


Fig. 2. Modelled probability of predation by plant substrate. The equation for mistletoe is $f(x) = \exp(-0.173 + 0.0026x) / 1 + \exp(-0.173 + 0.0026x)$, whereas for *Eucalyptus* the equation is $g(x) = \exp(-0.173 + 0.584 + 0.0026x) / 1 + \exp(-0.173 + 0.584 + 0.0026x)$.

The only other study that compared predation levels between mistletoe and other nest-sites was conducted on real nests of two species of honeyeater (Ford 1999). Ford (1999) found that the nests of red wattlebirds (*Anthochaera carunculata*) and noisy friarbirds that were in mistletoe were no less likely to be depredated than those in other plants, including *Eucalyptus* trees. This result is contrary to the findings of this study. The difference may be because, unlike an artificial nest without parents, a real nest is defended by a large honeyeater that is aggressive towards intruders and capable of driving off some potential predators. This highlights one of the limitations of using artificial nests in predation studies stated previously. Furthermore, Ford’s (1999) study was conducted in a different habitat, undoubtedly with a different predator community, potentially confounding direct comparisons between the two studies. Finally, although this

study had a sample size of 130 pairs of nests, Ford’s (1999) study was based on 93 nests in mistletoe (29 red wattlebird; 64 noisy friarbird). Hence, even if mistletoe nests did experience a lower predation rate, the difference would have needed to be 19% or more ($n = 64$ pairs, $\alpha = 0.1$, $P_1 < P_2$) to have been found significant.

This study has demonstrated that there are differences in the quality of nest-sites within one nesting substrate in this system. Much of the work on nest-site selection has focussed on comparisons between broad nesting substrates (i.e. ground versus tree versus hollow), with the implicit assumption that within-substrate differences are less important. Indeed, few studies explore this component of variation even though, in some cases, it outweighs between-substrate comparisons (Haskell 1994; Weidinger 2002). The fact that within-substrate variation can have an impact on nest outcome further strengthens the argument for conducting more rigorous artificial nest trials by controlling for, or measuring, more variables and by having larger sample sizes (Major and Kendal 1996). It also suggests that artificial nests placed by humans may miss subtle differences in the selection process made by a bird. The corollary of this is to emphasise that artificial nest experiments must be based on a particular model species so that the particular behaviours of each species can be reflected in the experimental design and also to recommend that a natural nest control is established to calibrate the results of the artificial nest outcomes (Major and Kendal 1996; Pärt and Wretenberg 2002).

More work is needed to evaluate the observed patterns of predation on other groups of birds and in other habitats worldwide to determine the generality of these results. Future studies should focus on experiments that explore this phenomenon in the context of real birds’ nests, the role of different predator assemblages, and the differences in habit and habitat exhibited by different species of mistletoe worldwide. An ideal candidate for such future studies would be the noisy friarbird as its nest is relatively large, conspicuous, placed moderately close to the ground (8.75 ± 0.25 m, Ford 1999) and is frequently found in mistletoe. A range of nest-site variables, such as nest height, concealment and nest patch density should be measured to understand the processes that may influence the predation rate. Finally, although traditional methods of predator identification

Table 3. Comparisons used to identify the most influential variables to model artificial nest predation, sorted by Akaike’s information criterion

For description of variables see Table 1. Numbers in each variable column are probabilities based on *F*-statistics

AIC	d.f.	ABOVE %	DBH	NEST HEIGHT	NEXT PLANT	PLANT	TREE HEIGHT
Best subsets with 1 term							
245.07	2	–	–	–	–	0.050	–
246.66	2	–	–	–	0.135	–	–
246.92	2	–	0.161	–	–	–	–
Best subsets with 2 terms							
243.64	3	–	0.089	–	–	0.024	–
245.15	3	–	–	–	0.166	0.061	–
245.97	3	0.295	–	–	–	0.034	–
Best subsets with 3 terms							
244.20	4	–	0.084	–	0.227	0.027	–
244.53	4	–	0.040	0.288	–	0.042	–
244.78	4	–	0.038	–	–	0.038	0.352

have had mixed success (Major 1991), the use of remotely triggered cameras will highlight any differences in the predator community between mistletoe and other otherwise comparable nest-sites.

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