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Research Paper

Nest box placement influences occupancy by Yellow-headed (*Amazona oratrix*) and White-fronted (*Amazona albifrons*) Parrots in the pine savannas of Belize

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ABSTRACT. Supplementation of nest boxes is a common practice to increase nesting opportunities for cavity nesters, such as psittacids (i.e., parrots), many of whom are species of conservation concern. However, understanding occupancy requirements of most psittacids remains an important challenge for effective conservation actions, including placement of nest boxes in the landscape. This study utilized logistic regression models to investigate factors that influence occupancy of nest boxes by two Amazon parrots in the lowland pine savannas of Belize. We performed combined and separate analyses of nest box occupancy by White-fronted (*Amazona albifrons*) and Yellow-headed Parrots (*Amazona oratrix*), in relation to understory cover, localized tree density, frontal visibility from the nest box entrance, tree height, tree canopy cover, nest box entrance orientation, and tree diameter at breast height. Overall, 60% of nest boxes were used by four species of Amazon parrots, with White-fronted and Yellow-headed Parrots accounting for majority of use; 27% and 28%, respectively. Tree height had a strong positive effect on nest box occupancy in the combined species analysis. Species-specific analysis revealed that Yellow-headed Parrots occupied nest boxes in taller trees, closer to previously successful nests, while White-fronted Parrots did not show strong preference for any measured characteristics. Our results demonstrate that these two species will utilize artificial nest boxes and specifically highlights the importance of selecting taller trees when installing nest boxes for use by Yellow-headed Parrots.

Le positionnement des nichoirs influence l'occupation par les perruches amazones à tête jaune (*Amazona oratrix*) et amazones à front blanc (*Amazona albifrons*) dans les savanes de pins du Belize

RÉSUMÉ. L'apport de nichoirs est une pratique courante pour augmenter les opportunités de nidification des espèces cavicoles, comme les psittacidés (tels que les perruches), dont un grand nombre sont menacées. Toutefois, il demeure difficile de comprendre les exigences de la plupart des psittacidés en termes d'occupation des nids afin de mettre en place des mesures de conservation efficaces, notamment en ce qui concerne le positionnement des nichoirs dans le paysage. Cette étude a utilisé des modèles de régression logistiques pour examiner les facteurs qui influencent l'occupation des nichoirs par deux perruches d'Amazonie dans les savanes de pins des plaines du Belize. Nous avons réalisé des analyses combinées et distinctes portant sur l'occupation des nichoirs par les perruches amazones à front blanc (*Amazona albifrons*) et amazones à tête jaune (*Amazona oratrix*), par rapport à l'épaisseur de la sous-végétation, la densité locale des arbres, la visibilité frontale de l'entrée du nichoir, la hauteur des arbres, l'orientation de l'entrée du nichoir et au diamètre des arbres à hauteur de poitrine. Globalement, 66 % des nichoirs étaient utilisés par quatre espèces de perruches d'Amazonie, les amazones à front blanc et les amazones à tête jaune représentant la majorité des occupants, avec 27 % et 28 % respectivement. L'analyse combinée des deux espèces révèle que la hauteur des arbres possède une forte influence positive sur l'occupation des nichoirs. L'analyse spécifique aux espèces a démontré que les perruches à tête jaune occupaient des nichoirs installés dans des arbres plus hauts, plus proches des nids antérieurs qui donnaient de bons résultats, tandis que les perruches à front blanc ne manifestaient pas d'influence marquée à l'égard d'une caractéristique mesurée. Nos résultats indiquent que ces deux espèces utiliseront les nichoirs artificiels et mettent particulièrement en évidence l'importance du choix d'arbres plus hauts pour installer des nichoirs destinés aux perruches à tête jaune.

Key Words: *Amazon parrots; cavity nesters; conservation; nest boxes; nest selection; White-fronted Parrot; Yellow-headed Parrot*

INTRODUCTION

The use of artificial nest boxes is an increasingly common conservation tool for cavity nesting birds in modified landscapes (Holt and Martin 1997, Cockle et al. 2008, 2010, Miller 2010, Norris et al. 2018). Recent research suggests that abundance and breeding density of secondary cavity nesters increase after nest boxes are added to the landscape (Cockle et al. 2010, Cuatianquiz Lima and Macías Garcia 2016). For example, the addition of nest boxes in an Argentinian logged subtropical forest led to an increase in breeding densities of White-throated (*Xiphocolaptes albicollis*) and Planalto Woodcreepers (*Dendrocolaptes platyrostris*; Cockle et al. 2010). Similarly, studies in Mexico and Switzerland have documented an increase in abundance of secondary cavity nesters following the addition of nest boxes (Berthier et al. 2012, Cuatianquiz Lima and Macías Garcia 2016). Despite frequent

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use of artificial nest boxes as a conservation tool, few studies have assessed if target species will readily occupy them and how occupancy of nest boxes is influenced by local nest tree and habitat characteristics.

Seventy-eight percent of Psittaciformes species are secondary cavity nesters, relying on available tree cavities (Renton et al. 2015). As a group, most parrots are medium to large secondary cavity nesters, which makes them of particular interest as they require nesting cavities that are both sufficiently large and maintain stable microclimates, but also reduce predation risk (Renton et al. 2015). Natural disturbances, human induced wildfires, and unsustainable logging practices can greatly reduce availability of nest sites for many species in the genus *Amazona* (Amazon parrots hereafter), highlighting the need for direct conservation actions to alleviate the destruction of nesting sites (Berkunsky and Reboreda 2009, Cockle et al. 2010). Studies that evaluate use and occupancy requirements of nest boxes by Amazon parrots are limited, with varying conclusions. Reported use of nest boxes by Red-spectacled (*Amazona pretrei*) and Yellow-shouldered Parrots (*Amazona barbadensis*) in Brazil and Venezuela was low (3 and 5% use, respectively) and neither species occupied boxes immediately after installation (Sanz et al. 2003, Kilpp et al. 2014). In contrast, most nesting activities of Puerto Rican Parrots (*Amazona vittata*) occur in artificial nests, but conservation practices and nest box experimentation with this species have been in place since the 1970s (Snyder et al. 1987, White et al. 2006).

Parrots are a highly endangered avian group; 28% of the species are classified as threatened or endangered worldwide, with much of this decline a result of habitat loss and poaching for the pet trade (Berkunsky et al. 2017, Birdlife International 2019). Given the potential importance of nest boxes for parrot conservation, some studies have assessed how occupation is influenced by nest box location and specific box characteristics. For example, successful occupation of nest boxes is linked with historical nesting occurrence and food availability, as has been observed for Swift Parrots (*Lathamus discolor*; Stojanovic et al. 2019), boxes with larger entrances and located in areas with varying degrees of disturbance affected use by native and exotic cavity nesters (Le Roux et al. 2016), and areas with higher nest site visibility were preferred by Puerto Rican Parrots (White et al. 2006). Similarly, selection of natural nests has been associated with cavity direction and with high-quality cavities located at greater height in larger trees and with larger entrances and depth (Heinsohn 2008, Cockle et al. 2011, Dias 2011, de la Parra-Martínez et al. 2015). Selection of larger trees with emergent crowns and no connecting canopy has been positively associated with nest survival of Scarlet Macaws (*Ara macao*) in Belize and Black-billed Parrots (*Amazona agilis*) in Jamaica as they limit access to the nest by non-volant predators (Koenig et al. 2007, Britt et al. 2014), and has been suggested to play a role in predator detection (White et al. 2006). Cavity orientation and large diameter nest trees have been found to be important for natural nests used by Northern Flickers (*Colaptes auratus*) and Yellow-faced Parrots (*Alipiopsitta xanthops*), potentially influencing the internal temperature of the nest cavity (Wiebe 2001, Dias 2011). Furthermore, nest success during the previous year and distance to nearby occupied nests influences nest site selection and reoccupation for natural and artificial cavities (White et al. 2006, Berkunsky and Reboreda 2009, Olah et al. 2014). For example, Scarlet Macaws in Peru were found to occupy cavities closer to active nests within a season and to reoccupy 85% of successful nest cavities in the next breeding season (Olah et al. 2014). Similarly, Turquoise-fronted Parrots (*Amazona aestiva*) were more likely to reuse a nest cavity if successful during the previous breeding season (Berkunsky and Reboreda 2009).

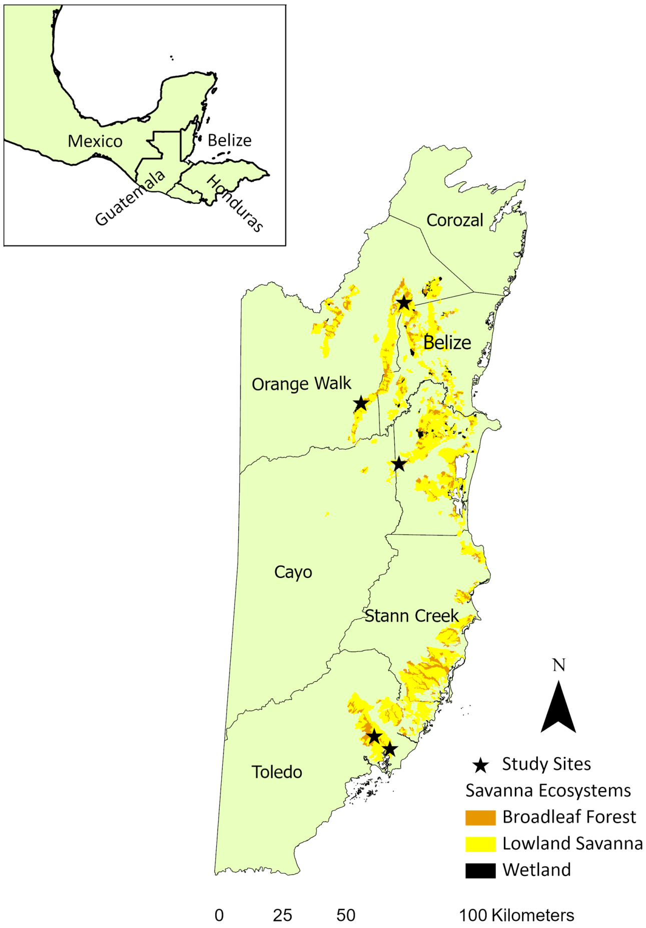
Here, we evaluated nest box use as a function of nest tree and habitat characteristics by supplementing boxes to parrots in areas with limited or no previous exposure to nest boxes prior to the initiation of this study. We examined nest box use by Yellow-headed (*Amazona oratrix*) and White-fronted Parrots (*Amazona albifrons*) in the lowland pine savannas of Belize, an ecosystem that has been historically impacted by hurricanes, logging, and fire. Given the high rate of predation experienced by nesting parrots in the Belizean savannas (Tarazona-Tubens et al. 2022), we hypothesized that parrots would select boxes with nest tree and habitat characteristics that facilitate detection of predators by nesting adults. Specifically, we predicted that nest box occupancy would be positively associated with increasing frontal visibility and tree height, but negatively associated with high tree density, canopy cover, and understory cover. These habitat characteristics are thought to influence nest predation and predator detectability (White et al. 2006, Britt et al. 2014, Jenkins et al. 2016), which may, in part, drive nest selection. Lastly, we predicted that parrots would select trees with larger diameter at breast height (DBH) and north-facing cavities as these could be associated with cooler internal temperatures.

METHODS

Study area

Research was conducted in lowland pine savanna habitat in Belize (Fig. 1). There were three study sites in the north separated by approximately 165 km from the study site in the south. All were selected based upon previous nest monitoring efforts at each site and include the following geographic coordinates and size: private farms adjacent to Crooked Tree Wildlife Sanctuary (17.7343º N, 88.5372º W, 1km²), Rio Bravo Conservation and Management Area (17.6889º N, 88.8070º W, 55.31km²), The Belize Zoo and Tropical Education Center (17.3589º N, 88.5562º W, 4.18km²), and Payne's Creek National Park (16.3301º N, 88.6022º W, 52.38km²). Mean elevation across sites was approximately 17 m above sea level (range: 9–40 m), while mean annual rainfall ranged from 1524 mm in the north, to 4064 mm in the south. All sites had marked transitions between the rainy (June to November) and dry (December to May) seasons with 62% of rainfall, on average, occurring in the rainy season (National Meteorological Service of Belize 2022). Mean temperature during the nesting season (February to July) ranged from 25.0–29.8 °C in the north, and 25.8–27.8 °C in the south. All sites were designated as private property or protected areas, but varied in terms of availability of resources allocated for active patrolling and site protection. As a result, intensity of human disturbance (e.g., illegal hunting, human caused fires, logging) varied among sites. We did not quantify the number of available cavities; however, we did know the number of active Yellow-headed Parrot nests at each site as part of a previous study (Tarazona-Tubens et al. 2022). Number of active nests varied across sites prior to nest box installation, suggesting that the number of available cavities likely varied across sites (F. Tarazona-Tubens, *unpublished data*).

Fig. 1. Map of Belize representing the districts in the country, habitat types within our study areas, and study sites where nest boxes were installed and monitored during the 2018 Amazon parrot breeding season.



All study sites had been historically logged, but intensity and time since logging activities varied among sites (Smith 2021). With the exception of the southern study area, nest boxes had not been previously installed at sites prior to the start of this study. Sites were primarily composed of lowland pine savannas surrounded by evergreen tropical forests, with small broadleaved forests occurring where riparian and wetland habitats exist. Dominant plants included Caribbean pine trees (*Pinus caribaea*) as the top canopy species, while the lower canopy contained species such as sandpaper tree (*Curatella americana*), palmetto (*Acoelorrhaphe wrightii*), oak (*Quercus oleoides*) and craboo (*Byrsonima crassifolia*). Understory plants consisted of various species of short grasses and forbs (Cameron et al. 2011). Plant species composition among sites was similar. However, within sites there was localized variation in the density of pines, particularly in the northern sites, which had higher pine density overall.

Focal parrot species

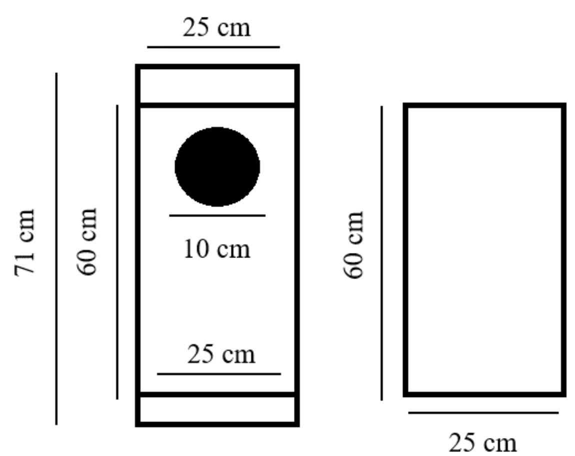
Given the threat of habitat loss and destruction in the pine savannas (Cameron et al. 2011), we focused on this habitat type and sought to add artificial nest boxes, using Yellow-headed Parrots as the target species. The Yellow-headed Parrot (length = 35 cm; Forshaw 1977) currently occurs in Mexico and Northern Central America and is currently classified as "Endangered" by the IUCN Red List and thought to be declining across its range (BirdLife International 2020). Population declines for this and other parrot species, are attributed to the pet trade and habitat loss, resulting in small, sometimes isolated populations (Lousada and Howell 1996, Monterrubio-Rico et al. 2010). We have been actively focusing on monitoring Yellow-headed Parrot nests in the Belizean pine savannas since 2016, which helped identify known nesting locations for the species, and also document other Amazon species nesting in the savannas. Yellow-headed Parrots had been known to nest at all study sites prior to the addition of nest boxes, with most nesting occurring within Rio Bravo Conservation and Management Area and Payne's Creek National Park. Number of Yellow-headed Parrot nests in Crooked Tree Wildlife Sanctuary was never greater than four nests during 2016–2017 nesting seasons, and the first nest at The Belize Zoo was documented during the 2017 season. Another similarly sized Amazon parrot observed in the savanna is the Red-lored Parrot (*Amazona autumnalis*; length = 34 cm); however, this species seems to be more abundant in dense, broad-leaf forests in Belize (F. Tarazona-Tubens, *personal observation*). Other smaller Amazon parrot species known to occur in the savannas are the White-fronted Parrot (length = 26 cm) and the Yellow-lored Parrot (*Amazona xantholora*; length = 26 cm). The former occurs as a common habitat generalist in Belize, whereas the latter is typically found in open savannas in northern Belize (Lee Jones 2005). With the exception of the Yellow-headed Parrot, the three Amazon parrots are currently classified as "Least Concern" species by IUCN (BirdLife International 2016, 2018a, 2018b); however, details on their status for Belize is currently unknown.

Nest box installation and monitoring

We installed 60 nest boxes from December 2017 to February 2018, before initiation of the nesting season for Amazon parrots in the pine savannas. Mean distance between installed nest boxes was 522.21 m (range: 139.15–3,941 m). The majority of nest boxes were installed on Caribbean pine; one box was installed on an oak tree. We installed the majority of boxes at Rio Bravo Conservation and Management Area (n = 20) and The Belize Zoo (n = 21). Remaining boxes were installed within two private farms adjacent to the Crooked Tree Wildlife Sanctuary (n = 6) and at Payne's Creek National Park (n = 13). We installed more boxes in the first two sites because pine density is higher in these areas, allowing for more substrate to install boxes. We limited the installation of boxes around Crooked Tree Wildlife Sanctuary to private farms because previous monitoring of Yellow-headed Parrot nests in the area indicated high levels of poaching. We had limited available locations to add additional nest boxes in Payne's Creek National Park because of lower tree density and previously installed nest boxes. Location of boxes at each site was opportunistically assigned, trying to balance equal number of boxes on dense and open areas within each site and based on recommendations from land managers/owners. Land managers usually have a good understanding of the landscape and provided suggestions on areas traditionally used by poachers, which we avoided for box installation. Selection of trees for nest box installation was done by systematically walking the area while looking for trees that were large enough (DBH range: 62–190 cm) to sustain the nest box. When possible, we kept a minimum distance of 200 m between trees selected for nest box placement, known active nests, and roads or marked paths. We initially sought to keep this minimum distance based on observed spacing of natural Yellow-headed Parrot nests; however, actual distances between nest boxes and natural nests ranged from 184 to 22,316 m. We also used the 200 m distance as a safety buffer from the road to avoid detection and potential taking of the nest box or nestlings by poachers.

Box dimensions followed a similar design to that developed by Allen (1991) and previously used at the southern site for parrot nesting. The design was modified to be installed externally (not inserted in trunk) and enlarged to provide additional space for incubating female and nestlings (Fig. 2). Each box was approximately 60 cm tall, 25 cm wide, and 25 cm deep, following internal diameter observed for cavities used by Yellow-headed Parrots (range: 13–40 cm; F. Tarazona-Tubens, *unpublished data*). A 10 cm diameter entrance hole was placed near the top. Before installation, we placed sawdust in the nest box and sprayed the outside with a diluted insecticide (Permethrin) to deter Hymenoptera insects from using the box. Mean height from the ground (± SD) to the nest box entrance was 5.72 m (0.72 m), which falls within observed height values of used cavities by this species (range: 1.16–13.07 m). We chose to keep height of the box relatively invariant to avoid needing specialized tree climbing equipment for monitoring of nest boxes. Direction of the nest box on the tree was randomly chosen, however, if direction faced the road (facilitating detection by poachers), the box was placed in the opposite direction.

Fig. 2. Frontal (left) and lateral (right) views of nest boxes installed in the pine savanna ecosystem in Belize during December 2017 through March 2018. The back side of the nest box (71 cm) was made larger than the frontal side (60 cm); these flanges in the back side were used for attachment of the box to the tree. A circular entrance hole (10 cm) was placed close to the top of the box, no perch was provided.



After installation, nest boxes were revisited four times to monitor use and identify species using the artificial cavity. The first two visits were conducted in March 2018, coinciding with the start of nesting activities (F. Tarazona-Tubens, *unpublished data*). Additional visits were conducted in April and May 2018. Monitoring of the nest box was done by climbing the nest tree and visually inspecting the inside of the nest box. Nest boxes were classified as used if adult parrots were observed flying out of the box, and eggs or nestlings were observed. Active nests continued to be monitored every 6 to 7 days by visual inspection or use of camera traps (Reconyx Hyperfire PC 900) as part of a separate study (Tarazona-Tubens et al. 2022). Nest boxes where nest contents (broken eggshells) and adults were present were also classified as used. Boxes where no adults were observed entering the cavity or egg laying could not be confirmed were classified as unused.

Spatial characteristics of habitat

Habitat and nest tree data were collected to examine nest box occupancy by Amazon parrots. Data were collected in June 2018, at the end of the breeding season, to minimize disturbances on active nests. For each nest box location, we determined the following: understory cover (classified as low/high) and tree density (no. of trees/plot) around the nest tree, frontal visibility (km^2), tree height (m), canopy cover of the nest tree (%), nest box direction, and diameter at breast height (cm; White et al. 2006, Cockle et al. 2010, 2011). Understory cover and tree density were estimated using a 25 m^2 plot centered at the tree where the next box was installed. Classification of understory cover was initially estimated by having a single observer systematically walk within the 25 m^2 plot and estimate the total percentage of understory cover within the plot. Given the structure of the habitat, most cover estimates were either very low or high estimates of cover, with few intermediate values. We later reclassified the cover estimate as a binary classification: low if cover was estimated to be less than 30%, areas above 30% were classified as high cover (Cameron et al. 2011). Short woody plants and tall grasses were considered as part of our cover estimate. Tree density surrounding the nest box was calculated based on an accurate count of the number of trees occurring within the 25 m^2 plot centered at the tree where the next box was installed. We obtained aerial imagery by flying a drone (DJI Mavic Pro) around the edges of the plot, from a standard height of 25 m; this proved to be a faster way to count trees than conducting ground surveys. The standardized height was selected because at this height we had good visualization of the trees for counting, and the images were able to capture clear delineation of where the plot was located, avoiding counting outside the plot. Frontal visibility was defined as the horizontal distance from the nest box entrance to the nearest visual obstruction by surrounding vegetation. Five measurements were taken in 45° increments: -90°, -45°, 0° (directly out from the entrance), 45°, and 90° (White et al. 2006). These distances were obtained with a rangefinder and used to calculate the mean area of the horizontal field of view, providing a measure of the degree of openness at the nest entrance (White et al. 2006). Tree height was measured using a clinometer and a rangefinder and calculated using the tangent method (Bragg 2008). Canopy cover at the nest tree was measured using the mean densiometer reading taken 1 m from the base of the tree, facing outward, in each of four cardinal directions. We did not collect data on food availability

Table 1. Summary of habitat characteristics of all occupied and unoccupied Amazon parrot nest boxes (n = 60) in Belize during the 2018 breeding season. Habitat characteristics on boxes occupied by Red-lored (n = 2; *Amazona autumnalis*) and Yellow-lored Parrots (*Amazona xantholora*; n = 1) are included here but were excluded from nest box occupancy analysis. Nest box height is included as a reference and was not included in occupancy analysis. Distance to previously successful nest was only included in the Yellow-headed Parrot (*Amazona oratrix*) nest box occupancy analysis. Included here are the mean and standard deviation (in parentheses) for each variable.

Variable	*A. oratrix* (*n* = 17)	*A. albifrons* (*n* = 16)	*A. autumnalis* (*n* = 2)	*A. xantholora* (*n* = 1)	Unoccupied (*n* = 24)
Tree height (m)	14.2 (4.4)	14.5 (4.7)	14.3 (5.4)	8.9	12.8 (3.6)
Canopy cover (%)	47.3 (28)	46.8 (27.9)	48.4 (27.5)	65.6	50.7 (28.0)
Frontal visibility area (km²)	4.1 (6.5)	4.1 (6.6)	4.3 (8.5)	0.8	4.8 (7.7)
Tree density (trees per plot)	20.1 (20.9)	18.8 (17.4)	20.9 (22.6)	10	18.6 (20)
Nest box height (m)	5.3 (0.7)	5.2 (0.8)	5.2 (0.4)	6.6	5.1 (0.5)
Diameter at breast height (cm)	119.8 (19.6)	122 (23.2)	119.3 (24.8)	133	123.8 (25.6)
Distance to previously successful nest (m)	1385 (636.9)	N/A	N/A	N/A	12,295.3 (9,695.7)

and tree inclination because our field observations suggested that feeding occurs outside of the savannas and because most pine trees in our sites had straight vertical growth with very little inclination.

Statistical analyses

We modeled nest box occupancy (used/unused) by Amazon parrots as a function of nest tree and habitat characteristics using generalized linear models (GLM) with a binomial error distribution and a logit link function utilizing the package AICcmodavg (version 2.2-2; Mazerolle 2019) in program R (version 3.5.1; R Core Team 2018). We developed a set of 17 a priori models that included univariate and additive combinations of the collected predictor variables, as well as a null (intercept-only) and a global model that included additive combinations of all the predictor variables, to determine the effect these were having on nest box occupancy. Prior to fitting any models, a Pearson's correlation coefficient was calculated, using $|r| \geq 0.70$ as our threshold, to detect collinearity between predictor variables. We found no high collinearity between our predictor variables. An information-theoretic approach using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) was used to compare fitted models; models with $\Delta AIC_c \leq 2$ were considered to have strong empirical support (Burnham and Anderson 2002). Predictors were considered to have a significant effect on nest box occupancy if 95% confidence intervals for the regression coefficients did not overlap zero. Model averaging was used to calculate parameter estimates across the model set (Burnham and Anderson 2002).

We performed an additional species-specific analysis to investigate nest box use by Yellow-headed and White-fronted Parrots, individually, utilizing predictors included in the top-ranked models from the combined nest box occupancy analysis. We evaluated 10 a priori models to explore if these species were occupying nests based on different nest site or habitat characteristics. To investigate nest box occupancy by Yellow-headed Parrots, we compared nest boxes not utilized by any species and those occupied by this species only. For this analysis we also included the distance to nearest Yellow-headed Parrot successful nest during the previous nesting season to investigate its influence on nest box occupancy. Data on locations of successful nests during the previous nesting season was available as part of another study (Tarazona-Tubens et al. 2022) and was calculated using the Near tool in ArcGIS (version 10.5.1.).

Nest box occupancy by White-fronted Parrots was evaluated using records of used and unused boxes by this species. In addition, boxes used by Yellow-headed Parrots were included in this analysis as unused boxes by White-fronted Parrots as this species initiates nesting earlier in the season than Yellow-headed Parrots (Lee Jones 2005; F. Tarazona-Tubens and C. Britt, *unpublished data*). Given the difference in timing of nesting activities, we assumed that nest boxes used by Yellow-headed Parrots would have been available, but unselected, during the nest prospecting and selection phase of White-fronted Parrot breeding pairs. Nest boxes located in the southern site were also excluded from analysis as White-fronted Parrots do not occur in the area. We did not have previous data on fates of White-fronted Parrots nests before the addition of nest boxes, therefore this variable was not considered for this analysis. Model selection for species-specific analysis was conducted using the criteria outlined above. All descriptive statistics were obtained from installed nest boxes; these are presented as the mean and standard deviation (SD), unless denoted.

RESULTS

We documented nesting activities in nest boxes by the first week of March 2018, indicating that breeding pairs quickly utilized the nest boxes. Nesting by four Amazon parrot species was confirmed in 36 of the 60 nest boxes (60%) and included: Yellow-headed (n = 17), White-fronted (n = 16), Red-lored (n = 2) and Yellow-lored Parrots (n = 1). However, only Yellow-headed and White-fronted Parrots were considered for statistical analysis, given the limited observations of other species. Additionally, nesting by a Brown-crested Flycatcher (*Myiarchus tyrannulus*) was confirmed in one nest box. Habitat characteristics informing the use and placement of nest boxes were obtained for all boxes occupied by Amazon parrots (Table 1).

The combined analysis of nest box occupancy by both species showed that five of the 17 candidate models were within 2 ΔAIC_c units and these models received 86% of the total model weight (Table 2). Variables included in these models were tree height, understory and canopy cover, frontal visibility, and tree density. Model-averaged estimates indicated that only tree height had a significant positive effect on nest box occupancy (Table 3, Fig. 3).

Table 2. Model selection results investigating the combined nest box occupancy (used/unused; n = 57), and species-specific use by Yellow-headed (*Amazona oratrix*, n = 41) and White-fronted (*Amazona albifrons*, n = 44) Parrots in Belize during the 2018 nesting season. Nest boxes located in the southern site were excluded from White-fronted Parrot species-specific analysis, boxes occupied by Yellow-headed Parrots in the northern sites were included. Boxes occupied by Red-lored (n = 2; *Amazona autumnalis*) and Yellow-lored Parrots (*Amazona xantholora*; n = 1) were excluded from analysis. Included for each model set are the number of parameters (*k*), model deviance (Deviance), the difference in Akaike's Information Criterion corrected for small sample size between each model and the top model (ΔAIC_c), and the model weight (wi).

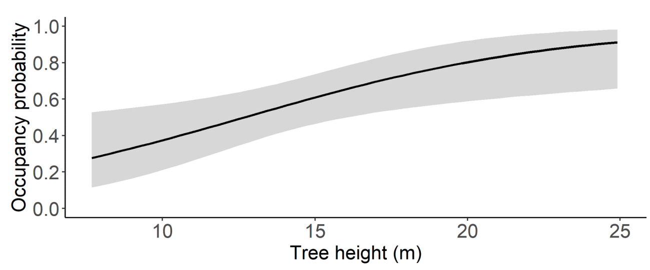
Model	*k*	Deviance	ΔAIC_c	w_i
Combined analysis (both species)				
Tree height[†]	2	69.46	0.00	0.26
Tree height + Understory cover	3	67.54	0.31	0.22
Canopy cover + Tree height	3	67.98	0.77	0.18
Tree height + Front. visibility	3	69.06	1.84	0.10
Tree density + Tree height	3	69.16	1.94	0.10
DBH[‡] + Tree height	3	69.40	2.17	0.09
Null	1	77.60	5.99	0.01
Front. visibility	2	77.22	7.77	0.01
Direction + Front. visibility	5	70.54	8.04	0.00
Tree density + Understory cover	3	75.28	8.06	0.00
DBH	2	77.60	8.14	0.00
Direction + DBH	5	71.54	9.04	0.00
Canopy cover + Tree density	3	76.82	9.59	0.00
Global[§]	10	58.64	9.75	0.00
Direction + Front. visibility + Understory cover	6	69.78	9.78	0.00
Tree density + Front. visibility + Understory cover	4	75.06	10.16	0.00
DBH + Canopy cover + Front. visibility	4	75.74	10.84	0.00
Species-specific analysis				
Yellow-headed Parrot				
Tree height + Dist. nearest previously successful nest[†]	3	33.72	0.00	0.54
Global[§]	7	23.36	0.37	0.45
Front. visibility + Dist. nearest previously successful nest	3	43.72	9.98	0.00
Dist. nearest previously successful nest	2	46.08	10.02	0.00
Tree height	2	46.20	10.15	0.00
Canopy cover + Tree height + Tree density	4	44.96	13.70	0.00
Null	1	55.64	17.36	0.00
Canopy cover + Front. visibility + Understory cover	4	52.72	21.45	0.00
Canopy cover + Tree density + Understory cover	4	52.76	21.49	0.00
Front. visibility + Tree density	3	55.56	21.84	0.00
White-fronted Parrot				
Null[†]	1	61.90	0.00	0.27
Tree height	2	60.32	0.59	0.20
Front. visibility + Tree height	3	58.72	1.25	0.15
Tree height + Understory cover	3	59.06	1.61	0.12
Front. visibility + Tree height + Understory cover	4	57.56	2.47	0.08
Front. visibility + Tree density	3	60.32	2.85	0.07
Canopy cover + Front. visibility + Understory cover	4	58.28	3.20	0.05
Canopy cover + Tree density + Tree height	4	59.88	4.81	0.02
Canopy cover + Tree density + Understory cover	4	60.06	4.98	0.02
Global[§]	6	56.32	6.32	0.01

[†] AIC_c value of the top-ranked model in each model set: $AIC_{c\ Combined}$ = 73.68, $AIC_{c\ Yellow\text{-}headed}$ = 40.38, $AIC_{c\ White\text{-}fronted}$ = 63.99.
[‡] DBH = Diameter at breast height.
[§] Model that includes additive combination of all variables.

Table 3. Model-averaged parameter estimates, unconditional standard errors, and 95% confidence intervals of parameters in the top models ($\Delta AICc \leq 2$) investigating combined, as well as species-specific, nest box occupancy by Yellow-headed (*Amazona oratrix*) and White-fronted Parrots (*Amazona albifrons*) in Belize during the 2018 nesting season. Parameter estimates for each analysis were obtained by model averaging across the set of considered models.

Parameter	Estimate	Standard error	LCL	UCL
Combined analysis				
Intercept	-2.31	1.35	-4.95	0.33
Tree height	0.20	0.08	0.05	0.34
Tree density	0.01	0.01	-0.02	0.03
Understory cover: Low	0.81	0.59	-0.35	1.97
Canopy cover	-0.01	0.01	-0.04	0.01
Frontal visibility	-0.03	0.05	-0.14	0.07
Species-specific analysis				
Yellow-headed Parrot				
Intercept	-3.97	3.38	-10.60	2.66
Tree height	0.47	0.19	0.10	0.84
Nearest previously successful nest	-0.23	0.10	-0.43	-0.03
Understory cover: Low	0.40	1.20	-1.96	2.75
Canopy cover	-0.07	0.04	-0.14	0.01
Frontal visibility	0.03	0.11	-0.17	0.24
Tree density	-0.01	0.03	-0.07	0.04
White-fronted Parrot				
Intercept	-1.46	1.16	-3.73	0.81
Tree height	0.08	0.07	-0.05	0.22
Understory cover: Low	0.75	0.66	-0.55	2.05
Canopy cover	-0.01	0.01	-0.03	0.02
Frontal visibility	-0.08	0.07	-0.23	0.07
Tree density	0.01	0.02	-0.04	0.04

Fig. 3. Nest box occupancy probability of Yellow-headed (*Amazona oratrix*) and White-fronted Parrots (*Amazona albifrons*) in Belize predicted by height of the nest tree. Predictions were obtained utilizing the model-averaged parameter estimates from the combined (both species) analysis, shaded areas represent 95% confidence intervals.



The species-specific analysis revealed specific nest box occupancy patterns by Yellow-headed, but not by White-fronted Parrots. Two of the 10 candidate models investigating nest box occupancy by Yellow-headed Parrots were within 2 ΔAIC_c units, receiving 100% of the total model weight (Table 2). The top-ranked model included additive combinations of tree height and distance to the nearest successful nest during the previous breeding season (Tables 2 and 3). The next top-ranked model included additive combinations of all the variables. Model-averaged parameter estimates show a significant positive effect of nest tree height and a negative effect on nest box occupancy with increasing distance to nearest successful nest during the previous breeding season (Table 3). Analysis of nest box occupancy by White-fronted Parrots revealed several supported models, with the null model ranked as the top model and confidence intervals of all model-averaged parameters bounded zero (Tables 2 and 3).

DISCUSSION

We documented 60% of nest boxes occupied soon after installation, indicating Amazon parrots readily utilized nest boxes in the Belizean pine savannas. Several studies have investigated the use of nest boxes by parrot species, with some contrasting results (Brightsmith and Bravo 2006, Olah et al. 2014, Wimberger et al. 2018). On average, nest box occupancy was approximately 10% (range: 0–32%) for four studies investigating species-specific use of nest boxes by Amazon parrots in areas with limited cavity availability (Sanz et al. 2003, White et al. 2006, Cockle et al. 2010, Kilpp et al. 2014). Occupancy rates found in our study were considerably higher, and nesting activities in nest boxes were initiated quickly after installation, suggesting that cavity availability in lowland pine savannas of Belize may be limited for Amazon parrots. Although we did not collect data to estimate availability of cavities across study sites, historic land use at most sites included large-scale unselective logging and surrounding areas are under the constant threat of land conversion for agriculture (Smith 2021). The effects of frequent fires in the savannas, as well as hurricanes may further reduce the availability of cavities; however, effects of these disturbances on cavity availability have not been thoroughly evaluated in Belize. Nonetheless, studies in the Neotropics where artificial nests were added in human altered and mature forests have shown an increase in density of cavity nesters after nest box addition, likely because cavity availability can be limited, even in mature forests (Cockle et al. 2010, Cuatianquiz Lima and Macías Garcia 2016).

Overall, Amazon parrots exhibited selection at the nest tree level by using nest boxes placed on taller trees. Models also indicated use of areas with less understory vegetation, canopy cover, and frontal visibility, but higher tree density; however, these variables did not strongly affect nest box occupancy. Although our data did not support selection of habitat characteristics surrounding the nest box, our results are only reflective of one year of observations in areas with limited or no previous exposure to a novel structure such as nest boxes. Continued nest box addition and monitoring could reveal an effect of these habitat characteristics on occupancy. Nonetheless, selection of taller trees, with less vegetation cover beneath the nest tree might facilitate detection of predators by nesting parrots. We observed male Yellow-headed Parrots perching at the nest tree tops, presumably scanning for predators, before entering the nest to feed the female or nestlings. On several occasions we also arrived at the nest to conduct monitoring and found the male perched nearby the nest, to which the male responded by producing alarm calls that resulted in quick departure from the area by both parents. Vigilant behavior and signaling is observed for Orange-winged Parrots (*Amazona amazonica*), where the male uses gestural communication to signal the female if it is safe to enter or leave the nest cavity (Moura et al. 2014). In addition, selection for taller trees supported by our data could indirectly reflect selection for emergent tree crowns with no connectivity to neighboring trees, which has been associated with increased nest survival in other parrot species (Koenig et al. 2007, Britt et al. 2014).

This study demonstrated that Yellow-headed Parrots showed a strong preference for tall nest trees in proximity to nests that were previously successful. Observations with camera traps documented Yellow-headed Parrot pairs visiting successful nest sites occupied by other breeding pairs after these nests had fledged. Furthermore, most previously successful nest sites remained occupied after the addition of nest boxes, suggesting that used boxes might have been occupied by new pairs. This may indicate that new pairs select an area in the vicinity of previously successful nests that are again occupied that breeding season, as there may be benefits to nesting in proximity to other successful pairs. Studies of nest box selection and cavity reoccupation by other Amazon parrots have suggested that nesting in proximity to previously successful conspecifics may be beneficial as successful nests may be clustered in areas with higher resources (Berkunsky and Reboreda 2009, Olah et al. 2014). Despite the support found in our data for higher occupancy of nest boxes closer to previously successful nests, additional research is needed to investigate any potential reproductive costs (e.g., competition with conspecifics) to nesting closer to other pairs, and evaluate if this pattern is also observed in areas with high availability of cavities (Renton 2004, Salinas-Melgoza et al. 2009).

Results from this study did not reliably identify nest site requirements for White-fronted Parrots, which might indicate that this species exhibits flexibility in nesting requirements, as is expected given its use of semi-open areas, woodlands, and forest patches in Belize (Lee Jones 2005). Alternatively, a larger sample size may be needed to detect specific occupancy requirements, if any, for this species. The limited use of nest boxes by other sympatric Amazon parrots, despite being abundant in our field sites, highlights the species-specific nesting requirements. Furthermore, inter-specific competition could have led to the limited use by other species; White-fronted Parrots actively chased other parrot species when close to their nest cavity (F. Tarazona-Tubens, *personal observation*). Investigation of species-specific nesting requirements and possible inter-specific competition for nest sites, would further clarify the nest selection process and inform placement of nest boxes on the landscape.

Supplementation of nest boxes on the landscape provides an effective short term management tool to increase nesting opportunities for secondary cavity nesters and mitigate the threats of habitat destruction and lack of available nesting sites for parrots (Cockle et al. 2010, Olah et al. 2014, Norris et al. 2018). This study demonstrated that two species of Amazon parrots in Belize will readily use nest boxes in pine savannas and that boxes in taller trees, closer to previously successful nests, are more likely to be selected by Yellow-headed Parrots. These findings provide valuable information that can be implemented for conservation of Yellow-headed Parrots and highlight the importance of species-specific occupancy patterns that may occur in sympatric parrot species. Conservation strategies in Belize should focus on increasing availability of nesting sites through supplementation of nest boxes, while considering species-specific nesting requirements. In addition, logging practices should preserve taller pines that can be used for placement of nest boxes and are more likely to develop natural cavities. Our findings on nest box occupancy by Yellow-headed Parrots also support placement of nest boxes in the proximity of previously successful nests. However, additional research with nest boxes should be utilized to closely examine if placing boxes near other breeding pairs will lead to increased agonistic interactions between pairs and to determine an appropriate distance between neighbors that minimizes aggressive interactions. Nest boxes are highly conspicuous on the landscape and might facilitate detection by poachers; therefore, supplementation of nest boxes should be accompanied by careful selection of nest trees to reduce nest detection and increased protection efforts to minimize poaching events. Lastly, the use of nest boxes provides a short-term solution to the problems of habitat destruction and limited availability of nesting sites, and does not address the serious threats presented by habitat destruction. Supplementation of nest boxes should be directly accompanied with habitat preservation and restoration actions, which will ultimately serve to increase availability of natural nesting sites.

Responses to this article can be read online at:
https://www.ace-eco.org/issues/responses.php/2234

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