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Nest-site selection and reproductive success of a critically endangered parrot, the Great Green Macaw (*Ara ambiguus*), in an anthropogenic landscape

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Nest-site selection is the principal way in which secondary cavity-nesting species mitigate the negative effects of factors such as predation, parasitism and exposure on reproductive success. Large-bodied secondary cavity-nesting birds rely on large cavities in mature trees that are often absent or reduced in anthropogenically disturbed forests. Hence, the availability of high-quality nest-sites may be limited for these species, potentially reducing reproductive success. The aim of this study was to investigate nest-site selection and the effect of nest-site features on reproductive success in the critically endangered Great Green Macaw *Ara ambiguus* in northern Costa Rica. We show that Great Green Macaws select nest-sites according to the characteristics of the cavity and the tree in which they are located. Moreover, reproductive success is a function of certain cavity features. However, the availability of high-quality cavities, those with features associated with higher reproductive success, is potentially limited. By studying nest-site selection and productivity together, we have identified that the availability of high-quality cavities could potentially limit the future recovery of the critically endangered Great Green Macaw.

Keywords: endangered species, limitation, nest-site availability, nest-site quality, reproduction.

Globally, there are 1307 secondary cavity-nesting bird species, of which 13% are threatened with extinction (van der Hoek *et al*. 2017). These species rely on cavities created by decay and other species to nest in. Large-bodied secondary cavity nesters are particularly reliant on mature trees that contain cavities of sufficient size (Marsden & Jones 1997, de la Parra-Martínez *et al*. 2015, Renton *et al*. 2015). However, the availability of large trees and cavities is often limited, especially in degraded and regenerating forests (DeWalt *et al*. 2003), potentially reducing reproductive success and affecting population dynamics. Understanding whether and how a population is limited by nest-site availability or other processes is essential information when designing a conservation strategy.

Nest-site limitation is influenced by three factors: quantity, quality and location (Newton 1998). However, the productivity of cavity-nesting birds – the number of new individuals recruited into a population – may be impacted more by the quantity of available cavities than by their quality (Lõhmus & Remm 2005). Many cavities are unoccupied in mature, semi-natural forests (e.g. Edington & Edington 1972, Carlson *et al*. 1998, Wesołowski 2007), yet cavity-nesting species often exhibit higher reproductive success in nestboxes than in cavities (Nilsson 1984, Jones *et al*. 1995, Brazill-Boast *et al*. 2013), suggesting that natural cavities may not always have optimal characteristics. Research also shows that the reproductive output of a nest-site is often associated with nest-site characteristics, such as orientation (Goodenough *et al*. 2008), nest height

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(Rottenborn 2000) and canopy connectivity (Britt *et al.* 2014). This indicates that the reproductive success of secondary cavity-nesting species may be limited by the availability of high-quality nest-sites in degraded forests, Stojanovic *et al.* 2021). Therefore, it is vital to understand nest-site selection and reproductive success to determine what makes a high-quality nest.

Multiple factors can affect an individual's reproductive success, for example, individual age (Forslund & Pärt 1995, Mauck *et al.* 2004) and food availability (Siikamäki 1998, Grames *et al.* 2023); these factors are completely outside an individual's control. However, the effect of other external factors such as weather (Stokes & Boersma 1998, McDonald *et al.* 2004, Coppes *et al.* 2021) and predation (Zhu *et al.* 2012, Stojanovic *et al.* 2014) can be mitigated through nest-site selection. Nest-site selection is particularly important for cavity-nesting birds, which rely on cavity characteristics to mitigate the risk of threats such as predation. Therefore, we might expect high-quality nest-sites, those that produce the most offspring, to share certain characteristics.

Parrots are one of the most endangered bird families, with 28% of species threatened with extinction globally (IUCN 2020), and most are secondary cavity nesters (Forshaw 2010, Parr & Juniper 2010). They are found throughout the tropics and subtropics (Forshaw 2010, Parr & Juniper 2010), where their major threats are poaching and habitat loss (Wright *et al.* 2001, Stojanovic *et al.* 2016, Berkunsky *et al.* 2017, Vergara-Tabares *et al.* 2020). For many parrot species, predation accounts for a significant proportion of nest failure (Renton & Salinas-Melgoza 2004, Pizo *et al.* 2008, Berkunsky *et al.* 2016), so we expect productivity to be correlated with physical nest-site characteristics that mitigate predation risk (Cockle *et al.* 2015). Parrots often select cavities that are deeper, higher above the canopy or larger than unused cavities (Saunders *et al.* 1982, Webb *et al.* 2012, Olah *et al.* 2014, de la Parra-Martínez *et al.* 2015, De Labra-Hernández & Renton 2016, Stojanovic *et al.* 2017, 2021). These characteristics have been shown to have a significant positive influence on productivity in the Papuan Eclectus *Eclectus polychloros* (Heinsohn 2008) and Scarlet Macaw *Ara macao* (Olah *et al.* 2014). This may be because deep cavities offer greater protection against predators (Zhu *et al.* 2012) and parasites (Tomás *et al.* 2020), or higher cavities have a better field of vision to detect predators (White *et al.* 2006). It follows that breeding at low-quality sites is often associated with lower reproductive success (Rendell & Robertson 1989, Stokes & Boersma 1998, Safran 2006, Carrete *et al.* 2006). Hence, we hypothesize that reproductive success might be limited in degraded ecosystems if constrained nest-site selection causes parrots to nest in low-quality cavities.

We investigated whether a link between nest-site selection and productivity exists in the critically endangered Great Green Macaw *Ara ambiguus* (BirdLife International 2020). The Great Green Macaw is a large neotropical parrot whose range extends from the Caribbean lowland forest in Honduras to Colombia and the Pacific coast of Panama to the dry forest in western Ecuador (Forshaw 2010, Parr & Juniper 2010). In Costa Rica, evidence suggests that their steep decline was the result of habitat loss; 90% loss of a critical nesting and food tree species, the Mountain Almond *Dipteryx oleifera* (Powell *et al.* 1999), and a 30% reduction in forest cover to ~50% by the year 2000 (Calvo-Alvarado *et al.* 2009). In this context, we aimed to (1) determine which cavity features Great Green Macaws use to select a nest-site, (2) discover which cavity features are associated with reproductive output and (3) quantify the availability of high-quality cavities.

METHODS

Study site

The study area is a c.1000-km^2 fragmented Caribbean lowland forest region situated in northern Costa Rica within the San Juan La Selva biological corridor (Fig. 1). Land use is split between cattle pasture, pineapple and other annual crops, and primary and secondary forests (Fagan *et al.* 2013, Jadin *et al.* 2016). Annual rainfall is c.4667 mm (2009–2014), with a slightly drier period between January and April (Gilman *et al.* 2016), which corresponds to the breeding season of the Great Green Macaw (Monge *et al.* 2003, 2012).

Cavity surveys

The locations of nest-cavities come from a database of Great Green Macaw nest-sites collated by Centro Cientifico Tropical (CCT 1995–2020) and Macaw Recovery Network (2017–2020). Nest cavities were entered into the database if they had a

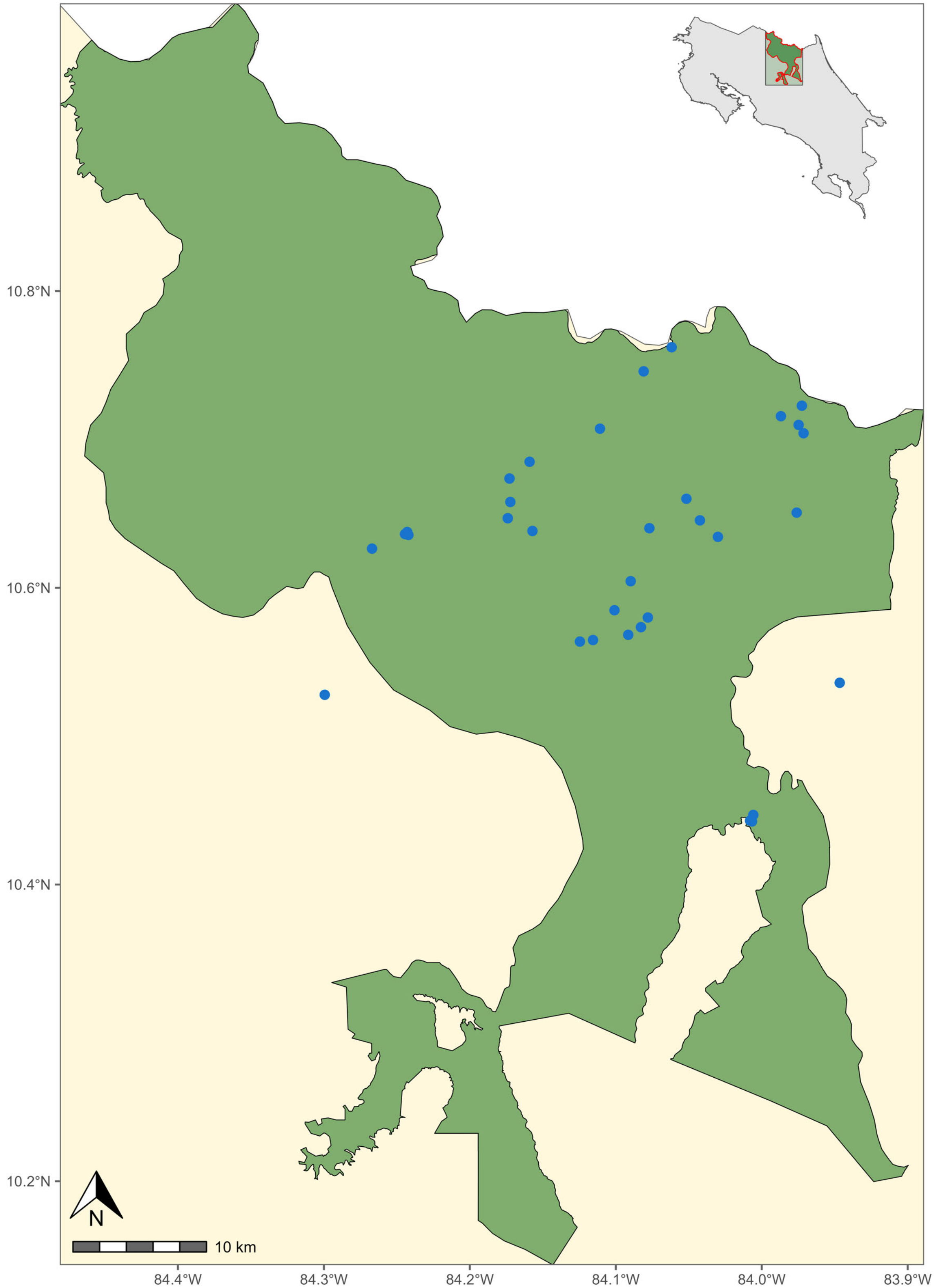

Figure 1. Study site map. Study site in the Caribbean lowlands within the San Juan La Selva (SJLS) biological corridor in northern Costa Rica, with nest-cavities (blue) marked. There were two monitored nests outside the SJLS biological corridor.

confirmed Great Green Macaw or Scarlet Macaw breeding attempt. We used this combined database to identify active nests (i.e. active in 2020) as potential 'focal nests' for the drone surveys. This involved identifying active nests from the previous year (2019) and monitoring these to determine if they were active in 2020. If a nest-cavity had previously been used by a Great Green Macaw but was occupied by a Scarlet Macaw in 2020, we included these in our study as focal nests, but we did not monitor the reproductive output of Scarlet Macaw breeding attempts. Around each active nest-cavity in the 2020 breeding season between December 2019 and May 2020, we surveyed a 500-m radius with a Mavic Pro Zoom drone to search for visible cavities. The drone was flown in transects 100 m apart and it searched for emergent trees. We focused on emergent trees because other studies have found that macaws select these types of trees in tropical forests (Renton & Brightsmith 2009), probably due to difficulties accessing cavities within a closed-canopy forest. We defined an emergent tree as one whose crown was entirely above the surrounding canopy. Once located, it was circled to attempt to detect any cavities; if we found a cavity, a picture was taken directly above the tree. The geo-location on the image was then entered into the GPS so the climbing team could navigate back to the tree on the ground; they then climbed the geo-tagged tree to measure all its cavities. We also recorded whether cavities were used by other interspecific competitors to help determine whether there is competition for cavities.

Cavity features

We took cavity measurements to calculate the entrance area, internal diameter and cavity depth. Because the internal shape of a cavity is not always circular, our measurement of internal diameter can be seen as a relative index of cavity diameter. Also, as cavity entrances are not commonly circular, we treated each entrance as five separate shapes to get the most accurate approximation of the area (see Supporting Online Information Fig. S1 and Equation S1). Cavity depth from the lip is the distance from the bottom lip of the cavity entrance to the cavity floor. Internal diameter was used instead of measuring the cavity floor because, in many cases, measuring this directly was impossible as the cavities were too deep. We also recorded the cardinal direction of the entrance.

The tree-level features measured were species identity, cavity height from the ground (metres), tree diameter at breast height (metres), which was obtained by dividing tree circumference by π, canopy connectivity (%) and vertical distance to the canopy to the nearest 5 m. We estimated the mean canopy height within a 50-m radius of each cavity using the dataset provided by Lang *et al.* (2022). This global dataset of mean canopy height at 10-m resolution was created using deep learning trained with GEDI and Sentinel-2 satellite data. We also estimated tree cover within 50 m using the dataset developed by Karra *et al.* (2021); this is a global dataset of landcover/land use created using deep-learning and Sentinel-2 data and trained on 5 billion human-labelled pixels (Fig. S3).

Reproduction

We monitored 40 known nest-sites during the 2020 breeding season (December 2019 to June 2020). However, we only monitored reproductive success at 33 active nest-sites; the rest were inactive. Reproductive success was measured as the number of chicks fledged per breeding attempt, estimated as the number of fully feathered chicks last seen in the nest before identifying an empty nest. We defined a breeding attempt as a clutch of eggs reaching a conclusion, either success or failure. Where possible, we recorded any evidence of the cause of a breeding attempt failure. We also used data collected over previous breeding seasons to help us understand common causes of failure. Potential causes were avian predation, aboreal animal predation and unknown.

Imputation

We could not acquire complete measurements for every cavity because of cavities being challenging to access or human error where measurements were missed in the field. We imputed these missing data to maximize the power of our statistical analyses. We used multivariate imputation by chained equations (mice package); this is a more robust way to deal with incomplete data sets compared with single imputation or data deletion approaches (Penone *et al.* 2014, Taugourdeau *et al.* 2014, Cooke *et al.* 2019). We used the mice package to generate our imputed values (van Buuren & Groothuis-Oudshoorn 2011). We used a random forest imputation method, with all numerical variables to impute missing values. Finally, we imputed 100 datasets to capture the uncertainty in the imputation process.

Statistical analysis

Cavity feature selection

To determine whether Great Green Macaws select cavity features, we fit a pair of intercept-only Bayesian regression models using the default flat prior. For each feature i to model the distribution of its values in occupied (x^{o}_{ij}) and unoccupied (x^{u}_{ij}) cavities:

$$x^{o}_{ij} \sim Norm\left(\mu^{o}_{i},\ \sigma^{o}_{i}\right) \tag{1}$$

$$x^{u}_{ij} \sim Norm\left(\mu^{u}_{i},\ \sigma^{u}_{i}\right) \tag{2}$$

where μ_i and σ_i are the mean and standard deviation of their distributions. We used the posterior distribution of the means and standard deviations to summarize their uncertainty and evaluate whether Great Green Macaws are selective for a cavity feature. We compare features of occupied and unoccupied cavities by calculating the posterior distribution of the difference in their means and standard deviations:

$$\mu^{o}_{i} - \mu^{u}_{i} \tag{3}$$

$$\sigma^{o}_{i} - \sigma^{u}_{i} \tag{4}$$

If the 95% credibility intervals of the differences did not cross zero, we treated the feature as selected for. By evaluating both standard deviation and mean, we can approach selection in different ways. The difference in the means and their distributions tells us whether they are actively selecting these features. We expect that the direction of the difference between means will vary depending on the cavity feature; for example, the difference would be positive if larger entrance holes were preferred compared to what is available. Standard deviation measures the specificity of selection of a feature. For this, we would expect strongly selected features to have a negative difference in standard deviation because occupied cavities would have a smaller standard deviation than unoccupied ones.

Nest suitability

To evaluate the suitability of each occupied cavity, we calculated the cavity suitability scores for each feature (s_{ij}), which differs among the occupied and unoccupied cavities:

$$s_{ij} = \frac{x^{o}_{ij} - \mu^{o}_{i}}{\sigma^{j}_{i}} \tag{5}$$

This gives the standardized score (s^{j}_{i}) for feature i associated with cavity j; the further away from the mean or suitable value, the lower the score will be. Therefore, less suitable cavities have lower scores. We combined these standardized scores into the nest suitability score by taking the mean of the selected features.

We carried out an ordinal regression with a logit link and a flexible threshold with the standardized score (s^{j}_{i}) for each feature and the combined nest suitability score as the individual predictor variables and reproductive output as the response variable. We then compared the performance of each model using the Widely Applicable Information Criterion (Watanabe 2010). We then used the top-performing model to estimate how many cavities not used by Great Green Macaws are within the nest suitability score range and, therefore, suitable for Great Green Macaw use. Finally, we determined how many high-quality cavities were available; we defined high-quality cavities as those with predicted productivity higher than the mean reproductive success.

We used the brms package to run all of our Bayesian models; this permitted the pooling of results across imputed datasets and the examination of posterior distributions (Bürkner 2017, 2018, 2021), which is crucial to our analysis. We carried out all analyses in R (R Core Team 2021).

RESULTS

We monitored 35 breeding attempts in 33 nest-cavities during the 2020 breeding season. A total of 47 Great Green Macaws fledged from these 35 breeding attempts, a mean of 1.34 (n = 35) fledglings per breeding attempt. Most trees held only one nest; however, two trees included in this study contained multiple (two and three) active nests. The tree that contained three nests fledged a total of seven chicks. Two trees not included in the study, because they were too dangerous to climb, also contained two active Great Green Macaw nests. We also found one nest tree that contained an active Great Green Macaw nest and an active Scarlet Macaw nest.

Nine nests failed at the first breeding attempt; birds at five of these nests did not re-lay. The maximum number of chicks fledged was three ($n = 1$). During the 2020 breeding season, we were able to attribute five failures to predation, one at the egg stage and four at the chick stage. Four of the failures at the chick stage were attributed to avian predators. During the 2019 breeding season, there were three confirmed predation events. One was attributed to avian predators; this nest was also predated in 2020. The other two were attributed to mammalian predators, as detached wings were found on the ground near the nests. Interestingly, the two nests that were apparently predated by arboreal predators have not been used again, that is, three breeding seasons later.

We measured a total of 192 cavities; 95 were found using a drone, 66 were from an existing CCT database and 51 were found incidentally by the field team of the Macaw Recovery Network. We found an additional 83 trees in the drone survey but did not include them in the study because of aggressive bees ($n = 2$), no cavities being found in the marked tree ($n = 2$) and fieldwork being cut short by the global coronavirus disease 2019 pandemic ($n = 79$). We excluded 22 cavities that were in entirely hollow trees. There was an average of 2.65 cavities per tree ($n = 192$). We found six species of trees with cavities; five were used as nest trees (Fig. S3). Most located cavities were in Mountain Almonds (88.5%; $n = 185$), as were the majority of nests (84.6%; $n = 33$; Fig. S3). These results indicate that Great Green Macaws use Mountain Almonds because this species is the most abundant source of cavities rather than actively preferring the species. Of the 192 cavities measured, we found interspecific competitors in 19; the most common were Scarlet Macaw ($n = 9$) and Red-lored Amazon *Amazona autumnalis* ($n = 5$; Table 1). Using Fichtler *et al.* (2003) we estimated the ages of all occupied nest trees (range 274–565 years old, mean 395 years; $n = 33$).

Cavity feature selection

We imputed 104 data points, which was 9% of our dataset ($n = 1160$). The difference in the posterior distributions of the mean cavity features in occupied and unoccupied cavities suggests that Great Green Macaws select certain nest-site characteristics. Mean differences between the types of cavities can either be positive or negative; those that are negative show that Great Green Macaws are selecting for features that are lower. For example, entrance height (mean − 0.69, 95% CI −1.06 to −0.33) was negative, suggesting that Great Green Macaws select cavities with lower entrances. However, cavity depth (mean 0.39, 95% CI 0.034–0.749), internal circumference (mean 1.14, 95% CI 0.83–1.46) and entrance area (mean 0.56, 95% CI 0.23–0.90) were all positive, suggesting that Great Green Macaw select for deeper, larger diameter and larger entranced cavities. At the tree level, all characteristics were lower around occupied than unoccupied cavities; they used canopy connectivity (mean − 0.54, 95% CI −0.93 to −0.19) when selecting nest-cavities, as well as canopy height (mean − 0.45, 95% CI −0.83 to −0.07) and tree cover (mean − 0.46, 95% CI −0.87 to −0.04) at the local area level (Fig. 2a,c). The difference in posterior distributions of the standard deviation shows that Great Green Macaws have a narrower preference for cavity entrance area (mean − 0.37, 95% CI −0.61 to −0.19), depth (mean − 0.28, 95% CI −0.53 to −0.01) and canopy connectivity (mean − 0.79, 95% CI −1.13 to −0.49) (Fig. 2b, d). A summary of the raw cavity measurements for occupied and unoccupied cavities can be found in Table S1.

Table 1. Nest suitability and cavity depth model predictions for all cavities.

		Predicted mean productivity	
Species	Number of cavities	Cavity depth	Nest Suitability Score
Red-lored Amazon	5	1.39	0.97
Great Green Macaw	37	1.40	1.26
Scarlet Macaw	9	1.10	0.97
Other interspecific competitors	5	1.55	1.43
Unoccupied	91	1.05	0.89

The two most numerous interspecific competitors, Scarlet Macaw and Red-lored Amazon, use cavities that have a predicted mean productivity that is lower than the Great Green Macaw, for cavity depth and nest suitability score. This suggests that on average these two species occupy cavities that are less suitable for Great Green Macaws.

Nest suitability

Cavity depth (1.05, 95% CI 0.20–1.99) was the only feature that was significantly positively

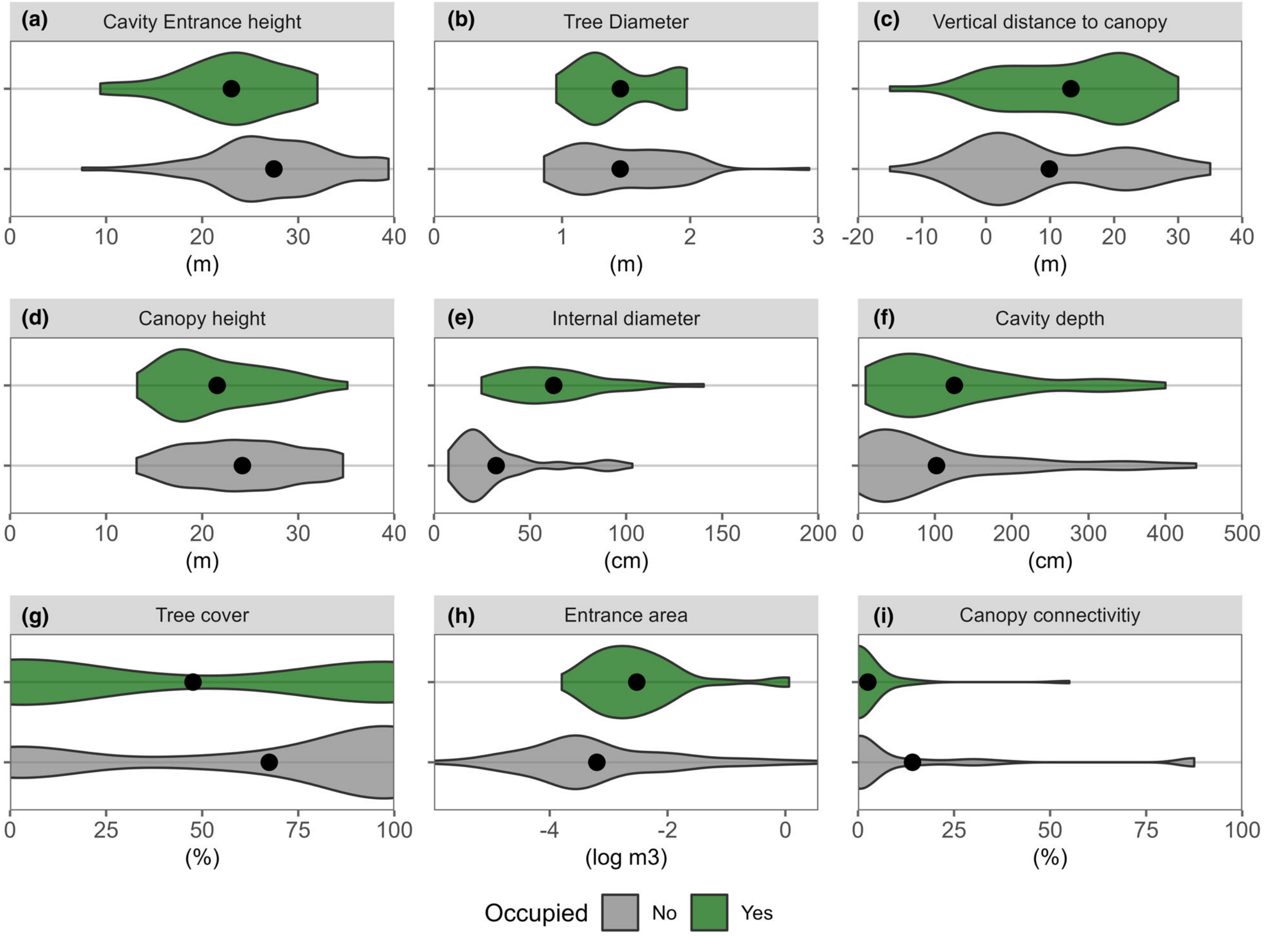

Figure 2. Cavity feature measurements ((a) cavity entrance height (m), (b) tree diameter (m), (c) vertical distance to canopy (m), (d) canopy height (m), (e) internal diameter (cm), (f) cavity depth (cm), (g) tree cover (%), (h) entrance area (cm2), (i) canopy connectivity (%)), after imputation, of occupied (*n* = 37) and unoccupied (*n* = 79) cavities, black dots show the mean for each feature and occupied status.

correlated with the number of fledglings per breeding attempt (Fig. 3). Our combined metric nest suitability score (2.20, 95% CI 0.33–4.34) was significantly positively correlated with the number of fledglings per breeding attempt.

The number of high-quality cavities available for Great Green Macaws to use varies depending on which metric is used to determine the quality. When we restricted the unoccupied cavities to within the range of scores used by Great Green Macaws, there were 39 high-quality available cavities when using cavity depth, although eight were used by competitors (Fig. 4). The number of high-quality cavities was much lower when using the nest suitability score, with only 17 cavities available; two were used by competitors (Fig. 5).

DISCUSSION

The Great Green Macaws in our study population prefer larger, deeper cavities in isolated trees, showing a strong selection for larger cavity entrance area, greater depth and low canopy connectivity. We have shown that high-quality nest-sites, those that produce more fledglings, are those that are deep. Our combined nest suitability score is also a good metric of nest quality, suggesting that although not significant on their own, other cavity features also contribute to reproductive success. This agrees with numerous other studies that found that parrots select for cavity depth (Saunders *et al.* 1982, Webb *et al.* 2012, Olah *et al.* 2014, de la Parra-Martínez *et al.* 2015, Renton *et al.* 2015, De Labra-Hernández &

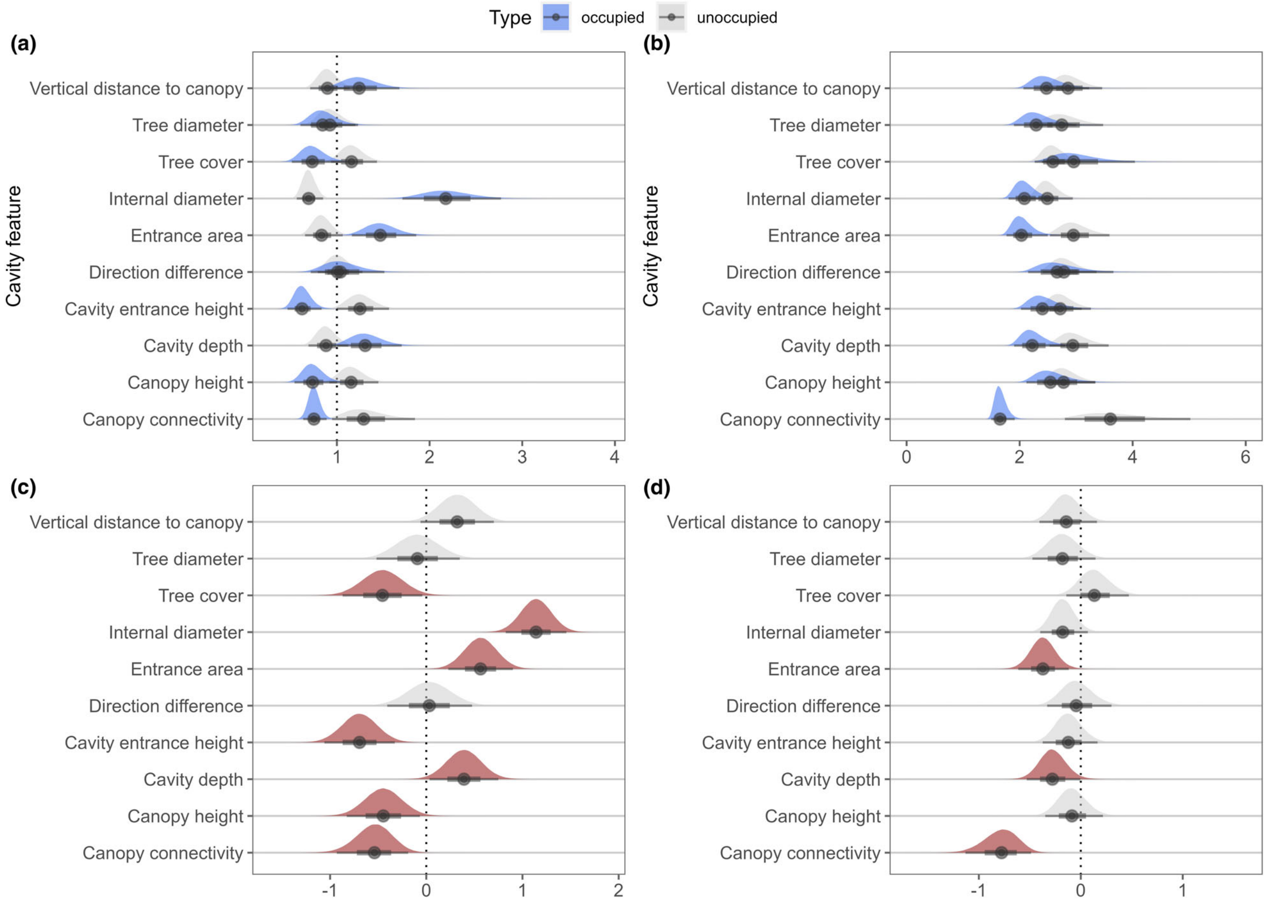

Figure 3. Univariate model outputs for cavity characteristics. Univariate model (a) means and posterior distributions and (b) variance and posterior distributions for occupied and unoccupied cavities. With the difference in (c) means and posterior distributions and (d) standard deviations and posterior distributions for each cavity feature with significant features, those with 95% credibility intervals not crossing zero are highlighted in red.

Renton 2016, Stojanovic *et al.* 2017, 2021) or tree isolation (Olah *et al.* 2014, Renton *et al.* 2015). We know that predation accounts for a significant proportion of nest failure in many parrot species (Pizo *et al.* 2008, Renton *et al.* 2015, Berkunsky *et al.* 2016); therefore, the selection of these specific features is probably driven by the need to reduce predation risk. By selecting isolated trees, parrots can passively reduce predation risk from non-volant predators (Britt *et al.* 2014, de la Parra-Martínez *et al.* 2015, Berkunsky *et al.* 2016), whereas deeper cavities reduce the risk from avian predators (Wesolowski 2002, Zhu *et al.* 2012, de la Parra-Martínez *et al.* 2015, Mejías *et al.* 2017).

For secondary cavity-nesting species, cavity location and morphology are the only way to reduce predation risk passively. Therefore, the relationship between cavity and tree characteristics and productivity can indicate which type of predators are the current primary threat to Great Green Macaw nesting success. Although it simplifies the suite of factors such as habitat quality (Dhondt 2010, Jones *et al.* 2014) and climatic conditions (McGillivray 1981, Borgman & Wolf 2016) that influence productivity, it is a valuable process because it might highlight potential information for conservation managers. Birds can attempt to reduce the risk from avian predators by selecting deeper cavities (Wesolowski 2002, Zhu *et al.* 2012). Therefore, if avian predation was the primary cause of nest failure, we might expect to see a relationship between cavity depth, as birds are more likely to predate shallow nests (Mejías *et al.* 2017). Alternatively,

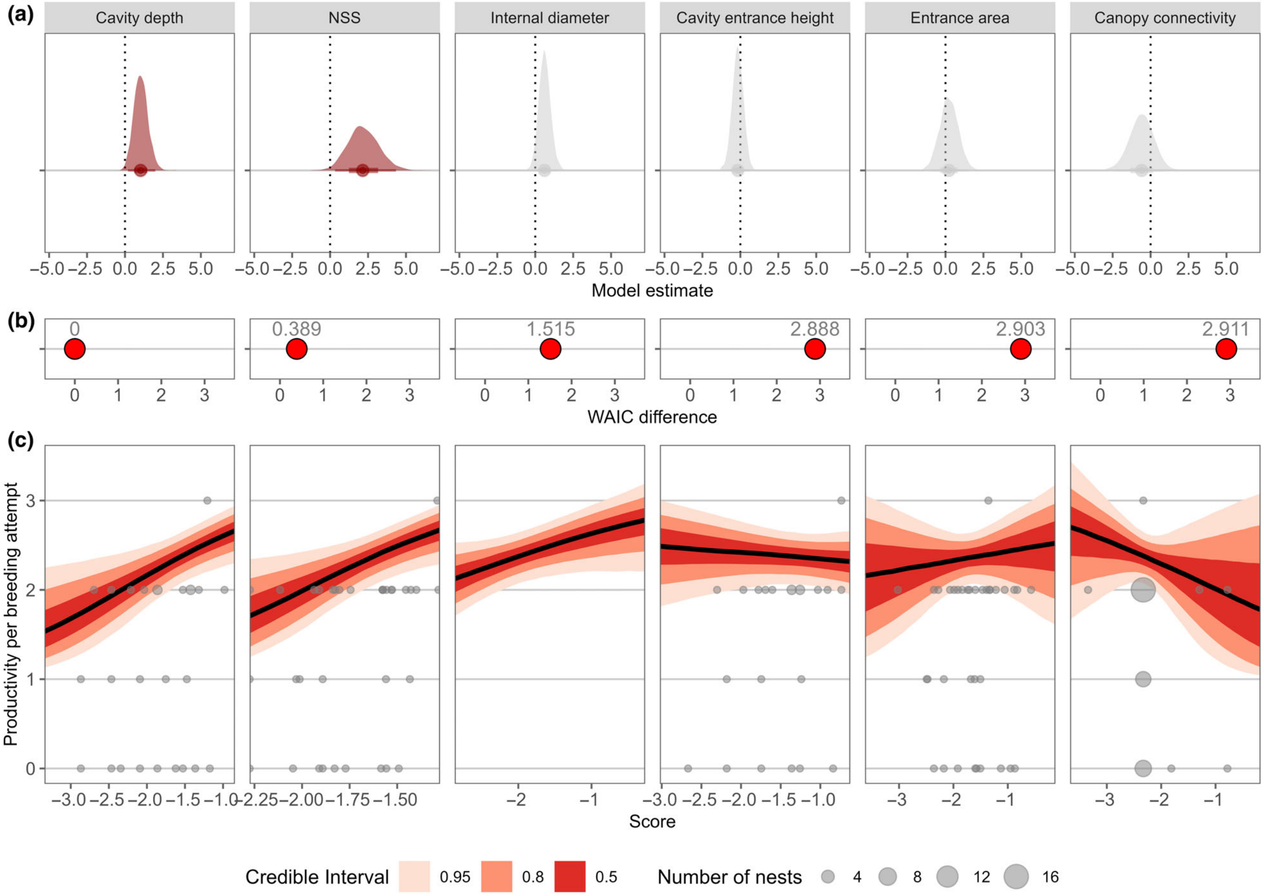

Figure 4. The relationship between productivity and cavity features. (a) Model estimates of the regression slopes and their posterior distributions from the univariate ordinal regression of each cavity feature, with the significant models in red. (b) Difference in the Widely Applicable Information Criterion (WAIC) scores compared with the best-performing model. (c) The relationship between each feature and predicted productivity alongside the data (grey).

individuals passively reduce accessibility to non-volant predators such as snakes and arboreal mammals by selecting isolated trees because they need access to cavities via connected canopy or vines (Koenig 2001, Britt *et al.* 2014, Berkunsky *et al.* 2016). Therefore, if non-volant predators are the primary source of nest predation, we expect to see a relationship between canopy connectivity and productivity. We have found a significant positive relationship between productivity and cavity depth, suggesting that avian predation is one of the primary drivers of nest failure. Indeed, we have evidence of this in our study population, where five of seven confirmed predation events from our study area were probably the result of avian predators. However, further research is needed to confirm this relationship between cavity characteristics and predation.

Great Green Macaws are apparently unique in their selection of cavities with entrance heights lower than surrounding cavities (Renton & Brightsmith 2009, de la Parra-Martínez *et al.* 2015). This may be an adaptation to fragmentation and degradation of habitat in this area of Costa Rica (Chassot *et al.* 2007, Grantham *et al.* 2020, Karra *et al.* 2021), where large cavities in large, emergent trees in the forest have probably been lost (DeWalt *et al.* 2003, Chassot *et al.* 2007). Cavity size is inversely related to height in the tree (Lindenmayer *et al.* 2000); therefore, low tree cover and canopy height could make large cavities lower down in trees accessible to Great Green Macaws. This might partially compensate for the loss of mature emergent trees in this region over the last 100 years (Sader & Joyce 1988). We monitored two active nests in 2020 that were 9.4 and 10.4 m

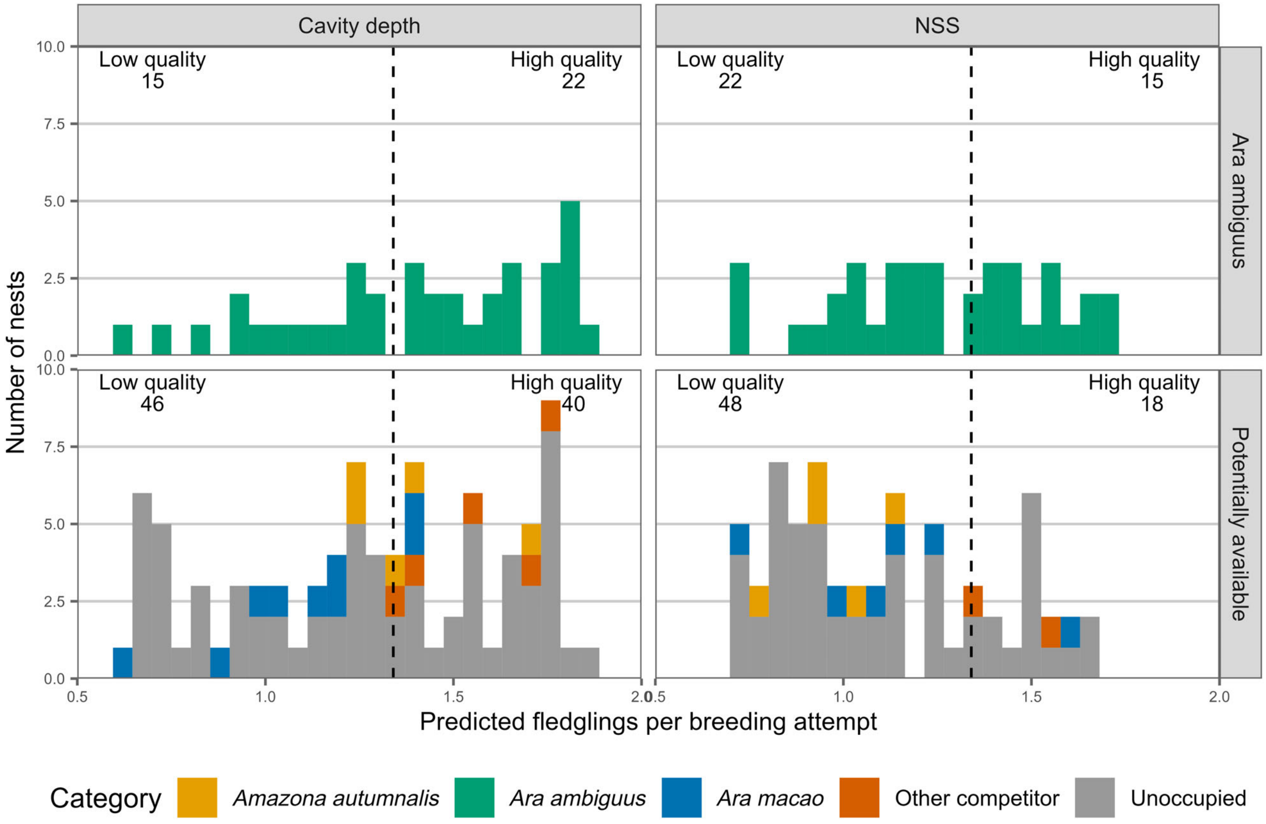

Figure 5. Comparison of occupied and unoccupied cavity features. Distribution of the predicted number of fledglings per breeding attempt from our univariate models. We restricted the unoccupied cavities to the range of the occupied cavities in both cases. The dashed line is the mean number of fledglings per breeding attempt from our monitoring data. The cavities to the right of the mean line are defined as high-quality and to the left as low-quality.

above the ground. The average canopy height across the San Juan La Selva biological corridor is 23.4 m (Lang *et al.* 2022), suggesting that if these trees were within the forest, they would not be accessible or suitable for Great Green Macaws.

We have shown that Great Green Macaws select for cavities that maximize reproductive success, which is not always the case, because other factors such as competition mean it is not possible (Zhu *et al.* 2012). Half of the cavities occupied by interspecific competitors were used by Scarlet Macaws (Table 1). However, cavities occupied by Scarlet Macaws were mostly considered low-quality cavities for the Great Green Macaws (Fig. 4). Research has shown that Scarlet Macaws have a broad nesting niche and compete directly with other large macaws for nesting cavities (Renton & Brightsmith 2009). Long-term data on known nest usage in Costa Rica suggest that only a small proportion of cavities are used by both Great Green Macaws and Scarlet Macaws (CCT unpubl. data). This suggests that Great Green Macaws are stronger competitors, meaning that there is either limited competition for cavities or Great Green Macaws are stronger competitors for cavities with their favoured characteristics. We have found evidence that high-quality cavities are in short supply (Fig. 4). Therefore, although Great Green Macaws may be stronger competitors, they are nesting in low-quality cavities, which is negatively impacting reproductive success.

Interestingly, we found multiple cases of trees holding more than one active Great Green Macaw nest. In addition, one tree contained both a Great Green Macaw and a Scarlet Macaw active nest, and others have also reported that Great Green Macaws and Scarlet Macaws in this region will occupy different nest-cavities in the same tree (Chassot *et al.* 2011, Jimenez *et al.* 2020). Gregarious nesting like this is not common in parrots, with only seven species of secondary cavity-nesting parrots, including Military Macaw *Ara militaris*, reported doing this (Rowley 1984, Forshaw 2010). We have found no other evidence in the literature of multispecies gregarious nesting in parrots in other regions. This could either mean that there is an abundance of cavities, so individuals are able to use cues from others to indirectly access the commodities (e.g. food and safety) necessary to breed and select cavities near successful nests (Danchin & Wagner 1997, Eberhard 2002). However, it could also suggest a lack of available cavities, forcing pairs to nest in close proximity. With the evidence from this study and the continuing extraction of large mature trees in this region (T.C. Lewis, pers. obs.), it is likely that there is a lack of high-quality nest-sites for Great Green Macaws.

Conservation implications

Cavity entrance height has often been found to be an important factor in nest-site selection for macaws, with species selecting for cavities higher than unused cavities (Olah *et al.* 2014, de la Parra-Martínez *et al.* 2015). However, we found that Great Green Macaws nest in cavities lower than unused cavities. This may be a result of the lack of forest around nest trees. Costa Rica reached a 17% forest cover low in the 1980s (Sader & Joyce 1988), and although logging continues in this region, large-scale deforestation no longer occurs (Fagan *et al.* 2013). In many areas, regenerating forest has replaced cattle pasture (Fagan *et al.* 2013, Jadin *et al.* 2016). However, as the forest continues to recover, there is a risk that cavities currently occupied by Great Green Macaws will become more connected to adjacent trees, increasing their accessibility for non-volant predators. This is a natural process that we have seen at a few nests in abandoned pastures; when the nests were first monitored 20 years ago, they were in isolated trees, and now they are within the canopy (U. Aleman, pers. comm.).

Trees around nest-sites could be managed to maintain limited connectivity with other trees and prevent access to the canopy for non-volant predators. However, installing artificial nestboxes may represent a better management option than preventing forest recovery around current nest trees. Before any nestbox programme is begun, we suggest experimenting with design features to counter predation, such as an entrance chamber like those used by the Mauritian Wildlife Foundation (Tatayah *et al.* 2007). There will obviously be a trade-off between practicality and design, but our results show that deep cavities are more productive, so deep nestboxes (up to 3.5 m deep, the deepest monitored active cavity) should be experimented with. As isolated trees are favoured by Great Green Macaws, we also recommend using trees whose canopy is not connected to the surrounding forest and that offer few opportunities for arboreal predators to climb to the nestbox. This is supported by evidence from Britt *et al.* (2014) who showed that canopy connectivity is a key factor determining nest success of Scarlet Macaws. The CCT carried out a small experiment with four nestboxes of one design between 2016 and 2020; one chick successfully fledged from a nestbox in 2020 (CCT unpubl. data). This demonstrates that wild Great Green Macaws will use nestboxes and suggests that further supplementation could be a viable management strategy.

Nestbox provision is a common conservation strategy to combat limited cavity availability in degraded habitats (Jones *et al.* 1995, Darling *et al.* 2004, Berthier *et al.* 2012, Tollington *et al.* 2013). For example, nestboxes have been successfully employed with another critically endangered macaw, the Blue-throated Macaw *Ara glaucogularis*, in Bolivia (Herzog *et al.* 2021). Research has shown that nestboxes can provide high-quality nest-sites, often producing larger clutches and fledging more offspring (Robertson & Hutto 2006, Brazill-Boast *et al.* 2013). A secondary benefit is that it would permit easier monitoring and active management of breeding attempts if necessary (Jones *et al.* 1995, Tollington *et al.* 2013). However, using nextboxes as a management tool does come with associated costs. It would have to be a long-term strategy to be able to mitigate the loss of cavities while others develop in maturing trees.

Mature Mountain Almond trees are a vital resource for the survival of Great Green Macaws. Evidence from this study suggests that Mountain Almonds need to be nearly 300 years old before their cavities can be used by Great Green Macaws. Furthermore, it is a species of conservation concern, with an alarming decline of approximately 90% observed in its Costa Rican populations (Chassot & Monge 2012). Additionally, the genetic diversity of these populations faces a significant challenge due to the limited gene flow between geographically disjunct groups, which could further impair their resilience (Chun 2008). The significance of the Mountain Almond tree has been internationally recognized, as evidenced by its inclusion in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2022).

Our study population of Great Green Macaw mainly nest in trees that are isolated or have low canopy connectivity. However, it is concerning that these isolated trees have a scarcity of seedlings or saplings (T.C. Lewis, pers. obs.). The primary factor contributing to this shortage can be attributed to cattle grazing in pasture lands, a practice found to have a significant negative impact on tree recruitment (de la Peña-Domene *et al.* 2013). As trees are not being recruited in these open areas the trees within the forest are therefore vital to the long-term survival of the Great Green Macaw. It is the availability of these mature trees and their cavities that will be instrumental in facilitating the recovery and potential growth of the Great Green Macaw population in the future.

Study limitations

We used a univariate approach due to the limited size of our dataset, because we did not have sufficient power to use multivariate approaches. The main limitation of this approach is that we are not capturing conditional effects. For example, our analysis suggests that Great Green Macaws select for cavities with lower entrances; however, our correlation analysis (Fig. S2) shows that this is strongly negatively correlated with entrance size and internal diameter. Future work with a larger dataset would enable the use of multivariate analysis, and could investigate these relationships further.

Secondly, we only used already known nests of the Great Green Macaw. These were not found using systematic methods and therefore there is observer bias in their selection. For example, nests in isolated trees in pasture are much easier to find than nests in forest. Therefore, our results cannot be used to generalize to Great Green Macaws in other habitats such as primary forest or other regions. Our study demonstrates that in degraded ecosystems Great Green Macaws will use low-quality nest-sites and that in these areas the availability of high-quality nest-sites is potentially limited.

CONCLUSIONS

Habitat loss and degradation have caused the loss of mature trees across the tropics, resulting in the loss of large cavities for large-bodied cavity nesters such as the Great Green Macaw (DeWalt *et al.* 2003, Degen *et al.* 2006, Cockle *et al.* 2010). As anthropogenic disturbance in tropical ecosystems grows, we need to understand how endangered species are affected and adapt to their new environment. Ecological traps can form if cues are used to select suitable nest-sites, and actual nest-site quality becomes uncoupled as the result of anthropogenic disturbance. This can lead to declines in productivity and subsequent population decline (e.g. Tozer *et al.* 2012, Zhu *et al.* 2012, Díaz & Kitzberger 2013). We found that reproductive success is associated with cavity features (Chassot *et al.* 2007, Grantham *et al.* 2020, Karra *et al.* 2021); however, the use of low-quality nest-sites suggests that high-quality nest-sites may be limiting reproductive output. It is unclear whether the reproductive success of 1.34 fledglings per breeding attempt is sufficient to maintain this population. More work studying the breeding biology of Great Green Macaw in less degraded regions will be important. By studying nest-site selection and productivity together, we have identified factors that could potentially limit the future recovery of the critically endangered Great Green Macaw. Finally, we suggest that nestbox provisioning could be a solution to the lack of high-quality nest-sites and the potential loss of nest-sites to forest regeneration in the future. This approach can be successful but does mean a long-term commitment to maintenance for conservationists.

AUTHOR CONTRIBUTIONS

Thomas C. Lewis: Conceptualization; methodology; data curation; formal analysis; investigation; visualization; project administration; resources; writing – review and editing; writing – original draft; software. **Ignacio Gutiérrez Vargas:** Investigation; data curation. **Claire Vredenbregt:** Investigation. **Mario Jimenez:** Investigation. **Ben Hatchwell:** Supervision; writing – review and editing; funding acquisition; validation. **Andrew P. Beckerman:** Funding acquisition; supervision; writing – review and editing; validation. **Dylan Z. Childs:** Conceptualization; methodology; supervision; funding acquisition; writing – review and

editing; writing – original draft; software; formal analysis; validation.

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CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest.

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ETHICAL NOTE

None.

Data Availability Statement

All data and code used in this paper can be found in Appendix S1.

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SUPPORTING INFORMATION

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

Figure S1. Cavity entrance diagram.

Figure S2. Visualization of a correlation matrix between all cavity features.

Figure S3. Species of trees that were occupied and unoccupied showing that there is no strong selection for any particular species.

Equation S1. Entrance area equation.

Table S1. Summary of all tree and cavity characteristics of occupied ($n = 37$) and unoccupied ($n = 79$) cavities.