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Perch proximity does not predict the probability of cuckoo parasitism in a woodland host

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Obligate avian brood parasites typically impose great costs on their hosts by replacing the host's offspring with their own. Multiple theories have been put forward regarding which factors influence the probability that a host nest will be parasitized. One of these, the perch proximity hypothesis, predicts that nests that are close to trees are more likely to be parasitized, as trees provide a vantage point for the parasite to observe nest building by the host. Substantial support for this hypothesis has been found in several species of brood parasites that occur in a range of open habitats, such as reed beds, marshlands and grasslands, where vantage points are likely to be scarce. However, it is unclear whether this prediction applies to species that occupy woodland habitats. Although brood parasites may be more likely to exploit nests with suitable vantage points nearby, it is possible that a high density of vegetation might obscure the nest, thereby reducing the likelihood of parasitism. Here we used a long-term data set of superb fairy-wren, *Malurus cyaneus*, nests to test this hypothesis in the brood-parasitic Horsfield's bronze-cuckoo, *Chalcites basalis*. Contrary to the prediction of the perch proximity hypothesis, parasitism risk did not increase with closer proximity of a perch to the nest; instead, we show that the risk of parasitism may decrease as tree density increases. These results suggest that exploration of the host activity hypothesis and nest exposure hypothesis may be fruitful for future work in this system.

Obligate avian brood parasites, such as cuckoos, lay their eggs in the nests of other birds, abandoning the care of their young to their chosen hosts (Davies, 2000). The costs of brood parasitism to hosts are typically enormous. In many cases, the hosts not only lose their own clutch, but also expend much time and energy in raising a foreign chick, which is usually much larger than their own young (Davies, 2000). While many hosts have evolved the ability to recognize and reject brood-parasitic eggs (Davies, 2000) or chicks (Langmore et al., 2003; Sato et al., 2010), these defences do not eliminate all the costs of parasitism, as the parasite typically removes one host egg when laying her own (Davies, 2000); and because even effective egg rejection still includes errors (in which hosts mistakenly reject one of their own eggs or fail to reject a parasitic egg, Davies, 2000). Thus, the most effective defence against brood parasitism is to avoid being parasitized altogether. How a host can achieve this will depend on which factors influence the probability of a nest being parasitized, which in turn depends on the methods that brood parasites use to locate host nests. The question of how brood parasites locate host nests has generated numerous hypotheses (Clotfelter, 1998; Hauber & Russo, 2000).

There are five nonmutually exclusive hypotheses that describe how brood parasites may find host nests to parasitize. These include the 'nest exposure hypothesis', which predicts that visually conspicuous nests are more likely to be parasitized (Clotfelter, 1998; Øien et al., 1996). Second, the 'host activity hypothesis' posits that host activity attracts brood parasites (Clotfelter, 1998; Gochfeld, 1979; Thompson & Gottfried, 1976). Third, the 'nesting cue hypothesis' states that hosts that are more aggressive to brood parasites are more likely to be parasitized, due to increased activity providing more evidence about the nest location (Clotfelter, 1998; Robertson & Norman, 1976; Seppä, 1969). The nesting cue hypothesis can be considered a special case or subset of the host activity hypothesis. Fourth, the 'habitat search hypothesis' states that brood parasites find nests by searching the habitat without relying on behavioural cues from the hosts (Norman & Robertson, 1975;

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Wiley, 1988). Finally, the ‘perch proximity hypothesis’ predicts that nests close to trees, where brood parasites can easily observe host behaviour, are more likely to be parasitized (Alvarez, 1993; Clotfelter, 1998; Hauber & Russo, 2000).

The ‘nest exposure hypothesis’ has broad support across several brood parasite species. Exposed nests have been found to be parasitized more by the common cuckoo, *Cuculus canorus* (Clarke et al., 2001; Jelínek et al., 2014; Moskát & Honza, 2000), as well as by brown-headed cowbirds, *Molothrus ater* (Burhans, 1997). Nest size also affects parasitism risk in several species, such as the Eurasian magpie, *Pica pica* (parasitized by the great spotted cuckoo, *Clamator glandarius*, Soler et al., 1995), long-tailed shrikes, *Lanius schach*, house crows, *Corvus splendens*, and common mynas, *Acridotheres tristis* (all hosts to the Asian koel, *Eudynamys scolopacea*, Begum et al., 2011) and the large-billed gerygone, *Gerygone magnirostris* (parasitized by the little bronze-cuckoo *Chalcites minutillus*, Noh et al., 2021). Bigger nests may be more conspicuous and hence exposed, but may also be an indicator of a high-quality pair or territory. Much of the support for the ‘host activity hypothesis’ and the ‘habitat search hypothesis’ come from cowbird systems (Banks & Martin, 2001; Clotfelter, 1998; Fiorini & Reboreda, 2006; Robinson & Robinson, 2001; Wiley, 1988), while the ‘perch proximity hypothesis’ has been supported by both studies on common cuckoo systems (Alvarez, 1993; Moskát & Honza, 2000; Øien et al., 1996) and studies in cowbird systems (Clotfelter, 1998; Hauber & Russo, 2000). Support for the ‘nesting cue hypothesis’ has been sparse, and several studies have been unable to find any support for it at all (Clotfelter, 1998; Fiorini et al., 2009; Gill et al., 1997).

The perch proximity hypothesis is likely to be most applicable to hosts and brood parasites that live in habitats that lack a canopy, such as grasslands, reed beds, wetlands and marshes, where a vantage point is likely to greatly increase a brood parasite’s opportunity to observe nest building by a host. However, it is unclear whether perch proximity is also important for brood parasites that occupy woodlands and forests. In these habitats, the higher density of trees may actually impede observations of host nest building by brood parasites. If so, we would predict that higher perch proximity may be associated with decreased risk of parasitism.

Here we aimed to test whether perch proximity influences the probability of parasitism among hosts that nest in open eucalypt woodland (see Fig. 1). We investigated the probability of brood parasitism by Horsfield’s bronze-cuckoos, *Chalcites basalis*, of superb fairy-wren, *Malurus cyaneus*, nests in eastern Australia in relation to the vegetation around the nest. Following the findings of previous studies (Alvarez, 1993; Moskát & Honza, 2000; Øien et al., 1996), we tested whether the distance to tree branches, vantage points (including trees and synthetic structures) and the closest tree were significant predictors of parasitism. In addition to these measurements, we also measured tree density (number of trees over 2 m in height, in a 10 m radius around the nest site) and took measurements to get an approximation of canopy cover.

METHODS

Study Site

This research was undertaken at Campbell Park/Mt Ainslie Nature Reserve (149°9′E, 35°16′S) in Canberra, Australia, from February to May 2020. Campbell Park comprises cleared land for grazing to the north and east and open dry sclerophyll forest to the south and west (Fig. 1). Since 1999, this site has been used for research on Australian cuckoos and their hosts, and parasitism rates have been monitored in a population of superb fairy-wrens that are mostly colour-banded for individual identification. The site has not been subjected to any substantial modification of vegetation (e.g. bushfire, clearing and grazing) during the study period.

Study Species

At Campbell Park, the Horsfield’s bronze-cuckoo’s primary host is the superb fairy-wren, which is a small (ca. 10 g), cooperatively breeding insectivore (Langmore & Kilner, 2010; Nias, 1984). At our site, superb fairy-wrens generally occupy habitat with a high number

Figure 1. Campbell Park is an open eucalypt woodland nature reserve in Canberra, Australia.

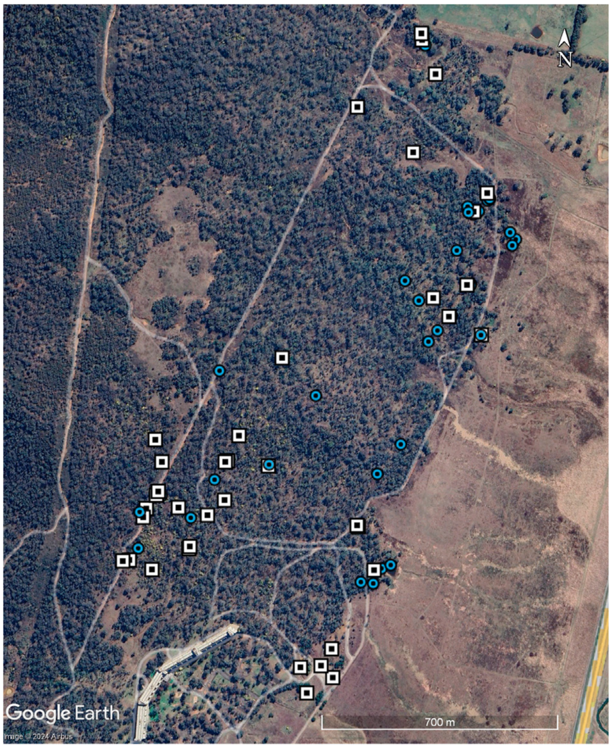

Figure 2. The study site with the GPS points of each nest included in this study. Circles represent locations of parasitized superb fairy-wren nests. Squares represent locations of unparasitized superb fairy-wren nests.

of shrubs and trees, with some open grassland nearby (Parsons et al., 2008; Rowley, 1964). They breed from September to February each year and generally prefer to build nests close to the ground (<1 m) in dense vegetation such as grass tussocks among fallen branches and in dense thorny shrubs (Nias, 1986; Rowley, 1964).

At Campbell Park, parasitism rates vary annually from 0% to 37% (Langmore & Kilner, 2007), as cuckoos are nomadic and do not return to their natal locations to breed (Brooker & Brooker, 1989; Langmore & Kilner, 2007). Horsfield's bronze-cuckoos are small (ca. 23 g; Brooker & Brooker, 1989), insectivorous cuckoos (Higgins, 1999; Langmore et al., 2007) that are widespread over Australia (Higgins, 1999). They arrive in southeastern Australia in late winter or early spring, where females stay at each breeding site for only a short period (2–8 weeks) before moving on to exploit hosts at a different site (Langmore et al., 2007). The male typically remains on the territory and may subsequently pair with a second, newly arrived female. Campbell Park holds at least two distinct cuckoo territories, which may be visited by up to three female cuckoos each year (Langmore et al., 2007). Given the nomadic movements and short-term tenure at territories by female cuckoos, we are confident that our results are not biased by the parasitism strategy of any single cuckoo.

Long-term Data Set

A long-term data set of superb fairy-wren nest locations with records of parasitism was collected for Campbell Park from 2011 to 2017. To test whether perch proximity influences the probability of parasitism, we paired each parasitized nest with another, unparasitized nest in the study site ($N = 76$, see Fig. 2). Nests were paired based on the date on which the first egg was laid by the host female. We matched nests into pairs based on hosts that had laid on the same date or the next closest date. Matching the nests based on egg-laying dates ensured that there was a cuckoo present at the study site during the laying period of both nests, and therefore they were equally vulnerable to parasitism. Thirty-eight parasitized nests across this period were used for this analysis. For 81.5% (31) of the pairs, the first eggs of the two nests were laid within 1 day of each other. The maximum number of days between nest pairs was 9 days for one pair.

Ethical Note

Vegetation data were collected during autumn, when superb fairy-wrens no longer maintain nesting territories and are instead in small feeding flocks. During the time measurements were taken there were no fairy-wrens present in the vicinity of the old nests. Nest GPS locations were collected as part of previous studies on the fairy-wren population at Campbell Park (Langmore et al., 2011, 2016; Medina et al., 2019; Medina & Langmore, 2019; Taylor & Langmore, 2020). This work was approved by the Australian National University Animal Experimentation Ethics Committee (Ethics protocol numbers: F.BTZ.39.09, A2012/47, A2016/33, A2017/35). Additionally, ACT government permits were required to work on these projects (Permit numbers: LT2011509, LT2012589, LT2013667, LT2014776, LT2015842 and LT2016895).

Field Measurements

Each nest location was visited between March and May 2020 using the GPS points recorded in the long-term data set. Our confidence in the GPS accuracy was supplemented by the consistent use of particular nest bushes by the wrens. This facilitated in identifying the precise nest locations from earlier years. The variables measured are described in Table 1. Several studies have found that distance to the nearest tree (Alvarez, 1993; Antonov et al., 2007; Clotfelter, 1998) and distance to the closest vantage point (Clotfelter, 1998; Moskát & Honza, 2000), generally a branch/perch (Øien et al., 1996), are significant predictors of parasitism. We measured the distances to both closest live branch (CLB) and the closest dead branch (CDB), as both could be potential vantage points. We separated live and

Table 1
A list of predictor variables measured in this study

Parameter	Measurement	Short description of how each measurement was collected
TD	Tree density	Number of trees over 2 m in height, in a 10 m radius around the nest GPS point
NT>2	Distance to nearest tree over 2 m	Distance from nest point to base of tree trunk. Trees must be 2 m or more in height
NT<2	Distance to nearest tree/plant under 2 m	Distance from nest point to base of tree or plant (must be able to support perching cuckoo). Trees/plants must be under 2 m in height
DistDBH	Distance to closest tree with a DBH ≥ 100 cm	Distance from nest point to base of closest tree with a diameter-at-breast-height of 100 cm or more
DBH	DBH of tree identified in DistDBH	Diameter-at-breast-height of tree identified in DistDBH
CLB	Distance to closest live branch	Closest living branch that could support a cuckoo
CDB	Distance to closest dead branch	Closest dead branch that could support a cuckoo
VP	Vantage points	Number of perching points that were visible at eye line from the nest point, included artificial structures such as phone lines and fences
CanCov	DBHbyBigTree	DBH variable divided by distDBH to create a new variable we used an approximation for canopy cover

dead branches as dead branches have been identified in other studies as potential brood parasite vantage points (Anderson & Storer, 1976). Because of the different ways superb fairy-wrens and Horsfield's bronze-cuckoos use their habitats, we measured the distance to the nearest vegetation across two categories. We divided the vegetation into 'Nearest tree over 2 m in height' ($NT > 2$) and 'Nearest tree/plant under 2 m in height' ($NT < 2$) as superb fairy-wrens usually move through the understorey, whereas cuckoos may use taller trees to observe their hosts. Owing to their high density, precise measurement of trees and shrubs under 1 m in distance away was not possible. In this case, a value of 0.5 was recorded. All measurements were recorded in metres to one decimal place, except for diameter-at-breast-height (DBH), which was measured to two decimal places. Tree density (TD) may also play a role in determining risk of parasitism, because more trees provide more vantage points and may also provide more cover for hosts and the nests. Artificial structures, such as electricity poles and fence posts, could also provide vantage points, so these were included in the variable vantage points (VP).

Vegetation may change in height and density over time. To reduce the impact of this on our analyses, we quantified variables that would show the least change between when the nest GPS points were collected (2011–2017) and when the above measurements were made (2020). We did not measure canopy cover directly or ground cover because the foliage cover fluctuates seasonally, and between years. We generated an approximation of canopy cover by creating a weighted variable from the distance to the closest tree with a DBH over 100 cm (DistDBH) and the DBH of that tree. We divided DBH by distance to create a new variable, CanCov. This meant that large trees that were close to nest sites had a high number and small trees that were far away had a low number. This helped capture large, long-limbed sprawling tree branches that provided much of the canopy cover. Because of the size of the trees included, we ensured that the same trees were present throughout the range of the long-term data set.

There are several habitat configurations for which VP might provide a benefit to brood parasites. Fig. 3 illustrates what the environment around the nest might look like if we found support for the perch proximity hypothesis among the various vegetation measurements we collected.

Analysis

The statistical software R (R Development Core Team, 2020) v4.0.2 was used for all data analyses. After an initial exploration of the data set, we removed two nests that were outliers and their corresponding pair (owing to missing data in one case and skewing of data in another). This left 36 pairs for analysis ($N = 72$). Additionally, we found that CDB and CLB were both highly correlated with $NT > 2$ (correlation between $NT > 2$ and $CLB = 0.751$, and between $NT > 2$ and $CDB = 0.761$). We removed the variable CLB due to the high correlation between it and $NT > 2$; however, we did not remove CDB because snags (dead trees and/or prominent protruding dead tree branches) have been a variable measured in other brood parasite - host nest-finding studies (Anderson & Storer, 1976; Brittingham & Temple, 1996), and brood parasites have been associated with watching hosts from such vegetation features (Robbins, 1979).

We initially modelled the probability of parasitism using a generalized linear mixed-effects model following a binomial

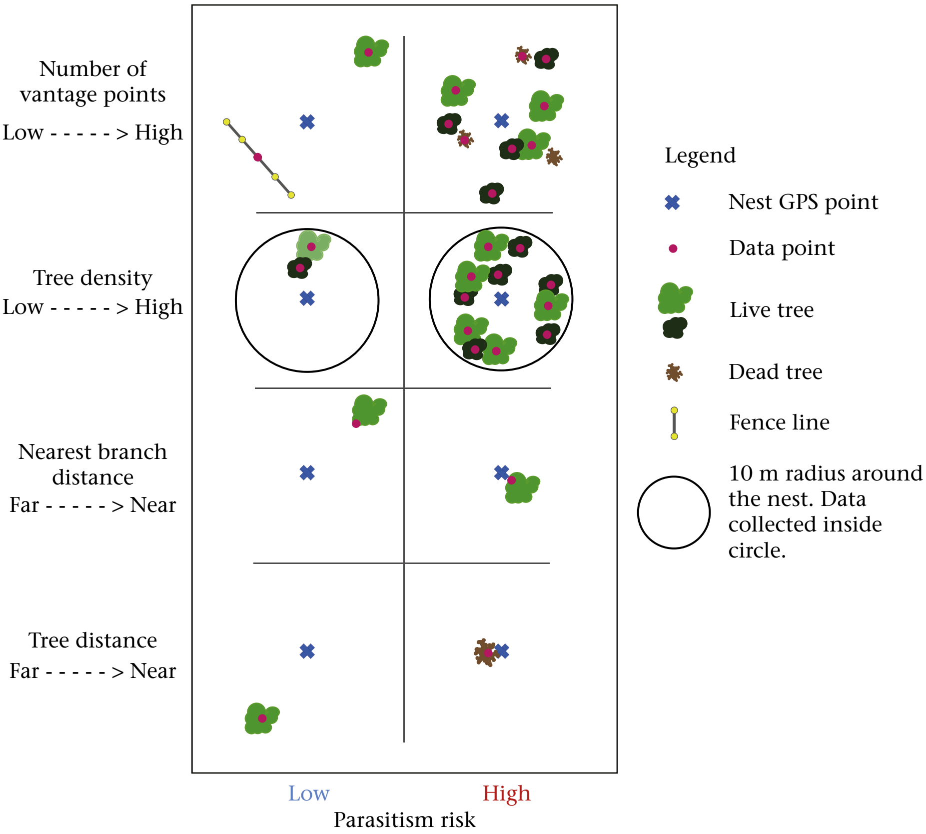

Figure 3. How the environment around the nest might look if we were to find support for the perch proximity hypothesis. Examples of habitat configurations with high and low number of vantage points, high and low tree density, near and far branch distance, and near and far tree distance. The perch proximity hypothesis predicts higher parasitism rates for configurations on the right-hand side of the illustration.

probability distribution with a logit link function using the package glmmTMB (Brooks et al., 2017). We fitted a full model with predictor variables TD, NT>2, NT<2, CDB, VP and CanCov, and three random effects, i.e. year, female ID and point pairs. This full model would not converge. We tested the significance of each random effect using a model comparison method. The models with random effects explained no meaningful amount of variation (log likelihood ratio test for all three model comparisons had the same results: $\chi^2{}_1 = 0, P = 0.9999$). In no model containing random effects did any of the fixed effects change. Therefore, the random effects were removed from the model.

To test perch proximity theory and explore other possible vegetative mechanisms that may influence a brood parasite's ability to find a nest in a woodland habitat, we built a suite of models (Table 2; ordered by the Akaike information criterion corrected for small sample size, AICc) that used a variety of combinations of predictor variables. We selected which variables were used in each model based on factors that have been found to be significant in studies where perch proximity was used by brood parasites, as well as variables that were of interest based on the specific study system. Significant predictors of perch proximity in other studies include distance to closest tree, vantage points and dead branches (Alvarez, 1993; Anderson & Storer, 1976; Begum et al., 2011). Variables specific to this study system include understory (trees/plants under 2 m, NT<2: as the hosts build their nests close to the ground in dense vegetation), and TD and CanCov, due to the woodland habitat approach of this study.

RESULTS

Vegetation Features of Nesting Sites

Vegetation at nesting sites was highly variable (Fig. 4). For example, distance to the nearest tree (both over and under 2 m in height) ranged from 0 to 23.9 m (Fig. 4b and c), and tree density ranged from 0 to 104 trees within a 10 m radius (Fig. 4a). Fig. 4f shows the data from the canopy cover proxy variable that was created from the data in Fig. 4d and e and shows that most nests were built under trees with large canopies, but there were a few exceptions. Most nests were within a few metres of a tree branch (dead or alive), but occasionally branches could be much further away, up to 16 m (Fig. 4g and h). The range of vantage points at each nest was 2—57, with a mean of 28.75 and SD 12.05 (Fig. 4i).

Table 2
Models used to test the perch proximity hypothesis in open woodland habitat

Models testing perch proximity hypothesis	AIC(c) value
(1) NT>2 + NT<2 + TD	100.5
(2) NT<2 + TD	100.7
(3) NT>2 + TD	100.7
(4) Null model	101.9
(5) NT<2 + VP	102.9
(6) NT>2 + VP	103.2
(7) NT>2 + NT<2 + VP	104.1
(8) VP + CDB	104.3
(9) NT<2 + NT>2	104.4
(10) NT>2 + CanCov	104.5
(11) VP + CDB + NT>2	104.9
(12) VP + CDB + CanCov	105.5
(13) NT>2 + NT<2 + CanCov	105.6

Additionally, model (1) explored the importance of understorey and surrounding vegetation in this system. AICc: Akaike information criterion corrected for small sample size; NT>2: nearest tree over 2 m; NT<2: nearest tree under 2 m; TD: tree density; VP: vantage points; CDB: closest dead branch; CanCOV: approximation for canopy cover.

Model Selection

Models with a Δ AICc < 2 of the top model were considered to fit the data significantly better than subsequent models, and only the predictors in these models were considered further. The model with the lowest AICc (100.5) contained the following variables: distance to nearest tree over 2 m (NT > 2), distance to nearest tree under 2 m (NT < 2) and tree density. In this model, tree density was significantly negatively associated with the probability of parasitism ($P = 0.029$; Table 3). Fig. 5 displays the predicted rate of parasitism for this model at varying tree densities. To see how this might look biologically, Fig. 6 gives an example of types of environments associated with higher parasitism risk according to our data.

The next two closest models had identical AICc values at 100.7. There were two predictors in each model; TD was in both, while one model contained NT>2 and the other contained NT<2 (Table 2). As these two models were similar to the top model, the conclusions from these three models remain broadly the same; tree density is the best predictor of parasitism risk when accounting for trees over and under a height of 2 m (Table 3). While trees over and under 2 m must be included in the model to determine the effect of tree density, they were not significant factors for parasitism risk in themselves.

It is of particular note, however, that the null model was very close to these three top models, with an AICc of 101.9, only 1.4 points from the highest model. This result diminishes the conclusions we can draw from the top three models because we cannot completely reject the null model in this case.

DISCUSSION

In previous studies on the impact of perch proximity on brood parasitism conducted in open habitats, a close perch was associated with a higher risk of parasitism (Alvarez, 1993; Clotfelter, 1998; Moskát & Honza, 2000). By contrast, our study found that close perches were not correlated with parasitism risk. We found some evidence that in eucalypt woodland the risk of parasitism may decrease with increasing number of available perches. The results rule out the perch proximity hypothesis and suggest that TD may influence how cuckoos find nests in eucalypt woodland, which has not been shown to be the case in previous studies.

The perch proximity hypothesis may not be applicable to woodland habitats, owing to the abundance of perching opportunities and the visual obstruction caused by dense vegetation. Studies that support the perch proximity hypothesis have been conducted in a variety of habitats, but many of these habitats have been open and perch-deficient, such as vineyards (Alvarez, 1993), grass and sedge meadow (Clotfelter, 1998) and reed beds (Antonov et al., 2007; Moskát & Honza, 2000; Øien et al., 1996). In sparsely wooded habitats with limited perching opportunities, the closest tree is likely to provide the clearest, or sometimes the only, vantage point for viewing host nesting activity. However, in habitats with more abundant perching opportunities, cuckoos may weigh the risk of a clear view with the risk of being seen by the host. Superb fairy-wrens mob Horsfield's bronze-cuckoos (Langmore et al., 2012), and after sighting them will increase their nest vigilance (Feeney & Langmore, 2015) and the probability of rejecting a cuckoo chick (Langmore et al., 2009). Because of these defences, Horsfield's bronze-cuckoos must avoid being detected by hosts while they observe nest construction to be successful in parasitizing the host nest (Feeney et al., 2013). This may result in cuckoos preferring to observe host nest building from a concealed or distant perch rather than the closest perch. However, this may be a poor strategy in heavily wooded habitats, where dense vegetation may hinder the cuckoo's view of host activity. This appears to be the case

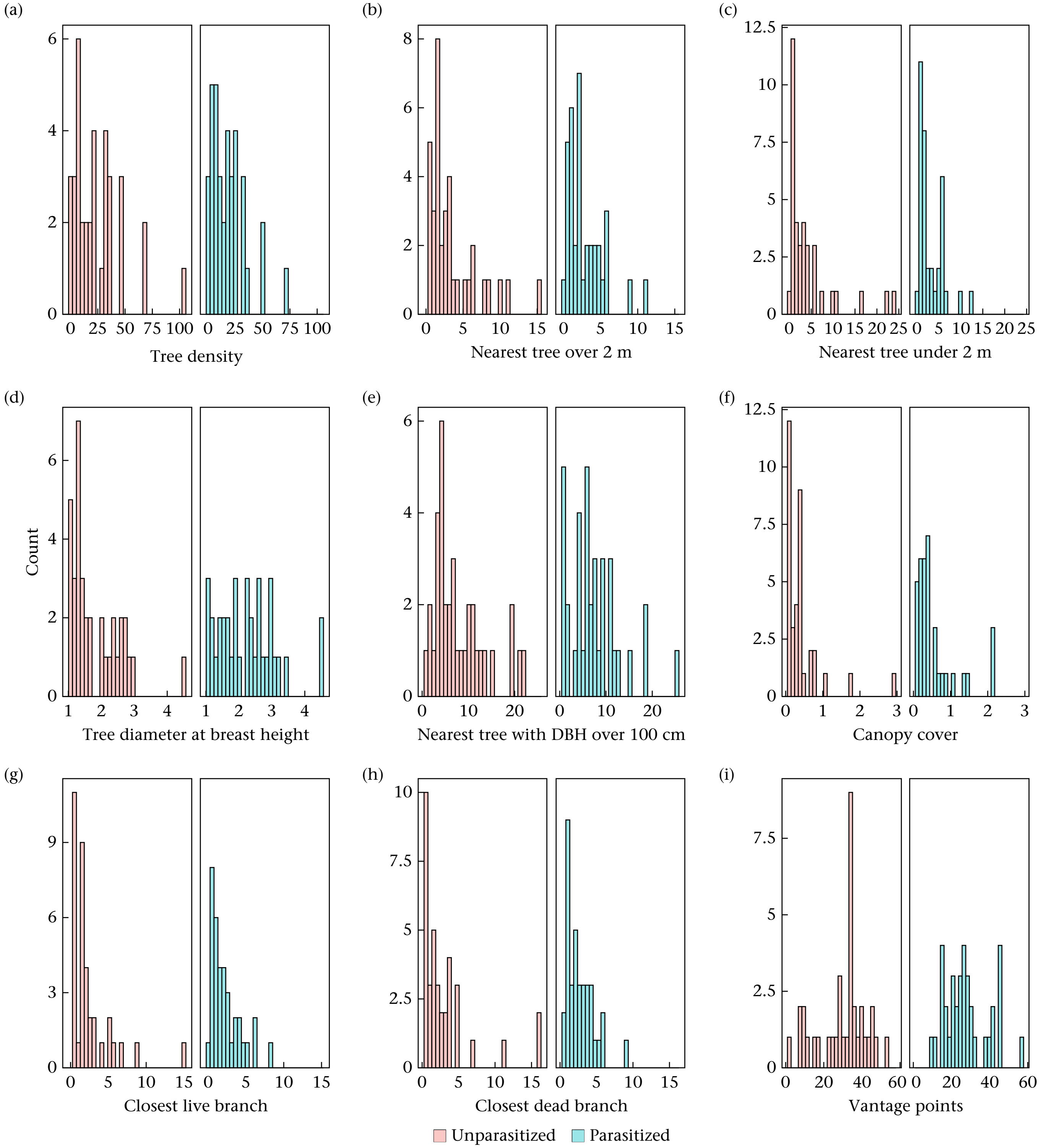

Figure 4. Frequency histograms of the vegetation features at nesting sites measured in this study. Outliers have been removed for this figure. The data are separated into parasitized and nonparasitized nests. (a) Tree density, (b) nearest tree over 2 m, (c) nearest tree under 2 m, (d) tree diameter at breast height (DBH), (e) nearest tree with DBH over 100 cm, (f) canopy cover, (g) closest live branch, (h) closest dead branch and (i) vantage points.

in our study; high tree densities were associated with a reduced risk of parasitism, but the distance to the closest tree did not explain the parasitism risk.

An alternative explanation for our results is that higher TD reflects higher quality habitat, which may support a higher density of superb fairy-wrens. Fairy-wrens nesting at high densities are less prone to parasitism than fairy-wrens nesting at intermediate densities, probably owing to higher rates of detection and mobbing of cuckoos (Medina & Langmore, 2019). Alternatively, a high density of nests within a cuckoo's territory may lower the possibility of any given nest being parasitized. To distinguish between these possibilities, a radiotracking study to monitor cuckoo nest

Table 3
Model output from binomial regression model testing the effects of tree density (V_1), trees over 2 m (V_2) and trees under 2 m (V_3) on the response variable parasitism

Coefficients	Estimate ± SE	z	*P* (>|z|)
Intercept	1.730 ± 0.732	2.364	**0.018***
Tree density (TD)	−0.041 ± 0.019	−2.187	**0.029***
Nearest tree over 2 m (NT>2)	−0.160 ± 0.107	−1.499	0.134
Nearest tree under 2 m (NT<2)	−0.103 ± 0.073	−1.415	0.157

P values are indicative only. Significant *P* values are in bold.
$^*P < 0.05$.

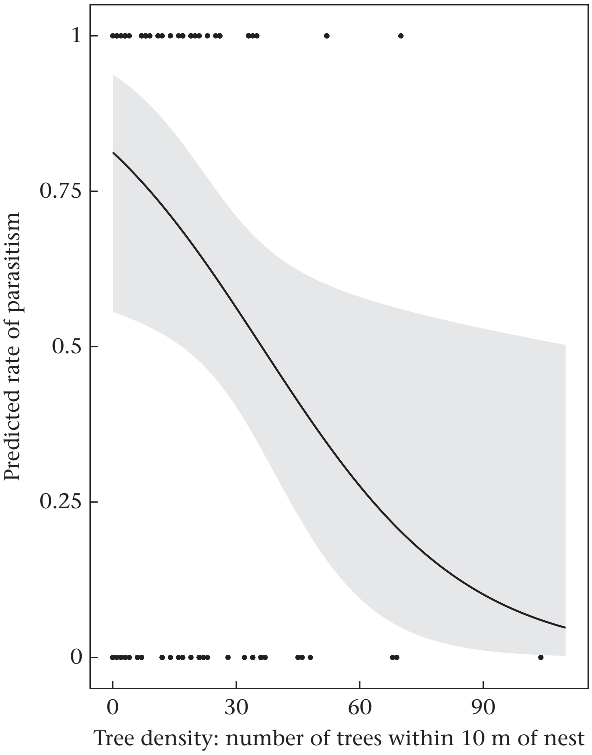

Figure 5. Predicted parasitism plot. The predicted risk of parasitism at varying tree densities (number of trees over 2 m, in a 10 m radius around the nest GPS point). The black solid line illustrates predictions of the final model for parasitism risk at varying tree densities (×) when holding ‘Distance to trees over 2 m’ and ‘Distance to trees under 2 m’ constant (in this example both = 1 m). A 95 % confidence interval is shown by the shaded grey area. The black points show the raw data for tree densities for each parasitized (top line, $y = 1$) and unparasitized (bottom line, $y = 0$) nest.

searching behaviour would be helpful. This would allow more direct quantification of perch proximity to parasitism risk.

To build a more comprehensive picture of how vegetation may influence cuckoo nest-finding methods, it would be beneficial to take measurements at the time of nesting. This would provide a more complete picture of which vegetation features may affect cuckoo nest-finding methods. In this study we were restricted in the vegetation features we could measure, as we could only collect data for features that were most likely or certainly present at the time of nesting. Although we are confident that the measurements we took reflect accurate traits of the nest sites that were present at the time of nesting, we were unable to include the ebb and flow of annual vegetation.

Although these results do not support the perch proximity hypothesis, they are consistent with the host activity hypothesis. If Horsfield's bronze-cuckoos find nests through host activity, higher TD might impede the cuckoo's ability to detect host movements, which may in turn reduce its ability to locate the nest. Future work should aim to test other hypotheses in this system. Additionally, it would be interesting to investigate whether Horsfield's bronze-cuckoos use the same nest-finding methods in different habitats and host species.

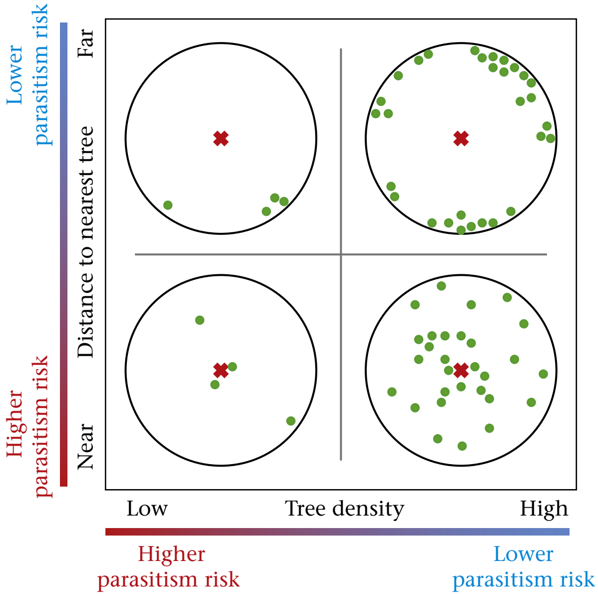

Figure 6. Example of types of environments associated with higher parasitism risk according to our data. The red crosses represent host nests, and the circle represents a 10 m radius around each nest. The green dots represent example of variables such as trees and shrubs. We found significant evidence that tree density affects parasitism, but not the distance to the nearest tree. Although trees over and under 2 m must be included in the model to determine the effect of tree density, they were not significant factors for parasitism risk.

Author Contributions

Cassandra J. Taylor: Formal analysis, Investigation, Methodology, Project administration, Resources, Writing – original draft, Writing – review & editing. **Claire J. Taylor:** Data curation, Writing – review & editing. **Naomi E. Langmore:** Conceptualization, Data curation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing. **Timothée Bonnet:** Formal analysis, Methodology, Supervision, Writing – review & editing.

Data Availability

The data set and code used to analyse the data are available in the Supplementary Material.

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2024.10.019.

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