

Trapped between popular fruit and preferred nest location – cafeterias are poor places to raise a family

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Summary

1. Nest-site location is a critical component of habitat preference in birds, reflecting a balance between minimizing the likelihood of nest predation while maximizing access to nutritional resources. While many studies have demonstrated the influence of predators in nest-site selection, few studies have explicitly quantified nutritional resources or considered the interacting effects of predation and food availability in determining nest survival.

2. The painted honeyeater *Grantiella picta* is a mistletoe-specialist frugivore, with fruit from grey mistletoe *Amyema quandang* representing the main food source for breeding adults and nestlings. Previous work demonstrated that painted honeyeaters prefer to place their nests within mistletoe substrates. Here, we measured the outcome of 63 nests over two years, relating survival to various structural and resource-based variables to discern whether nests placed in mistletoes were more likely to succeed.

3. Twenty-one nests survived the 33 day nest period, with 35 of the 42 failed nests predated. While few significant differences were discerned between successful and unsuccessful nests in terms of nest tree or surrounding habitat, nest substrate emerged as the most important predictor of nest fate. Survival of nests in mistletoe was 16.6% across a 33 day active nest period compared with a mean of 43.1% for nests in other substrates, a difference consistent across both years.

4. Rather than having a positive effect on nest outcome (via access to nutritional resources), proximity to mistletoe had a marked negative effect, with nests in mistletoe suffering a predation rate 2.6 times higher than nests elsewhere. Rather than predators targeting mistletoe clumps, we suggest that this pattern arises from other species visiting fruiting mistletoe clumps, opportunistically predated the nest contents and disturbing attending parents. We interpret this finding as evidence that the painted honeyeater may be caught in an ecological trap; the cues used to select nesting locations are a poor predictor of success.

Key-words: ecological trap, frugivory, *Grantiella picta*, Loranthaceae, Meliphagidae, mistletoe, nest survival, Program MARK, threatened species

Introduction

Determinants of nest-site selection are some of the most critical components of habitat preference in birds, with breeding habitats often representing a very small subset of the range of habitats occupied (Huhta, Jokimaeki & Rahko 1998; Clark & Shutler 1999). The survival of nests is primarily influenced by predation at the nest site (Ricklefs 1969), hence choosing nests sites that minimize predation risk should be adaptive (Martin 1993; Chalfoun & Martin 2007), and the survival of nests has been linked to habitat selection in many

species (Martin & Roper 1988; Huhta, Jokimaeki & Rahko 1998; Zanette, Doyle & Trémont 2000; Olsson *et al.* 2001). Few studies investigating patterns of nest-site selection or nest survival, however, evaluate the influence of food abundance in their design (but see Crampton 2004; Zanette, Clinchy & Smith 2006) despite food availability directly affecting nest survival by influencing the amount of food provisioned to nestlings (Martin 1987; Visser, Holleman & Gienapp 2006; Zanette, Clinchy & Smith 2006).

The importance of food resources for breeding birds is exemplified by the matching of breeding effort to variation (in both space and time) in the availability of food in a range of systems (e.g. Ligon 1978; Hahn 1995; Barea & Watson 2007). Food abundance and its availability do not necessar-

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ily act alone but can influence nest survival by interacting with predation risk, either synergistically (Zanette *et al.* 2003) or as a function of time available for nest vigilance and defence (Martin 1992). When nutritional resources are spatially aggregated, trade-offs would be expected, especially for food sources that are exploited by a wide range of species – any nutritional or energetic benefits associated with locating nests closer to these resources may be offset by increased disturbance and higher rates of nest failure.

Mistletoe represents a spatially aggregated resource in forest and woodland canopies, widely used by birds as a source of abundant nectar and fleshy fruits (Watson 2001). One group of birds – mistletoe-specialist frugivores – depends on these fruits as their principal food source (Watson 2013), enabling nutritional resources to be estimated accurately and the interactions between nest-site selection, nest success and food availability to be disentangled. The painted honeyeater (*Grantiella picta* Meliphagidae; Fig. 1a) is one of the better-studied members of this group, a migratory passerine endemic to eastern Australia which feeds almost exclusively on the fruits of mistletoe in the genus *Amyema*, Loranthaceae (Higgins, Peter & Steele 2001; Barea & Herrera 2009). In addition to water and carbohydrates, mistletoe fruit is an important source of protein for painted honeyeater adults and nestlings (Barea 2008b; Barea & Herrera 2009) and the species matches reproductive timing with mistletoe fruiting phenology (Barea & Watson 2007). As well as their principal food source, mistletoe also represents a favoured nest-site for painted honeyeaters (Barea 2008a) and mistletoe abundance and its proximity to nest trees are important drivers of nest-site selection patterns (Barea 2012). Mistletoe clumps represent favoured nest sites for other species (Ford 1999; Cooney, Watson & Young 2006) including another mistletoe specialist (Crampton 2004) but, to date, studies of mistletoe as a food source and a nest site have been conducted in parallel, with no consideration given to interactions or potential conflict between these two uses.

Here, we build on previous work on the nutritional ecology, timing of reproduction and nest-site selection of painted honeyeaters to evaluate the role of nutritional and structural resources in determining nest survival and likelihood of predation. Specifically, we asked the following questions:

1. Is nest survival explained by variation in mistletoe abundance near the nest tree?
2. Does habitat structure explain nest survival?
3. Does nest predation vary between nests placed in mistletoe substrates and those placed in other substrates?

Materials and methods

STUDY AREA

The study was conducted between October 2004 and February 2006 in Binya State Forest, a 4229-ha woodland 20 km east of Griffith, New South Wales, Australia (34°13'S, 140°16'E; Fig. 1b). The forest has a history of management for timber production,



Fig. 1. (a) A male painted honeyeater *Grantiella picta*, singing from a perch beneath a grey mistletoe *Amyema quandang*. (Photograph by Chris Tzaros, used with permission). (b) A stand of yarran *Acacia homalophylla* showing the open crown with occasional dense clumps of grey mistletoe. The sparse understorey with occasional shrubs and herbs is characteristic of the study area. (Photograph by Laurence Barea)

which is reflected in the plant communities currently present. The upper stratum is dominated by White Cypress-pine (*Callitris glaucophylla*) interspersed with Bimble Box (*Eucalyptus populnea*), mallee (*Eucalyptus* spp.), Buloke (*Allocasuarina luehmannii*), Belah (*Casuarina cristata*), corkwood (*Hakea* spp.) and Yarran (*Acacia homalophylla*), the principal host for Grey Mistletoe (*Amyema quandang*) at this site. Grey Mistletoe fruit was available in all months of the year but abundance followed a unimodal seasonal pattern characterized by an extended period of scarcity from late summer through winter followed by a peak in abundance between October and January in both years (Barea & Watson 2007). The shrub layer is dominated by saplings of the main canopy species, various acacias (*Acacia* spp.) and hop-bush (*Dodonaea* spp.). The

herbaceous layer is sparse and dominated by annual introduced species, such as Capeweed (*Arctotheca calendula*) and mustards (Brassicaceae), while native chenopods, such as Ruby Saltbush (*Enchylaena tomentosa*), are also common. The study area experiences hot summers and cool winters with an annual average of 21.3 days with maximum temperatures above 35°C and 19.1 days with minimum temperatures below freezing (BOM 2012). Rainfall is winter/spring dominant (April–October) and highly variable, averaging 406 mm per annum over a 74-year record, with mean monthly rainfall in these months ranging from 32.5 mm to 41.3 mm (BOM 2012).

LOCATING AND MONITORING NESTS

Nests were located during the breeding seasons of 2004 and 2005 by following individual birds and monitoring their behaviour from a distance of approximately 15–20 (through binoculars). Most nest sites were found by following birds carrying nesting material or food items, with each nest site given a unique identifier and its location recorded using a handheld global positioning system unit. We checked nests every 1–2 days, with occasional intervals spanning up to 4 days. Data recording commenced the day a clutch was initiated, or the day a nest was found if it already contained a clutch or brood. Painted honeyeater nests were very lightly constructed, consistent with their description as ‘frail, with eggs and daylight clearly visible through sides’ (Higgins, Peter & Steele 2001), enabling nest contents to be easily quantified by direct observation through the nest floor from beneath (Barea 2008b). All nests, except one containing nestlings (verified by parental behaviour – both sexes incubate and brood nest contents (Barea 2008b) – and nestlings visible above the nest rim), permitted their contents to be visually quantified in this manner. Thus, we monitored nests by initially observing them from a concealed position approximately 30 m distant, waiting for the attending adult to leave the nest of its own accord and then moving into a position immediately beneath the nest, checking the contents and leaving before the parent returned. As such, we were able to monitor nests frequently and reliably, while minimizing observer influences on nest survival.

We defined a successful nest in accordance with its conventional definition as a nest that fledged at least one nestling (Zanette, Clinchy & Smith 2006 and references therein); daily nest survival rate (DSR) was defined as the probability that a nest survives a single day and nest survival as the probability that a nest will be successful (*sensu* Dinsmore, White & Knopf 2002). If the entire nest contents simultaneously disappeared between visits, we considered the nest to have been depredated. The start of the nesting season was defined as the day the first observed clutch was initiated, and we calculated the age of each subsequent nest at day one of the nesting season (i.e. first observed clutch initiation date; after Cooch & White 2007) and then standardized day one between years to account for the earlier start to the nesting season in 2005 (Barea & Watson 2007). For nests where laying or hatching dates were unknown, dates were estimated by back-calculating from observed hatching or fledging dates using the mean incubation period ($15.8 \pm \text{SE } 0.16$ days, $n = 19$; defined as the first day an egg appeared in the nest; Barea 2008b) and/or the mean nestling period ($16.8 \pm \text{SE } 0.31$ days, $n = 15$; calculated from the day the first egg hatched; Barea 2008b) calculated from nests where they were explicitly known. For nine nests discovered when active but where age was uncertain, we assigned them the average age (after Dinsmore, White & Knopf 2002).

MODELLING NEST SURVIVAL

We used the nest survival model in program MARK (White & Burnham 1999; Dinsmore & Dinsmore 2007) using a logistic link function to model DSR of painted honeyeater nests. The model best

explaining nest survival was selected using an information theoretical approach (Burnham & Anderson 2002; Johnson & Omland 2004) based on the second-order variant of Akaike Information Criterion (AICc, Burnham & Anderson 2002).

Modelling followed a hierarchical approach. First, two *a priori* time-dependent models were constructed to assess competing hypotheses regarding temporal variation in DSR and recognizing that the nests were initiated at different times across the three-month nesting season (Barea & Watson 2007), rather than assuming constancy (Grant *et al.* 2005);

1. $S_{(c)}$ – Constant DSR (i.e. maximum likelihood version of the Mayfield method).
2. $S_{(date)}$ – A logit-linear time-trend model modelling DSR across the nesting season.

Although a quadratic model assessing variation in survival across time can be appropriate to nest survival analyses, we did not include such a model because an initial assessment considering sample size did not support such an approach. Similarly, we pooled data across the incubation and nestling stages to avoid over-parameterizing the models.

RESOURCE MODELS

Following initial modelling, we used the best AICc criterion-selected time-trend model as a platform for all subsequent models and allowed remaining time-trend models to compete with resource models in the final model set. We built 11 *a priori* resource models based on nine environmental variables (Table 1) to model their influence on nest survival. Resource model structure reflected that of a previous study of painted honeyeater nest-site selection (Barea 2012; see Barea 2008a for associated methods and rationale). We also constructed three additional resource models and a model assessing between-year variation as described below;

1. $S_{(substrate)}$ – Assesses the hypothesis that DSR is a function of nest substrate (i.e. mistletoe or nonmistletoe) because painted honeyeaters in the study area preferred mistletoe substrates (Barea 2008a).
2. $S_{(nest \text{ height})}$ – Assesses the hypothesis that DSR varies with nest height.
3. $S_{(nest \text{ orientation})}$ – Measured as the number of degrees deviation from the mean nest orientation; assesses the hypothesis nest orientation drives DSR.
4. $S_{(year)}$ – Assesses the hypothesis that year of study best explains DSR.

The final candidate set of models consisted of 17 models; that is, the 14 resource models, one time-dependent model, the constant model and the single model assessing between-year differences in DSR. Finally, we used hierarchical partitioning (Mac Nally 2000) to assess the independent contribution of the explanatory variables using R and the package ‘hier.part’ (Mac Nally & Walsh 2004) based on 1000 randomizations of the binary data matrix in a GLM using the statistical package R (R Development Core Team 2012). The utility of this technique is that it can identify a single variable (or perhaps several) containing a high level of independent explanatory power thus alleviating potential multicollinearity problems often associated with selecting a single best model (Mac Nally 2002).

Results

We located 77 painted honeyeater nests in which a clutch was laid (34 in 2004; 43 in 2005). Fourteen nests were known or suspected to be re-nesting attempts by previously recorded pairs and were excluded from analysis to mini-

Table 1. Habitat variables measured at painted honeyeater nest sites in Binya State Forest, NSW, Australia

Variable	Method of Measurement
DISTHOST	Average distance (m) to the nearest mistletoe-bearing host – excluding mistletoe-bearing nest trees – (with at least 1 mistletoe clump >0.3 m canopy diameter) in each quarter – measured to a maximum of 100 m using a laser rangefinder.
MISTAbund	Number of mistletoe clumps (>0.3 m canopy diameter) in closest infected host tree in each quarter – summed for all quarters.
DISTTree	Distance (m) to the nearest tree (DBH > 76 mm – corresponding to the DBH of the smallest observed nest tree) in each quarter expressed as a mean – measured to a maximum of 100 m using a laser rangefinder.
SNAG	Distance (m) to the nearest dead tree or dead-topped tree with emergent branches and measured to a maximum of 100 m using a laser rangefinder.
CANOPY	Percentage of canopy cover measured by sighting through a 25 mm diameter tube extended vertically above 13 sample points placed along the centre line of four 25 m × 2 m strip transects and estimating the percentage of the view through the tube that was obscured by vegetation in 10% increments (modified after Luck 2002). Strip transects originated at the base of the nest tree and extended towards four randomly oriented cardinal points. Sample was pooled for each nest tree to represent percentage canopy cover in surrounding 0.02 ha
SHRUBS	Number of shrubs/saplings with a DBH <76 along four 25 m × 2 m strip transects originating at the base of the nest tree and extending towards four randomly oriented cardinal points (James and Shugart 1970). Sample was pooled to reflect the density of shrubs/saplings within in 0.02 ha.
NEST HEIGHT	Height (m) of nest above-ground measured with a clinometer.
NEST SUBSTRATE	Vegetation within which nest is placed recorded as mistletoe or nonmistletoe (Barea 2008a).
NEST ORIENTATION	Number of degrees (rounded to the nearest 5 degrees) from magnetic north and assessed as deviation from circular mean (Batschelet 1981) of all nests.

mize issues of nonindependence. Hence, all analyses presented here were calculated using data for 63 painted honeyeater nests (2004 $n = 27$; 2005 $n = 36$) where a clutch was initiated and each nest tree is only represented once in the data set. All painted honeyeater nests were located in trees, with most placed in Yarran ($n = 49$), of which 29 were in Grey Mistletoe clumps (Barea 2008a).

Based on the combined incubation and nestling period (mean incubation 15.8 days \pm SE 0.16, $n = 19$; mean nestling period 16.8 days \pm 0.31, $n = 15$), the mean total nest period was 32.6 days (median 33 days; Barea 2008b). Twenty-one nests survived for the total nest period, while 42 nests failed – an apparent nest success rate of 33.3%. Thirty-five of the failed nests were considered to have been depredated; each case characterized by the simultaneous loss of all eggs or nestlings between nest visits. No predation events were observed directly, rendering predator identity unknown.

NEST TREE CHARACTERISTICS AND FATE

Successful nest trees were surrounded by fewer trees than failed nest trees and, although farther from trees hosting mistletoe, there were more mistletoe plants in the closest infected trees (Table 2), but 95% confidence intervals for successful and failed nests overlapped broadly for all three variables. Canopy closure was similar for failed and successful nest trees and, although there were fewer shrubs beneath successful nest trees and the orientation of successful nests deviated less from the mean ($51^\circ \pm 73^\circ$ SD; Barea 2008a; Table 2), 95% confidence intervals for both overlapped broadly. The mean height of successful nests was greater than that of failed nests (6.95 > 5.50 m) and, although their 95% confidence intervals overlapped, the degree of overlap was lower than other variables (Table 2).

MODELLING NEST SURVIVAL

Constant daily survival ($S_{(.)}$; model weight 0.73) was selected as the most parsimonious model explaining nest survival using AICc. The β estimate for $S_{(DATE)}$ was weakly negative and the 95% confidence interval contained zero (Table 3). Consequently, we modelled the influence of environmental variables on DSR by building on the most parsimonious time-trend model, that is $S_{(.)}$.

The best AICc-selected model explaining variation in nest survival was $S_{(SUBSTRATE)}$ (Table 4). The next best selected model, $S_{(NEST HEIGHT)}$ also received considerable support ($\Delta i < 2$), however the evidence ratio between these models ($w_{i_{best}}/w_{ij}$), indicated that $S_{(SUBSTRATE)}$ was supported 2.4 times more than $S_{(NEST HEIGHT)}$. $S_{(DISTHOST)}$ and $S_{(.)}$ were ranked third and fourth in the model set, respectively, each receiving less support ($\Delta i > 2 < 4$), than the two former models and their Akaike weights were low (Table 4).

EFFECT OF SUBSTRATE ON DAILY SURVIVAL RATES

The cumulative survival rate of the $S_{(.)}$ model was 29.9% (95% CI 19.6–41.0%) over the 33-day nesting period which was marginally lower than the apparent success rate of 33.3%, which also assumes that survival rates are constant over time. Mean DSR values for $S_{(SUBSTRATE)}$ and $S_{(NEST HEIGHT)}$ were 0.9644 (\pm 0.005) and 0.9647

Table 2. Mean, standard deviation and 95% confidence intervals for variables of successful and failed painted honeyeater nests in Binya State Forest and surrounding habitat, NSW, Australia. (see Table 1 for a description of variables)

Variable	Successful			Failed		
	Mean (\pm SD)	Range	95% CI	Mean (\pm SD)	Range	95% CI
DISTHOST	22.52 (12.28)	5.75–43.50	16.93–28.11	17.57 (13.86)	2.75–67.25)	13.25–21.89
MISTAbund	40.29 (12.28)	5.00–100.00	28.54–52.03	33.26 (25.81)	6.00–149.00	25.22–41.30
DISTTree	10.54 (5.71)	4.44–30.50	7.94–13.14	9.29 (7.36)	0.87–33.94	7.00–11.58
SNAG	25.45 (17.53)	2.50–60.00	17.47–33.43	26.90 (20.99)	3.00–100.00	20.36–33.45
CANOPY	8.69 (2.91)	3.65–14.62	7.37–10.01	8.91 (3.35)	1.92–17.98	7.87–9.96
SHRUBS	45.14 (55.04)	0.00–170.00	20.09–70.20	52.43 (81.49)	0.00–313.00	27.03–77.82
NEST ORIENTATION	49.48 (43.23)	4.00–139.00	29.80–69.15	61.45 (44.76)	6.00–174.00	47.50–75.40
NEST HEIGHT	6.95 (2.71)	3.40–15.20	5.72–8.19	5.50 (1.94)	1.80–12.03	4.89–6.10

Table 3. Time-dependant model selection summary for painted honeyeater daily nest survival rates in Binya State Forest, NSW, Australia. AICc = Akaike Information Criterion adjusted for small sample sizes. Models are ranked by ascending Δ AICc, w_i is the model weight, K is the number of parameters. Beta values are only presented for models assessing covariates

Model	K	Δ AICc	w_i	β	SE	95% CI lower	95% CI upper
$S_{(.)}$	1	0.00	0.73	–	–	–	–
$S_{(date)}$	2	2.01	0.27	–0.00	0.01	–0.02	0.02

AICc $S_{(.)}$ = 325.38.

(\pm 0.005), reflecting cumulative survival rates of 30.3% (95% CI 19.7–41.7%) and 30.6% (95% CI 19.9–42.0%), respectively. The β estimate for $S_{(NEST HEIGHT)}$ was 0.15 (\pm 0.08), and its 95% confidence interval (–0.00–0.30) contained zero.

The DSR for nests placed in mistletoe was substantially lower than for nests placed in other substrates (i.e. 0.9471 (\pm 0.010) and 0.9748 (\pm 0.001), respectively), the β estimate was negative (–0.77), and the 95% confidence interval (–1.39 to –0.15) did not contain zero. This difference corresponds to cumulative survival rates across the 33 day nest period of 16.6% (95% CI 6.9–30.2%) for nests in mistletoe and 43.1% (95% CI 26.4–58.9%) for those placed in nonmistletoe substrates. The β estimate for nests located in nonmistletoe substrates was positive (0.77), and its 95% confidence interval (0.15–1.39) did not contain zero.

Hierarchical partitioning revealed that both substrate and nest height contributed significant independent effects in explaining nest outcome for painted honeyeaters, while the independent effects attributable to all other variables were low and nonsignificant (Fig. 2).

Discussion

Painted honeyeater cumulative nest survival was low (29.9%), but within the range reported for other Australian open-cup nesters (Ford 1999; Ford *et al.* 2001) and comparable with other honeyeaters (Ford & Trémont

2000). The $S_{(.)}$ model assumed that the daily nest survival rate is constant over the nesting season, a similar finding to that of Ford (1999) for red wattlebirds and noisy friarbirds. More than half of the 63 nests studied (55.6%) were predated, with predation accounting for 83.3% of the 42 failed nests. Although substantially higher than that reported for canopy/subcanopy nesting species in Northern hemisphere forests (Martin 1992) and Australian passerines (Robinson 1990; Berry 2001; Debus 2006), these proportions are similar to those reported for other honeyeaters (Franklin *et al.* 1995; Boulton & Clarke 2003; Remeš, Matysioková & Cockburn 2012).

Whereas availability of food (mistletoe fruit) and habitat structure were important predictors of nest-site selection in this system (Barea 2012), they had little influence over nest survival, suggesting a lack of bottom-up control on nest survival for this study. Crampton (2004) also found weak support for a link between nest survival and availability of food resources in the phainopepla, another mistletoe-specialist frugivore. The lack of support for any of the mistletoe food resource models could be explained if mistletoe food abundance exhibits a threshold effect, above which influences are not observed (e.g. Shochat *et al.* 2005a). Mistletoe fruit abundance may have been above such a threshold during this study – in addition to dominating nestling diet (Barea 2008b), painted honeyeater reproduction tracked mistletoe fruiting phenology, so that fruit abundance peaked when adults were provisioning nestlings (Barea & Watson 2007). Fruit availability was further increased by selecting nest sites close to high mistletoe densities (Barea 2008a, 2012).

Although consistent over two years, we acknowledge that nutritional resources may drive nest survival in years when the mistletoe fruit crop either fails or is less productive. Indeed, there are reports of painted honeyeater populations failing to breed despite arriving in their breeding habitat during such years (Higgins, Peter & Steele 2001). A similar failure to breed during periods of fruit crop failure has also been observed in phainopeplas, (Chu 1999). Painted honeyeaters also consume arthropods and provide them to their nestlings (Barea 2008b; Barea & Herrera 2009) and their availability could influence reproduction.

Table 4. Summary of model selection results for nest survival of painted honeyeaters in Binya State Forest, NSW, Australia. AICc = Akaike Information Criterion adjusted for small sample sizes. Models are ranked by ascending $\Delta AICc$, w_i is the model weight, $K = n$ environmental parameters + constant)

Model	K	$\Delta AICc$	w_i	Model definition
$S_{(SUBSTRATE)}$	2	0.00	0.40	Mistletoe or nonmistletoe substrate
$S_{(NEST HEIGHT)}$	2	1.70	0.17	Nest height
$S_{(DISTHOST)}$	2	3.21	0.08	Mistletoe spatial distribution
$S_{(.)}$	1	3.96	0.06	Nest survival is constant over time
$S_{(ORIENTATION)}$	2	4.33	0.05	Orientation of nest in tree crown
$S_{(SHRUBS)}$	2	4.74	0.04	Combined shrub and sapling density
$S_{(YEAR)}$	2	4.96	0.03	Study year
$S_{(DISTTree)}$	2	5.00	0.03	Tree density
$S_{(MISTAbund + DISTHOST)}$	3	5.22	0.03	Additive effects of mistletoe abundance and its spatial distribution
$S_{(MISTAbund)}$	2	5.63	0.02	Mistletoe abundance
$S_{(SNAG)}$	2	5.88	0.02	Snag proximity
$S_{(DATE)}$	2	5.96	0.02	Nest survival varies across the nesting season
$S_{(CANOPY)}$	2	5.96	0.02	Canopy closure
$S_{(DISTHOST + DISTTree + CANOPY + SHRUBS + SNAG)}$	6	8.31	0.01	Additive effects of mistletoe spatial distribution and habitat structure
$S_{(DISTTree + CANOPY + SHRUBS + SNAG)}$	5	9.58	0.00	Habitat structure
$S_{(MISTAbund + DISTHOST + DISTTree + CANOPY + SHRUBS + SNAG)}$	7	10.33	0.00	Additive effects of all resources measured (global model)
$S_{(MISTAbund + DISTTree + CANOPY + SHRUBS + SNAG)}$	6	11.29	0.00	Additive effects of mistletoe abundance and habitat structure

AICc $S_{(SUBSTRATE)} = 321.42$.

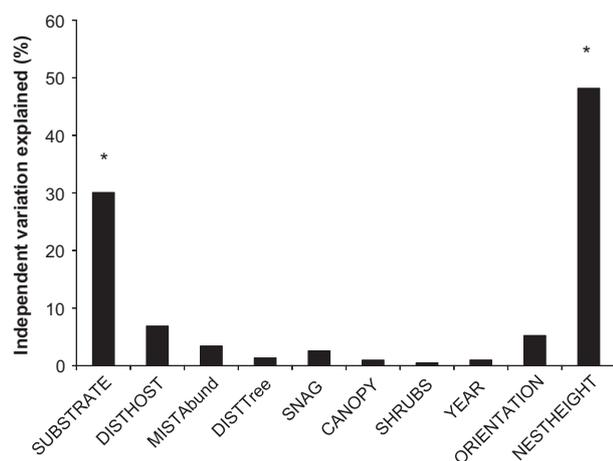


Fig. 2. Hierarchical partitioning results showing the percentage of total independent variation attributable to each variable in explaining painted honeyeater nest success. Only SUBSTRATE and NEST HEIGHT have a significant Z-score value at the 95% confidence level, suggesting that only these variables contribute significant independent effects to variation in painted honeyeater nest success. Z-scores calculated as [observed mean (1000 randomizations)]/SD (1000 randomizations).

Although arthropod abundance was not measured during this study, nestling starvation was not a major mortality factor in this study, suggesting that food abundance (mistletoe fruit or arthropods) did not limit nestling survival.

Rather than nutritional resources, habitat structure or characteristics of the nest tree, nest survival was best explained by whether the nest was placed in a mistletoe

clump: survival rates of mistletoe nests were 16.6%, 2.6 times lower than those placed elsewhere and the associated 95% confidence intervals support a strong effect size. Mistletoe is used as a nest substrate by at least 66% of Australia's arboreal nesting bird species (Cooney, Watson & Young 2006), potentially leading to the formation of specific search images by predatory birds (the major nest predators in many Australian systems (Ford 1999; Boulton & Clarke 2003). Previous research evaluating the basis of mistletoe nesting found that artificial nests in mistletoe experienced significantly decreased predation than nests placed in other arboreal substrates (Cooney & Watson 2006), while Ford's (1999) work on red wattlebirds and noisy friarbirds reported that nest success was independent of mistletoe or other substrate types.

Unlike both previous studies, the nesting period for painted honeyeaters coincides with peak availability of mistletoe fruit (Barea & Watson 2007). We suggest the higher failure rate for nests in mistletoe results from the direct and indirect effects of honeyeaters and other passerines foraging in mistletoe clumps (Zanette 1997; Boulton & Clarke 2003; Debus 2006), via opportunistic predation and increased agonistic interactions with nesting birds resulting in reduced nest attendance. Fruiting mistletoe plants attract large numbers of visiting animals, many of them opportunistic frugivores including species that include eggs or nestlings in their diet (Watson 2001). Brown-headed honeyeater (*Meliphreptus brevirostris*) and spiny-cheeked honeyeaters (*Acanthagenys rufogularis*) were commonly observed in the study area foraging on mistle-

toe nectar and fruit, and both species are known to be occasional nest predators (Zanette 1997; Higgins, Peter & Steele 2001). We observed numerous antagonistic interactions between painted honeyeaters and spiny-cheeked honeyeaters, with the former physically attacking or driving off spiny-cheeked honeyeaters when they approached their nest, consistent with previous work implicating spiny-cheeked honeyeaters as possible egg predators of painted honeyeaters (Whitmore & Eller 1983). We observed a female painted honeyeater driving off a brown-headed honeyeater that had its bill inside the painted honeyeater's nest which contained eggs. The nest was subsequently found depredated. Although neither species were confirmed as preying on painted honeyeater nests in this study, they were directly implicated in interference competition (Barea 2008b) which could result in increased conspicuousness of the nest to other potential predators due to defensive behaviour by the nest owner.

While we are confident that mistletoe represents a popular nest substrate for painted honeyeaters (Barea 2008a), it is unclear how representative our estimates of nest success are for this species in other regions and years, nor how the potential predator guild varies through space and time. Although arboreal marsupials are absent from this region, several species are known nest predators that favour mistletoe foliage and occur elsewhere in their range, so establishing predator identity is a key priority for further work.

Reduced nest survival associated with nesting in close proximity to mistletoe has also been reported for the phainopepla (Crampton 2004), consistent with a generalized and hitherto overlooked drawback of mistletoe as a nesting substrate – increased potential of nest predation. In addition to the strong effect of nest substrate, this mechanism would also explain the unexpected finding that successful nests were farther from the nearest mistletoe-bearing host, suggesting the mechanism may operate beyond the nest-tree scale. Although mistletoe is a popular nest-site location in forested habitats world-wide (Watson 2001), the fact that these interactions have not previously been noted, suggests that nesting periods overlapping with fruit availability are rare. Mistletoe phenology has been described in many systems and is characterized by long, even continuous fruiting seasons, with peak fruit availability often coinciding with periods of regional shortages. The potential for interference between mistletoe frugivores and mistletoe nesters would be greatest for the group of species that depend on mistletoe fruit as their primary food source – the mistletoe-specialist frugivores – which often time their breeding to coincide with periods of maximum fruit availability. It is noteworthy that very few of these species have been reported using mistletoe as a nest substrate (Watson 2013 and references therein), with higher nest success for nesting locations further away from fruiting mistletoes (Crampton 2004; this study).

Given that habitat selection can have a genetic basis and it is expected to be an adaptive process positively influenc-

ing individual fitness (Martin & Roper 1988; Clark & Shuttler 1999; Misenhelter & Rotenberry 2000; Chalfoun & Martin 2007), our results suggest that nesting in mistletoe may be maladaptive in this system, a surprising result given the high incidence of Australian birds nesting in mistletoe (Cooney, Watson & Young 2006). Nest-site selection by painted honeyeaters may represent a response to predictable variation in mistletoe fruit abundance over evolutionary time (*sensu* Martin 1992) as well as to nest predation rates over similar time frames. However, reproductive outcome may have become decoupled from the consequences of nest-site selection if painted honeyeaters are unable to predict and respond to fluctuations in the composition or behaviour of predator populations if they primarily cue of fruit abundance as suggested by Barea 2008a; Barea & Watson 2007; Barea 2012). As a consequence, any adaptive advantages associated with placing nests in mistletoe clumps may be either neutralized or overwhelmed by chance predation consistent with the ecological trap hypothesis (Gates & Gysel 1978; Kokko & Sutherland 2001), invoked for various bird species and systems (Misenhelter & Rotenberry 2000; Boulton & Clarke 2003; Shochat *et al.* 2005b).

This mismatch between preferred nest site and likelihood of success may be quite recent, reflecting changes in habitat occurrence and the distribution of mistletoe plants within the painted honeyeater's restricted breeding range and potentially contributing to widespread declines in this species (recently listed as nationally Vulnerable). The acacia-dominated woodland used as breeding habitat for this species was subjected to broad-scale clearing for agricultural development, with large initial losses in the late 1800s and a second phase when irrigation expanded in the 1950s (Ford *et al.* 2001; Barea 2008b and references therein). These extensive changes coupled with intensive disturbance associated with commercial logging in the largest remnants restricted the species preferred habitats to roadside stands and small patches within *Callitris*-dominated woodland. As with many other agriculture-dominated landscapes in southern Australia, increases in mistletoe density coincided with his habitat fragmentation (Watson 2011), leading to a small number of resource-rich patches. Although advantageous for regular mistletoe consumers (Watson 2013), we suggest this concentration underlies the high density of breeding pairs (Barea 2012), far closer to one another than reported for any other honeyeaters (Franklin *et al.* 1995; Ford 1999).

Rather than necessarily restricted to mistletoes, this phenomenon may apply to other fruiting plants, with their popularity and suitability as nest sites both predicted to be lower during fruiting seasons. In addition to opportunistic predation, nests within fruiting plants may exhibit lower success rates due to parents spending more time defending the nest tree and less time attending to their chicks (Martin 1992). Indeed, this pattern may reflect a more widespread trade-off for frugivores, with energetic advantages associated with nesting close to food plants offset by greater risk

of nest failure, especially in disturbed areas where resources are more concentrated.

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References

- Barea, L.P. (2008a) Nest-site selection by the Painted Honeyeater (*Grantiella picta*), a mistletoe specialist. *Emu*, **108**, 213–220.
- Barea, L.P. (2008b) *Interactions between frugivores and their resources: case studies with the painted honeyeater Grantiella picta*. PhD dissertation, Charles Sturt University, NSW, Australia.
- Barea, L.P. (2012) Habitat influences on nest-site selection by the Painted Honeyeater (*Grantiella picta*): do food resources matter? *Emu*, **112**, 39–45.
- Barea, L.P. & Herrera, M.L.G. (2009) Sources of protein in two semi-arid zone mistletoe specialists: insights from stable isotopes. *Austral Ecology*, **34**, 821–828.
- Barea, L.P. & Watson, D.M. (2007) Temporal variation in food resources determines onset of breeding in an Australian mistletoe specialist. *Emu*, **107**, 203–209.
- Batschelet, E. (1981) *Circular Statistics in Biology*. Academic Press, London.
- Berry, L. (2001) Breeding biology and nesting success of the Eastern Yellow Robin and the New Holland Honeyeater in a southern Victorian woodland. *Emu*, **101**, 191–197.
- BOM (2012). *Australian Bureau of Meteorology*. Available at http://www.bom.gov.au/climate/averages/tables/cw_075028_All.shtml. Verified 18 September, 2012.
- Boulton, R.L. & Clarke, M.F. (2003) Do yellow-faced honeyeater *Lichenostomus chrysops* nests experience higher predation at forest edges? *Wildlife Research*, **30**, 119–125.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd Edition, Springer-Verlag, New York.
- Chalfoun, A.D. & Martin, T.E. (2007) Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *Journal of Applied Ecology*, **44**, 983–992.
- Chu, M.C. (1999) *Ecology and breeding biology of Phainopepla (Phainopepla nitens) in the desert and coastal woodlands of Southern California*. PhD dissertation, University of California, Berkeley, California.
- Clark, R.G. & Shuttler, D. (1999) Avian habitat selection: pattern from process in nest site use by ducks. *Ecology*, **80**, 272–287.
- Cooch, E. & White, G. (2007). *Program Mark: A Gentle Introduction*. 6th edition. <http://www.phidot.org/software/mark/docs/book/>. Verified 18 September 2012.
- Cooney, S.J.N., Watson, D.M. & Young, J. (2006) Mistletoe nesting in Australian birds; a review. *Emu*, **106**, 1–12.
- Crampton, L.H. (2004) *Ecological determinants of the distribution, abundance and breeding success of phainopepla (Phainopepla nitens: Aves) at the northern edge of their range*. PhD dissertation, University of Nevada, Reno, Nevada.
- Debus, S.J.S. (2006) Breeding and population parameters of robins in a woodland remnant in northern New South Wales, Australia. *Emu*, **106**, 147–156.
- Dinsmore, S.J. & Dinsmore, J.J. (2007) Modeling avian nest survival in Program Mark. *Studies in Avian Biology*, **34**, 73–83.
- Dinsmore, S.J., White, G.C. & Knopf, F.L. (2002) Advanced techniques for modeling avian nest survival. *Ecology*, **83**, 3476–3488.
- Ford, H. (1999) Nest site selection and breeding success in large Australian honeyeaters: are there benefits from being different? *Emu*, **99**, 91–99.
- Ford, H.A. & Trémont, S. (2000) Life-history characteristics of two Australian honeyeaters (Meliphagidae). *Australian Journal of Zoology*, **48**, 21–32.
- Ford, H.A., Barrett, G.W., Saunders, D.A. & Recher, H.F. (2001) Why have birds in the woodlands of Southern Australia declined? *Biological Conservation*, **97**, 71–88.
- Franklin, D.C., Smales, I.J., Miller, M.A. & Menkhorst, P.W. (1995) The reproductive biology of the helmeted honeyeater, *Lichenostomus melanops cassidix*. *Wildlife Research*, **22**, 173–191.
- Gates, J.E. & Gysel, L.W. (1978) Avian nest dispersion and fledging success in field-forest ecotones. *Ecology*, **59**, 871–883.
- Grant, T.A., Shaffer, T.L., Madden, E.M. & Pietz, P.J. (2005) Time-specific variation in passerine nest survival: new insights into old questions. *Auk*, **122**, 661–672.
- Hahn, T.P. (1995) Integration of photoperiodic and food cues to time changes in reproductive physiology by an opportunistic breeder, the red crossbill (*Loxia curvirostra*: Aves, Carduelinae). *Journal of Experimental Zoology*, **272**, 213–226.
- Higgins, P.J., Peter, J.M. & Steele, W.K. (2001). *Handbook of Australian, New Zealand and Antarctic Birds. Vol. 5: Tyrant Flycatchers to Chats*. Oxford University Press, Melbourne.
- Huhta, E., Jokimaeki, J. & Rahko, P. (1998) Distribution and reproductive success of the Pied Flycatcher *Ficedula hypoleuca* in relation to forest patch size and vegetation characteristics: the effect of scale. *Ibis*, **140**, 214–222.
- James, F.C. & Shugart Jr, H.H. (1970) A quantitative method of habitat description. *Audubon Field Notes*, **24**, 727–736.
- Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution*, **19**, 101–108.
- Kokko, H. & Sutherland, W.J. (2001) Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effects. *Evolutionary Ecology Research*, **3**, 537–551.
- Ligon, J.D. (1978) Reproductive interdependence of Piñon Jays and Piñon Pines. *Ecological Monographs*, **48**, 111–126.
- Luck, G.W. (2002) The habitat requirements of the rufous treecreeper (*Climacteris rufa*). 1. Preferential habitat use demonstrated at multiple spatial scales. *Biological Conservation*, **105**, 383–394.
- Mac Nally, R. (2000) Regression and model-building in conservation biology, biogeography and ecology: the distinction between—and reconciliation of—‘predictive’ and ‘explanatory’ models. *Biodiversity and Conservation*, **9**, 655–671.
- Mac Nally, R. (2002) Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. *Biodiversity and Conservation*, **11**, 1397–1401.
- Mac Nally, R.M. & Walsh, C.J. (2004) Hierarchical partitioning public-domain software. *Biodiversity and Conservation*, **13**, 659–660.
- Martin, T.E. (1987) Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics*, **18**, 453–487.
- Martin, T. E. (1992). Interaction of nest predation and food limitation in reproductive strategies. *Current Ornithology* (ed D. M. Power), **9**, pp. 163–197.
- Martin, T.E. (1993) Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist*, **141**, 897–913.
- Martin, T.E. & Roper, J.J. (1988) Nest predation and nest site selection of a western population of the hermit thrush. *Condor*, **90**, 51–57.
- Misenhelter, M.D. & Rotenberry, J.T. (2000) Choices and consequences of habitat occupancy and nest site selection in sage sparrows. *Ecology*, **81**, 2892–2901.
- Olsson, O., Wiklander, U., Malmqvist, A. & Nilsson, S.G. (2001) Variability of patch type preferences in relation to resource availability and breeding success in a bird. *Oecologia*, **127**, 435–443.
- R Development Core Team. (2012). *R: A Language and Environment for Ecology and breeding biology of Phainopepla Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org> [accessed 18 September 2012].
- Remeš, V., Matysioková, B. & Cockburn, A. (2012) 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.
- Ricklefs, R.E. (1969) An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology*, **9**, 1–48.
- Robinson, D. (1990) The nesting ecology of sympatric scarlet robin *Petroica multicolor* and flame robin *P. phoenicea* in open eucalypt forest. *Emu*, **90**, 40–52.
- Shochat, E., Wolfe, D.H., Patten, M.A., Reinking, D.L. & Sherrill, S.K. (2005a) Tallgrass prairie management and bird nest success along roadsides. *Biological Conservation*, **121**, 399–407.

- Shochat, E., Patten, M.A., Morris, D.W., Reinking, D.L., Wolfe, D.H. & Sherrod, S.K. (2005b) Ecological traps in isodars: effects of tallgrass prairie management on bird nest success. *Oikos*, **111**, 159–169.
- Visser, M., Holleman, L. & Gienapp, P. (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia*, **147**, 164–172.
- Watson, D.M. (2001) Mistletoe—a keystone resource in forests and woodlands worldwide. *Annual Review of Ecology and Systematics*, **32**, 219–249.
- Watson, D.M. (2011) *Mistletoes of Southern Australia*. CSIRO Publishing, Collingwood, 188 pp.
- Watson, D.M. (2013). The relative contribution of specialists and generalists to mistletoe dispersal: insights from a Neotropical forest. *Biotropica*, **45**, 195–202.
- White, G.C. & Burnham, K.P. (1999) Program MARK: Survival estimation from populations of marked animals. *Bird Study*, **46**, 120–139.
- Whitmore, M.J. & Eller, C.M. (1983) Observations at a nest of Painted Honeyeaters. *Emu*, **83**, 199–202.
- Zanette, L. (1997) Predation of an eastern yellow robin nest by a small bird, the brown-headed honeyeater. *Australian Bird Watcher*, **17**, 158–159.
- Zanette, L., Clinchy, M. & Smith, J. (2006) Combined food and predator effects on songbird nest survival and annual reproductive success: results from a bi-factorial experiment. *Oecologia*, **147**, 632–640.
- Zanette, L., Doyle, P. & Trémont, S.M. (2000) Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology*, **81**, 1654–1666.
- Zanette, L., Smith, J.N.M., van Oort, H. & Clinchy, M. (2003) Synergistic effects of food and predators on annual reproductive success in song sparrows. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 799–803.

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