Biological Conservation 250 (2020) 108754

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Policy analysis

Harpy Eagle (*Harpia harpyja*) nest tree selection: Selective logging in Amazon forest threatens Earth's largest eagle

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ARTICLE INFO

Keywords:
Bertholletia excelsa
Breeding
Ceiba pentandra
Emergent tree
Habitat degradation
Nest site selection
Nest tree selection
Raptor

ABSTRACT

Characterizing wildlife conservation problems is essential to properly inform conservation planning, and requires detailed knowledge on critical life stages, such as reproduction. Large tropical raptors often require large emergent trees to build their huge nests. However, large emergents are also in heavy demand by the timber industry. Here, we review the literature to characterize nesting structures used by Earth's largest eagle, Harpy Eagles (*Harpia harpyja*) and examine to what extent nest-tree selectivity is targeted by selective logging. We show that Harpy Eagles selected specific forest canopy structures as nesting platforms. Nests were large (mean size 152 × 99 cm) and typically located on the main fork of 28 emergent tree species, 92.8% of which are commercially targeted by the timber industry. AIC-based stepwise regression indicated that, compared with non-nesting emergent trees, nest trees were 19.6% taller at the first bifurcation; had crowns 26.6% wider; had 33.3% fewer branches < 45°, which were on average 35% lower-angled. Tree size varied widely across the range of nesting tree species, but peaked near the Equator, and were high-statured in unflooded forest compared with flooded forests. Our results show that commercial loggers target the same set of species and individuals on which Harpy Eagles nest, questioning whether large tracts of selectively logged Amazonian primary forests still provide suitable nesting habitat for this mega-raptor. We conclude that suitable Harpy Eagle nesting trees have been rapidly lost over the species last stronghold, and this information may prove useful to the upcoming species evaluation by IUCN.

1. Introduction

Pragmatic solutions to preclude or mitigate anthropogenic threats to wildlife present a raft of challenges for conservation scientists throughout the tropics. With burgeoning human populations, available habitat for wildlife has both declined severely and become increasingly degraded (Dobrovolski et al., 2013; Woodroffe, 2000). Yet as conservation practices are developed, researchers have strived to make their science more policy-relevant and inform practitioners in implementing feasible solutions (Campos-Silva and Peres, 2016; Macdonald et al., 2017). Logging is the most widespread driver of habitat degradation in tropical forests worldwide. Production forests account for ~53% of all natural tropical forest in permanent timber estates (Blaser et al., 2011), and remaining forests are still threatened by illegal logging, deforestation, and wildfires (Gibson et al., 2011). Although selective logging may have limited impact on the overall biodiversity (Tobler et al., 2018; Wilcove et al., 2013), species relying on commercially valuable emergent trees for at least part of their life cycle will likely succumb to highly degraded habitat structure, declining resource availability and smaller populations of mutualistic species (Barrientos and Arroyo, 2014).

Large raptors that are directly dependent on towering emergent trees for nesting may be impacted by forest management practices, such as removal of commercially valuable trees and direct mortality of nestlings induced by tree-felling (Alvarez-Cordero, 1996; Chebez et al., 1990). Harpy Eagles (*Harpia harpyja*) are the largest extant raptor on Earth. They were formerly distributed through much of the Neotropics, from Southern Mexico to Northern Argentina (Miranda et al., 2019; Vargas-González et al., 2006). Harpies have been extirpated from over 40% of their former range in Mesoamerica, mainly by shooting and habitat loss (Miranda et al., 2019; Trinca et al., 2008). In South America, the species is virtually extinct across the Atlantic Forest ecoregion, where extensive forest loss (amounting to 85% of all forest cover, Hirota and Ponzoni, 2014) restricted the species to a few isolated

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https://doi.org/10.1016/j.biocon.2020.108754
Received 2 January 2020; Received in revised form 28 July 2020; Accepted 12 August 2020

Fig. 1. Mother and chick at the nest. Harpy Eagle nest at a Brazil-nut tree (*Bertholletia excelsa*) in southern Amazonia. Photo: Roy Toft.

pairs scattered across the largest remaining forest tracts (de Lucca, 1996; Suscke et al., 2016). The last stronghold of Harpy Eagles is therefore extensive areas of relatively intact forests across the lowland Amazon, representing 93% of the present species range distribution (Miranda et al., 2019). Amazonian forests have been rapidly incinerated into cattle pastures and cropland across a vast frontier known as the Amazonian 'Arc of Deforestation' (Fearnside, 2005), particularly in Brazil (Peres et al., 2010). However, Amazonia still retains extensive areas of largely pristine forest habitat, which presently precludes Harpy Eagles from being listed by IUCN into higher conservation threat categories; the species is currently assessed as Near Threatened (Birdlife International, 2017).

Like other large eagles, Harpy Eagles build huge nests, usually on the primary bifurcation of large-girthed emergent trees (Giudice et al., 2007; Fig. 1). Because active nests consist of large structures, some minimum structural requirements must be met by suitable host trees and landscape (Vargas-González et al., 2020). General descriptions of Harpy Eagle nests and nest trees were reported in early works (e.g. Rettig, 1978), but an objective analysis of their nesting habitat requirements is still lacking, and remains a priority for reproductive studies (Monsalvo et al., 2018). Harpy Eagles occur at relatively low population densities (4–6 nests/100km^2 in Panama; Vargas-González and Vargas, 2011; 5 nests/100km^2 in Ecuador; Muñiz López, 2016) across some of the most remote Neotropical regions. Locating a statistically meaningful number of active nests has been achieved by only a few studies (Vargas-González and Vargas, 2011), to the point that finding even a single nest becomes a highly prized ornithological achievement (Rotenberg et al., 2012; Ubaid et al., 2011). Some studies have provided a checklist of nesting tree species, but they typically describe site-specific patterns of nesting that are typically affected by local tree species composition and geographic location. Consequently, a systematic review of nesting structures used by Harpy Eagles throughout their range is timely to identify nesting tree preferences across a wide range of forest landscapes and canopy tree architecture.

In this study, we compiled continental-scale data on Harpy Eagle nests across the species' distribution range to identify their nesting tree preferences and better inform selective logging policies and forest management planning. Our motivation is to prevent or reduce the detrimental effects of forest degradation on the critical nesting habitat requirements of the world's largest extant aerial predator. We first review nesting tree data obtained across all studies conducted throughout the Harpy Eagle distribution range. We then determined patterns of nest-tree preference or avoidance by Harpy Eagles in relation to tree architecture and surrounding land cover. We also examined the variation in nest-tree size over the species distribution range. Finally, we provide a checklist of Harpy Eagle nest-tree species, and the present extractive market demand on these species, particularly in relation to the most commercially-valuable timber species. We therefore attempt to understand the nesting requirements of Harpy Eagles in light of expanding areas of commercial logging concessions in the Amazon, and the conservation implications of nest-tree preferences for Harpy Eagle persistence. We predicted that Harpy Eagles select the highest emergent canopy tree species as nest sites throughout their distribution range. We further predicted that these tree species are congruent with timber species that are highly sought after for commercial logging and trade.

2. Methods

2.1. Review and data standardization

We searched Google Scholar using several combinations of the following keywords: Aguila Arpía, Harpia, Harpy Eagle and Nido, Anidación, Ninho or Nest, as well as the species Latin binomial. This allowed us to obtain published and unpublished studies in Spanish, Portuguese and English. We also consulted raptor biologists working on Harpy Eagles to obtain additional unpublished data sources or supplementary material from published sources. Our search lead to 17 published and 3 unpublished studies. The study of Vargas-González et al., 2014 was excluded a priori because it presents no raw data and we failed to obtain supplementary information from these authors. We used data from unpublished studies – including undergraduate, MSc and PhD theses – because we sought to obtain raw data on nest-trees, rather than secondary interpretations. Altogether, the studies we compiled presented raw data on 98 nests.

We obtained detailed information on the surrounding vegetation structure for 23 nests, and detailed data on nest-tree structure for 32 nests. We also had data on the tree structure and surrounding vegetation for 58 non-nest emergent trees, which we define here as pseudo-controls. The variables measured at nesting trees and the surrounding

Table 1
Checklist and description of the structure of 20 nest-tree species and predictor variables related to the surrounding vegetation explaining Harpy Eagle nest site colonization of emergent trees. Sources: 1) Alvarez-Cordero, 1996; 2) Giudice, 2005; 3) da Luz, 2005.

Variable	Description	Type	Source
Crown radius	Distance from tree trunk to borders of tree crowns in meters, taken at two or four points. Mean values were used to calculate crown diameter.	Nest tree	1,2,3
Trunk diameter	Diameter of the nest tree or control emergent at breast height, in cm.	Nest tree	1,2,3
Nest height	Height of the fork sustaining the nest. In control emergent trees, it was measured at tree main fork. Measured in m, by climbing the tree or using a hypsometer.	Nest tree	1,2,3
Tree height	Total tree height. Estimated or measured by the climber, or measured with a hypsometer from the ground.	Nest tree	1,2,3
Branch number	Refers to the number of branches (living or dead) supporting nest structure.	Nest tree	2,3
Branches lower than 45°	Number of branches with an angle lower than 45°, having the ground as 0°. Estimated from the ground.	Nest tree	2
Number of emergents trees	Number of emergent trees in a plot of 25 × 40 m around nest tree and in a control site ≥3.7 km from it.	Vegetation structure	2
Nearest emergent	Distance from the nest tree or control emergent tree to the nearest emergent.	Vegetation structure	2
Mean number of trees > 0.1DBH	Mean number of trees with more than 10 cm of diameter at breast height in five plots of 25 × 40 m around nest tree and around a control emergent tree.	Vegetation structure	2
Wood cover	Wood cover in the same plots, in m^2/ha.	Vegetation structure	2
Wood density	Recovered from the literature for each emergent tree species.	Nest tree	
External fork angle	Mean of the external angles of all branches sustaining the nest. Angular measurements using a compass.	Nest tree	3
Internal fork angle	Same as above, but measure in the internal face of the branch.	Nest tree	3
Fork branches diameter	Summed diameter of the branches sustaining the nest, in cm. Measured during climbing.	Nest tree	3
Nest exposition	Index composed by fork height, minus far canopy height, minus distance from the nest fork to the center of the trunk.	Nest tree	3
Canopy under the tree	Canopy height, in meters, under the nest tree or control. Estimated by the climber during ascension.	Vegetation structure	3
Canopy height around the tree	Canopy height, in meters, around the nest tree or control. Estimated by the climber during tree ascension.	Vegetation structure	3
Height difference	Difference between the height of the canopy under and around emergent tree.	Vegetation structure	3
Density of trees	Number of trees with > 25 cm of trunk diameter at breast height in a 60-m^2 plot around the nest tree.	Vegetation structure	3
Declivity	Mean declivity, measured with a clinometer, in six points in the 60-m^2 plot.	Vegetation structure	3

vegetation differed across studies (Table 1). Ordinarily, available data for the vast majority of nest site trees included trunk diameter at breast height, total tree height, above-ground nest height, crown diameter and tree species identity, which allowed analyses on the effects of tree size for nest site trees.

Regarding the nest itself, measures of nest diameter were obtained assuming a roughly circular nest. Two perpendicular measures of diameter were obtained by most authors. Nest height, as measured by all authors, was defined from the base of the tree fork to the nest rim.

To compare tree species demanded by the logging industry with those used by nesting Harpy Eagles, we used the benchmark index for timber prices of the State of Para, Brazil (DOEPA, 2010). Para accounts for roughly one half of all natural timber harvested in Latin America (Richardson and Peres, 2016) and over 96% of our nest-tree species checklist were listed in this single source. This was used as a proxy of international timber market prices. In addition, it is virtually impossible to find credible timber prices for all countries/regions within the natural range of Harpy Eagles. To include tree species that were not listed on this source, we grouped them into a timber category of similar wood density, since wood densities of desirable timber species demanded by Brazilian and international markets are fairly consistent with timber prices (Richardson and Peres, 2016). DOEPA (2010) presents timber species according to four wood price classes (all in Brazilian Reais R $/$m^3$ ~ 1 US$ = 4.24 R$) into four groups of decreasing market desirability: Class 1 (11 species): > R$75; Class 2 (18 species): R$45 to R$74; Class 3 (40 species): R$25 to R$44; and Class 4 (all other 245 species): R$1 to R$24.

2.2. Statistical analysis

We evaluated the spatial variation in Harpy Eagle nesting-tree size by fitting trunk diameter, nest height, tree height and crown diameter to geographic latitude using a Generalized Additive Model (GAM). As semiparametric extensions of generalized linear models, GAMs have an additive predictor rather than a linear predictor. As the relationship between response and predictor variables is determined by the data instead of an a priori presumed parametric function, these models are described as more data-driven than model-driven (Logan, 2011). Thus, we selected GAMs to avoid a priori assumptions about the relationship between tree size and latitude. We also compared the stem density and tree size with available data for Amazonian canopy trees using 2345 plots of 1-ha each, which were surveyed throughout the Brazilian Amazon during the RADAMBRASIL tree inventory (Peres et al., 2016). This network of tree plots was carried out from 1968 to 1973 and predates any major forest disturbance in Amazonia, and is therefore considered the best available baseline on tree species composition, abundance and size structure for any major tropical forest region anywhere.

We relied on a null model to test whether differences in tree size between flooded and unflooded Amazonia were larger than expected by chance. We used 1000 iterations of the means of randomly labeled groups (i.e. random categorization of forest type), which were later compared with real differences between forest types in trunk diameter, nest height, tree height and crown diameter. While bootstrapping samples in each simulation we used the sample size (n) of the smallest group (flooded forest).

As Table 1 shows, a long list of variables have been selected by many researchers to describe the trees in which Harpy Eagles nest and their surrounding vegetation. We used information theoretic model selection based on Akaike's Information Criterion (AIC) to perform a logistic stepwise regression to determine a well-supported model for inference (Crawley, 2007), including all predictor variables (Table 1). By using both trees with nests and pseudocontrol samples we produced a binary response variable. Since da Luz (2005) and Giudice, 2005 quantified variables of similar biological meaning using different methods, we ran the analysis for each dataset independently. Statistical analyses were carried out with the R platform, using the *vegan*, *MGCV* and *MASS* packages (Oksanen et al., 2007; Ripley et al., 2013; Wood and Wood, 2007).

3. Results

3.1. Nests and nest trees

Harpy Eagle nests were on average 152 cm wide (SD ± 27 cm, n = 21) and 99 cm in height (SD ± 49 cm, n = 12; Table 2). These nests were located on the main fork (85.7%), primary branches (12.2%) and secondary branches (2.1%) of emergent trees (n = 98; Fig. 2).

Table 2
Summary of Harpy Eagle nest morphology. Nest diameter and nest height were calculated by two perpendicular diameters, and measurements of the distance between the fork and the nest rim, respectively.

	Mean	SD	Maximum	Minimum	n
Mean nest diameter (cm)	152.9	27.8	200.0	81.5	21
Nest height (cm)	99.8	49.5	200.0	21.0	12
Diameter 1 (cm)	158.4	36.6	240.0	78.0	21
Diameter 2 (cm)	148.4	30.1	218.0	85.0	19

Harpy Eagle nests were observed in 28 species of emergent trees, of which ceiba (*Ceiba pentandra* Gaertn.) was the most common nesting tree species in Amazonia, tauari (*Couratari guianensis* Aubl.) in the Guiana Shield, cuipo (*Cavanillesia platanifolia* Humb. & Bonpl.) in Mesoamerican dry forests, earpod (*Enterolobium contortisiliquum* Vell.) in the Atlantic Forest, and courbaril (*Hymenaea courbaril* L.) in the Brazilian Cerrado (Table 3). Of those 28 species, most (92.8%) were of commercial interest and highly prized by the timber industry. The other two tree species included an arborescent palm and the Brazil nut tree *Bertholletia excelsa* Bonpl. (which cannot be legally harvested in most of its distribution; Nepstad et al., 1992). The 26 remaining tree species were distributed as follows: 54.7% were species of relatively low commercial value (~US$3.10/m^3), 15.4% were species with average commercial value (~US$6.19/m^3), 19.2% species were of high commercial value (~US$9.20/m^3) and 7.7% species were commercially very valuable (> US$16.32/m^3).

3.2. Spatial patterns of tree size

Regardless of forest type, Harpy Eagles always selected the largest available trees in which to build their nests (Fig. 3). Nest tree size – measured in terms of total height, above-ground nest height, trunk diameter at breast height or crown diameter – increases in low-latitude regions towards the Equator (Generalized Additive Model; $P < 0.05$ for all variables except for crown diameter; Fig. 4). In Amazonia, total height of selected trees, nest height above ground, trunk diameter and crown diameter were all higher in upland unflooded forests compared to seasonally flooded forests, but only the first two were statistically significant (Null model; $P < 0.05$ $n = 9$ flooded and 16 unflooded nest trees; Fig. 5).

3.3. Vegetation structure

The number of emergent trees, distance to nearest emergent tree and the number of trees larger than 10 cm in diameter did not affect the probability of nest-tree selection for Harpy Eagles. However, surrounding forest cover had a marginal negative effect on tree colonization probability (AIC-based stepwise regression, SE = 0.475, 16 DF, R^2 = 0.149, F = 3.97, P = 0.063).

Canopy height under and around any given emergent tree, density of trees with trunk diameter > 25 cm and canopy openness were not included in the most parsimonious models. However, differences in canopy height between the forest under and around any given emergent tree, combined with terrain declivity, had a positive effect on nest-tree selection probability (AIC-based stepwise regression, SE = 0.4523, 29 DF, R^2 = 0.258, F = 5.05, P = 0.0131).

3.4. Tree architecture

Considering the structure of nest-trees, the best models explaining Harpy Eagle nest-tree selection included crown diameter (10.19 m vs. 8.05 m, 26.6% wider in selected nest-trees) and number of branches lower than 45° at the nest fork (3.56 vs. 2.67, 33.3% more < 45° branches in selected trees), both of which suggest selectivity of a large platform structure in selected nest-trees (AIC-based stepwise regression; SE 0.333, 47 DF, R^2 = 0.191, F = 6.785, P = 0.002). However, trunk

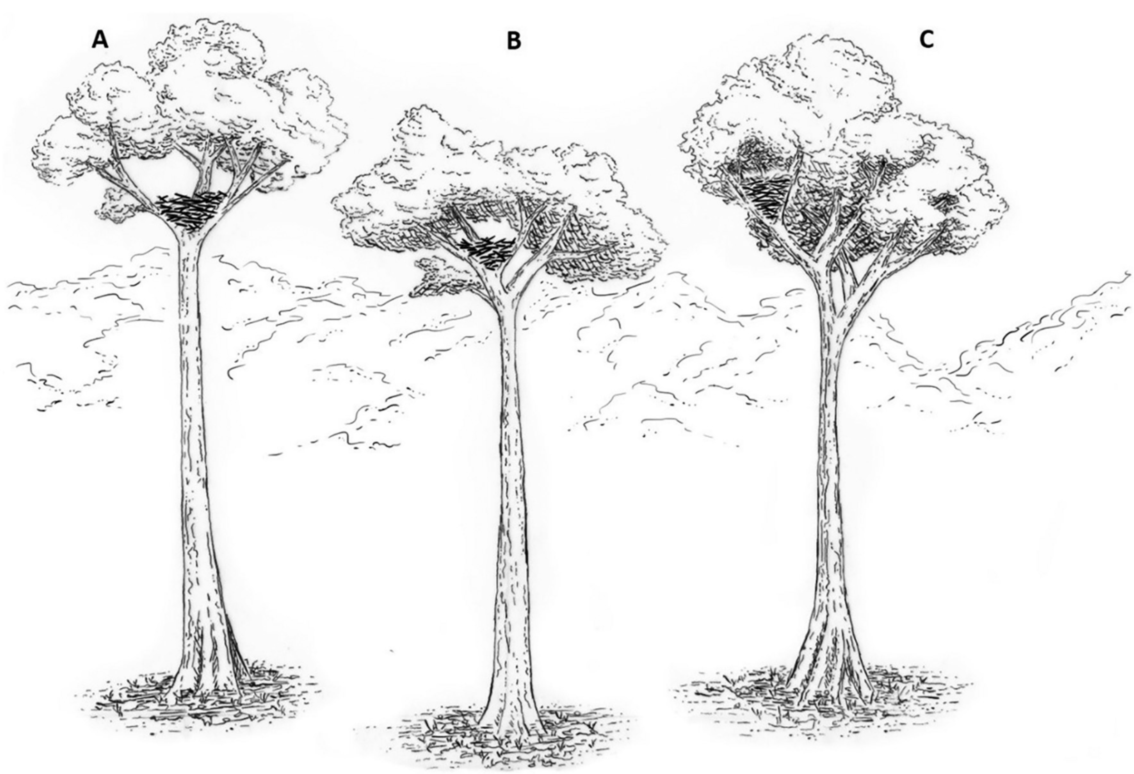

Fig. 2. Nest size and position. Harpy Eagle nests exhibited a mean width of 152 cm and a mean height of 99 cm. These nests were located at the main fork of nest trees (85.7%, A), primary branches (12.2%, B), and secondary branches (2.1%, C) of 28 species of emergent trees averaging 33.5 m in height at the main bifurcation (illustration: Paula Viana).

Table 3
Harpy Eagle nesting on a variety of emergent tree species shown as frequency of occurrence. Tree families: [a] Malvaceae; [b] Lecythidaceae; [c] Fabaceae; [d] Chrysobalanaceae; [e] Anacardiaceae; [f] Combretaceae; [g] Myristicaceae; [h] Vochysiaceae; [i] Arecaceae. Price class represents the benchmark primary market wood prices of timber species (source: DOEPA, 2010), on a scale of 1 to 4, where 1 represents the most expensive species and 4 the cheapest.

Nest tree species	Price class	Unflooded Amazon	Flooded Amazon	Guiana Shield	Mesoamerican Forests	Atlantic Forest	Cerrado and Pantanal	Source
Ceiba pentandra [a]	4.0	31.7	60.0					6, 8, 11, 12, 13, 17, 18
Bertholletia excelsa [b]	–	29.3						4, 8, 9, 11, 19
Cavanillesia platanifolia [a]	4.0				90.9			2
Couratari guianensis [b]	4.0			30.0				2
Dinizia excelsa [c]	1.0	12.2	6.7					10, 11
Catostemma commune [a]	4.0			20.0				2
Dipteryx micrantha [c]	2.0	2.4	20.0					8
Hymenaea courbaril [c]	2.0			20.0			50.0	2, 4, 9, 11, 19
Parinari excelsa [d]	4.0			20.0				2
Cedrelinga cateniformis [c]	4.0	7.3						12
Enterolobium contortisiliquum [c]	4.0					42.9		3, 5
Peltogyne sp. [c]	3.0			10.0				2
Hymenolobium sp. [c]	3.0	2.4						11
Apuleia leiocarpa [c]	3.0	2.4						9
Astronium concinnum [e]	2.0					14.3		1
Astronium graveolens [e]	2.0					14.3		15
Cariniana legalis [b]	4.0					14.3		4
Huberodendron ingens [a]	4.0	2.4						11
Huberodendron sp. [a]	4.0	2.4						12
Hymenaea parvifolia [c]	2.0		6.7					11
Hymenolobium petraeum [c]	3.0	2.4						7
Schizolobium amazonicum [c]	4.0	2.4						19
Sterculia apetala [a]	4.0		6.7					14
Handroanthus impetiginosa [c]	1.0					14.3		5
Terminalia sp. [f]	4.0	2.4						4
Virola koschny [g]	4.0				9.1			16
Vochysia divergens [h]	4.0						25.0	20
Mauritia flexuosa [i]	–						25.0	21
Number of Species		12	5	5	2	5	3	
Number of Nests		41	15	20	11	7	4	

Data sources: 1. Aguiar-Silva et al., 2012, 2. Alvarez-Cordero, 1996, 3. Anfuso et al., 2008, 4. Sousa et al., 2015, 5. Chebez et al., 1990, 6. Fowler and Cope, 1964, 7. Galetti and de Carvalho-Jr, 2000, 8. Giudice, 2005, 9. Gusmão et al., 2016, 10. Kuniy et al., 2015, 11. da Luz, 2005, 12. Muñiz-López, 2008, 13. Muñiz-López et al., 2007, 14. Olmos et al., 2006, 15. Pereira and Salzo, 2006, 16. Rotenberg et al., 2012, 17. Sanaiotti et al., 2015, 18. Seymour et al., 2010, 19. This work, 20. Ubaid et al., 2011, 21. Sick, 1984.

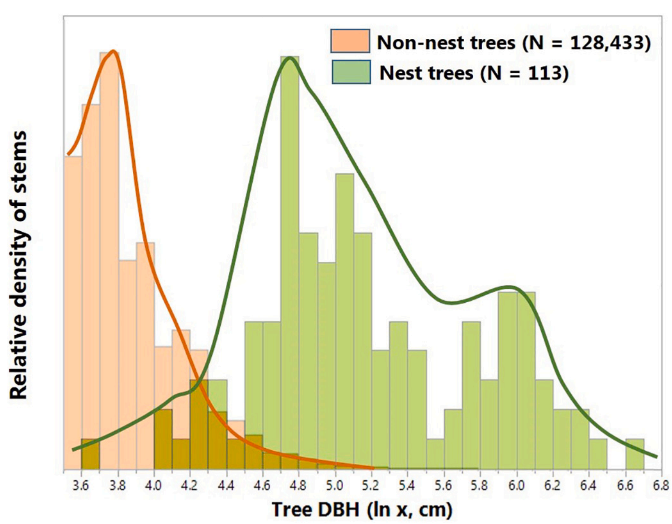

Fig. 3. Tree size. Double-histogram showing the tree size distribution (log of DBH, cm) of Harpy Eagle nest trees (green bars) across the Neotropics and non-nest trees (orange bars) across the Brazilian Amazon. Dark green bars show the overlap in tree sizes. Data for non-nest trees were sourced from the RADAM-BRASIL floristic inventories (Peres et al., 2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

diameter, nest height above ground, tree height, wood density and number of branches at the nest fork were not included in the most parsimonious models. Higher nest heights (33.5 m vs. 28.0 m, 19.6% taller in selected trees) and low internal fork angles (82.5° vs. 61.0°, 35% less inclined in selected trees) positively affected tree colonization probabilities (AIC-based stepwise regression; SE 0.4173, 29 DF, $R^2 = 0.325$, $F = 8.47$, $P = 0.001$). On the other hand, models did not include diameter of fork branches, external fork angle, degree of nest exposure, number of branches at the nest fork, nest height above ground, crown diameter, wood density, and trunk diameter at breast height. All models indicated a T-shaped primary bifurcation structure in large trees selected for successful nesting (Fig. 6).

4. Discussion

Our findings provide strong empirical evidence that Harpy Eagles are selective in their choice of nesting sites throughout their distribution range and, as predicted, these are the highest emergent canopy trees. The average nest size—1.5 m in diameter and 1 m in height—requires a strong structure that can withstand a very large stable nest safely for many years. When compared with pseudocontrol non-nest trees, nest-trees were higher statured, and had wider crowns and forks containing large low-angled primary branches. This tree structure better accommodates a large Harpy Eagle nest, as well as provides branches that ensure safe exercising to the young and facilitates landing by the parents. Nest tree size varied throughout the wide range of Harpy Eagles, peaking near the equator where the tallest trees and highest primary productivity occurs (Gorgens et al., 2019). Although

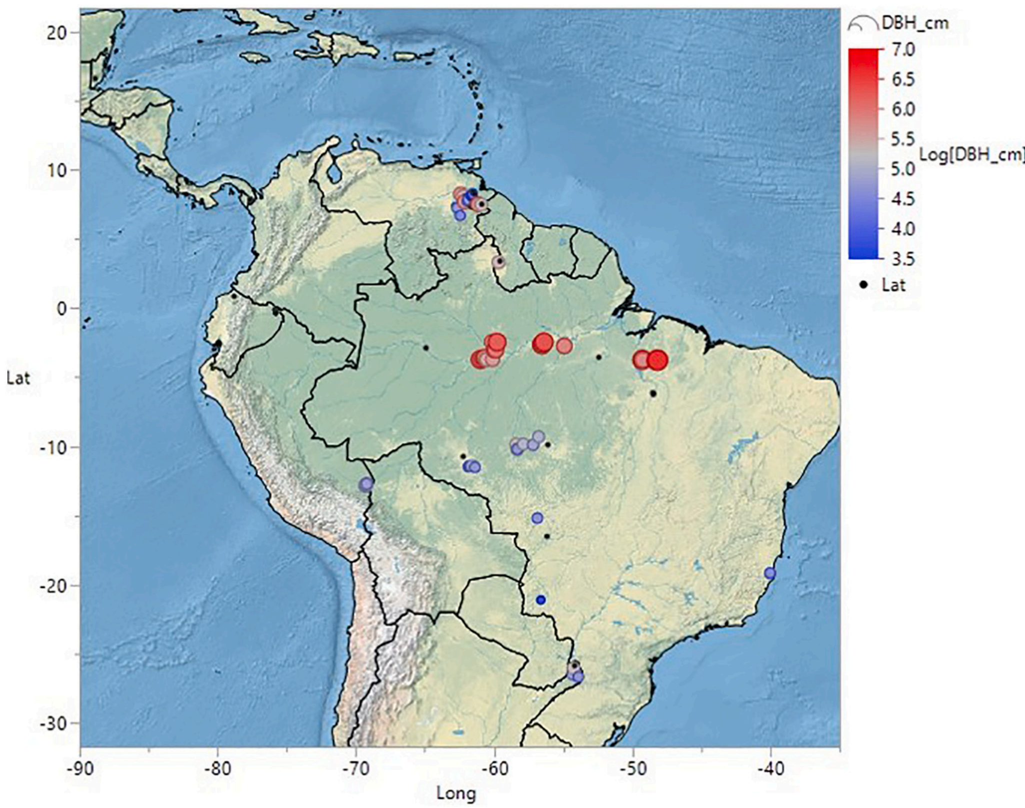

Fig. 4. Nest-tree size across South America. Wide variation in the size of observed nest-trees across the Harpy Eagle range distribution showing the spatial increase in tree diameter at breast height (DBH) towards the equator (GAM, R^2 0.0014, $n = 52$, $p > 0.05$). The same pattern of increase towards the equator was shown in nest height (GAM, R^2 0.151, $n = 63$, $p > 0.05$), tree height (GAM, R^2 0.165, $n = 42$, $p > 0.05$) but not in crown diameter (GAM, R^2–0.015, $n = 31$, $p < 0.05$). Solid black represent nest-trees lacking any information on tree size.

consistently selecting the tallest individual tree species at any given site, those trees are typically smaller in environments where forest canopy was lower, such as in seasonally flooded forests of Amazonia. Considering the vast tree diversity in the Amazon which contains more than 10,000 tree species (ter Steege et al., 2019), not to mention other Neotropical biomes, Harpy Eagles' choice of nest-trees includes a very short checklist of only 28 tree species. We, therefore, show that Harpy Eagles are highly selective in their choice of nest-trees and that they select specific features in emergent tree species that can provide those features. Given the cascading effects of Harpy Eagle predation in any forest environment (Gil-da-Costa, 2007; Terborgh et al., 2001), this represents considerable conservation and management interest.

The vegetation surrounding the Harpy Eagle nest-tree is apparently of limited importance in tree selection. The negative effect of wood cover was unimportant in nest tree selection in one dataset in our review, as well as in other studies (Vargas-González et al., 2014). Other variables with a significant result, such as the height difference between the forest canopy underneath and around the nest tree, may be a secondary effect of the larger crowns and low-angled forks exhibited by selected nest-trees. The amount of light that reaches the canopy around those huge T-shaped nest-trees is likely lower, thereby strongly suppressing vegetation growth directly underneath the tree, thus further increasing this difference. Topographic slope may be an effect of selection of nest-trees that are located at local elevated terrains that confer nest-trees greater heights than the surrounding landscape. Indeed, we do not expect that a large raptor that essentially spends all of its life cycle in the upper layers of the forest canopy would carry out habitat selection based on a stratum of the forest it rarely visits. It is more likely that those expectations are driven by the ease with which understory vegetation variables can be sampled by researchers on the ground, compared to the challenges of climbing observed or potential nest-trees.

The very large Harpy Eagles nests—up to 2.4 m across—are among the largest nests built by any living eagle. Even subjected to the high decomposition rates of tropical climates, their nests rival the enormous of Golden Eagle (*Aquila chrysaetus*) nests, that are around 1.33–1.75 m in diameter and used by unfledged chicks for much shorter periods (Grubb and Eakle, 1987; Watson, 2010). A close look at the measurements provided in Table 2 reveals that there is a wide variation in Harpy Eagle nest size, mostly resulting from the succession of decay and their rebuilding at each 3-year long reproductive cycle. Like other very large raptors, Harpy Eagles use the same nest sites for several decades, but nests must be repaired, if not completely overhauled, after each breeding event (Muñiz-López et al., 2016; Urios et al., 2017). We consider the extreme measures of nest diameter to represent the upper and lower points of the reproductive cycle, with smaller nests found during periods between breeding events and larger structures representing recently rebuilt nests.

With such very large nests, the emergent tree structure required to support them is not trivial. Generally, low-angled forks provide a wide platform where the nest can be built. Their highly elevated positions render nests largely inaccessible to scansorial predators (Aguiar-Silva et al., 2017) and even less so to terrestrial predators including humans. Body parts of Harpy Eagles are often highly prized by native Amerindians (Reina and Kensinger, 1991; Rosa, 2010), and they are hunted as food source (Freitas et al., 2014) or for curiosity (Trinca et al., 2008). In addition, nest-trees provide a better panoramic view well above the forest canopy as a mere consequence of being taller. This confers foraging advantages in providing a higher perch from which a large area can be scanned as well as is an easy point where nestlings can be guarded by adults at distant perches. The wide crown provides a safe and extensive training ground for the "branch-hoping" young during their slow process of flight learning (Muñiz-López et al., 2012), which may be mandatory for tree selection, since falling from the nest is an important cause of fledgling mortality (Muñiz-López, 2017).

The consistent increase in nest-tree size towards the equator reported here relates to the high variation in forest canopy tree size observed along this gradient (Moles et al., 2009). High levels of variation in trunk size at low latitudes are also related with the extensive occurrence of buttressed trees in Amazonia (Parolin et al., 2016). The

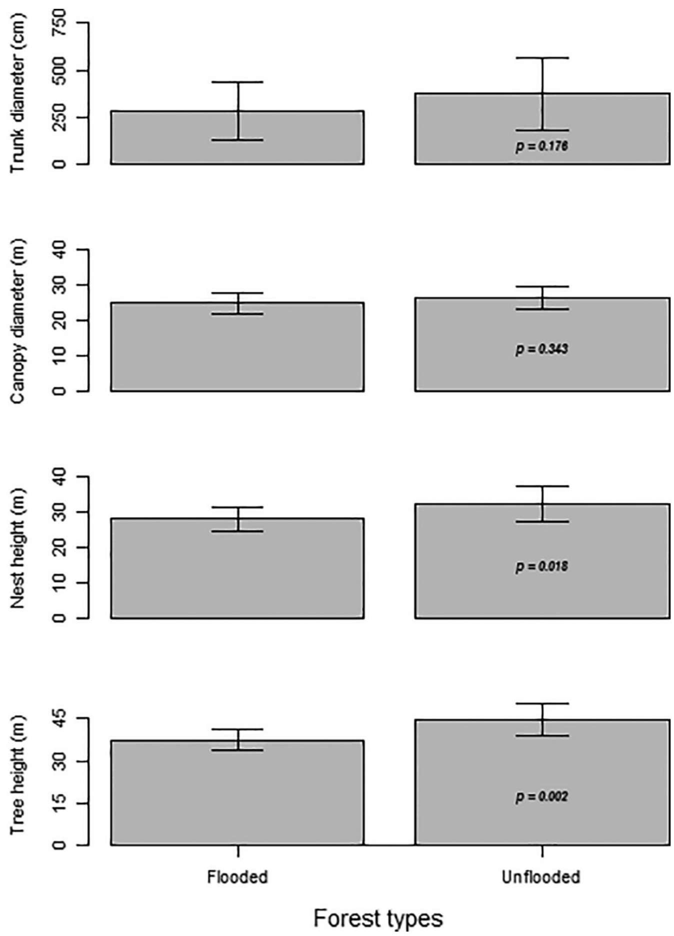

Fig. 5. Tree size in different forest types. Mean value for each variable and its standard deviation in flooded and unflooded Amazonian forests for Harpy Eagles nest tres. Trees are lower-statured in seasonally flooded forest, but this difference only held statistical significance for nest height and tree height.

same occurs when we consider the cuipo trees which have bulky trunks relative to their size (Murawski and Hamrick, 1992) in the northern portion of the Harpy Eagle range, creating wide variation in trunk size and reducing the explanatory power of latitude. Tree crown diameter is also subjected to wide variation as crown architecture is species-specific, and also shows extensive individual variation induced by phenotypical plasticity (Pretzsch, 2014). This study poses the question of whether or not nesting habitat is a limiting factor in the ecological distribution of Harpy Eagles, since potential nest-trees are downsized at the latitudinal limits of their range, and large emergent tree are rare in the Cerrado savannah scrublands of Central Brazil. The use of giant palms as *Mauritia flexuosa* as nesting trees in the extensive grasslands of the Cerrado (Sick, 1984) suggests that this subject merits further investigation, but Harpy Eagles have now been essentially extirpated from this ecoregion (Miranda et al., 2019). Our findings are relevant to experts climbing nest-trees as well as enterprises interested in Harpy Eagle-centric ecotourism, given that knowing expected height can favor tailored planning before searching a specific areas for climbing or installing an observation canopy tower.

While frequently used as Harpy Eagle nest-trees in the Amazon, Brazil-nut trees is a poor candidate as a nest site choice. Brazil-nut trees produce cannonball-like fruits (Mori and Prance, 1990) that whenever falling can easily cause severe damage to the nest structure and/or directly injure the eagles (EPBM, pers. obs.), and we believe that its heavy use in unflooded (*terra firme*) forests is related to these trees being frequently visited by Brazil-nut collectors. Any nest is more likely to come to attention of nut harvesters, which is eventually communicated to researchers, thereby overinflating estimates of nest-tree use. However, considering that Brazil-nut trees are strictly protected by law against felling in much of Amazonia (i.e. Brazil, Bolivia and Peru), they can provide an option for Harpy Eagle breeding sites in forests that otherwise have lost other emergent species to selective logging. This further emphasizes the advantages of the complete ban on felling Brazil-nut trees, and the indirect positive effects of natural Brazil-nut stands as Harpy Eagle nesting sites.

Biologically available soil nitrogen and phosphorus has been perceived as important to the processes that controls tropical forest dynamics (Marklein et al., 2016). By concentrating nutrients underneath the crowns of nest-trees through long-term deposition of prey carcasses and feces over decades, Harpy Eagles may provide a key mutualistic relationship with the trees in which they nest. The impact of Harpy Eagle presence over seed predators and dispersers of nest trees, combined with the possibility of secondary seed dispersal from prey stomach contents (Nogales et al., 2002), may be the underlying reason explaining a larger number of families of trees found underneath nest-tree crowns (Vargas-González et al., 2014). These possibilities pose many interesting lines of enquiry on how Harpy Eagles and other large tropical forest raptors can operate as ecosystem engineers, in addition to their better understood ecological roles as keystone predators.

Only emergent trees are selected by Harpy Eagles for nesting and, as predicted, those are congruent with the same set of individuals in demand by the Neotropical timber industry (Sist et al., 2014). We emphasize that excluding the giant palm *Mauritia flexuosa* and the Brazil-nut tree, all other observed nest-trees (> 92%) are commercially harvested tree species sought by logging operations. This is of extreme concern considering that generally these Neotropical forests are poorly managed for timber extraction and whether it is actual sustainable use. Furthermore law enforcement in most low-governance forest areas is scant and most timber trees continue to be harvested illegally (Nellemann, 2012). Brazilian law, for instance, endorses a cutting cycle of 25–35 years for all timber species, which is far too short to safeguard the life-history requirements of most commercially-valuable timber species (Fernandez et al., 2012; Richardson and Peres, 2016). In Panama, recent research suggests to improve the legislation of natural resources extraction by local communities in Panama to keep suitable nesting habitat for Harpy Eagles (Vargas-González et al., 2020). In most cases, following the local commercial extinction of many hard-wooded timber species, formerly managed stands are deforested and converted into cattle pastures, with disastrous effects on forest biodiversity.

The relationship between forest governance and the ecological impacts of logging in other Amazonian countries is equally concerning. In Ecuador, there are five different timber extraction systems (Bonilla-Bedoya et al., 2017), each of which tied to different environmental and social contexts. Species frequently used as nest-trees—*Ceiba pentandra* and *Cedrelinga cateniformis*, for instance—are among the species with highest extracted timber volumes. The Environmental Ministry of Ecuador estimates that 40–50% of all timber in the Ecuadorian Amazon is illegally harvested, and in Colombia, at least 42% of all timber harvested in natural forests is illegal (Orozco et al., 2014). While Peru and Bolivia have improved forest governance laws to accommodate local communities and indigenous people's demands (Cano et al., 2019), they also function under the minimum size paradigm (Piponiot-Laroche et al., 2019). In other words, they ignore mega-trees that are valuable for Harpy Eagle nesting (although forbidding the felling of Brazil-nut trees; Nepstad et al., 1992). Venezuela's current political turmoil has harmed its governance over environmental resources, with entire timber concessions clear-cutted (Pacheco-Angulo et al., 2017). On the other hand, the long-term conservation project in Venezuela stimulates loggers to leave active Harpy Eagle nest-trees alone (Alexander Blanco, pers. com.). To make the problem worse, timber theft is extensive across Amazonia (Asner et al., 2006), including protected areas and indigenous reserves. These examples highlight the effects of forest governance over multiple countries covered by the Amazon Forest,

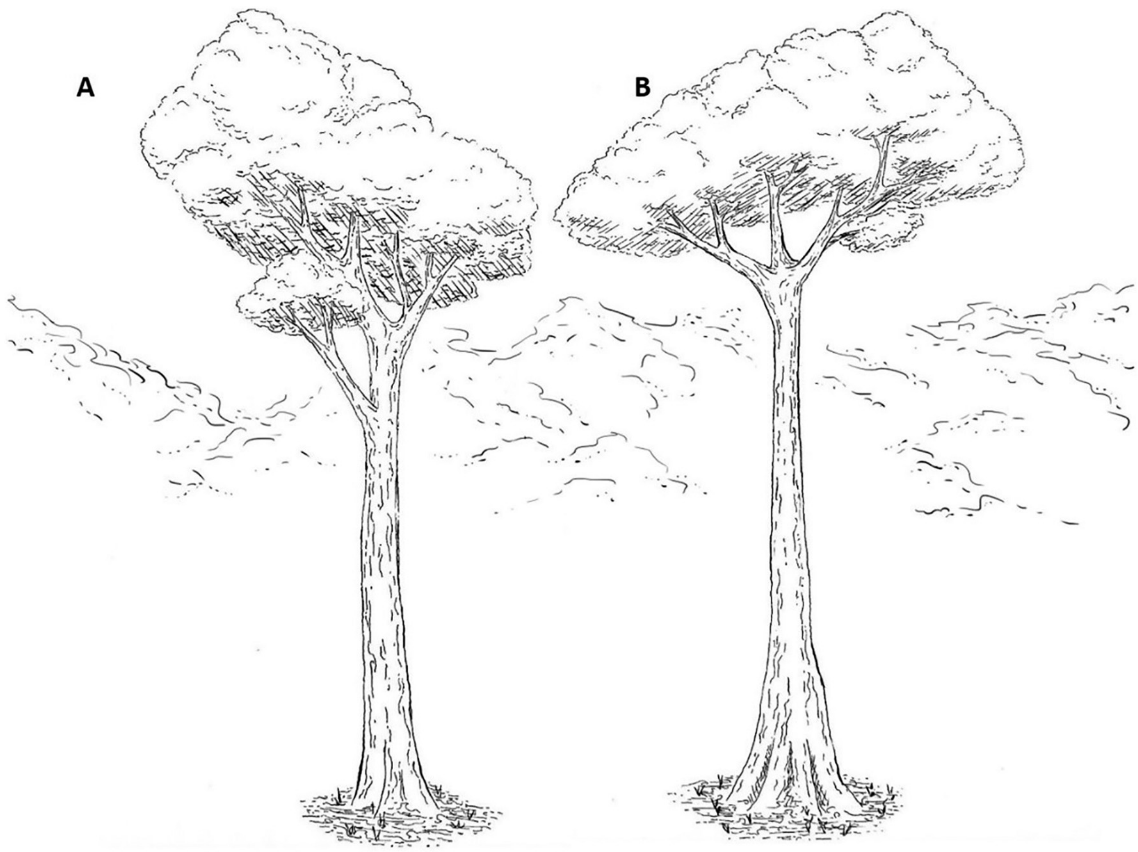

Fig. 6. Comparison of tree architecture. Pseudocontrol emergent trees (A) were 26.6% narrower in crown diameters, had 33.3% less < 45° branches, were 19.6% shorter, and their branches were 35% steeper compared with selected Harpy Eagle nest-trees (B) (illustration: Paula Viana).

suggesting extensive habitat degradation.

In addition to this, Harpy Eagle nestlings are frequently killed during tree felling (Chebez et al., 1990; Alvarez-Cordero, 1996; pers. obs.). The overall consequence is a 'perfect storm' for extensive habitat degradation across the last stronghold of Harpy Eagles, the Amazon basin; and over half of the nest-trees reported here include species sold for US$3.10 per cubic meter or less. As suggested elsewhere (Pinho et al., 2020), we believe that the minimum size paradigm for timber harvesting does not serve the interests of biodiversity conservation and should be complemented by simply sparing all very large ancient trees from logging altogether. This can be seen as a further addition to the plethora of hardly useful natural history-based conservation recommendations. However, we emphasize that sparing very large emergent trees would support a wide range of both biodiversity and ecosystem services benefits (Lindenmayer et al., 2014; Pinho et al., 2020).

In conclusion, we have shown that Harpy Eagles select the largest emergent trees in which to build their enormous nests in any region where they persist. Tree size is highly variable across Neotropical ecoregions and habitats, but selected nest-trees are consistently in the top-ranking size class in any ecoregion. Selected nesting trees are the tallest emergent individuals, exhibit a T-shaped crown architecture, and contain low-angled large branches at the main fork. The surrounding vegetation appears to have a limited role in nesting site selection. We emphasize that our findings indicate a strong overlap between tree species selected by Harpy Eagles and those selected by the growing selective logging industry in the Amazon – and this includes both the composition of tree species and key features in tree architecture. The availability of suitable nesting habitat for Harpy Eagles is unquestionably becoming more restricted, and the extensive habitat degradation in the last stronghold of this species is of prime interest to the upcoming IUCN species evaluation.

CRediT authorship contribution statement

Everton B. P. Miranda: Conceptualization, Writing - Original Draft, Visualization, Formal analysis, Methodology, Software, Validation, Data Curation, Investigation, Resources, Project administration, Funding acquisition. **Carlos A. Peres**: Formal analysis, Methodology, Software, Validation, Writing - Review and Editing. **Miguel Â. Marini**: Writing - Review and Editing, Supervision. **Colleen Downs**: Writing - Review and Editing, Supervision.

Declaration of competing interest

Other than academic rivalries, we declare no conflict of interest.

Acknowledgements

This paper has only been possible thanks to many raptor biologists who bravely overcame the challenges associated with finding an extensive number of nests in remote regions where Harpy Eagles still persist, overcoming the hardships of climbing those nests. CTD is grateful to the University of KwaZulu-Natal and the National Research Foundation (ZA) for funding. Paula Viana produced the nest trees illustrations. Thales Martins, Saulo Thomas and Thaíssa Cabreira provided thoughtful comments on the manuscript. English review was performed by Nickolas Lormand. We thank the financial support of Rufford Small Grants (18743-1, 23022-2 and 31091-B), Rainforest Biodiversity Group, Idea Wild, The Explorer's Club Exploration Fund – "Mamont Scholars Program", Cleveland Metroparks Zoo and SouthWild.com conservation travel system. This work received logistical support from the Peugeot-ONF Carbon Sink Reforestation Project, based at Fazenda São Nicolau, Mato Grosso, Brazil. This Project is a Peugeot initiative to fulfill the Kyoto Protocol directives and is operated by ONF-Brasil. Finally, we thank ICMBio for authorising the project activities under the permit SISBIO 58533.

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