Building a conservation strategy for the harpy eagle in the Amazon Forest

Everton B. P. de Miranda

Submitted in fulfilment of the academic requirements for the degree of

Doctor of Philosophy

in the Discipline of Ecological Sciences

School of Life Sciences

College of Agriculture, Engineering and Science

University of KwaZulu-Natal

Pietermaritzburg Campus

2020

ABSTRACT

Apex predators are threatened worldwide and are considered a priority in the conservation biology agenda. Their decline is associated with habitat loss and degradation, and persecution arising from perceived and actual conflict with humans. The trophic cascades emerging from the loss of apex predators can disrupt the regulation of prey populations, seed dispersal, tree composition and nutrient cycles derived from carcass deposition, with widespread consequences for biodiversity. The harpy eagle (*Harpia harpyja*) is the Earth's largest eagle and is considered a flagship species for Amazon Forest conservation. Harpy eagles are threatened by poaching and by loss and degradation of habitat.

This thesis is comprised of nine chapters—being seven of them data chapters—related to harpy eagle biology and conservation. Chapters 1 and 9 are respectively an introduction and a synthesis about the subjects I approached. In Chapter 2, I created a predictive model of the species range aimed at understanding the current distribution, the contraction of the species distribution compared with the original range, and sites that currently have notable potential for reintroduction of harpy eagles. In Chapter 3, I analyse the effects of environmental parameters such as moonlight and temperature on prey selection probability. In Chapter 4, I aimed to establish the factors that drive the killing of harpy eagles by local people, including the relation between livestock predation and harpy killing. Chapter 5, I explore the nesting, timing and rates of visitation to nests by parent and fledged eagles as it relates to the viability of harpy nests as ecotourism attractions. In Chapter 6, I conducted a meta-analysis that synthesises data on nest tree selection by harpy eagles with the tree species preferences by loggers. In Chapter 7, I test the hypothesis that harpy eagles are agents of accumulation of nutrients, by concentrating decaying remains of prey items at nest sites over decades, thereby biomagnifying soil and foliage nutrient profiles. In Chapter 8, I describe rates of prey delivery by harpy eagles to their nests, and the composition of this prey, to understand the effects of forest loss on harpy eagle feeding ecology.

This multi-faceted set of topics were combined in the field with a new, responsible ecotourism strategy focused on harpy eagles. Subsequently, I hope to build an evidence-based, economically-viable conservation strategy for the largest eagle on Earth, as well as to understand their keystone function of harpy eagles in Neotropical forest ecosystems.

Keywords: Amazon canopy; apex predator; ecotourism; habitat loss; *Harpia harpyja*; livestock predation; nutrient cycling; top predator.

PREFACE

The data described in this thesis were collected in southern Amazonia, Mato Grosso state, Brazil from March 2016 to August 2020. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Professor Colleen T. Downs, and co-supervision of Professor Carlos A. Peres.

This thesis, submitted for the degree of Doctorate of Philosophy in Science in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, School of Life Sciences, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.

[redacted]

Everton Bernardo Pereira de Miranda

October 2020

I certify that the above statement is correct, and as the candidate's supervisor, I have approved this thesis for submission.

[redacted]

……………………………..

Professor Colleen T. Downs

Supervisor

October 2020

COLLEGE OF AGRICULTURE, ENGINEERING AND SCIENCE

DECLARATION 1 - PLAGIARISM

I, Everton Bernardo Pereira de Miranda, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.

2. This thesis has not been submitted for any degree or examination at any other university.

3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
   a. Their words have been re-written, but the general information attributed to them has been referenced
   b. Where their exact words have been used, then their writing has been placed in italics and inside quotation marks, and referenced.

5. This thesis does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the thesis and in the References sections.

Signed: [redacted]

Everton Bernardo Pereira de Miranda

October 2020

COLLEGE OF AGRICULTURE, ENGINEERING AND SCIENCE
DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

Publication 1

EBP Miranda, JFS Menezes, CCL Farias, CA Munn & CA Peres

Species distribution modeling reveals strongholds and potential reintroduction areas for the world's largest eagle

Author contributions:

EBPM conceived the paper, performed data curation, investigation, funding acquisition and wrote the original draft. JFSM performed formal analyses, defined methodology and produced data visualisation. CCLF collected and curated data and reviewed the final draft. CAM performed funding acquisition, reviewed and edited the final draft. CAP contributed valuable comments to the manuscript, reviewed and edited the final draft.

Publication 2

EBP Miranda, CF Kenup, E Campbell-Thompson, FH Vargas, A Muela, R Watson, CA Peres & CT Downs

High moon brightness and low ambient temperatures affect sloth predation by harpy eagles

Author contributions:

EBPM conceived and designed the experiments, analysed the data and authored the draft of the paper. CFK analysed the data, prepared figures, reviewed drafts of the paper. ECT and AM performed the experiments and reviewed drafts of the paper. FHV and RW reviewed drafts of the paper, performed project administration and fundraised. CAP and CTD contributed valuable comments on the manuscript, reviewed drafts of the paper, and approved the final draft.

Publication 3

EBP Miranda, CA Peres & CT Downs

Landowners perceptions of livestock predation: implications for persecution of a keystone apex predator

Author contributions:

EBPM conceived, designed and performed the sampling, analysed the data, produced the figures, performed project administration, fundraised and authored the first draft of the paper. CAP and CTD contributed valuable comments on the manuscript, reviewed drafts of the paper, and approved the final draft.

Publication 4

EBP Miranda, CF Kenup, CA Munn, N Huizinga, N Lormand & CT Downs

Harpy Eagle *Harpia harpyja* nest activity patterns: Potential ecotourism and conservation opportunities in the Amazon Forest

Author contributions:

EBPM formulated research ideas, goals and aims, management activities to collect, curate and store research data, performed project administration, fundraised, and wrote the first draft. CFK performed the analyses, produced the figures and developed the methodology. NH and NL conducted data collection, storing and curation, and reviewed the final draft. CAM performed the fundraising and reviewed the drafts. CTD provided useful comments on the original draft, its critical review and approval.

Publication 5

EBP Miranda, CA Peres, MÂ Marini & CT Downs

Harpy Eagle (*Harpia harpyja*) nest tree selection: Logging in Amazonian Forests threatens Earth's largest eagle

Author contributions:

EBPM formulated research ideas and aims, performed the analyses, management activities to curate and store research data and wrote the first draft. CAP produced the figures, commented and reviewed the drafts. CTD and MÂM provided useful comments on the original draft, its critical review and approval.

Publication 6

EBP Miranda, CA Peres, V Carvalho-Rocha, BV Miguel, N Lormand, N Huizinga, CA Munn, TBF Semedo, TV Ferreira, JB Pinho, VQ Piacentini, MÂ Marini & CT Downs

Tropical deforestation induces thresholds of reproductive viability and habitat suitability in Earth's largest eagles

Author contributions:

EBPM formulated research ideas, goals and aims, performed the analyses, management activities to collect, curate and store research data, raised funds and wrote the first draft. VCR produced the maps and GIS analyses, and reviewed the drafts. BVM, NL and NH curated and stored data, and reviewed the first draft. CAM performed fundraising and the critical review of the first draft. TBFS, TVF, JBP, VQP identified prey species and performed the review of the first draft. CAP, MÂM and CTD provided useful comments on the original draft, its critical review and approval.

Publication 7

EBP Miranda, CA Peres, LG Oliveira-Santos, CT Downs

Long-term concentration of tropical forest nutrient hotspots is generated by a central-place apex predator

Author contributions:

EBPM formulated research ideas, goals and aims, produced the figures, project management, management activities to collect, curate and store research data, raised funds and wrote the first draft. LGOS performed the analyses, produced the figures and critical review of the final draft. CAP developed the methodology, sampling design, critical review and approval of the final draft. CTD provided useful comments on the original draft, its critical review and approval.

[redacted]

Signed: ………………………………………………

Everton Bernardo Pereira de Miranda

October 2020

ACKNOWLEDGEMENTS

Four years ago, when I submitted the first funding proposal to a grant program, one of the referees said that my ideas were not viable, because he had worked in the Amazon Forest for more than 30 years but only saw 2-3 harpy eagle nests. Consequently, my proposal was rejected. The present thesis tells how the lives of a giant eagle, a settler and his gang of Brazil-nut collectors, a tourism entrepreneur, and several cattle ranchers intertwined with my life in tales of violence, desolation, beauty and redemption. Our aim was to build a conservation strategy for harpy eagles while simultaneously disproving this referee—and many other sceptics.

Moving to Mato Grosso tore me from my beloved family and friends, which are mostly based in Rio de Janeiro. Despite being far from them, I was never alone. Rather, they have been with me every time I hum to myself the verses of Bethânia: "*Não mexe comigo, que eu não ando só*". Being distant from you robbed my peace of mind, but thinking of you helped me summon the strength to soldier on when my despair about deforestation threatened to dominate my days. Therefore, I would like to thank my dear Jessica Martins, for patiently waiting for me on countless occasions—I am always late—with eyes full of equal measures of anger and forgiveness. Jessica is still trying to wheedle a harpy eagle feather out of me, as it would be a precious addition to her feather collection, but it continues to be a scientific sample for me. This feather continues to evade a Solomonic solution. I thank Carol Starling and Lara Renzeti for the companionship and never-ending talks about nature, Caio Kenup, 'O Poderoso' Jorge Menezes, and Pedro Uchoa for the patience with my infinite requests for evaluating figures, maps and data analyses. To Heliz, Anna and Michi for making my days happier. I also thank Renato Senden for hilarious talks. I am immensely grateful to my worst friends: Reginaldo 'Regi' Honorato, Igor 'Mazi' Simões, Souza, Daniel 'Caxias' Cerqueira, Gabriel 'Virgem' Cardiano, Jeferson Tinoco, Fernando 'Moita' Martins, Ginayan 'Clamídia' Silveira and Robert

Castilho. I hope you all continue to serve as outstanding examples of what to avoid in life. I thank Bruno Moraes and Bernardo Araujo for being bold enough to choose the writer's path, one I could never walk myself. To my friends at Unemat: Marcos 'Marquinhos' Garcia, Mendelson Lima, Juliana Garlet, Wescley Viana, Vinícius Moraes. To my new friends in Mato Grosso, Jéssica Mudrek, Saulo Thomas, Lorena Castilho, Luciano Ferreira, Domingos Rodrigues, Angele Oliveira, and Eldile Oliveira, for being so very goodhearted and teaching me the ways of this new land. To Ana Tourinho, Sidnei Dantas, and Carlos Tuyama for the many tips and talks. To Harry Greene and Kelly Zamudio for the stimulus: I'm still planning a visit to yours! To Jesus Rivas for reviewing the first version of the project of this thesis. To Leandro Silveira, Anah Jácomo and Christine Strüssmann for the support. To my friends Leandro Macedo and Marcelo Rheingantz, who guided my first steps in science. To my personal illustrator Paula Viana, who with her art, made this thesis far more enjoyable (less boring?). To Raíssa Sepúlvida, of whom I am so proud. To Iris Parrot who brought joy to my days in São Nicolau Farm. To Liz Bonin and Rachel Nuwer, who made my work visible to the world. To my many friends at 'SouthWild.com': Flavia, Wellen, Alex, Nego, Miguel, Lailson and Layra Martins. Leaving home again, this time towards South Africa, gave me the opportunity to forge new bonds. South Africa is now the only other place on Earth besides Brazil where I feel truly at home. There I made excellent new friends: Céline Hanzen, Camille Fritsch, Cormac Price, Cameron Cormac, Jarryd Streicher, Islamiat Abidemi and Matthew Burnett, who made my days so much more wonderful in their company. Cameron, you are the most unique human being I ever met. I hope my friendship has been as rewarding to all of you as much as your outstanding friendship has been for me.

I would like to thank my various financial supporters for very generous support. Firstly, I thank Rufford Small Grants for approving the first grant to start this project. Regarding Rufford, I thank all team members, particularly Jane Raymond, for being so helpful and patient over these years. Additionally, I thank Idea Wild for essentials to climb towering Brazil nut trees. I am grateful to the Explorers Fund, the Rainforest Biodiversity Group and the Cleveland Metroparks Zoo for supporting various parts of this project. I would also like to thank my partners at SEMA Danny Franciele da Silva Dias Moraes, Gabriel Conter de São José and Marcos Ferramosca for the support. Finally, I must thank the major, ongoing support provided by SouthWild.com, a conservation-oriented tourism company that since 2017 has been investing heavily in tourism to protect harpy eagles. Charles Munn, its CEO, has been one of the most amazing human beings I have met. Even if at least once a week he manages to irritate everyone who loves him. Charlie has drawn back the green curtain to reveal a gamut of new, conservation-oriented methods of wildlife tourism that can produce ongoing support for conservation. Of course, it is very important that I thank the French government's "ONF Brasil", particularly two impressive managers of that spectacular reforestation project: Cleide Arruda, who first invited me to set up my project at their ambitious carbon-capture property, and Estelle Dugachard, who continue to this day the outstanding hospitality and logistical support for my project. The two years of my life lived in the Amazon Forests of ONF-Brasil made a long-lasting impression on my worldview.

Many people have helped me on the day-to-day activities on the fieldwork in the Amazon Forest. Firstly, I must thank the man who was my eyes, hands and feet when I arrived in the Amazon Forest: Gilberto Araújo. This thesis would not exist without him, and I most apologize to Alaíde, Luis and Matheus for keeping him out of home for so long. Roberto Stofel, our climber, driver, boat driver, chainsaw operator, porter, bush guide and cameraman (plus everything else you may imagine) has seen much of the worst I have to show as a human being, and endured with me the toughest days imaginable of fieldwork in the Amazon, never complaining for a single second. I—twice his mass and half his stamina—was complaining all the time. I thank Jonas Medeiros, Nickolas Lormand, Niki Huizinga and Bruna Miguel, who left their comfy homes for long periods to join me in adventures in the Amazon Forest. I also thank Elaine Dione for the outstanding help regarding rescued eaglets. Additionally, I would like to thank the many landowners who allowed us to work with the harpy eagles on their properties and partnered with my project in the harpy tourism ventures. In addition to the landowners, it is critical that I thank the hundreds of Brazil nut collectors, thousands of indigenous people, and dozens of field biologists who helped me to find harpy eagle nests, something I could never do all by myself.

Other than assistance in the difficult fieldwork, I also benefited tremendously from outstanding intellectual help from brilliant scientists. In particular, I would like to thank Colleen Downs and Carlos Peres for accepting the challenge to advise someone as stubborn and arrogant as myself. I hope that the collaboration that we established during these years will be the seeds of a much longer relationship, and that my rough ways did not overly stress these extremely busy scientists. I must further thank Jorge Menezes, Caio Kenup and Gustavo Oliveira-Santos for saving me when my bumbling statistical skills were flagging, and I required serious assistance. Finally, I must thank every single friend who helped me to polish and improve my English, which frequently was found lacking.

I would like to thank my family for the endless support for me as a scientist. Through all these years, I never heard a word from them that was anything but patience and encouragement. When I was a kid, my brothers Cássio and Guto, my sister Letícia, and my sister-in-law Tatiana sparked and encouraged my curiosity towards nature, and they played a large role in my education. I cannot say less about the proud eyes of Mariana and Simone, my second family, where I always enjoy a very warm reception when I visit Rio. Finally, I must thank my father, José Luís Barros de Miranda. His failing senses now sometimes mask the powerful intellect that he displayed in his earlier years. The progressive fading of his former brilliance can serve as a cautionary tale for young, vain persons such as myself.

Finally, I would like to offer a word of advice to all people that read these words and consider following a similar path in conservation. The hardest lesson that I learned in the last few years is that you can also make a mistake from love. Love for nature does not make anyone infallible. Love rather makes you more vulnerable to making a mistake in the conservation path. I have committed many mistakes: against myself, against nature and against others. If you are reading these words and I have ever made a mistake towards you, please forgive me. In those fiery years, I have been blunt, impolite and tremendously rude on countless occasions, often with people who did not deserve it. I am sorry. Mea culpa. If otherwise, I have helped you—perhaps with just a little smirk—I would like you to know:

I will love to do much more.

CONTENTS

FIGURES

TABLES

CHAPTER 1

INTRODUCTION

1.1 Background

Burgeoning human populations with increasing living standards have pressed natural habitats in ever-growing rates all over the world (Motesharrei *et al.* 2016). That has been causing the clearing of many ecoregions to give space to cattle ranching and agriculture (Crist *et al.* 2017). Summed to this is the degradation of the remaining habitats in the form of logging and poaching (Fa *et al.* 2002, Richardson & Peres 2016). Those trends have been particularly worrisome regarding tropical forests (Giam 2017), because of their role as ecoregions of highest biodiversity levels (Keil & Chase 2019, ter Steege *et al.* 2019), not to mention the extensive environmental services in the form of carbon-storing and water cycling (Sampaio *et al.* 2007, Dargie *et al.* 2017). Tropical forests have thus been a major topic of environmental conservation.

Between the tropical forests threatened by the issues pointed above are the Congo Basin, the Southeast Asia Rainforest, and the Amazon Forest (Dargie *et al.* 2017, Tölle *et al.* 2017, Carrero *et al.* 2020). The latter stands out as the most biodiverse ecoregion on Earth (ter Steege *et al.* 2019), being also the largest rainforest (Fearnside 2005). In Brazil, the Amazon Forest has been incinerated from the outside-in by a cattle-ranching frontier know as Arc of Deforestation (Nogueira *et al.* 2008). Amazon's South, Southeast and Western borders have been subjected to extensive human migration starting in the 70s, sponsored by the state (Villas Boas & Villas Boas 1994, Schneider & Peres 2015). The usual succession of economic activities in this region starts with logging, later giving space to pasture after the forest is carbonised (Junior & Lima 2018, Carrero *et al.* 2020, Eri *et al.* 2020). Finally, soybean and corn cultivation is established in plain sections of land (Junior & Lima 2018). Since this region has been occupied after the promulgation of the main legal regulation regarding nature protection in private lands of Brazil—the Forest Code (Anonymous 2012)—substantial portions of land remain covered in forest as demanded by law (known as 'Legal Reserves'), with relatively high structural connectivity given by the corridors formed by riparian forests that are also demanded by law (Lees & Peres 2008, Michalski *et al.* 2010, Zimbres *et al.* 2018). This mosaic of habitats allows extensive presence of larger vertebrates within productive lands (Lima *et al.* 2019, Oliveira *et al.* 2019), including several apex predators (Michalski *et al.* 2006, Trinca *et al.* 2008, Miranda *et al.* 2016).

The conservation of top predators is vital for the functioning of ecosystems (Terborgh & Estes 2013). A wide range of ecosystems are losing their top predators (Ripple *et al.* 2014), generating multiple cascading effects because of the loss of population regulation of prey species (Ripple & Beschta 2007, Heithaus *et al.* 2014). Examples of trophic cascades resulting from large-vertebrate loss include the degradation of riparian environments by ungulates following the extirpation of wolves (*Canis lupus*) from Yellowstone National Park, USA (Dobson 2014), or the degradation of seagrass beds by green turtles (*Chelonia mydas*) where sharks had been extirpated (Heithaus *et al.* 2014). Consequently, top predators are prioritised in the conservation agenda globally (Sergio *et al.* 2014).

The harpy eagle (*Harpia harpyja*) is an apex predator of the Amazon Forest (Aguiar-Silva *et al.* 2014). Additionally, the harpy eagle is the largest eagle in the world, averaging 5.9 kg for males and 7.3 kg for females (EBPM, unpublished data). Its key role as a predator has been demonstrated by the dynamics of prey populations in their absence, altering herbivory and seed dispersal processes, with drastic consequences for the forest ecosystem (Terborgh *et al.* 2001, Orihuela *et al.* 2014). The harpy eagle is directly threatened by shooting in retaliation or prevention from depredation of domestic animals (Trinca *et al.* 2008, Watson *et al.* 2016). It is further threatened by habitat loss and degradation (Aguiar-Silva 2016). Much like other apex predators, harpy eagles have disproportionately large ecological requirements, consuming about 800 g of prey per day (Touchton *et al.* 2002). The harpy eagle occurs at relatively low densities, ranging from 4-6 nests per 100 km² (Vargas-González & Vargas 2011), and they feed mainly on medium-sized, arboreal vertebrates, such as sloths and primates, but also prey upon large birds and some reptiles (Miranda 2015, 2018). Conserving harpy eagles is a major challenge because of conflicts between these large eagles and rural communities, their natural rarity, the high cost of research, the logistical complications of implementing viable conservation programs, and the current low return on investment for society when public money is spent on predator conservation.

Monitoring the decline of top predators, however, is far from trivial, inexpensive, or safe (Terborgh & Estes 2013). Harpy eagles nearly disappeared from Atlantic Forests and Central America (Anfuso *et al.* 2008, Sánchez-Lalinde *et al.* 2011, Vargas-González & Vargas 2011, Watson *et al.* 2016), and much of the range contraction happened decades before any conservation initiatives were established. However, mapping this decline from the ground is unfeasible. Harpy eagles are highly secretive and even finding a single nest is a prized event for ornithologists (Pereira & Salzo 2006, Ubaid *et al.* 2011, Rotenberg *et al.* 2012). Considering that the harpy eagle has a prolonged range contraction and that the Amazon Forest is their last stronghold, a distribution range modelling effort is timely to establish conservation priorities in a landscape scale (D'Elia *et al.* 2015). It also facilitates understanding how this species is faring in anthropogenic degraded landscapes, where retaliation for livestock predation is a driver of its decline (Trinca *et al.* 2008, Gusmão *et al.* 2016).

Several theoretical frameworks have been proposed to advance knowledge about the conservation of predators that are threatened by human-wildlife conflict resulting from the predation of domestic livestock (Cavalcanti & Gese 2010, Miranda *et al.* 2016). The Theory of Planned Behaviour, which assumes that a person's attitude is formed by a subjective social norm and perception of behavioural control, can be applied to solving this problem (Marchini & Macdonald 2012). Predators can include domestic prey in their diet as a response to habitat loss or degradation, but predation over easy-to-capture domestic livestock is also known (Odden *et al.* 2013, Mondragón *et al.* 2017). Understanding the in-depth composition of their diet, and the landscape where they live can be used to identify which forms of land use can boost or facilitate livestock predation (Das 2014). Prey composition can be affected by subtle variation in traits related with seasonality for apex predators, which can also affect the toll over prey species (Azevedo & Verdade 2012) or even the predation of livestock (Edge *et al.* 2011). Landscapes traits can also help to predict up to which point apex predators can tolerate habitat loss, as this permanently impact feeding ecology (Schweiger *et al.* 2015, Ellis & Gombobaatar 2020). Combining this with knowledge on the socioeconomic and psychological vectors that motivate the preventive or retaliatory killing of harpy eagles can predict its occurrence and, consequently, prevent it. Additionally, we can calculate the costs of those losses and plan to compensate for them, since Brazil is one of the few countries that lack a compensation program for predator's damages to private property. These costs can be estimated and then matched by NGOs, state-owned environmental bureaus or the private sector such as birding and ecotourism companies.

Besides providing funds for compensation, integrating predators into local economies through ecotourism is another option available for the conservation of predators. Tourism is a tool that has shown potential to overcome obstacles like livestock predation (Macdonald *et al.* 2017, Tortato *et al.* 2017). For establishing an ecotourism alliance, however, it is necessary to learn when and for how long harpy eagles are active to allow successful observation experiences. This prevents harm to the animals, as observed for other species (Haskell *et al.* 2015, Muntifering *et al.* 2019), as well as determining how many nests are necessary to observe the eagles year-round. Understanding harpy eagle activity patterns using research creates functional systemic and economic links between conservation, research and tourism companies, consequently benefiting local people (Kirkby *et al.* 2011). Furthermore, that strategy is self-funding and alleviates problems arising from livestock predation through compensation programs. Considering that harpy eagles are a highly sought-after sighting by ecotourists (Pivatto *et al.* 2007), we aim to structure our initiative so that the ecotourism visits will gain their own momentum and continue after the present project has finished. Harpy eagles are rare but at the same time predictable in spatial occurrence, since they nest over the same trees for decades in a row (Alvarez-Cordero 1996).

Harpy eagles nest sites are typically located in giant emergent tropical forest trees that have an average height of primary branch forks of >30 m (Giudice 2005). The repeated use of the same nest trees and the open architecture of the high forks in these trees allow close monitoring of the diet of these eagles during one of the most critical phase of their life cycles: reproduction. The harpy eagle has the longest known reproductive cycle of any of the world's ~10,000 bird species, as 2.5-3 years are required to produce only a single fledgling (Muñiz-López *et al.* 2012, Muñiz-López 2017). Many of the emergent tree species used by the eagle as nest sites are also targets of the timber industry (Giudice 2005). No study to date, however, has analysed the harpy eagle's selection of nest trees in either structural, economic or ecological terms, although several papers describe more than 100 nest trees throughout the distribution of the species (Giudice 2005, Luz 2005, Miranda *et al.* 2017, 2018). A combined meta-analysis of existing databases on the floristic composition and trade of commercially-valuable timber can provide essential information on the selection of trees as breeding habitat, as well as the taxonomic and structural overlap with the timber industry. This analysis will also provide essential knowledge about the conservation of large emergent trees that harbour both harpy eagle nests and many other ecological functions (Clark & Clark 1996, Lindenmayer *et al.* 2014).

Nesting within a single nest tree for decades has potential to strongly alter nutrient cycles through the spatially-heterogeneous deposition of prey carcasses, as it has been shown for many apex predators (Ben-David *et al.* 1998, Hurteau *et al.* 2015). Soil and foliar nutrient heterogeneity is an important determinant of both above and below-ground biodiversity (Tuomisto *et al.* 2003, Bump *et al.* 2009). The harpy eagle is a large-bodied central foraging predator because of the close and long association with the same nest tree (Alvarez-Cordero 1996). Testing the hypothesis that harpy eagles affect soil heterogeneity and vegetation quality by the accumulation of carcass remains would demonstrate for the first time a mechanism by which a top predator affects soil mosaics and therefore biodiversity in a tropical forest ecosystem.

1.2 Study area

This research project was carried out in southern Amazonia, in the northern part of Mato Grosso State in a region known by conservationist as the "Arc of Deforestation" (Nogueira *et al.* 2008). This region of the Amazon Forest is composed by the southern, south-eastern and eastern regions of the Amazon Basin. Between 2016 and 2020, I worked in the northern part of Mato Grosso State, Brazil, using ONF-Brasil's São Nicolau farm as headquarters (9°51'20.7"S, 58°14'53.9"W). The climate is humid and hot, with annual mean temperatures of 24ºC, 80% humidity (Vourlitis *et al.* 2002) and annual rainfall averaging 2000 mm (Noronha *et al.* 2015) decreasing in a southwestern gradient. The dry season occurs between April and September and the rainy season between October and March. The region includes primary and secondary open ombrophilous Amazon

Forest (Veloso *et al.* 1991). The succession of anthropogenic land-use changes and related economic activities in the region generally starts with selective logging (Richardson & Peres 2016), followed by forest incineration and planting of pasture for cattle (Eri *et al.* 2020), with smaller amounts of land occupied by plantations of soybeans and other grains (Junior & Lima 2018). State-sponsored migrants from Southern Brazil (where harpy eagles have been extirpated for several human generations) now inhabit this region (Schneider & Peres 2015). Therefore, these settlers have relatively little knowledge of forest use or the existence and importance of harpy eagles. Mato Grosso's high deforestation rate (representing 34.5% increase of Amazon Forest loss in 2020 when compared with 2019, according to PRODES; Anonymous 2020) has a profound impact on biodiversity (Boubli *et al.* 2019, Costa-Araújo *et al.* 2019).

1.3 Problem statement

Conservation of an apex predator in a complex environmental and societal mosaic is a dilemma requiring novel and creative solutions for multi-scale set of problems, ranging from distribution range modelling and flow of nutrients across the ecosystem to tourism and socio-economic relationship with locals. Combining the above towards a conservation strategy focused on harpy eagles has the potential to be an important contribution. This will, for the first time, allow the development of an evidence-based, economically-viable conservation strategy for the largest eagle on Earth, the harpy eagle, in its threatened Amazon Forest habitat.

1.4 Aims and objectives

The overall aim of this study was to assess harpy eagle conservation at several levels:

(1) I described the suitability of Neotropical forests for harpy eagles, with emphasis on Amazon and Atlantic Forests. I aimed to assess the suitability of Amazon Forest, harpy eagle's last stronghold, where habitat loss and degradation is advancing at a rapid pace. Additionally, I evaluated Atlantic Forest sites for harpy eagle suitable for reintroduction.

(2) I explored environmental determinants of prey capture rates of reintroduced harpy eagles, focusing on: (a) assessing the effects of seasonality—like temperature, rainfall and leaf deciduousness—on sloth capture rates by harpy eagles; and (b) assessing how moonlight could affect sloth and nocturnal prey predation rates;

(3) I interviewed locals to establish socio-economic and environmental parameters capable of predicting the occurrence of livestock predation and magnitude of retaliatory or preventive killings by local people, through structured questionnaires;

(4) Using camera-traps, I collected fine-grain data on the timing of harpy eagle visits to nests, as well as uniquely detailed data on probabilities of viewing eagles during different stages of the nest cycle. Because ecotourism is a prospective tool to help solve several conservation issues of harpy eagles, I also investigated how many nests are necessary to offer the basis for it to happen reliably;

(5) I 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. My motivation was to prevent or reduce the detrimental effects of forest degradation on the critical nesting habitat requirements of the harpy eagle. I determined patterns of nest-tree preference or avoidance by harpy eagles in relation to tree architecture and surrounding land cover. Finally, I provided a checklist of harpy eagle nest-tree species, and the present extractive market demand on these tree species, particularly in relation to the most commercially-valuable timber species;

(6) I aimed to understand the impacts of forest loss on harpy eagle feeding ecology, through the following different questions: (*i*) effects of harpy eagle sexual dimorphism on feeding ecology; (*ii)* effects of landscape degradation on predation of non-forest and disturbance-tolerant species; (*iii)* effects of landscape degradation over prey delivery rates and biomass delivered to eaglets; (*iv)* tolerance threshold of harpy eagles to deforestation levels and associated prey scarcity. By exploring the above, I estimated the consequences of the extensive Amazon deforestation on the persistence of breeding pairs of harpy eagles.

(7) I tested the hypothesis that harpy eagle nests represent macro- and micro-nutrient centralisers by concentrating discarded prey carcasses underneath nest sites over decades, thereby bio-magnifying the nutrient profile in both the soil and associated plants. As heterogeneity is one of the main aspects that correlates with biodiversity, loosing harpy eagles may means loosing landscape engineers that create this heterogeneity.

1.5 Structure of the thesis

This thesis is organised with data chapters prepared for publication or published in international peer-reviewed journals. Chapter 1 represents an introduction to the subject of harpy eagles and the conservation problems, scientific concepts and solutions provided by this thesis. The next seven data chapters are four published, one accepted, one submitted and one in preparation to peer-reviewed journals. Each of these is formatted according to the respective journal formats in which it was published, or to which we intend or have submitted it. Some repetition of the “study area” section was therefore unavoidable because of most data was collected over the same region. However, this is deemed to be of little concern as this format allows the reader to read each chapter separately without losing the overall context of the thesis. Figures and tables follow a continuous numbering through the thesis followed by the numbering per specific chapter. The hypotheses or predictions are presented in each chapter.

1.6 References

AGUIAR-SILVA, F., T. SANAIOTTI, and B. LUZ. 2014. Food habits of the Harpy Eagle, a top predator from the Amazonian rainforest canopy. J. Raptor Res. 48: 24–45.

AGUIAR-SILVA, H. 2016. Uso e seleção de recursos por harpia em múltiplas escalas espaciais: persistência e vulnerabilidade. INPA.

ALVAREZ-CORDERO, E. 1996. Biology and conservation of the harpy eagle in Venezuela and Panama. DSc Thesis. University of Florida, Florida, USA.

ANFUSO, J., M. SUAREZ, and J. CHEBEZ. 2008. Nuevo Registro de Nidificación de la harpía (*Harpia harpyja*) en la provincia de Misiones, Argentina y Consideraciones sobre su conservación. Nótulas Faunísticas 21: 1–13.

ANONYMOUS. 2012. Novo Código Florestal, Lei 12.651 de 25 de maio de 2012, Dispõe sobre a proteção da vegetação nativa. Subchefia de assuntos jurídicos, Brasília Available at: http://www.planalto.gov.br/ccivil_03/_ato2011-2014/2012/lei/l12651.htm.

ANONYMOUS. 2020. Monitoramento do Desmatamento da Floresta Amazônica Brasileira por Satélite. PRODES Rep. Available at: http://www.obt.inpe.br/OBT/assuntos/programas/amazonia/prodes.

AZEVEDO, F. C. C., and L. M. VERDADE. 2012. Predator-prey interactions: jaguar predation on caiman in a floodplain forest. J. Zool. 286: 200–207.

BEN-DAVID, M., T. A. HANLEY, and D. M. SCHELL. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. Oikos 83: 47–55.

BOUBLI, J. P. ET AL. 2019. On a new species of titi monkey (Primates: *Plecturocebus* Byrne et al., 2016), from Alta Floresta, southern Amazon, Brazil. Mol. Phylogenet. Evol. 132: 117–137.

BUMP, J. K., R. O. PETERSON, and J. A. VUCETICH. 2009. Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. Ecology 90: 3159–3167.

CARRERO, G. C., P. M. FEARNSIDE, D. R. DO VALLE, and C. DE SOUZA ALVES. 2020. Deforestation Trajectories on a development frontier in the Brazilian Amazon: 35 years of settlement colonization, policy and economic shifts, and land accumulation. Environ. Manage. 1–19.

CAVALCANTI, S., and E. GESE. 2010. Kill rates and predation patterns of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. J. Mammal. 91: 722–736.

CLARK, D. B., and D. A. CLARK. 1996. Abundance, growth and mortality of very large trees in Neotropical lowland rain forest. For. Ecol. Manage. 80: 235–244.

COSTA-ARAÚJO, R., F. R. DE MELO, G. R. CANALE, S. M. HERNÁNDEZ-RANGEL, M. R. MESSIAS, R. V. ROSSI, F. E. SILVA, M. N. F. DA SILVA, S. D. NASH, J. P. BOUBLI, I. P. FARIAS, and T. HRBEK. 2019. The Munduruku marmoset: a new monkey species from southern Amazonia. PeerJ 7: e7019.

CRIST, E., C. MORA, and R. ENGELMAN. 2017. The interaction of human population, food production, and biodiversity protection. Science 356: 260–264.

D'ELIA, J., S. M. HAIG, M. JOHNSON, B. G. MARCOT, and R. YOUNG. 2015. Activity-specific ecological niche models for planning reintroductions of California condors (*Gymnogyps* *californianus*). Biol. Conserv. 184: 90–99.

DARGIE, G. C., S. L. LEWIS, I. T. LAWSON, E. T. MITCHARD, S. E. PAGE, Y. E. BOCKO, and S. A. IFO. 2017. Age, extent and carbon storage of the central Congo Basin peatland complex. Nature 542: 86–90.

DAS, C. S. 2014. Causes, consequences and cost-benefit analysis of the conflicts caused by tiger straying incidents in Sundarban, India. Proc. Zool. Soc 68: 120–130.

DOBSON, A. P. 2014. Yellowstone wolves and the forces that structure natural systems. PLoS Biol. 12: e1002025.

EDGE, J. L., D. E. BEYER JR, J. L. BELANT, M. J. JORDAN, and B. J. ROELL. 2011. Livestock and domestic dog predations by wolves in Michigan. Human-Wildlife Interact. 5: 66–78.

ELLIS, D. H., and S. GOMBOBAATAR. 2020. Ecology of the Golden Eagle in Mongolia, Part 2: Prey. J. Raptor Res. 54: 30–37.

ERI, M., C. A. DA S. JUNIOR, M. LIMA, N. L. S. JÚNIOR, J. F. DE OLIVEIRA-JÚNIOR, P. E. TEODORO, G. F. CAPRISTO-SILVA, G. CAIONE, and C. A. PERES. 2020. Capitalizing on opportunities provided by pasture sudden death to enhance livestock sustainable management in Brazilian Amazonia. Environ. Dev. 4: 100499.

FA, J. E., C. A. PERES, and J. MEEUWIG. 2002. Bushmeat exploitation in tropical forests: an intercontinental comparison. Conserv. Biol. 16: 232–237.

FEARNSIDE, P. M. 2005. Deforestation in Brazilian Amazonia: History, rates, and consequences. Conserv. Biol. 19: 680–688.

GIAM, X. 2017. Global biodiversity loss from tropical deforestation. Proc. Nat. Acad. Sci. 114: 5775–5777.

GIUDICE, R. 2005. Arquitectura de árboles y estructura de la vegetación del bosque como factores determinantes en la anidación del Águila Arpía (*Harpia harpyja* Linnaeus 1878) en la cuenca baja del Río Tambopa. Universidad Nacional Agraria La Molina.

GUSMÃO, A. C., A. BANHOS, F. H. AGUIAR-SILVA, L. S. DE SOUZA, T. M. SANAIOTTI, TANIA MARGARETE SILVA, ADRIANO MARTINS DA COSTA, L. E. OLIVEIRA, W. G. DE MORAIS, and S. F. FERRARI. 2016. Records of the occurrence, nesting, and hunting of the Harpy Eagle (*Harpia harpyja*) (Aves: Accipitridae) in Rondônia. Atualidades Ornitológicas 190: 18–23.

HASKELL, P. J., A. MCGOWAN, A. WESTLING, A. MÉNDEZ-JIMÉNEZ, C. A. ROHNER, K. COLLINS, M. ROSERO-CAICEDO, J. SALMOND, A. MONADJEM, A. D. MARSHALL, and S. J. PIERCE. 2015. Monitoring the effects of tourism on whale shark *Rhincodon typus* behaviour in Mozambique. Oryx 49: 492–499.

HEITHAUS, M. R., T. ALCOVERRO, R. ARTHUR, D. A. BURKHOLDER, K. A. COATES, M. J. A. CHRISTIANEN, N. KELKAR, S. A. MANUEL, A. J. WIRSING, W. J. KENWORTHY, and J. W. FOURQUREAN. 2014. Seagrasses in the age of sea turtle conservation and shark overfishing. Front. Mar. Sci. 1: 28.

HURTEAU, L. A., A. MOOERS, J. D. REYNOLDS, and M. D. HOCKING. 2015. Salmon nutrients are associated with the phylogenetic dispersion of riparian flowering-plant assemblages. Ecology 15-0379.1.

JUNIOR, C. S., and M. LIMA. 2018. Soy Moratorium in Mato Grosso: deforestation undermines the agreement. Land Use Policy 71: 540–542.

KEIL, P., and J. M. CHASE. 2019. Global patterns and drivers of tree diversity integrated across a continuum of spatial grains. Nat. Ecol. Evol. 3: 390–399.

KIRKBY, C. A., R. GIUDICE, B. DAY, K. TURNER, B. S. SOARES-FILHO, H. OLIVEIRA-RODRIGUES, and D. W. YU. 2011. Closing the ecotourism-conservation loop in the Peruvian Amazon.

Environ. Conserv. 38: 6–17.

LEES, A. C., and C. A. PERES. 2008. Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. Conserv. Biol. 22: 439–449.

LIMA, M., C. A. PERES, M. I. ABRAHAMS, C. A. DA SILVA JUNIOR, G. DE MEDEIROS COSTA, and R. C. DOS SANTOS. 2019. The paradoxical situation of the white-lipped peccary (*Tayassu pecari*) in the state of Mato Grosso, Brazil. Perspect. Ecol. Conserv. 17: 36–39.

LINDENMAYER, D. B., W. F. LAURANCE, J. F. FRANKLIN, G. E. LIKENS, S. C. BANKS, W. BLANCHARD, P. GIBBONS, K. IKIN, D. BLAIR, L. MCBURNEY, A. D. MANNING, and J. A. R. STEIN. 2014. New policies for old trees: averting a global crisis in a keystone ecological structure. Conserv. Lett. 7: 61–69.

LUZ, B. B. DA. 2005. Características de árvores emergentes utilizadas por Gavião-real (*Harpia harpyja*) para nidificação no centro e leste da Amazônia Brasileira.

MACDONALD, C., A. J. GALLAGHERB, A. BARNETTD, J. BRUNNSCHWEILERE, D. S. SHIFFMANF, and N. HAMMERSCHLAGA. 2017. Conservation potential of apex predator tourism. Biol. Conserv. 215: 132–141.

MARCHINI, S., and D. W. MACDONALD. 2012. Predicting ranchers' intention to kill jaguars: case studies in Amazonia and Pantanal. Biol. Conserv. 147: 213–221.

MICHALSKI, F., R. L. P. BOULHOSA, A. FARIA, and C. A. PERES. 2006. Human-wildlife conflicts in a fragmented Amazonian Forest landscape: Determinants of large felid depredation on livestock. Anim. Conserv. 9: 179–188.

MICHALSKI, F., J. P. METZGER, and C. A. PERES. 2010. Rural property size drives patterns of upland and riparian forest retention in a tropical deforestation frontier. Glob. Environ. Chang. 20: 705–712.

MIRANDA, E. 2015. Conservation implications of harpy eagle *Harpia harpyja* predation patterns. Endanger. Species Res. 29: 69–79.

MIRANDA, E. B. P. 2018. Prey composition of harpy eagles (*Harpia harpyja*) in Raleighvallen, Suriname. Trop. Conserv. Sci. 11: 1–8.

MIRANDA, E. B. P., E. CAMPBELL-THOMPSON, A. MUELA, and F. H. VARGAS. 2018. Sex and breeding status affect prey composition of Harpy Eagles *Harpia harpyja*. J. Ornithol. 159: 141–150.

MIRANDA, E. B. P., R. P. RIBEIRO-JR., and C. STRÜSSMANN. 2016. The ecology of human-anaconda conflict: a study using internet videos. Trop. Conserv. Sci. 9: 26–60.

MONDRAGÓN, J., A. CASTILLO, A. HOOGESTEIJN, and H. MEYER. 2017. Livestock predation by jaguars *Panthera onca* in south-eastern Mexico: the role of local peoples' practices. Oryx 51: 254–262.

MOTESHARREI, S., J. RIVAS, E. KALNAY, G. R. ASRAR, A. J. BUSALACCHI, R. F. CAHALAN, M. A. CANE, R. R. COLWELL, K. FENG, R. S. FRANKLIN, and K. HUBACEK. 2016. Modeling sustainability: population, inequality, consumption, and bidirectional coupling of the Earth and Human Systems. Nat. Sci. Rev. 3: 470–494.

MUÑIZ-LÓPEZ, R. 2017. Harpy Eagle (*Harpia harpyja*) mortality in Ecuador. Stud. Neotrop. Fauna Environ. 30: 1–5.

MUÑIZ-LÓPEZ, R., R. LIMIÑANA, G. CORTÉS, and V. URIOS. 2012. Movements of harpy eagles *Harpia harpyja* during their first two years after hatching. Bird Study 59: 509–514.

MUNTIFERING, J. R., W. L. LINKLATER, R. NAIDOO, S. URIKHOB, P. D. PREEZ, P. BEYTELL, S. JACOBS, and A. T. KNIGHT. 2019. Sustainable close encounters: integrating tourist and animal behaviour to improve rhinoceros viewing protocols. Anim. Conserv. 22: 189–197.

NOGUEIRA, E. M., B. W. NELSON, P. M. FEARNSIDE, M. B. FRANÇA, and Á. C. A. DE OLIVEIRA. 2008. Tree height in Brazil's 'arc of deforestation': Shorter trees in south and southwest Amazonia imply lower biomass. For. Ecol. Manage. 255: 2963–2972.

NORONHA, J. C., M. M. LIMA, C. L. VELASQUEZ, E. J. ALMEIDA, A. B. BARROS, and D. J. RODRIGUES. 2015. Update das espécies de anuros da Fazenda São Nicolau, Mato Grosso, Brasil. Sci. Electron. Arch. 8: 15–25.

ODDEN, J., E. B. NILSEN, and J. D. C. LINNELL. 2013. density of wild prey modulates lynx kill rates on free-ranging domestic sheep. PLoS One 8: e79261. Available at: http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0079261#pone-0079261-g002 [Accessed February 17, 2015].

OLIVEIRA, A. T. M., C. S. SÃO BERNARDO, F. R. MELO, M. SANTOS-FILHO, C. A. PERES, and G. R. CANALE. 2019. Primate and ungulate responses to teak agroforestry in a southern Amazonian landscape. Mamm. Biol. 96: 45–52.

ORIHUELA, G., J. TERBORGH, N. CEBALLOS, and K. GLANDER. 2014. When top-down becomes bottom up: behaviour of hyperdense howler monkeys (*Alouatta seniculus*) trapped on a 0.6 Ha Island. PLoS One 9: e82197.

PEREIRA, A. D. M. M., and I. SALZO. 2006. Primeiro registro da nidificação de *Harpia harpyja* (Falconiformes, Accipitridae) na Serra da Bodoquena (Mato Grosso do Sul, Brasil). Rev. Bras. Ornitol. 14: 157–160.

PIVATTO, M. A. C., J. SABINO, S. FAVERO, and I. L. MICHELS. 2007. Perfil e viabilidade do turismo de observação de aves no Pantanal Sul e Planalto da Bodoquena (Mato Grosso do Sul) segundo interesse dos visitantes. Rev. Bras. Ornitol. 15: 520–529.

RICHARDSON, V. A., and C. A. PERES. 2016. Temporal Decay in Timber Species Composition and Value in Amazonian Logging Concessions. PLoS One 11: e0159035.

RIPPLE, W. J., and R. L. BESCHTA. 2007. Restoring Yellowstone's aspen with wolves. Biol. Conserv. 138: 514–519.

RIPPLE, W. J., J. A. ESTES, R. L. BESCHTA, C. C. WILMERS, E. G. RITCHIE, M. HEBBLEWHITE, J. BERGER, B. ELMHAGEN, M. LETNIC, M. P. NELSON, O. J. SCHMITZ, D. W. SMITH, A. D. WALLACH, and A. J. WIRSING. 2014. Status and ecological effects of the world's largest carnivores. Science 343: 151–164.

ROTENBERG, J., J. MARLIN, L. POP, and W. GARCIA. 2012. First record of a Harpy Eagle (*Harpia harpyja*) nest in Belize. Wilson J. Ornith. 124: 292–297.

SAMPAIO, G., C. NOBRE, M. H. COSTA, P. SATYAMURTY, B. S. SOARES-FILHO, and M. CARDOSO. 2007. Regional climate change over eastern Amazonia caused by pasture and soybean cropland expansion. Geophys. Res. Lett. 34: L17709.

SANCHEZ-LALINDE, C., L. F. SILVEIRA, F. VELEZ-GARCIA, A. CA. CORNÉLIO, and M. R. ALVAREZ. 2011. Records of the Harpy Eagle (*Harpia harpyja*) in the Serra Bonita reserves complex, Camacan, Bahia, with evidence of breeding. Rev. Bras. Ornitol. 19: 436–438.

SCHNEIDER, M., and C. A. PERES. 2015. Environmental costs of government-sponsored agrarian settlements in Brazilian Amazonia. PLoS One 10: e0134016. Available at: http://dx.plos.org/10.1371/journal.pone.0134016 [Accessed August 3, 2016].

SCHWEIGER, A., H.-J. FÜNFSTÜCK, and C. BEIERKUHNLEIN. 2015. Availability of optimal-sized prey affects global distribution patterns of the golden eagle *Aquila chrysaetos*. J. Avian Biol. 46: 81–88.

SERGIO, F., O. J. SCHMITZ, C. J. KREBS, R. D. HOLT, M. R. HEITHAUS, A. J. WIRSING, W. J. RIPPLE, E. RITCHIE, D. AINLEY, D. ORO, Y. JHALA, F. HIRALDO, and E. KORPIMÄKI. 2014. Towards a cohesive, holistic view of top predation: a definition, synthesis and perspective. Oikos 123: 1234–1234. Available at: http://doi.wiley.com/10.1111/oik.01468 [Accessed August 22, 2014].

TER STEEGE, H., S. MOTA DE OLIVEIRA, N. C. A. PITMAN, D. SABATIER, A. ANTONELLI, J. E. GUEVARA ANDINO, G. A. AYMARD, and R. P. SALOMÃO. 2019. Towards a dynamic list of Amazonian tree species. Sci. Rep. 9: 3501.

TERBORGH, J., and J. ESTES. 2013. Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington, USA

TERBORGH, J., L. LOPEZ, P. NUNEZ, M. RAO, G. SHAHABUDDIN, G. ORIHUELA, M. RIVEROS, F. ASCANIO, G. ADLER, T. LAMBERT, and L. BALBAS. 2001. Ecological meltdown in predator-free forest fragments. Science 294: 1923–1926. Available at: http://www.sciencemag.org/content/294/5548/1923.short [Accessed January 16, 2015].

TÖLLE, M. H., S. ENGLER, and H. J. PANITZ. 2017. Impact of abrupt land cover changes by tropical deforestation on Southeast Asian climate and agriculture. J. Clim. 30: 2587–2600.

TORTATO, F. R., T. J. IZZO, R. HOOGESTEIJN, and C. A. PERES. 2017. The numbers of the beast: Valuation of jaguar (*Panthera onca*) tourism and cattle depredation in the Brazilian Pantanal. Glob. Ecol. Conserv. 11: 106–114.

TOUCHTON, J., Y. HSU, and A. PALLERONI. 2002. Foraging ecology of reintroduced captive-bred subadult harpy eagles (*Harpia harpyja*) on Barro Colorado Island, Panama. Ornitol. Neotrop. 13: 365–379.

TRINCA, C., S. FERRARI, and A. LEES. 2008. Curiosity killed the bird: arbitrary hunting of Harpy Eagles *Harpia harpyja* on an agricultural frontier in southern Brazilian Amazonia. Cotinga 30: 12–15.

TUOMISTO, H., A. D. POULSEN, K. RUOKOLAINEN, R. C. MORAN, C. QUINTANA, J. CELI, and G. CAÑAS. 2003. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. Ecol. Appl. 13: 352–371.

UBAID, F., L. FERREIRA, and P. ANTAS. 2011. Primeiro registro de *Harpia harpyja* para o bioma Pantanal, com dados sobre atividade reprodutiva. Rev. Bras.

VARGAS-GONZÁLEZ, J. DE J., and F. H. VARGAS. 2011. Nesting density of Harpy Eagles in Darien with population size estimates for Panama. J. Raptor Res. 43: 199–210.

VELOSO, H., A. RANGEL FILHO, and J. LIMA. 1991. Classificação da vegetação brasileira adaptada a um sistema universal. Rio de Janeiro.

VILLAS BOAS, O., and C. VILLAS BOAS. 1994. A marcha para o oeste: a epopéia da expedição Roncador-Xingu. Globo, São Paulo.

VOURLITIS, G., N. FILHO, M. HAYASHI, J. NOGUEIRA, F. CASEIRO, and J. CAMPELO JR. 2002. Seasonal variations in the evapotranspiration of a transitional tropical forest of Mato Grosso, Brazil. Water Resour. 38: 11.

WATSON, R. T., C. J. W. MCCLURE, F. H. VARGAS, and J. P. JENNY. 2016. Trial restoration of the harpy eagle, a large, long-lived, tropical forest raptor, in Panama and Belize. J. Raptor Res. 50: 3–22.

ZIMBRES, B., R. B. MACHADO, and C. A. PERES. 2018. Anthropogenic drivers of headwater and riparian forest loss and degradation in a highly fragmented southern Amazonian landscape. Land use policy 72: 354–363.

CHAPTER 2

Species distribution modeling reveals strongholds and potential reintroduction areas for the world's largest eagle

Everton B. P. Miranda*[1, 2, 3], Jorge F. S. Menezes[4], Camila C. L. Farias[5], Charles Munn[6], Carlos A. Peres[7]

1 - Universidade Estadual de Mato Grosso, Alta Floresta, Mato Grosso Brazil

2 - School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa

3 - Programa de Pós-graduação em Ecologia, IB, Universidade de Brasília, Brasília, Distrito Federal, Brazil

4 - Mitrani Department of Desert Ecology, Ben Gurion University of the Negev, Beersheba, Israel

5 - Faculdade de Medicina Veterinária, Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brazil

6 – SouthWild, Várzea Grande, Mato Grosso, Brazil

7 – Center for Ecology, Evolution and Conservation, School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK.

*Corresponding author: mirandaebp@gmail.com

Published in PLOS One. For the published version, please visit: https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0216323

2.1 Abstract

The highly interactive nature of the predator-prey relationship is essential for ecosystem conservation. Predators have been extirpated, however, from entire ecosystems all over the Earth. Reintroductions comprise a management technique to reverse this trend. Species Distribution Models (SDM) are preemptive tools for release-site selection, and can define levels of habitat quality over the species distribution. The Atlantic Forest of South America has lost most of its apex predators, and Harpy Eagles *Harpia harpyja* – Earth's largest eagle – are now limited to few forest pockets in this domain. Harpy Eagles are supposedly widespread in the Amazon Forest, however, where habitat loss and degradation are advancing at a rapid pace. We aim to describe the suitability of threatened Amazonian landscapes for this eagle. We also aim to assess the suitability of remaining Atlantic Forest sites for Harpy Eagle reintroductions. Here we show that considerable eagle habitat has already been lost in Amazonia because of the expansion of the "Arc of Deforestation", and that Amazonian Forests currently represent 93% of the current distribution of the species. We also show that the Serra do Mar protected areas in southeastern Brazil is the most promising region for Harpy Eagle reintroductions in the Atlantic Forest. Reintroduction and captive breeding programs have been undertaken for Harpy Eagles, building the technical and biological basis for a successful restoration framework. Our distribution range for this species represents a 41% reduction of what is currently described by IUCN. Furthermore, habitat loss in Amazonia, combined with industrial logging and hunting suggest that the conservation status of this species should be reassessed. We suggest researchers and conservation practitioners can use this work to help expand efforts to conserve Harpy Eagles and their natural habitats.

Keywords: Arc of Deforestation; Atlantic Forest; *Cebus*; *Euterpe edulis*; top predator; reintroduction; *Sapajus*; trophic cascades.

2.2 Introduction

Extensive losses of apex predators is a pervasive conservation problem in ecosystems around the world [1]. Since the appearance of hominids ~2 million years ago, competition for wild prey, fear of direct attack on humans, and predation on domestic animals has led to the decimation of predator populations [2–4]. The subsequent cascading effects of predator-free populations of herbivores on plant communities can thus damage both natural vegetation and associated biodiversity [5–7]. These issues have placed predators near the top of the conservation biology agenda [8,9], and reintroductions have emerged as one of the main conservation tools to reverse these trends [10,11].

Few living predators are as quintessential creatures of legend as the Harpy Eagle (Fig. 2.1, *Harpia harpyja*; [12,13]). Averaging 6.6 kg, the Harpy Eagle is the largest extant raptor on Earth, and is surpassed in size by only the extinct, island-living Haast Eagle (*Harpagornis moorei*; [14]), which humans wiped out from New Zealand's South Island 600 years ago. The Harpy Eagle is a forest species with the lowest known reproductive rate of any living bird, producing a single offspring every 30-36 months [15,16]. Harpy Eagles have been persecuted over their entire range [17–20], and their feathers and talons are ubiquitous ornaments, with feathers often part of Amerindian arrows and headdresses [21,22]. Live eagles are also captured and kept by Amerindians as sources of feathers ([21]; personal observation). These factors, combined with habitat loss and degradation through logging, have already led to the rarity or extirpation of Harpy Eagles in much of their geographic distribution [23], especially in the Brazilian Atlantic Forest biodiversity hotspot [24].

Fig 2.1. Harpy Eagle *Harpia harpyja* adult female perched in the Atlantic Forest of Sooretama Reserve, state of Espirito Santo, Brazil [25].

The Atlantic Forest has suffered widespread losses of top predators [26]. Jaguars *Panthera onca* survive in the Atlantic Forest in only eight forest pockets, with a total estimated remaining population of only 300 individuals [27]. Relictual populations of Harpy Eagles in the Atlantic Forest are currently known from around ten breeding pairs and a few scattered individuals [28–31]. Harpy Eagles have been shown to exert strong behavioural and demographic control over their prey species [6,32]. In the absence of Harpy Eagles, prey populations often experience unfettered growth [33]. Consequently, they can be described as a keystone predator. Cascading consequences arising from the absence of Harpy Eagles are known to affect prey species. For instance, hyper-abundant populations of Black Capuchin Monkeys (*Sapajus nigritus*) cause high mortality of an arborescent palm (*Euterpe edulis*) of the Atlantic Forest because they rip out and eat the apical meristem, known as "palmito" [34,35]. This palm species is itself a threatened key species of the Atlantic Forest, and benefits many species of frugivores by producing year-round infructescences, which are particularly important during the annual period of general, community-wide fruit scarcity [36]. Throughout the entire distribution of the Harpy Eagle, various species of capuchins represent its second most common primate prey [37]. Restoring Harpy Eagle populations would restore balanced communities in the ecosystem by reducing capuchin monkey densities, thereby preventing harmful plant-herbivore interactions. Management guidelines could therefore benefit considerably from prioritising which forest regions are most suitable for restoration of Harpy Eagle populations. Species Distribution Modeling (SDM; *sensu* [38]) can help obtain those answers.

Harpy Eagles are currently considered Near Threatened by the International Union for Conservation of Nature, IUCN [39]. Whereas the species has vanished throughout much of its historical distribution [23], its widespread occurrence in vast tracts of Amazonian Forests prevents Harpy Eagles from being listed in a higher threat category [39]. Meanwhile, questions remain about the quality of the supposedly homogeneously-pristine tracts of eagle habitat across Amazonia. Improving knowledge on this topic has high value for conservation since the ever-expanding cattle ranching frontier in a region of the southern Amazon known as the "Arc of Deforestation" has rapidly converted vast tracts of Amazonian Forests into pasture and soy fields [40]. This forest destruction has led to the loss of genetic diversity in Harpy Eagles [41]. SDMs could provide an improved basis for discussions about Harpy eagle distribution in neotropical forests as well as in fringe forest habitats such as the Brazilian Cerrado and Pantanal wetlands, thereby helping delineate the biogeographic boundaries of future reintroduction programs. Therefore, building SDMs for Harpy Eagles is central to a sound conservation strategy for this apex predator.

A significant challenge to building a Harpy Eagle SDM is that to produce a robust result; one requires a significant amount of widely distributed geographic records [42]. Existing records, however, might be either too few or too patchy to produce a reliable SDM for such an elusive species. Finding Harpy Eagle nests has proven so difficult that the discovery of a single nest often sparks widespread excitement among ornithologists [43–45]. Furthermore, the few museum records of this species are severely restricted in range [46]. Finally, most museum skins include no data on the breeding status of the specimens, information that can greatly improve the quality of SDMs. We further highlight the unmet potential of the only attempt to compile a sufficient number of geographic records to unravel the Harpy Eagle distribution [23]; but this study failed to produce even the simplest map. Although two different, long-term Harpy Eagle field projects have each located more than a hundred nests, they have failed to compile and publish more than a small fraction of these valuable data. Meanwhile, many amateur birders have managed to painstakingly obtain numerous records of Harpy Eagles, many of which are available from online databases. Such databases have become extensive and provide considerable, often underutilised, information. Could a combination of citizen science and published scientific data, therefore, result in a major advance in an SDM for Harpy Eagles?

Here, we investigate two related topics in Harpy Eagle ecology and conservation: (1) we develop SDMs throughout the species range to identify strongholds and ecologically-suitable areas. We do so by generating and testing the SDMs using environmental variables that are directly linked to Harpy Eagle ecology, which can help produce better conservation policies; and (2) we use these SDMs to identify suitable reintroduction sites in the Atlantic Forest. SDM maps can help identify new field sites for future surveys, help create new protected areas specifically designed to conserve Harpy Eagles, and identify marginal or suboptimal habitats as well as potential reintroduction sites. All of these results can help improve conservation policies for the world's largest eagle.

2.3 Methods

Data collection

We compiled occurrence records using two main methods: standardised literature searches from Google Scholar and birders' records at WikiAves (www.wikiaves.com.br). At Google Scholar, we used scientific and vernacular names of the species (in Portuguese, English and Spanish) to look for papers that may contain geographic data. We relied on geographic coordinates provided by authors, but occasionally only maps were available, because some researchers believe that nest sites should remain undisclosed to avoid loss of chicks to wildlife traffickers. When we were unable to contact the authors, we extracted coordinates directly from the maps, but for records that included maps that were not sufficiently precise, we excluded those records. The WikiAves data retrieval was done up to 2016, with records spanning any date. To determine the location of a documentary photo or sound recording, we used municipal county (*município*) information from WikiAves in addition to the location description, consulting the author whenever necessary. Data were double-checked for pseudo-replicates, meaning that we use only one confirmed record for specific nests or individual eagles that had been photographed by multiple birders. We also searched the following georeferenced sound and photo databases: www.birdforum.net, www.xeno-canto.org, and www.macaulaylibrary.org. All records and their geographic coordinates can be found in **Supporting Information S2.1 Table 1**.

Breeders

Harpy Eagles are selective in their nest tree choice and almost exclusively nest in giant "T-shaped" bifurcations of emergent trees providing a stable platform [47,48]. Those trees used for breeding are of direct interest to the timber industry and are now absent from vast tracts of Amazonian logged forest [49]. We, therefore, distinguished records of breeding and non-breeding individuals because animals in logged landscapes may not be able to reproduce given the absence of appropriate trees. We concluded that there was evidence of breeding if any of the following conditions were met: (1) eagles with greyish-white plumage, as such eagles are fledglings that are known to be unable to traverse flight distances longer than 2-km from their natal tree [15,16]; (2) adult individuals with brown breast colouration, which typically result from weeks of contact with tannin-rich leaves of the fresh nest material branches during incubation, and then brooding of the young chick [50]; and (3) any individual recorded at a nest. Consequently, we were able to identify locations that were, in fact, breeding sites for this eagle.

Databases

For our SDMs, we used remotely sensed large-scale metrics as environmental variables. Specifically, we used data on bioclimatic variables and elevation [51], human population density (CIESIN, 2016), enhanced vegetation index, which is a measure of the amount of vegetative greenness (NASA LP DAAC, 2016), canopy cover (NASA LP DAAC, 2016), and canopy height

[54]. All environmental variables had a 1-km^2 resolution, and analyses were cut to fit our study area, namely the Americas south of 40°N latitude.

Species distribution modelling

To calculate the species distribution model, we followed three consecutive steps similar to the procedure of “random selection with environment profiling” [55]. First, we performed a rough classification of “suitable” and “unsuitable” habitat areas using an on-class support vector machine. To calculate this area, we set the condition that 90% of the observations must be within a suitable area, a procedure that has been shown to increase overall model discrimination [55]. Pseudo-absences were selected from the “unsuitable area”. However, this sample was not random. We were concerned that detection of Harpy Eagles might be positively correlated with human population density, because detection may be inflated in an area simply because of the presence of more human observers. To minimise the bias on our model estimates, we selected pseudo-absences, giving weights for each cell, with weights proportional to the human population density of a given cell. In this manner, as the bias is present in both presences and pseudo-absences, it would not affect the model outcome [56]. We created as many pseudo-absences as our number of actual observations. Most of the models used here performed best when presented with an equal number of pseudo-absences and presences [57]. A direct test for the presence of bias on our models is at **Supporting Information S2.2**.

After pseudo-absences were sampled, we ran multiple environmental models: BIOCLIM, MAXENT, multivariate adaptive regression splines, logistic regression, generalised additive model, random forest, and support vector machine (SVM) networks, a machine learning approach. With this selection, we attempted to select most families of models, namely climatic envelopes, maximum entropy, splines, linear models, classification tools and SVMs. Since some of these models are sensitive to collinearity, we excluded bioclimatic variables that were correlated with one another. To do so, we ran a principal component analysis on the environmental values of our observations and pseudo-absences. We then scanned the variables in descending order of their eigenvalues. If a variable was not correlated by >0.7 with a previously-selected variable, it was retained in the model. With this procedure, we reduced our variable list to: seasonality of temperature (BIO4), annual precipitation (BIO12), precipitation in the coldest quarter of the year (BIO19), precipitation in the warmest quarter (BIO18), precipitation in the driest quarter (BIO17), mean temperature of the wettest quarter (BIO8), mean diurnal temperature range (BIO2), enhanced vegetation index, canopy cover, and canopy height. Using linear models, we added variables only to the main-effects model, as GAM models failed to converge if they contained interactions. In all models, we reserved 20% of our observations and pseudo-absences for testing the models. We then used the model to predict the quality of each cell in the study area. The third step was to combine all of these prediction maps. We used a weighted average, whereby each map was weighted by its Area Under the Curve (AUC) values. The weighted average was indicated as a robust method for building model consensus [58].

We were concerned that many of these observations did not relate to reproductive individuals, so we added a new step to the analysis. We performed all three of the previous steps again, but this time using only observations of Harpy Eagles that prove breeding is occurring. The results of this new analysis were then combined with all samples (including records of eagles that had been shown to be breeding and those of eagles that showed no sign of reproduction). We considered that for an area to adequately support sustainable Harpy Eagle populations, it must be close enough to an area suitable for its reproduction. To represent that, we drew a circle around each cell that showed suitability for reproduction, and the area of the circle was equivalent to the mean home range size of a typical Harpy Eagle pair. Using the same logic with a continuous metric of habitat quality for reproduction, we used a Gaussian blur on the reproductive predictions with a standard deviation of 25000/1.96 km. This value was chosen considering that a home range area equals 95% of an individual eagle's total range of movements [59], and that home ranges of Harpy Eagles are approximately 25 km² [60,61]. Merging different distribution models for different activities has been successfully used for California Condors (*Gymnogyps californianus*), showing robust predictive ability [62]. Once the final distribution was set, we used the criteria of equal sensitivity and specificity to categorise habitat quality as either "presence" or "absence" [63].

2.4 Results

We obtained records of Harpy Eagles with geographic references for all 19 countries that encompass their historical distribution. These include a total of 322 occurrences, 174 records of which consist of individuals that offer no clear evidence of breeding, while 148 records showed evidence of breeding. The largest number of records came from WikiAves (121), followed by scientific articles (118), unpublished theses and dissertations (49), governmental reports (17), birdforum.com (13), and four records from miscellaneous sources. According to the AUC values, all models yielded higher predictive power than random models (AUC range for non-reproductive models: 0.7553 (BIOCLIM) to 0.8867 (SVMs); AUC range for reproductive models: 0.7731 (BIOCLIM) to 0.8849 (SVMs, Table 2.1)). The distribution of those records and the overall potential geographic distribution of Harpy Eagles can be seen in Fig 2.2.

Table 2.1. Area under the curve of several isolated models, the consensus between them, and the final model, where "All" refers to all records and "Reproductive" refers to records with credible evidence of breeding.

Model	Data	Isolated models	Consensus	Final
BIOCLIM	All	0.7547		
GLM	All	0.8224		
GAM	All	0.8429		
MARS	All	0.8099	0.7788	
RF	All	0.7698		
MAXENT	All	0.8381		
SVM	All	0.8416		0.8414
BIOCLIM	Reproductive	0.7189		
GLM	Reproductive	0.8549		
GAM	Reproductive	0.7163		
MARS	Reproductive	0.8846	0.8026	
RF	Reproductive	0.8657		
MAXENT	Reproductive	0.8491		
SVM	Reproductive	0.9029		

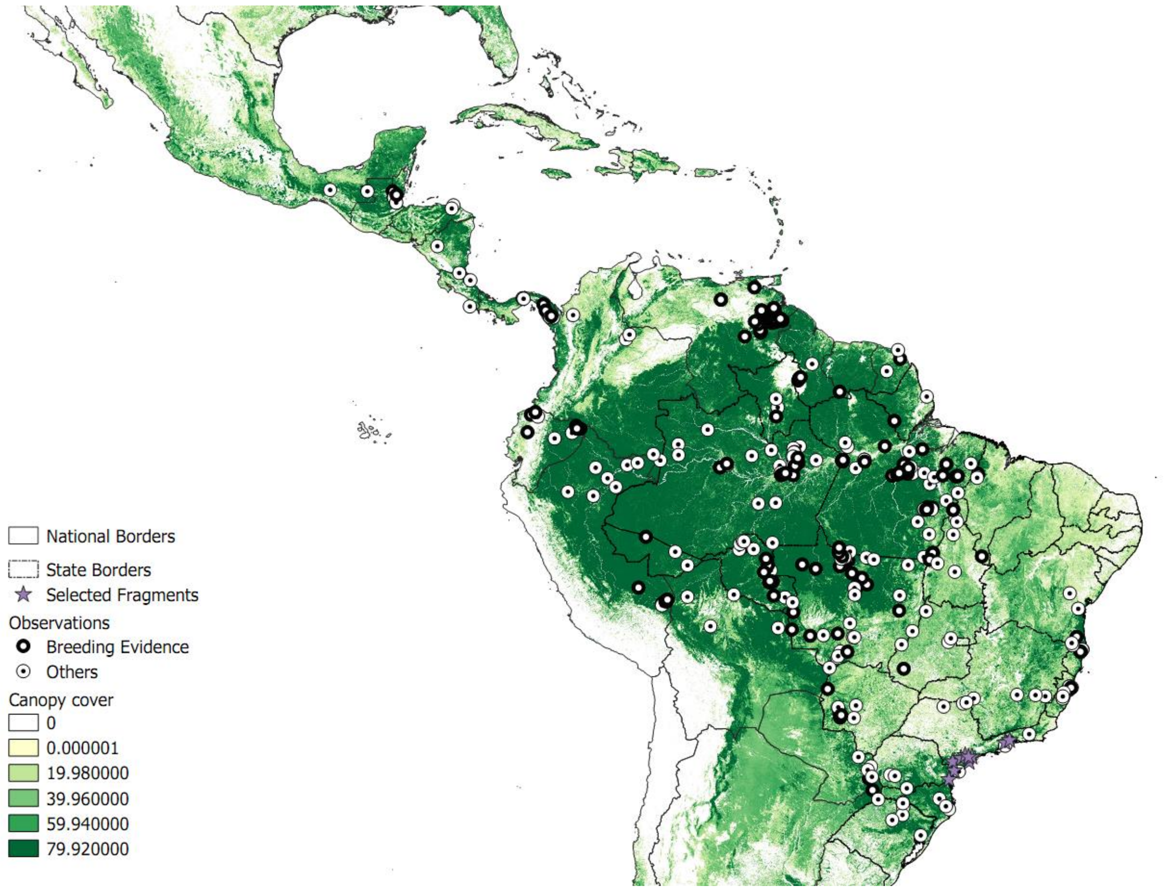

Fig. 2.2. Spatial distribution of the 322 breeding (black circles) and not breeding (white circles) records of Harpy Eagles in Central and South America. Forest cover is shown as a green scale gradient from white (no forest) to dark green (tall canopy forest). Lines represent political country boundaries, and in the case of Brazil, state boundaries. Purple stars are potential reintroduction sites (i.e. predicted suitable habitat areas at present lacking Harpy Eagle populations).

The predicted distribution of Harpy Eagles throughout the Neotropics is shown in Fig. 2.3. The model suggests that the Amazon forest is still the largest stronghold for the species, with a continuous area comprising 93% of all currently available habitat (Fig. 2.4). The northern *cerrado* scrubland to wooded savanna macromosaic, mainly located in Brazil's state of Tocantins, has an extensive patch of intermediate quality Harpy Eagle habitat. Important habitat pockets remain in Mesoamerica, including southeastern Panamá near the Isthmus of Darien, the mosaic of protected areas that straddle Nicaragua and Honduras, and the Selva Maya protected areas that stretch across southern Mexico, Belize and Guatemala.

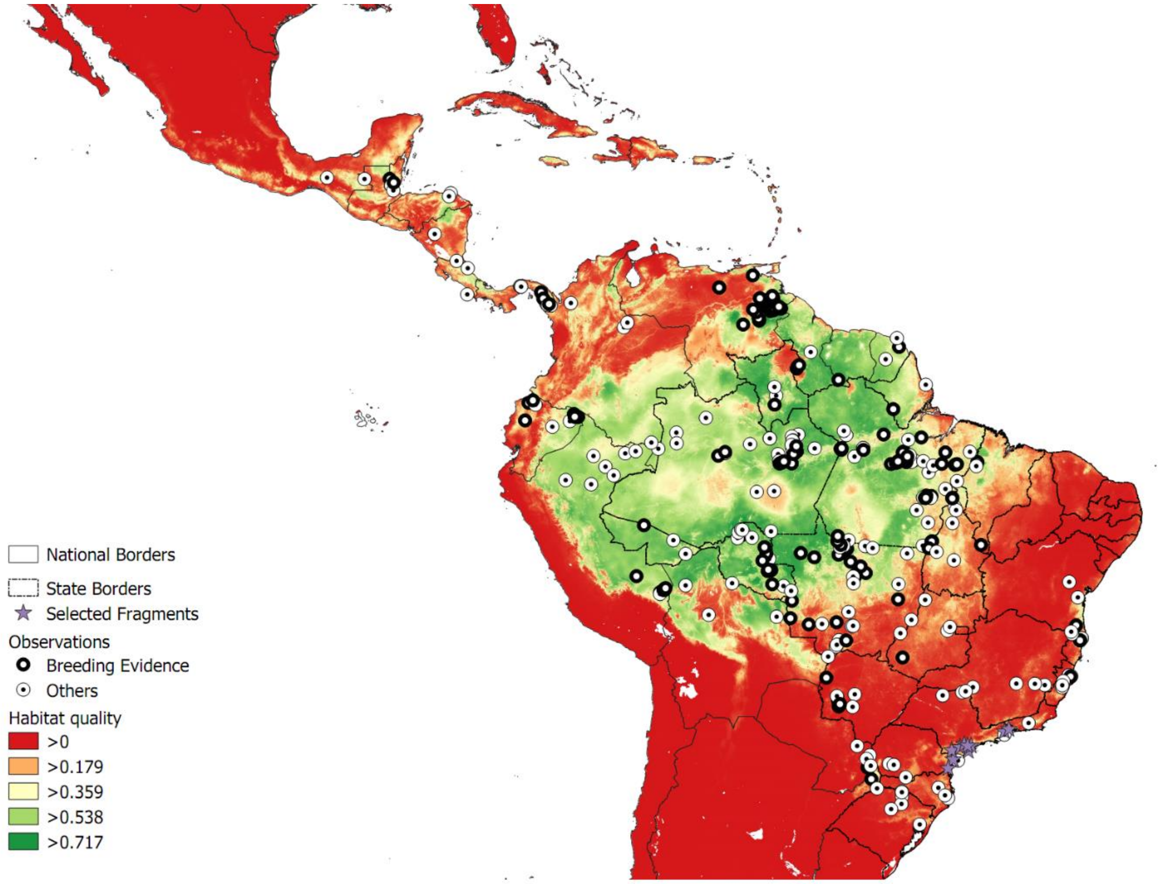

Fig. 2.3. Prediction of the current geographic distribution of conditions fitting the ecological demands of Harpy Eagles in Central and South America under contemporary forest cover. Records of breeding (black circles) and not breeding (white circles) are also shown. The areas considered to be suitable habitat at present are shown in dark green, and uninhabitable areas are shown in red. Purple stars represent suitable reintroduction sites (i.e. predicted suitable habitat areas at present lacking Harpy Eagle populations). Lines represent political country boundaries, and in the case of Brazil, state boundaries.

The hyperfragmented landscape of the Atlantic Forest biome retains few available remaining habitat pockets that could currently support viable Harpy Eagle populations. One of them, in the lowland coastal forests of Brazil's northern Atlantic Forest (in the states of Espírito

Santo and southern Bahia) has yielded recent evidence of current populations, including breeding pairs. The other, in northeastern Argentina (Misiones Province), has evidence of breeding in the last decade and recent records of non-breeding individuals. Finally, a ~7,000 km^2 cluster of forest habitat patches in a large mosaic of coastal protected areas — on the southern section of the Serra do Mar (Fig. 2.5) — potentially shows the best area for future reintroduction attempts across the Brazilian Atlantic Forest. Yet for several decades, this region has yielded no confirmed records of Harpy Eagles.

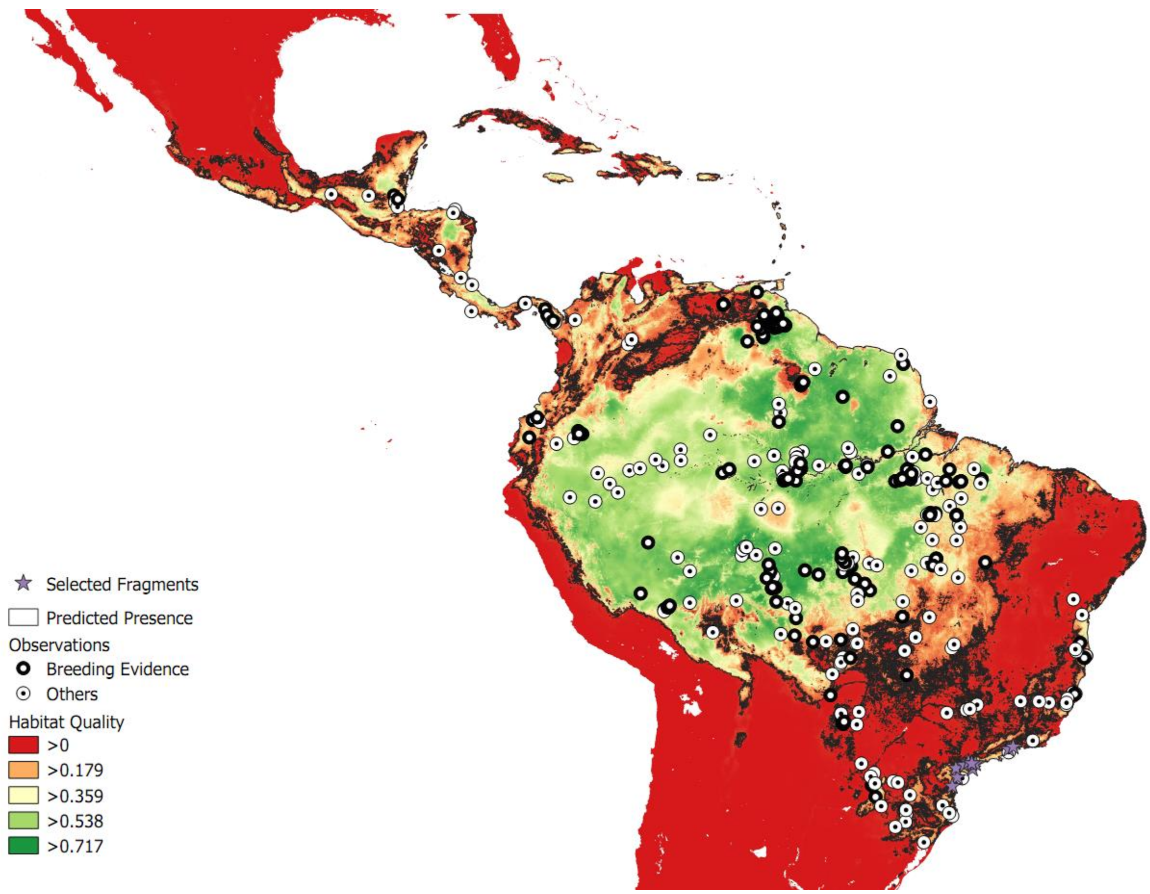

Fig. 2.4. Categorical prediction of the current geographic distribution of conditions fitting the ecological demands of Harpy Eagles in Central and South America under contemporary forest cover (see Methods section for thresholds criteria). Black lines represent the limit between predicted presence and absence. Records of breeding (black circles) and not

breeding (white circles) are also shown. The areas considered to be suitable habitat at present are shown in dark green, and uninhabitable areas are shown in red. Purple stars represent suitable reintroduction sites.

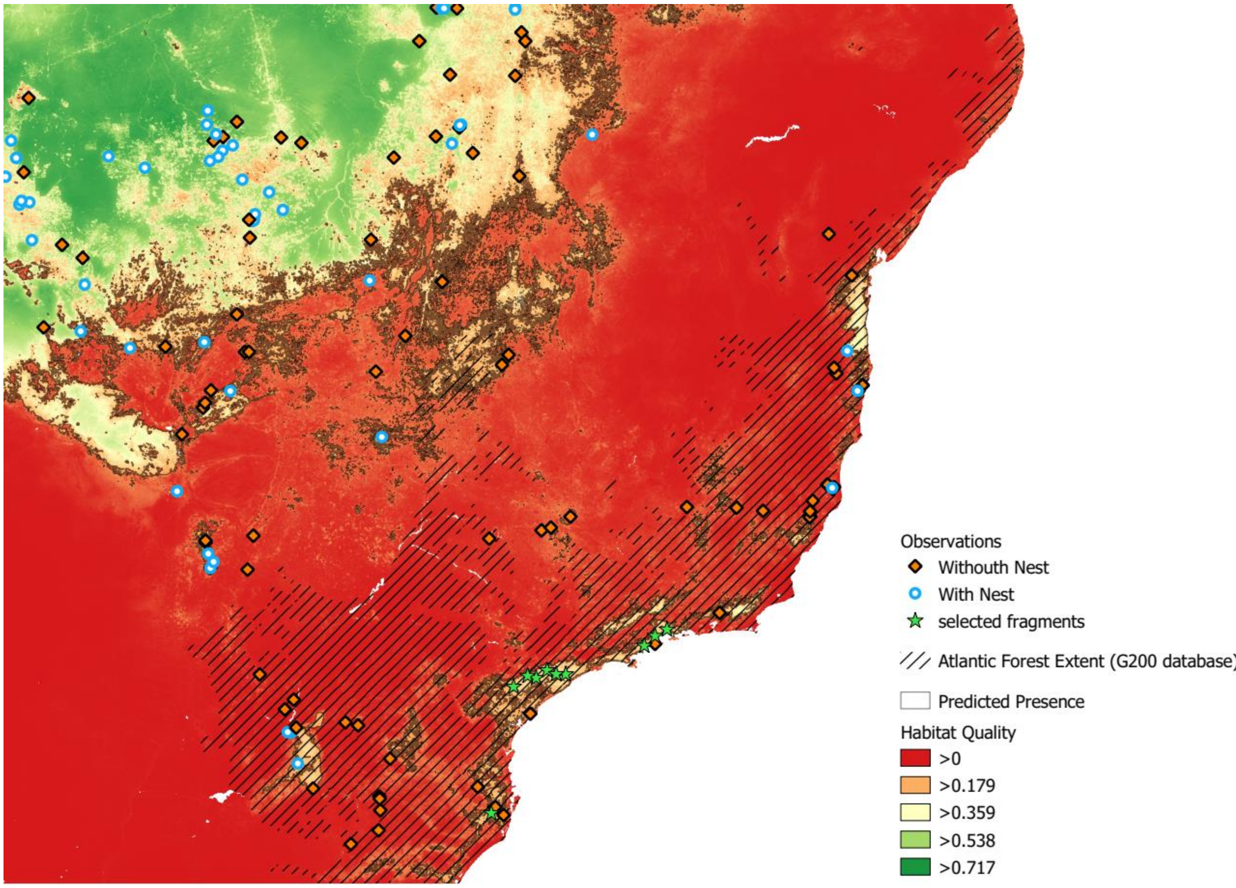

Fig 2.5. Prediction of the potential Harpy Eagle reintroduction sites in the Atlantic Forest, showing the largest forest fragments that could bear reintroduced populations (i.e. predicted suitable habitat areas at present lacking Harpy Eagle populations), pointed by green stars. They are mainly located along the protected areas of Serra do Mar.

2.5 Discussion

Careful selection of sites for reintroductions is key to successful species conservation and restoration. Here we delineate for the first time the plausible, global-scale distribution of Earth's largest extant eagle, a result that is of prime management and conservation interest. Three relatively-small sections of the Atlantic Forest biome demonstrate good habitat suitability for

Harpy Eagles, namely: (*i*) the lowlands of the northern Atlantic Forest in Brazil; (*ii*) the Misiones green corridor of Argentina, and (*iii*) the Serra do Mar region of southeastern Brazil. Indeed, the Serra do Mar region has no current records of Harpy Eagles but could host successful reintroduction programs, while other suitable Atlantic Forest sites have recent or current evidence of breeding populations. The Serra do Mar forest corridor could host reintroduced populations that could become viable in the long term, much like the case of the Harpy Eagle reintroduction into Mesoamerica [64]. In contrast, the Amazon Forest currently has extensive tracts of high-suitability forest habitat, mainly concentrated in Brazil, eastern Peru and northern Bolivia. Additional vast tracts of well-suited habitat lie in southeastern Colombia, the Sierra Imataca of eastern Venezuela, and in Guyana, Suriname and French Guyana. Ecuador shows two pockets of suitable habitat, both east and west of the Andes. Mid-elevation tropical Andean forests above 1000 a.s.l. apparently provide suboptimal habitat for Harpy Eagles. Finally, our proposed distribution of over ten million square kilometres (10,401,993 km^2) represents a reduction of 41% of the neotropical distribution area of 17,600,000 km^2 that is currently proposed by IUCN [39].

A shortcoming of our methods is that it is not possible to obtain an even distribution of records, leading to some remote regions of the Amazon forest with few records of Harpy Eagles. Those are regions where they certainly occur, whereas our model shows a limited quality habitat section. However, we added two layers of corrections, the random selection with environmental profiling and selecting pseudo-absence using a sampling proportional to the human population. We consequently believe in having constrained this limitation adequately. If going further than that on additional corrections, we could incur in the opposite problem where we give a disproportionally large weight for samples in pristine locations, leading us to falsely conclude the species has stronger conservation requirements than it has indeed. Having recognised and addressed that issue, we will hereafter focus on meaningful elements of the results and in understanding their implications.

Harpy Eagle Range

The Amazon has long been considered the Harpy Eagle's last stronghold [39,65], and 93% of the current Harpy Eagle range is indeed encompassed by the Pan-Amazonian region. When we attempt to examine the status of Harpy Eagles in what we presume to be its primary Amazonian stronghold, we can simplify the analysis by looking at three broad areas of concern: (A) food, (B) habitat, and (C) mortality.

(A) Regarding the question of an adequate prey base, bushmeat hunting and the resulting competition with humans is a minor issue. Harpy Eagles feed primarily on sloths [66], which in addition to being abundant [67,68], are of minor importance as game species [69]. The effects of secondary forest, hunted or highly degraded forests on the foraging ecology of Harpy Eagles remains an open question because few have been published on their diet in unhunted, primary forests [70]. Recent observations in Mato Grosso, Brazil, and Sierra Imataca, Venezuela, suggest that this mega-raptor fares well in secondary forest landscapes as long as it is not hunted by local people. Therefore, competition with humans over wild prey is hardly a problem. The ability of these eagles to feed their young with wild prey – chiefly sloths – even in otherwise-hunted landscapes [60,71,72], suggests that Harpy Eagles are able to coexist well with humans.

(B) Concerning habitat, the extensive section of degraded forest that we found in much of the southeastern Amazon poses two problems regarding the "last stronghold" assumption: (1) habitat loss by deforestation and (2) habitat degradation by logging and wildfires. The cattle-ranching frontier along the Arc of Deforestation continues to advance [73,74], and has already destroyed 23% of all primary *terra firma* forests of Amazonia. This impact has already led to a reduction in the genetic diversity of Harpy Eagles in this region [41]. Brazil's recent economic and political crisis and the massive decline in funding directed towards prevention of deforestation, combined with widespread relaxation of environmental laws, has effectively resulted in an unprecedented renewed increase in forest loss [74]. Up to 19,000 km² of primary Amazon Forest becomes highly-graded each year by mechanised timber extraction [75], removing low-density giant emergent trees that Harpy Eagles require for nesting. Felling of nest trees by loggers is also a direct source of mortality of eagle chicks [60,76]. The relentless advance of cattle pastures was responsible for another 7,900 km² of forest loss in 2018 alone, which is increasing since 2012 [77]. Population densities of Harpy Eagles have been estimated at only 3-6 nests per 100 km² [78], thereby reiterating the crucial need for megareserves in Amazonia [79].

(C) Eagle killings by humans is another serious issue in the Amazon [20]. Amerindian reserves cover approximately 27% of the Brazilian Amazon [80]. In these Amerindian reserves, Harpy Eagles are universally considered to be prized birds for headdresses and arrow fletching [13,22]. Whereas indigenous societies may have gradually acquired a dynamic equilibrium with the wildlife that remained following the Pleistocene extinctions [81], the acquisition of firearms by Amerindians places much greater powers of destruction in the hands of indigenous people throughout the Amazon [82]. Native Amazonians wielding firearms, combined with the high prices commanded by indigenous feather headdresses when sold illegally as handicrafts, has greatly increased the pressure on Harpy Eagle populations inside Indigenous Lands. Although we are clearly in favour of indigenous land rights, sustainable use of wildlife often fails within indigenous territories and extractive reserves [83–85]. The discussion about the hunting of threatened species cannot be trivialised or swept under the rug using the clichéd term “traditional practice”. Rather, sensible rules and bag-limits, if any offtake can be defined as sustainable, as well as effective law enforcement are required to prevent endangered wildlife from melting away through careless use by communities who are directly connected to outside markets. Furthermore, when government land reform agencies settle millions of poor socio-economic migrants in primary Amazonian Forest [86], the settlers tend to shoot in rapid succession every Harpy Eagle as well as other large, diurnal raptors [17,18,87].

The Harpy Eagle’s “last stronghold” is therefore far from an adequate safety net, as they are caught in the crossfire generated by market-integrated indigenous groups, high-grading loggers, land reform settlers, and cattle ranchers. These threats should, therefore convince IUCN board-members to reassess the conservation status of the Harpy Eagle.

The occasional occurrence of Harpy Eagles in some marginal habitats has been the subject of some discussion [44,45,88]. While early naturalists recorded this species in the Cerrado of central Brazil [65], Harpy Eagles were apparently never abundant in this ecosystem. The eagle’s strong preference for giant, T-shaped emergent trees for nesting [47,48], and their specialised feeding habits concentrated on sloths (which are absent outside tropical forests) should render the Cerrado a marginal habitat for this species. Perhaps because of this, many maps show an erroneously disjunct distribution for the species with two separated pockets in South America, excluding the savanna regions between them. This is the case of IUCN map, which makes our proposed 41% reduction in range size even more shocking. Our results suggest that a pocket of acceptable Harpy Eagle habitat exists in the northern Cerrado and in much of the transition zone between the Cerrado and the Amazon, which could explain occasional reports of individuals shot and nests found in such areas. In the Pantanal wetlands, our SDMs suggests that this species is expected to occur only in its northern parts (with very limited habitat quality and range), where the few direct records have been documented for the species [44]. An extensive search of the entire Pantanal for the similarly-huge nests of Jabiru storks (*Jabiru mycteria*) found no Harpy nests whatsoever, suggesting absence [89]. A pair of Harpy Eagles have been recently documented at the Calileuga National Park in the Yungas of northwestern Argentina, which contains a small habitat patch that our SDM shows to be of low quality. Another peripheral habitat area that shows several pockets of good suitability are the Caribbean Antilles. It is interesting to note that none of the bird-rich fossil records of Antillean Islands have uncovered any remains of Harpy Eagles. Several species of giant raptors that humans drove to global extinction are known from this archipelago [90,91]. These extinct predators include a giant flightless owl (*Ornimegalonyx oteroi*), a giant flying owl (*Tyto pollens*) and a giant, buteo-type hawk (*Amplibuteo woodwardi*). It would be interesting to investigate if those extinct Antillean raptors performed a similar predation role on both terrestrial and arboreal sloths of the Antilles as Harpy Eagles exert on arboreal sloths in continental forest ecosystems. These musings open many interesting lines of inquiry regarding convergent predator-prey relationships in the Caribbean islands and continental Neotropical forests.

Atlantic forest reintroduction

Range models can be interpreted as related to environmental suitability for the target species, where higher index values suggest better habitat conditions [92][93]. The Harpy Eagle's best sections of remaining habitat in the Atlantic Forest biome primarily consist of high-stature, lowland forest. One of these sections is the region that harbours some of the last breeding pairs of the species in the Atlantic Forest, specifically in the forest reserves of Sooretama, Linhares, Serra Bonita, Descobrimento, and Pau Brasil [28,29,94]. Over the last five centuries, Atlantic Forest landscapes have become highly degraded by conversion into sugarcane, coffee, and cacao plantations, slash-and-burn agriculture, and timber extraction [95], followed by extensive cattle ranching and eucalyptus monocultures, the latter two of which tolerate the resulting nutrient-poor soils. Thus, the Atlantic Forest has been an epicenter of forest loss in South America, beginning several centuries prior to the consolidation of the “Arc of Deforestation” in the southern, eastern and southeastern Amazon [96]. After centuries of various direct sources of forest depletion, the Atlantic Forest currently presents small – but still worthwhile – hotspots for Harpy Eagle conservation. A highly-biodiverse, shade-grown-cacao-based economy [97] can still host successful conservation programs in the northern Atlantic Forest [98], and that includes Harpy Eagles. At the other extreme of the land use spectrum, the strictly-protected reserve network in the Serra do Mar forest corridor could provide promising habitat for a “rewilding” reintroduction project that would rebuild long disrupted forest trophic cascades in the southern Atlantic Forest. We recommend that conservationists planning significant reintroduction efforts for Harpy Eagles and other apex predators consider the findings from our models. We also emphasise that the parks within the Serra do Mar Atlantic Forest region should be given highest priority for release sites if any rehabilitated individuals become available near or in the Atlantic Forest.

A key factor regarding site selection in the Serra do Mar Atlantic Forest, where we recommend reintroductions, is that a sizable portion of this region falls outside the distribution of sloths in the Atlantic Forest [99]. In the absence of sloths, Harpy Eagles may take a disproportionately high toll on other arboreal mammal prey species, such as capuchin monkeys. In the Serra do Mar, capuchins have densities as high as 32 individuals per km^2 [100], and these monkeys are known to seasonally decimate threatened arborescent palms [101]. Problems related to capuchins crop-raiding forest plantations have also been reported elsewhere in the southern Atlantic Forest [102], where reintroduced Harpy Eagles could regulate monkey populations [32,33]. In the southern Atlantic Forest, remarkable work to connect fragmented landscapes is being carried out for jaguars [103], and this model could be replicated for Harpy Eagles. Cross-fertilisation between research programs for both of these top predator species could provide highly positive synergistic outcomes. Reintroductions have become a central focus of attention in the Atlantic Forest conservation agenda [104,105]. Reintroductions of top predators must, however, take into consideration issues related to a number of threatened arboreal mammals of the Atlantic Forest. Blonde Capuchins (*Sapajus flavius*; [106]), Maned Sloths (*Bradypus torquatus*; [107]) and Bristle Porcupines (*Chaetomys subspinosus*; [108]) are just a few examples of endangered species that may be further imperilled by reintroduced predators, as has been shown elsewhere [109]. Fortunately, none of those prey species are in the set of regional sites where we propose reintroducing Harpy Eagles.

In Brazil, at least several conservation breeders have successfully reproduced Harpy Eagles (e.g. Bela Vista Biological Refuge, Roberto Ribas Lange Zoo and CRAX). Each of these breeders holds over several adult individuals, and other private breeders have a smaller number of adults and young animals totalling several dozens in Brazil [110]. Meanwhile, The Peregrine Fund has developed a huge amount of know-how on Harpy Eagle reintroductions during a directed restoration effort for the species in Mesoamerica [64,111–113]. In addition, the Brazilian Harpy Eagle Conservation Program successfully released several rehabilitated individuals [61]. Eliminating the causes of extirpation must be addressed before embarking on any reintroduction effort in the Atlantic Forest. Given that large remaining portions of the historically-overexploited

Atlantic Forest are no longer losing additional forest, the main threat to reintroduced Harpy Eagles would be reprisal or prophylactic killings by local residents [20,64]. Harpy Eagles also present a unique opportunity for ecotourism development that has shown positive results for both predators and local economies when implemented in a controlled, responsible manner [114,115]. Therefore, given the current amount and high quality of expertise, we believe that if appropriate funding can be raised, a successful reintroduction effort can become feasible.

In conclusion, we show that in the Amazon Forest – the Harpy Eagle's last stronghold – much of the forest that could be considered prime habitat for the species may in fact already be badly degraded by the rapidly-expanding Arc of Deforestation and associated logging frontiers. Regarding reintroductions at the Atlantic Forest, the most suitable sites for Harpy Eagle are located in the Serra do Mar forest corridor. In the currently hyperfragmented landscapes of the Atlantic Forest, this habitat corridor represents the largest tropical forest continuum available that could host a healthy population of Harpy Eagles. Much of this forest corridor lies within protected areas that could support a reintroduction project for Harpy Eagles, so environmental authorities should prioritise this corridor as a release site for Harpy Eagles. Here we sound the alarm that the supposedly uniformly high-quality of Amazonian Forests as a long-term refugium for Harpy Eagles are far from ideal. Rather, a perverse mix of anthropogenic threats has been driving Harpy Eagles to local extinction long before the forest cover is completely removed. We, therefore, suggest that in light of these findings, the IUCN status of this keystone predator should be reassessed.

2.6 Acknowledgements

We are greatly indebted to the many intrepid birders and Brazilian bird photographers who contributed Harpy Eagle records to the rapidly-growing WikiAves database. This work received major logistical support from the Peugeot-ONF Brasil Carbon Sink Reforestation Project, based at Fazenda São Nicolau in the Municipality of Cotriguaçu, Mato Grosso, Brazil. This project is an initiative of Peugeot Auto Maker to fulfil directives of the Kyoto Protocol.

2.7 References

1. Estes JA, Terborgh J, Brashares JJS, Power ME, Berger J, Bond WJ, et al. Trophic downgrading of planet Earth. Science 2011; 333: 301–306.
2. Darimont CT, Fox CH, Bryan HM, Reimchen TE. The unique ecology of human predators. Science 2015; 349: 855–860.
3. Swanepoel LH, Lindsey P, Somers MJ, Hoven W V., Dalerum F. Extent and fragmentation of suitable leopard habitat in South Africa. Anim. Conserv. 2013; 16: 41–50.
4. Werdelin L, Lewis ME. Temporal change in functional richness and evenness in the eastern African Plio-Pleistocene carnivoran guild. PLoS One 2013; 8: e57944.
5. Terborgh J, Estes J. Trophic cascades: predators, prey, and the changing dynamics of nature. Washington, USA: Island Press; 2013.
6. Terborgh J, Lopez L, Nunez P, Rao M, Shahabuddin G, Orihuela G, et al. Ecological meltdown in predator-free forest fragments. Science 2001; 294: 1923–1926.
7. Ripple WJ, Beschta RL. Restoring Yellowstone's aspen with wolves. Biol. Conserv. 2007; 138: 514–519.
8. Sérgio F, Newton I, Marchiesi L, Pedrini P. Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. J. Appl. Ecol. 2006; 43: 1049–1055.
9. Terraube J, Bretagnolle V. Top-down limitation of mesopredators by avian top predators: a call for research on cascading effects at the community and ecosystem scale. Ibis 2018; 160: 693–702.
10. Davies AB, Tambling CJ, Kerley GI, Asner GP. Limited spatial response to direct predation risk by African herbivores following predator reintroduction. Ecol. Evol. 2016; 6: 5728–5748.
11. Hunter DO, Britz T, Jones M, Letnic M. Reintroduction of Tasmanian devils to mainland Australia can restore top-down control in ecosystems where dingoes have been extirpated. Biol. Conserv. 2015; 191: 428–435.
12. Rosa JM. Harpia. Belo Horizonte: Editora Nitro; 2010.
13. Tufiño P. Cunsi Pindo: The Mistress of the Monkeys. Quito: Simbioe; 2007.
14. Holdaway R. Systematics and palaeobiology of Haast's eagle (*Harpagornis moorei* Haast, 1872)(Aves: Accipitridae). University of Canterbury. 1991.
15. Muñiz-López R, Limiñana R, Cortés G, Urios V. Movements of harpy eagles *Harpia*

harpyja during their first two years after hatching. Bird Study 2012; 59: 509–514.
16. Urios V, Muñiz-López R, Vidal-Mateo J. Juvenile Dispersal of Harpy Eagles (*Harpia harpyja*) in Ecuador. J. Raptor Res. 2017; 51: 439–445.
17. Trinca C, Ferrari S, Lees A. Curiosity killed the bird: arbitrary hunting of Harpy Eagles *Harpia harpyja* on an agricultural frontier in southern Brazilian Amazonia. Cotinga 2008; 30: 12–15.
18. Freitas MA, Lima DM, Gomes FB. Registro de abate de gaviões-reais *Harpia harpyja* (Accipitridae) para consumo humano no Maranhão, Brasil. Atualidades Ornitológicas 2014; 178: 12–15.
19. Curti M, Valdez U. Incorporating community education in the strategy for Harpy Eagle conservation in Panama. J. Environ. Educ. 2009; 40: 3–16.
20. Muñiz-López R. Harpy Eagle (*Harpia harpyja*) mortality in Ecuador. Stud. Neotrop. Fauna Environ. 2017; 30: 1–5.
21. Villas Boas O, Villas Boas C. A marcha para o oeste: a epopéia da expedição Roncador-Xingu. São Paulo: Globo; 1994.
22. Reina RE, Kensinger KM. The Gift of Birds: Featherworking of Native South American Peoples. Pennsylvania: University Museum of Archaeology & Anthropology; 1991.
23. Vargas-González J de J, Whitacre D, Mosquera R, Albuquerque J, Piana R, Thiollay J-M, et al. Estado y distribucion actual del aguila arpia (*Harpia harpyja*) en Centro y Sur America. Ornitol. Neotrop. 2006; 17: 39–55.
24. Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA, Kent J. Biodiversity hotspots for conservation priorities. Nature 2000; 403: 853–8.
25. Briso AL. [WA2508198, *Harpia harpyja* (Linnaeus, 1758)]. In: Wiki Aves - A Enciclopédia das Aves do Brasil. 2017.
26. Jorge M, Galetti M. Mammal defaunation as surrogate of trophic cascades in a biodiversity hotspot. Biol. Conserv. 2013; 163: 49–57.
27. Paviolo A, De Angelo C, Ferraz KM, Morato RG, Pardo JM, Srbek-Araujo AC, et al. A biodiversity hotspot losing its top predator: The challenge of jaguar conservation in the Atlantic Forest of South America. Sci. Rep. 2016; 6: 37147.
28. Suscke P, Verderane M, de Oliveira RS, Delval I, Fernández-Bolaños M, Izar P. Predatory threat of harpy eagles for yellow-breasted capuchin monkeys in the Atlantic Forest. Primates. 2017; 58:141-147.
29. Sánchez-Lalinde C, Silveira LF, Vélez-García F, Cornélio ACa, Alvarez MR. Records of the Harpy Eagle (*Harpia harpyja*) in the Serra Bonita reserves complex, Camacan, Bahia, with evidence of breeding. Rev. Bras. Ornitol. 2011; 19: 436–438.
30. Meller DA, Guadagnin DL. Rediscovery of the Harpy Eagle *Harpia harpyja* (Accipitriformes: Accipitridae) for Rio Grande do Sul state, Brazil. Brazilian J. Ornithol. 2016; 24: 53–57.
31. Anfuso J, Suarez M, Chebez J. Nuevo Registro de Nidificación de la harpía (*Harpia harpyja*) en la provincia de Misiones, Argentina y Consideraciones sobre su conservación. Nótulas Faunísticas. 2008; 21: 1–13.
32. Gil-da-Costa R, Palleroni A, Hauser MD, Touchton J, Kelley JP. Rapid acquisition of an alarm response by a neotropical primate to a newly introduced avian predator. Proc. Biol. Sci. 2003; 270: 605–610.
33. Orihuela G, Terborgh J, Ceballos N, Glander K. When Top-down becomes bottom up: Behaviour of Hyperdense howler monkeys (*Alouatta seniculus*) trapped on a 0.6 ha Island.

PLoS One 2014; 9: e82197.
34. Portela R de CQ, Bruna EM, Santos FAM dos. Are protected areas really protecting populations? A test with an Atlantic rain forest palm. Trop Conserv. Sci. 2010; 3: 361–372.
35. Lacerda R. Predação de plantas jovens de *Euterpe edulis* e invasão de lavouras de milho por *Sapajus nigritus* em remanescentes de floresta atlântica no sul do Brasil. Unioeste. 2013.
36. Garcia VA, Barbedo CJ. Phenology of *Bactris gasipaes* Kunth, *Euterpe edulis* Mart. e *Syagrus romanzoffiana* (Cham.) Glassman in the Vale do Ribeira, São Paulo State, Brazil. Hoehnea 2016; 43: 135–149.
37. Miranda E. Conservation implications of harpy eagle *Harpia harpyja* predation patterns. Endanger. Species Res. 2015; 29: 69–79.
38. Peterson AT, Soberón J. Species distribution modeling and ecological niche modeling: getting the concepts right. Nat. Conserv. 2012; 10: 102–107.
39. Birdlife International. *Harpia harpyja* (American Harpy Eagle, Harpy Eagle). In: Species factsheet: *Harpia harpyja*. 2017.
40. Nogueira EM, Nelson BW, Fearnside PM, França MB, Oliveira ÁCA de. Tree height in Brazil's 'arc of deforestation': Shorter trees in south and southwest Amazonia imply lower biomass. For. Ecol. Manage. 2008; 255: 2963–2972.
41. Banhos A, Hrbek T, Sanaiotti TM, Farias IP. Reduction of Genetic Diversity of the Harpy Eagle in Brazilian Tropical Forests. PLoS One 2016; 11: e0148902.
42. Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 2011; 17: 43–57.
43. Rotenberg J, Marlin J, Pop L, Garcia W. First record of a Harpy Eagle (*Harpia harpyja*) nest in Belize. Wilson J. Ornith. 2012;124: 292–297.
44. Ubaid FK, Ferreira LP, de Oliveira SB, Antas PDTZ. Primeiro registro de *Harpia harpyja* para o bioma Pantanal, com dados sobre atividade reprodutiva. Rev. Bras. Ornitol. 2011; 19: 88–92.
45. Pereira ADMM, Salzo I. Primeiro registro da nidificação de *Harpia harpyja* (Falconiformes, Accipitridae) na Serra da Bodoquena (Mato Grosso do Sul, Brasil). Rev. Bras. Ornitol. 2006; 14: 157–160.
46. Banhos A, Hrbek T, Gravena W, Sanaiotti T, Farias IP. Genomic resources for the conservation and management of the harpy eagle (*Harpia harpyja*, Falconiformes, Accipitridae). Genet. Mol. Biol. Sociedade Brasileira de Genética; 2008; 31: 146–154.
47. Granados RG. Arquitectura de árboles y estructura de la vegetación del bosque como factores determinantes en la anidación del Águila Arpía (*Harpia harpyja* Linnaeus 1878) en la cuenca baja del Río Tambopa. Universidad Nacional Agraria La Molina. 2005.
48. Luz BB da. Características de árvores emergentes utilizadas por Gavião-real (*Harpia harpyja*) para nidificação no centro e leste da Amazônia Brasileira. 2005.
49. Richardson VA, Peres CA. Temporal Decay in Timber Species Composition and Value in Amazonian Logging Concessions. Zia A, editor. PLoS One 2016; 11: e0159035.
50. Rettig N. Breeding behavior of the harpy eagle (*Harpia harpyja*). Auk 1978; 95: 629–643.
51. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 2005; 25: 1965–1978.
52. Center for International Earth Science Information Network - CIESIN - Columbia University. Gridded Population of the World, Version 4 (GPWv4): Population Density [Internet]. 2016. doi:http://dx.doi.org/10.7927/H4NP22DQ
53. NASA Land Processes Distributed Active Archive Center (LP DAAC). Vegetation Indices

Monthly L3 Global 1km [Internet]. 2006.
54. Simard M, Pinto N, Fisher JB, Baccini A. Mapping forest canopy height globally with spaceborne lidar. J. Geophys. Res. 2011; 116: G04021.
55. Iturbide M, Bedia J, Herrera S, del Hierro O, Pinto M, Manuel J. A framework for species distribution modelling with improved pseudo-absence generation. Ecol. Model. 2015; 312: 166–174.
56. Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, et al. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol. Appl. 2009; 19: 181–197.
57. Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. Selecting pseudo-absences for species distribution models: how , where and how many ? Methods Ecol. Evol. 2012;3: 327–338.
58. Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W. Evaluation of consensus methods in predictive species distribution modelling. Divers. Distrib. 2009; 15: 59–69.
59. Burt WH. Territoriality and home range concepts as applied to mammals. J. Mammal. 1943; 24: 346.
60. Alvarez-Cordero E. Biology and conservation of the harpy eagle in Venezuela and Panama. DSc Thesis. University of Florida, Florida, USA. 1996.
61. Aguiar-Silva H. Uso e seleção de recursos por harpia em múltiplas escalas espaciais: persistência e vulnerabilidade. INPA. 2016.
62. D'Elia J, Haig SM, Johnson M, Marcot BG, Young R. Activity-specific ecological niche models for planning reintroductions of California condors (*Gymnogyps californianus*). Biol. Conserv. 2015; 184: 90–99.
63. Liu C, White M, Newell G. Selecting thresholds for the prediction of species occurrence with presence-only data. J. Biogeogr. 2013; 40: 778–789.
64. Watson RT, McClure CJW, Vargas FH, Jenny JP. Trial Restoration of the harpy eagle, a large, long-lived, tropical forest raptor, in Panama and Belize. J. Raptor Res. 2016; 50: 3–22.
65. Sick H. Ornitologia brasileira, uma introdução. Brasília, Brasil: Universidade de Brasília; 1984.
66. Aguiar-Silva F, Sanaiotti T, Luz B. Food habits of the Harpy Eagle, a top predator from the Amazonian rainforest canopy. J. Raptor Res. 2014; 48: 24–45.
67. Alho C. Environmental effects of hydropower reservoirs on wild mammals and freshwater turtles in Amazonia: a review. Oecologia Aust. 2011; 15: 593–604.
68. Taube E, Vie J-C, Fournier P, Genty C, Duplantier J-M. Distribution of two sympatric species of sloths (*Choloepus didactylus* and *Bradypus tridactylus*) along the Sinnamary River, French Guiana1. Biotropica 1999; 31: 686–691.
69. Peres CA, Palacios E. Basin-wide effects of game harvest on vertebrate population densities in Amazonian Forests: Implications for animal-mediated seed dispersal. Biotropica 2007; 39: 304–315.
70. Miranda EBP. Prey Composition of harpy eagles (*Harpia harpyja*) in Raleighvallen, Suriname. Trop. Conserv. Sci. 2018; 11: 1940082918800789.
71. Piana R. Anidamiento y dieta de *Harpia harpyja* Linnaeus en la Comunidad Nativa de Infierno, Madre de Dios, Perú. Rev. Peru Biol. 2007; 14: 135–138.
72. Muñiz-López R. Revisión de la situación del Águila Harpía *Harpia harpyja* en Ecuador. Cotinga 2008; 29: 42–47.
73. Fearnside PM. Deforestation in Brazilian Amazonia: History, rates, and consequences.

Conserv. Biol. 2005; 19: 680–688.
74. Roriz PAC, Yanai AM, Fearnside PM. Deforestation and Carbon Loss in Southwest Amazonia: Impact of Brazil's Revised Forest Code. Environ. Manage. 2017; 60: 367-382.
75. Asner G, Knapp D, Broadbent E, Oliveira P, Keller M, Silva J. Selective Logging in the Brazilian Amazon. Science 2006; 310: 483.
76. Chebez J, Croome M, Serret A, Taborda A. La nidificación de la Harpía (*Harpia harpyja*) en Argentina. Hornero 1990;13: 155–158.
77. INPE. PRODES - Taxas anuais de desmatamento na Amazônia Legal Brasileira (AMZ). 2018.
78. Vargas-González J de J, Vargas FH. Nesting density of Harpy Eagles in Darien with population size estimates for Panama. J. Raptor Res. 2011; 43: 199–210.
79. Peres CA. Why we need megareserves in Amazonia. Conserv Biol. 2005; 19: 728–733.
80. Crisostomo AC, Alencar A, Mesquita I, Silva I, Dourado M. Terras Indígenas Na Amazônia Brasileira: reservas de carbono e barreiras ao desmatamento. Brasília; 2015.
81. Araujo BB, Oliveira-Santos L, Lima-Ribeiro M, Diniz-Filho J, Fernandez FA. Bigger kill than chill: The uneven roles of humans and climate on late Quaternary megafaunal extinctions. Quat. Int. 2017;431: 216–222.
82. Shepard Jr GH, Levi T, Neves EG, Peres CA, Yu DW. Hunting in ancient and modern Amazonia: rethinking sustainability. Am. Anthropol. 2012;114: 652–667.
83. Fernandez F dos S, Antunes P, Macedo L, Zucco CA. How sustainable is the use of natural resources in Brazil? Nat. Conserv. 2012;10: 77–82.
84. Terborgh J, Peres CA. Do community-managed forests work? A Biodiversity Perspective. Land. 2017; 6: 1–7.
85. Koster J. The impact of hunting with dogs on wildlife harvests in the Bosawas Reserve, Nicaragua. Environ. Conserv. 2008; 35: 211–220.
86. Schneider M, Peres CA. Environmental costs of government-sponsored agrarian settlements in Brazilian Amazonia. PLoS One 2015; 10: e0134016.
87. Gusmão AC, Banhos A, Aguiar-Silva FH, Souza LS de, Sanaiotti, Tânia Margarete Silva, Adriano Martins da Costa TM, Oliveira LE, et al. Records of the occurrence, nesting, and hunting of the Harpy Eagle (*Harpia harpyja*) (Aves: Accipitridae) in Rondônia. Atualidades Ornitológicas 2016; 190: 18–23.
88. Silva D, Melo F de, Júnior I. Historical and recent records of the Harpy Eagle (*Harpia harpyja*) in the Cerrado biome of the state of Goiás, Brazil. Rev. Bras. Ornitol. 2014; 21: 4.
89. Mourão G, Tomas W, Campos Z. How much can the number of jabiru stork (Ciconiidae) nests vary due to change of flood extension in a large Neotropical floodplain? Zoologia 2010; 27: 751–756.
90. Suárez W, Olson SL. Systematics and distribution of the giant fossil barn owls of the West Indies (Aves: Strigiformes: Tytonidae). Zootaxa 2015; 4020: 533–553.
91. Steadman DW, Albury NA, Kakuk B, Mead JI, Soto-Centeno JA, Singleton HM, et al. Vertebrate community on an ice-age Caribbean island. Proc. Nat. Acad. Sci. 2015; 112: 201516490.
92. Weber MM, Stevens RD, Diniz-Filho JAF, Grelle CE V. Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. Ecography 2016; 40: 817–828.
93. Tôrres NM, De Marco P, Santos T, Silveira L, Jácomo ATA, Diniz-Filho JA. Can species distribution modelling provide estimates of population densities? A case study with jaguars

in the Neotropics. Divers. Distrib. 2012; 18: 615–627.
94. Aguiar-Silva FH, Sanaiotti TM, Jaudoin O, Srbek-Araujo AC, Siqueira G, Banhos A. Harpy Eagle sightings, traces and nesting records at the “Reserva Natural Vale”, a Brazilian Atlantic Forest remnant in Espírito Santo, Brazil. Rev. Bras. Ornitol. 2012; 20: 148–155.
95. Dean W. A ferro e fogo: a história e a devastação da Mata Atlântica brasileira. São Paulo, Brasil: Companhia das Letras; 1996.
96. de Marques AAB, Schneider M, Peres CA. Human population and socioeconomic modulators of conservation performance in 788 Amazonian and Atlantic Forest reserves. PeerJ 2016; 4: e2206.
97. Middendorp RS, Vanacker V, Lambin EF. Impacts of shaded agroforestry management on carbon sequestration, biodiversity and farmers income in cocoa production landscapes. Landsc. Ecol. 2018; 33: 1953–1974.
98. Cassano CR, Schroth G, Faria D, Delabie JH, Bede L. Landscape and farm scale management to enhance biodiversity conservation in the cocoa producing region of southern Bahia, Brazil. Biodivers. Conserv. 2009; 18: 577–603.
99. Moraes-Barros N de, Giorgi AP, Silva S, Stenghel J, Morgante. Reevaluation of the geographical distribution of *Bradypus tridactylus* Linnaeus, 1758 and *B. variegatus* Schinz, 1825. Edentata. 2010; 11: 53–61.
100. Galetti M, Brocardo CR, Begotti RA, Hortenci L, Rocha-Mendes F, Bernardo CSS, et al. Defaunation and biomass collapse of mammals in the largest Atlantic forest remnant. Anim. Conserv. 2016; 1–12.
101. Brocardo CR, Gonçalves HS, Zipparro VB, Galetti M. Predation of adult palms by black capuchin monkeys (*Cebus nigritus*) in the Brazilian Atlantic Forest. Neotrop. Primates. 2010; 17: 70–74.
102. Mikich SB, Liebsch D. Damage to forest plantations by tufted capuchins (*Sapajus nigritus*): Too many monkeys or not enough fruits? For. Ecol. Manage. 2014; 314: 9–16.
103. Pardo J, Paviolo A, Saura S, De Angelo C. Halting the isolation of jaguars: where to act locally to sustain connectivity in their southernmost population. Anim. Conserv. 2017; doi:0.1111/acv.12354
104. Galetti M, Pires AS, Brancalion PH, Fernandez FA. Reversing defaunation by trophic rewilding in empty forests. Biotropica 2017; 49: 5–8.
105. Fernandez FAS, Rheingantz ML, Genes L, Kenup CF, Galliez M, Cezimbra T, et al. Rewilding the Atlantic Forest: Restoring fauna and ecological interactions in a protected area. Perspect. Ecol. Conserv. 2017;15: 308–314.
106. Kierulff MCM, Mendes SL, Rylands AB. *Sapajus xanthosternos*. In: The IUCN Red List of Threatened Species. 2015.
107. Giné GAF, Cassano CR, de Almeida SS, Faria D. Activity budget, pattern and rhythm of maned sloths (*Bradypus torquatus*): Responses to variations in ambient temperature. Mamm. Biol. 2015; 80: 459–467.
108. Catzeflis F, J. P, Percequillo A, Bonvicino C, Weksler M. *Chaetomys subspinosus*. In: The IUCN Red List of Threatened Species. 2008.
109. Lovari S, Boesi R, Minder I, Mucci N, Randi E, A. D, et al. Restoring a keystone predator may endanger a prey species in a human-altered ecosystem: the return of the snow leopard to Sagarmatha National Park. Anim. Conserv. 2009; 12: 559–570.
110. Oliveira MJ de. Manejo reprodutivo de harpia em cativeiro no Brasil [Internet]. Universidade Federal do Paraná. 2018. Available:

https://acervodigital.ufpr.br/handle/1884/58629
111. Muela A, Watson R, Mutch B, Heinrich W. The Harpy Eagle: biology, restoration and hacking procedures. Fondo Peregrino-Panamá. Ciudad de Panamá; 2003.
112. Campbell-Thompson E, Vargas FH, Watson RT, Muela A, Cáceres NC. Effect of sex and age at release on the independence of hacked harpy eagles. J. Raptor Res. 2012; 46: 158–167.
113. Miranda EBP, Campbell-Thompson E, Muela A, Vargas FH. Sex and breeding status affect prey composition of Harpy Eagles *Harpia harpyja*. J. Ornithol. 2017;
114. Macdonald C, Gallagher AJ, Barnett A, Brunnschweiler J, Shiffman DS, Hammerschlag N. Conservation potential of apex predator tourism. Biol. Conserv. 2017;215: 132–141.
115. Tortato FR, Izzo TJ, Hoogesteijn R, Peres CA. The numbers of the beast: Valuation of jaguar (*Panthera onca*) tourism and cattle depredation in the Brazilian Pantanal. Glob. Ecol. Conserv. 2017;11: 106–114.

CHAPTER 3

High moon brightness and low ambient temperatures affect sloth predation by harpy eagles

Everton B. P. Miranda[1], Caio Fittipaldi Kenup[2], Edwin Campbell-Thompson[3, 4], Félix Hernán Vargas[4], Angel Muela[4], Richard Watson[4], Carlos A. Peres[5, 6], Colleen T. Downs[1]

[1] Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, P/Bag X01. Pietermaritzburg, 3209, South Africa

[2] Wildlife and Ecology Group, Massey University, Palmerston North, New Zealand

[3] Fundación Águilas de Los Andes, Pereira, Colombia

[4] The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, Idaho 83709 U.S.A

[5] School of Environmental Sciences, University of East Anglia, Norwich NR47TJ, UK

[6] Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Brazil

Corresponding Author:
Everton Miranda
Rua F2, nº220, Alta Floreta, Mato Grosso 78580-000, Brazil
Email address: mirandaebp@gmail.com

Running header: Sloth predation by harpy eagles

Published in PeerJ. For the published version, please visit: https://peerj.com/articles/9756/

3.1 Abstract

Background. Climate plays a key role in the life histories of tropical vertebrates. However, tropical forests are only weakly seasonal compared with temperate and boreal regions. For species with limited ability to control core body temperature, even mild climatic variation can determine major behavioural outcomes, such as foraging and predator avoidance. In tropical forests, sloths are the arboreal vertebrate attaining the greatest biomass density, but their capacity to regulate body temperature is limited, relying on behavioural adaptations to thermoregulate. Sloths are largely or strictly nocturnal, and depend on crypsis to avoid predation. The harpy eagle (*Harpia harpyja*) is a sloth-specialist and exerts strong top-down control over its prey species. Yet the role of environmental variables on the regulation of predator-prey interactions between sloths and harpy eagles are unknown. The harpy eagle is considered Near Threatened. This motivated a comprehensive effort to reintroduce this species into parts of Mesoamerica. This effort incidentally enabled us to understand the prey profile of harpy eagles over multiple seasons.

Methods. Our study was conducted between 2003 and 2009 at Soberanía National Park (SNP), Panamá. Telemetered harpy eagles were seen hunting and feeding on individual prey species. For each predation event, field assistants systematically recorded the species killed. We analysed the effects of climatic conditions and vegetation phenology on the prey species profile of harpy eagles using generalised linear mixed models.

Results. Here we show that sloth predation by harpy eagles was negatively affected by nocturnal ambient light (i.e. bright moonshine) and positively affected by seasonally cool temperatures. We suggest that the first ensured low detectability conditions for sloths foraging at night and the second posed a thermally unsuitable climate that forced sloths to forage under riskier daylight. We showed that even moderate seasonal variation in temperature can influence the relationship between a

keystone tropical forest predator and a dominant prey item. So predator-prey ecology in the tropics can be modulated by subtle changes in environmental conditions. The seasonal effects shown here suggest important demographic consequences for sloths, which are under top-down regulation from harpy eagle predation, perhaps limiting their geographic distribution at higher latitudes.

3.2 Introduction

Predation is a central theme in ecology and evolution, driving morphological, physiological, and behavioural responses in prey species to the threat of death or injury (Genovart et al., 2010). Both the nature and magnitude of predation as a dominant ecological force are affected by seasonality (Darimont & Reimchen, 2002). However, the seasonality of predator-prey relationships in tropical forests is at best considered to be subtle compared with temperate and boreal regions, because of the comparatively low variation in day length and ambient temperature (Forsythe et al., 1995). Nevertheless, tropical forests can experience considerable seasonality in leaf flushing and fruiting as a response to climatic variables (Mendoza, Peres & Morellato, 2016). While available data suggests that climatic conditions in tropical environments have strong effects on animal activity (Foster et al., 2013; Cid, Oliveira-Santos & Mourão, 2015), there are relatively few studies about the nature of such effects on predator-prey interactions.

Seasonally elevated rainfall and the resulting responses in vegetation growth can provide food and cover for many arboreal taxa in tropical forests (Haugaasen & Peres, 2009). Conversely, the dry season often induces leaf abscission in trees and woody lianas (Souza, Gandolfi & Rodrigues, 2014), which may limit food availability and shelter to arboreal folivores. The combination of reduced cover and limited food resource availability can enhance predation risk (Menezes, Kotler & Mourão, 2014; Menezes, Mourão & Kotler, 2017). The seasonal variation may modify the range of thermal microhabitats available to a prey species. As endothermic forest specialists, sloths (genus *Bradypus* and *Choloepus*, order Pilosa) exhibit relatively low basal metabolic rates and can only partially regulate body temperature (Pauli et al., 2016). Therefore, they need to bask and can be affected by even mild variation in habitat cover and thermally inappropriate microhabitats (Peery & Pauli, 2014; Giné et al., 2015), to the extent that temperature seasonality is highly influential on sloth behavioural ecology (Moreira et al., 2014).

Sloths from the *Bradypus* and *Choloepus* genus differ in their biology. *Choloepus* are more vigorous (Pauli et al., 2016), larger (~6kg, Wetzel & Montgomery, 1985), have a higher body temperature (Vendl et al., 2016), and a more diversified diet (Dill-McFarland et al., 2016). *Bradypus* sloths fit the stereotypical sluggish behaviour of sloths (Pauli et al., 2016), are smaller (~4kg; Wetzel & Montgomery, 1985), have a relatively low body temperature (Vendl et al., 2016), and feed on leaves exclusively (Dill-McFarland et al., 2016). Finally, two-toed sloths (*Choloepus* spp.) are nocturnal, whereas three-toed sloths (*Bradypus* spp.) are cathemeral (Sunquist & Montgomery, 1973; Giné et al., 2015).

Likewise, moonlight is likely to alter animal behaviour by affecting the detectability of both predators and prey at night (San-Jose et al., 2019). Lunar phobia by mammals is widely justified as a strategy to prevent predation (Cozzi et al., 2012). However, a metanalysis by Prugh and Golden (2014) showed that the response to lunar light was typically idiosyncratic. While visually-oriented mammals have an increased activity response to lunar light, mammals that have weak vision—like sloths—generally decrease activity on bright nights (Prugh & Golden, 2014) and therefore are less likely to suffer predation.

We expected that the seasonality of predator-prey relationships involving sloths might be affected by even subtle climatic fluctuations in ambient temperature. Sloths are important prey species that rely heavily on crypsis to avoid predation, rather than evasive responses once they are detected (Touchton, Hsu & Palleroni, 2002). However, studies attempting to identify the cues leading to seasonal changes in prey activity and predation are inherently hindered by small sample sizes. While apex predators have profound effects on ecosystem structure and function (Terborgh et al., 2001), they are difficult to study, rendering this lack of knowledge almost impossible to overcome.

The harpy eagle (*Harpia harpyja*; Fig. 3.1) is considered Near Threatened by the IUCN (Birdlife International, 2017), mainly because of human persecution (Muñiz-López, 2017) and habitat loss, which have extirpated these mega-raptors from 41% of their former historical range distribution (Miranda et al., 2019). Harpy eagles are an apex predator that specialises on sloths, relying heavily on these prey species wherever they co-occur (Aguiar-Silva, Sanaiotti & Luz, 2014; Miranda, 2015). Harpy eagles hunt passively by visually scanning and listening to the forest canopy (Touchton, Hsu & Palleroni, 2002). They are unique among eagles having a large retractable facial disc to enhance their hearing (Ferguson-Lees & Christie, 2001). Harpy eagles are the Earth's largest eagles. Being large-sized, they can prey on sloths of any age (Aguiar-Silva, Sanaiotti & Luz, 2014), including adult individuals of all continental sloth species (Miranda, 2018). Harpy eagle-sloth predator-prey systems are therefore ideal candidates to investigate how changes in climate and moonlight may affect multispecies predation rates.

The Peregrine Fund has lead a comprehensive effort to reintroduce this species into parts of Mesoamerica (Campbell-Thompson et al., 2012; Watson et al., 2016). This effort, spanning from 2003 to 2009, incidentally enabled us to understand, for the first time, the prey profile of harpy eagles over multiple seasons.

Fig. 3.1 Harpy eagle preying over sloth. Adult female harpy eagle (*Harpia harpyja*) eating a young Two-toed sloth (*Choloepus didactylus*; Photo: Danilo Mota).

We explored environmental determinants of prey capture rates of reintroduced harpy eagles in Soberanía National Park; a tropical protected area in Panamá. Our goals were twofold: (1) to assess the effects of seasonality—like temperature, rainfall and leaf decidousness—on sloth capture rates by harpy eagles; and (2) to assess how moonlight could affect sloth and nocturnal prey predation rates. We predicted that: (1) sloth predation rates would increase with low temperatures, high rainfall and low leaf cover; (2) sloth and nocturnal prey predation rates would increase with low moon brightness.

3.3 Methods

STUDY SITE. — Our study was conducted between 2003 and 2009 at Soberanía National Park (hereafter, SNP), a 19,545 ha protected area in eastern Panama along the banks of the Panama Canal (9°07'13" N, 79°39'37" W). The vegetation of SNP consists of semi-deciduous, seasonally moist tropical forest, most of which is now advanced (>80 years) secondary forest (Bohlman, 2010). The area has most of the staple prey species targeted by harpy eagles (Aguiar-Silva, Sanaiotti & Luz, 2014), including three-toed sloths (*Bradypus variegatus*), Hoffman's two-toed sloths (*Choloepus hoffmanni*), white-nosed coati (*Nasua narica*), northern lesser anteater (*Tamandua mexicana*) and mantled howler monkeys (*Alouatta palliata*), all of which are either strictly arboreal or scansorial mammals. The Peregrine Fund had conducted experimental harpy eagle releases within SNP since 1997 (Muela et al., 2003; Watson et al., 2016), therefore we assumed that none of the prey species here were predator-naïve during our study.

The SNP has a marked dry season from December to April and a wet season from May to November. The wet season concentrates 85.3% of the annual rainfall, which averaged 2,242 mm p.a. for 2003-2009. During the dry season, the mean, minimum and maximum ambient temperatures were 27.3, 22.1, 33.0°C, respectively, and slightly warmer than the corresponding temperatures during the wet season (26.5, 23.2, 30.9°C, respectively). Daily weather data were obtained from ETESA (http://www.hidromet.com.pa/), using Hodges Hill Meteorological Station data for rainfall (15 km from the release site) and the Tocumen Station for data on temperature (43 km from the release site). A Walter-Lieth climate diagram describing the seasonality of rainfall and ambient temperature in the park was created (https://peerj.com/articles/9756/#supp-3).

HARPY EAGLE PREY PROFILE.—Before final release, captive-bred harpy eagles were soft-released at SNP by a process known as hacking (Muela et al., 2003). This allowed harpy eagles to learn how to hunt, as would occur in the wild (Muñiz-López et al., 2016). Further details on the harpy eagle reintroduction protocols and results are available in Campbell-Thompson et al. (2012) and Watson et al. (2016). Harpy eagles were fitted with both VHF and GPS tags. During soft releases, they were fed thawed rats and rabbits, always using a blind to avoid food conditioning with humans. Foraging independence was defined on the basis on an eagle being able to make two unassisted successive kills within 20 days or survive 30 days without food provisioning, thereby demonstrating that it was able to hunt self-sufficiently. Both regular radio- and global position system (GPS)-tracking, leading to visual contact with each telemetered eagle was required to check its body condition.

As the reintroduced harpy eagles were captive-born sub-adults (5-22 months; Campbell-Thompson et al., 2012) from captive stock maintained by The Peregrine Fund, we performed an *a priori* graphical analysis to ensure that the diet of reintroduced harpy eagles was similar to that of wild adult individuals. We did so by dividing the number of captured prey items within blocks of 25 samples (which adequately represents the main prey species; Miranda 2015) and distributed them according to ontogeny or experience. We defined ontogeny as age in months of any given prey killing event, whereas we defined experience as any given predation event relative to the number of days since the first wild prey item was captured. Neither ontogeny nor experience affected harpy eagles' patterns of predation as there was no evidence of nested patterns that would be expected if shifts in prey preferences occurred (Supplementary information Fig. S3.2 and S3.3).

We therefore consider hunting patterns by reintroduced harpy eagles comparable with those of wild adults, and this was consistent with previous reports (Touchton, Hsu & Palleroni, 2002). The spatial distribution of those kill sites, as well as the location of the release site and meteorological stations within SNP are shown in Fig. 3.2.

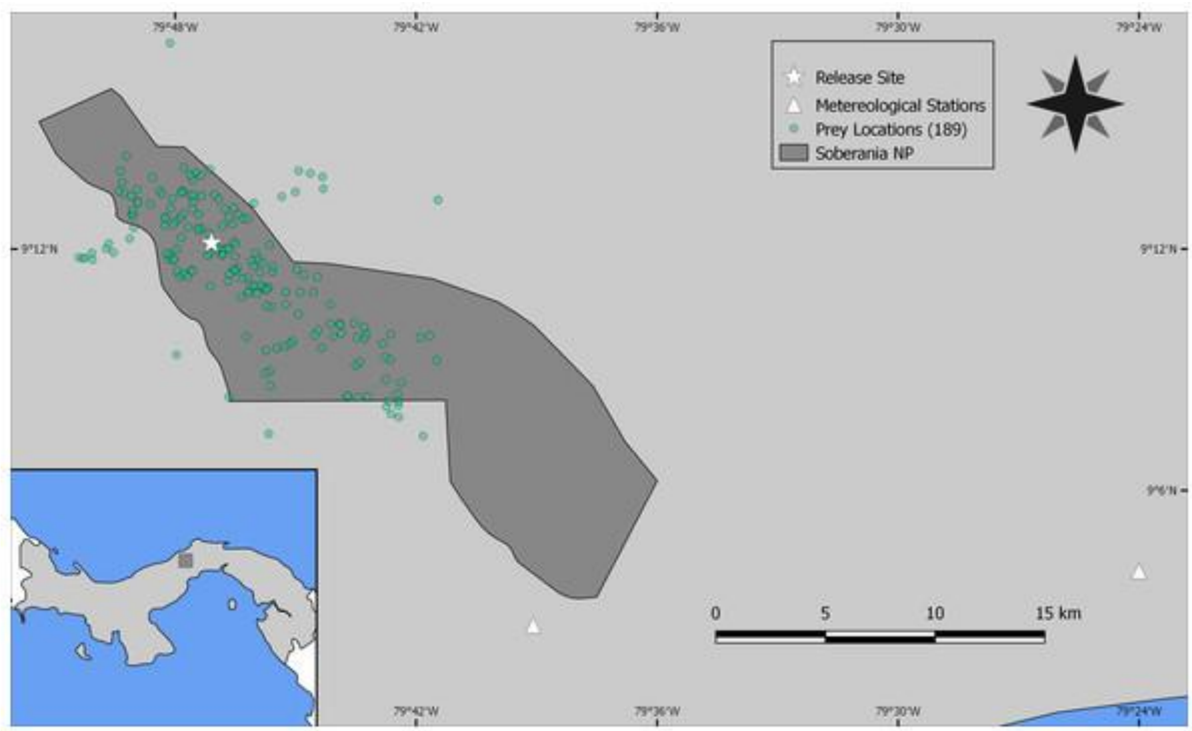

Fig. 3.2 Study site. Location of Soberanía National Park in central Panama (lower left inset map), showing the location of 189 predation events (green dots), release site (white star) and meteorological stations (white triangles).

PREDATION AND ENVIRONMENTAL DETERMINANTS.— During observations, while tracking, harpy eagles were seen hunting and feeding on individual prey species. For each predation event, field assistants systematically recorded all species killed (whenever identification to the level of species was possible). Field assistants were instructed to remain as inconspicuous as possible and leave the eagles alone as soon as observations were recorded. Prey items of known species identity were recorded during all months of the year, over the 7-year study, although observations were typically sparser during the month of November.

We related measures of climatic seasonality and vegetation phenology to the prey species profile of harpy eagles. Daily weather data on precipitation and ambient temperature, were obtained from nearby meteorological stations. Data on the phases of the lunar cycle at a daily resolution over the entire study period were obtained from http://www.astronomyknowhow.com. We used the percentage of moon shade cover per night as a proxy for light availability. NDVI is a measure of vegetation 'greenness', rather than deciduousness, but is highly correlated to leafing cycles (Bohlman, 2010).We used the normalised difference vegetation index (NDVI) as a proxy for canopy leaf deciduousness, where NDVI = (IR – R)/(R + IR), IR being the near-infrared LANDSAT band 4 and R the red LANDSAT band 3. NDVI values were calculated using georeferenced LANDSAT images obtained for all months of the year during the study period. For each prey detection event, we estimated the NDVI score of all 30 m x 30 m pixels within a 1 km radius of the location of each predation event for the nearest five dates of LANDSAT images available for that period. We then interpolated these indices to estimate the composite NDVI metric for the detection date of each prey item.

We ran two batches of generalised linear mixed-effects models (GLMM) using as response variables (1) the probability of any given prey item being a sloth (either *Bradypus* or *Choloepus*) and (2) the probability of any given prey item being nocturnal. Because the set of environmental covariates for each model was large, we used a backwards AIC-based stepwise algorithm to select the most important variables for each fixed-effect model, adding the random effect afterwards. All GLMMs were run using a binomial error structure and the logit link function, and bird identity as a random effect on the intercept. All variables used were checked for covariance using the Variance

Inflation Factor (VIF). All analyses were run using the R 3.6.1 platform. Environmental covariates used in each GLMM are presented in Supplementary information Table S1. All source codes used in the analyses are available at https://github.com/KenupCF/HarpySlothPredation.

The Peregrine Fund Harpy Eagle Restoration Program complied with the laws of Panamá during the time in which the project was performed, with permits granted by National Environmental Authority of Panama (ANAM, at present MiAmbiente and SISBIO#58533-5).

3.4 Results

We recorded a total of 200 harpy eagle predation events, from which we obtained positional data for 189 prey items, 173 of which were identified. These prey items were killed by 33 harpy eagles during six dry seasons and six wet seasons during the 7 years of study. This amounted to 88 prey samples during the dry seasons and 85 samples during the wet seasons. The temporal distribution of predation records and the functional groups of prey species showed that sloths were by far the most important prey species for harpy eagles (Fig. 3.3). Two sloth species represented 65.3% of the harpy eagle diet in terms of the overall numeric prey profile, of which brown-throated sloths, Hoffman's two-toed sloths and unknown sloths represented 34.1%, 15.6% and 15.6% of all prey items, respectively. Second to sloths, the next most significant dietary contributors to harpy eagles were white-nosed coatis (7.5%), northern lesser anteaters (6.9%) and mantled howler monkeys (5.2%). Further information on the prey species composition are shown in Table 3.1.

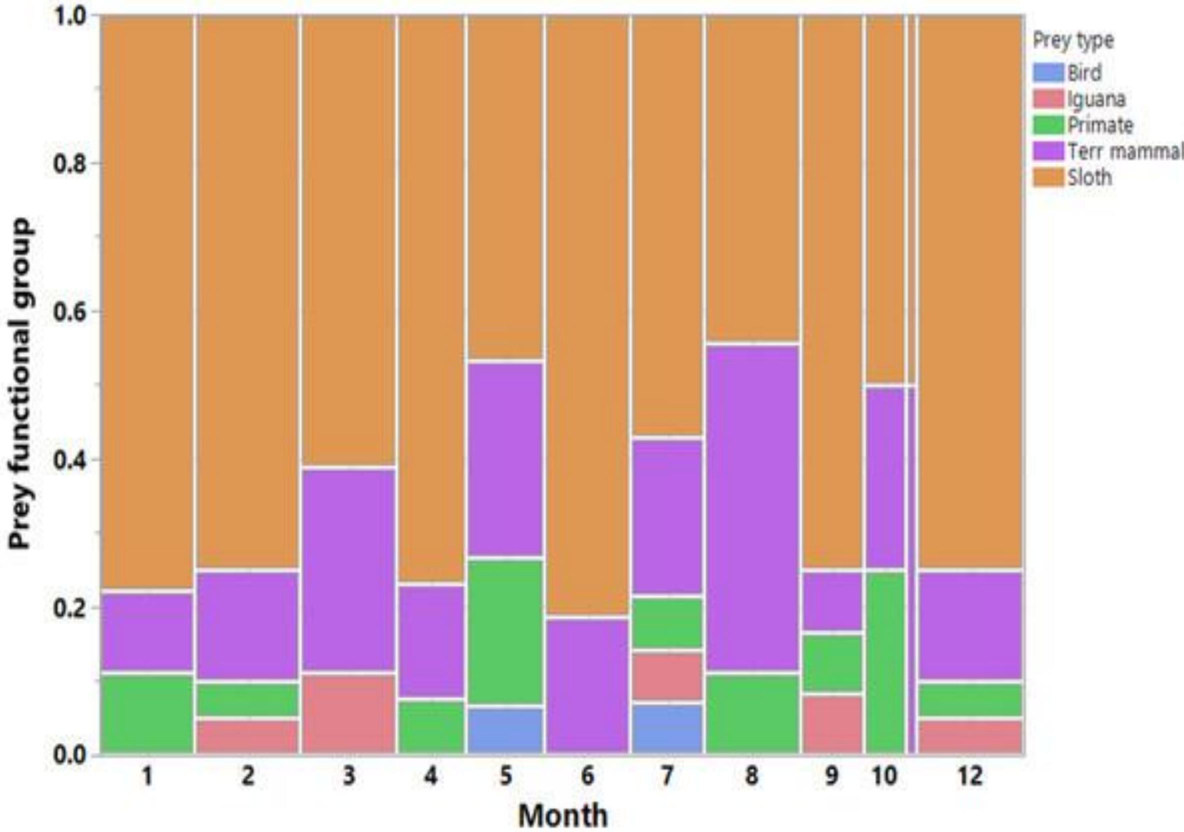

Fig. 3.3 Prey composition and effort. Monthly distribution of harpy eagle kills throughout the year. Vertical bars are colour-coded according to the main prey functional groups. Observations were made in all months of the year, however more scantly in November.

Table 3.1: Prey composition in the diet of harpy eagles. Seasonal changes in the incidence of kills by harpy eagles shown in percentages, combining frequencies for both wet and dry seasons across the seven years of study (2003–2009). Overall column shows percentages of prey items for all periods combined, and sample sizes (in parentheses). See “Study Site” section of Methods for further details of season definition.

Species	Dry %	Wet %	Overall % (n)
Brown-throated sloth *Bradypus variegatus*	36.8	31.4	34.1 (59)
Hoffmann's two-toed sloth *Choloepus hoffmanni*	24.1	7.0	15.6 (27)
Unidentified sloths	11.5	19.8	15.6 (27)
White-nosed coati *Nasua narica*	5.7	9.3	7.5 (13)
Northern lesser anteater *Tamandua mexicana*	2.3	11.6	6.9 (12)
Mantled howler monkey *Alouatta palliata*	3.4	7.0	5.2 (9)
Green iguana *Iguana iguana*	4.6	2.3	3.4 (6)
Common opossum *Didelphis marsupialis*	2.3	2.3	2.3 (4)
White-headed capuchin *Cebus capucinus*	2.3	2.3	2.3 (4)
Collared peccary *Tayassu tajacu*	1.1	2.3	1.7 (3)
Nine-banded armadillo *Dasypus novemcinctus*	1.1	1.2	1.1 (2)
Central American agouti *Dasyprocta punctata*	2.3	0.0	1.1 (2)
Crab-eating raccoon *Procyon cancrivorus*	1.1	0.0	0.5 (1)
Tayra *Eira barbara*	1.1	0.0	0.5 (1)
Black vulture *Coragyps atratus*	0.0	1.2	0.5 (1)
Unidentified parrot	0.0	1.2	0.5 (1)
Unidentified monkey	0.0	1.2	0.5 (1)

Sloth predation rates increased significantly during low moon brightness (β = –0.648, p = 0.0116) and low ambient temperatures with marginal statistical significance (β = –0.508, p = 0.0535; Fig. 3.4). Harpy predation on nocturnal animals was weakly affected by low moon brightness (Fig. 3.4), but this lacked sufficient statistical significance (β = –0.392, p = 0.1461). Rainfall and leaf deciduousness had no discernible effect in any of our models. Statistical results are summarised in Table 3.2.

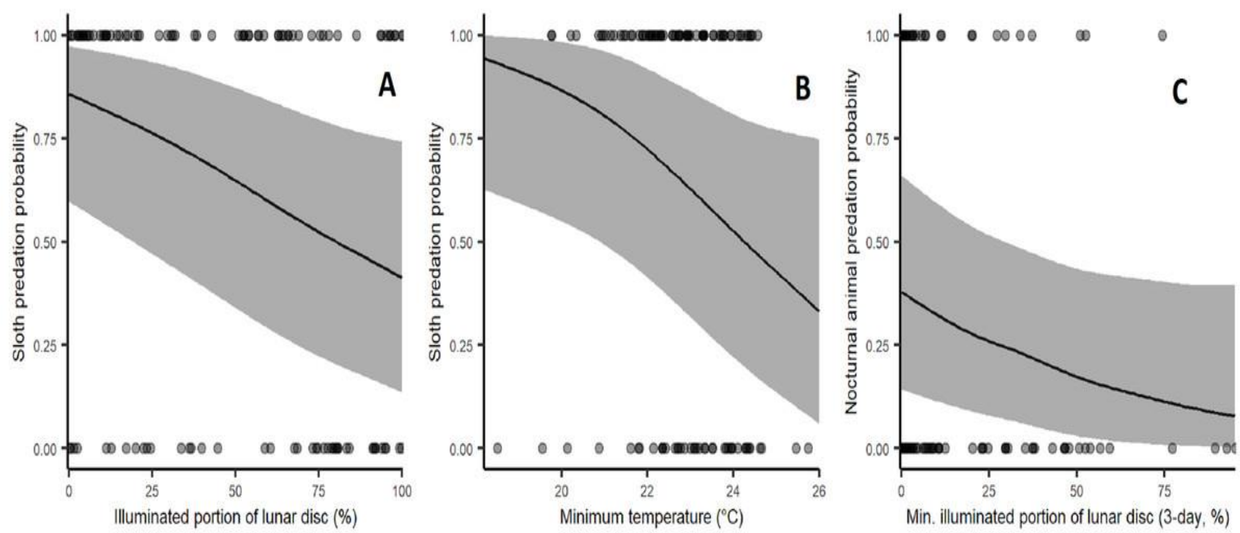

Fig. 3.4 Effect of environmental variables on the probability of predation events by harpy eagles. (A) Effect of moon brightness on sloth predation probability: fewer sloths were taken during bright moonlit nights (p = 0.0134). (B) Effect of minimum temperature on sloth predation probability: fewer sloths were taken under cooler conditions (p = 0.0413). (C) Effect of moon brightness on nocturnal mammal predation: fewer nocturnal prey were killed. During bright nights, but this lacked statistical significance (p = 0.12).

Table 3.2 Results of generalised linear mixed models of harpy eagle prey profile. The first model predicts the probability that a given animal preyed by a harpy eagle is a sloth, while the second model predicts the probability of prey being a nocturnal animal. Both models use a logit link because of the binomial natural of the data. Both models use tracked individuals and years sample as random effects over the intercept.

Model	Variable	Estimate	Standard Error	p-value	Random Individual Variance	Random Yearly Variance
Sloth	Intercept	0.588	0.470	0.2109	1.001	0.513
	Lunar disc (%)	-0.648	0.257	0.0116	-	-
	Minimum temperature (°C)	-0.508	0.263	0.0535	-	-
Night	Intercept	-0.933	0.422	0.0271	0.336	0.367
	Minimum lunar disc (3-Day; %)	-0.392	0.269	0.1461	-	-

3.5 Discussion

Although environmental conditions either increase prey vulnerability or provide an advantage to sit-and-wait and pursuit predators (Doody, Sims & Letnic, 2007; Prugh & Golden, 2014), little has been documented on this topic in closed-canopy tropical forest ecosystems. In harpy eagle-sloth predator-prey systems, sloth nocturnal activity under elevated moon brightness and cryptic behaviour during the day are putative mechanisms of escaping detection by harpy eagles. We also showed an increase in predation rates under cool temperatures, which may induce further diurnal activity of sloths. Finally, we examined the roles of leaf flush and rainfall on harpy eagle prey choice, but neither had a detectable effect on sloth predation rates. These results pose interesting questions about the consequences of temperature and moon brightness to this keystone Neotropical forest predator and its dominant prey species.

Moonlight has been shown to have contradictory effects on nocturnal mammal activity patterns in terms of their antipredator strategies. Prey species that can detect predators visually and anticipate their attacks with evasive manoeuvres may increase foraging activity under high levels of moonlight, whereas those that cannot decrease activity (Prugh & Golden, 2014). Sloths, however, typically prefer to sleep at night in environments where they evolved with predator presence (Voirin et al., 2014), and in other areas generally showing greater fear of diurnal predators as harpy eagles. Indeed, there is anecdotal evidence of increased sloth activity during full moon phases (Beebe, 1926). Sloths are known to be lethargic and have extremely poor vision, while harpy eagles typically attack from distances of less than 30 m during daylight (Touchton, Hsu & Palleroni, 2002). We, therefore, expected that sloths reduce their overall activity during the day, instead foraging at night under bright moonlit to reduce predation risk, which significantly reduces the probability of successful attacks by diurnal harpy eagles. Success rates of harpy eagles predation on sloths is generally high compared with visually oriented prey: 55% of all attacked sloths are successfully killed, while only 33% of visually oriented prey are successfully killed if they had been attacked (Touchton, Hsu & Palleroni, 2002). This may be the underlying adaptive reason why sloths are inactive during the day if bright nights are available as foraging time, neutralising search images of diurnal predators and greatly reducing their detection probability by harpy eagles. Further sloth telemetry studies would provide confirmatory evidence.

In addition to the reduced predation levels of sloths during bright moon nights, we showed that as ambient temperatures increased, predation rates declined. Presumably, this happened because of the increased daytime activity levels of this endotherm, which is prone to metabolic torpor under cooler weather conditions, especially at night (Giné et al., 2015). It has been shown, for instance, that the nocturnal activity of the maned sloth (*Bradypus torquatus*) is inhibited by lower ambient temperatures (Chiarello, 1998). Predation rates of sloths by harpy eagles were higher during colder conditions, which likely induce compensatory activity by sloths during the warmer daytime. Basking behaviour of sloths increases with lower ambient temperatures along altitudinal gradients in mountainous areas (Urbani & Bosque, 2007). Another possible explanation for the temporal changes in sloth predation rate could result from its reproductive behaviour. However, the literature shows weak and idiosyncratic evidence for seasonal breeding for both sloth species present in our study area (Taube et al., 2001). These features reinforce our premise that behavioural crypsis is the main antipredator strategy of sloths, which we suggest to be the underlying reasons for the patterns observed in our study. Indeed, the latitudinal boundaries of the geographic distribution of sloths are far more restricted than those of harpy eagles (Moreira et al., 2014; Miranda et al., 2019). Sloths of the *Choloepus* genus are distributed over tropical Central America and the pan-Amazonian region, while *Bradypus* also occur over the northern section of Atlantic Forest (Emmons & Feer, 1997). Predation by harpy eagles may play a key role in limiting sloth geographic distribution—and altitudinal ranges—given that sloths would be required to compensate for cooler temperatures in the southern Atlantic Forest or higher regions by increasing levels of diurnal activity (Chiarello, 1998; Urbani & Bosque, 2007). Therefore, this would inhibit extended periods of inactivity induced by cool temperatures, but increase temporal activity overlap with diurnal predators.

Rainfall apparently had no effect in any of our models explaining the incidence of sloth predation, a pattern that could also be explained by low predation risk resulting from the cessation of harpy eagle activity during rainy weather (Touchton, Hsu & Palleroni, 2002), or even distance from the meteorological stations, inducing error. Leaf abscission presented no effects on predation of sloths. Although we predicted increased probability of arboreal prey detection under leafless conditions in the semi-deciduous forests of central Panama, forest areas dominated by leafless trees and/or woody lianas may be consistently avoided by prey species relying on concealed foraging activity (Menezes, Kotler & Mourão, 2014; Menezes, Mourão & Kotler, 2017). For a sloth, leafless tree crowns offer little if any protective cover and no food resources. Our robust methods to estimate levels of deciduousness combined with a wide buffer describing the likely sight range of potential kills suggest that arboreal habitats lacking foliage cover would be avoided not only by prey species but also by harpy eagles, thereby at least partly explaining why deciduousness had no effects in any of our models.

Nocturnal prey capture by harpy eagles was not significantly affected by any of the environmental covariates, and the fact that these large diurnal raptors can frequently successfully kill several strictly nocturnal prey species remains puzzling. Modest increases in predation rates of nocturnal mammals were associated with darker nights, when nocturnal species typically preyed by harpy eagles (anteaters, opossums, and armadillos) are expected to be more active given their poor ability to anticipate incoming predators visually (Caro, 2005; Prugh & Golden, 2014). The harpy eagle sit-and-wait predation strategy is further enhanced by their retractable facial disc, which performs the same function as in strictly nocturnal raptors (i.e. owls), of improving acoustic detection of prey. Combined with extremely acute vision, which is likely associated with a high density of photoreceptor cells in the retina typical of many diurnal raptors (Lisney et al., 2013), harpy eagles are superbly capable of locating inconspicuous prey, enabling them to be the only Neotropical apex predator to specialise on the highly secretive sloths (Miranda, 2015; Miranda, Menezes & Rheingantz, 2016). Harpy eagle activity patterns can be investigated with further research using either intensive telemetry-assisted follows or camera-trapped nests. By including nocturnal telemetry or motion-sensitive telemetry devices on monitoring schedules or confirming that harpy eagles can deploy crepuscular/nocturnal hunting effort at the time of nesting (e.g. evidenced by nocturnal prey delivery) would largely solve this question.

Our results suggest important consequences for patterns of prey mortality through the tropical seasons of Neotropical forests. We, therefore, suggest that researchers, conservationists and practitioners can learn from natural fluctuations in predator-prey systems when designing management actions (such as reintroduction, release and translocation efforts) of both harpy eagles and their prey, since some of these prey species are also threatened (Catzeflis et al., 2008; Moreira et al., 2014; Suscke et al., 2017). For instance, consequences of the harpy eagle reintroduction on the endemic maned sloth, which is listed as Vulnerable in the Brazilian Atlantic Forest needs careful evaluation.

3.6 Conclusions

We showed that the probability of harpy eagles preying on sloths decreased in response to nocturnal high moon brightness and increased with low temperatures. This almost certainly occurs because sloths respond to low temperatures foraging more in the daytime, and circumvent high diurnal detectability by foraging on bright moonlit nights when they are not exposed to visually oriented predators. These conceptually simple conclusions result from overcoming the formidable challenges of monitoring the diet of apex predators in tropical forests for extended periods. We further note that the seasonal effects we uncovered here suggest important consequences for herbivore prey species, whose populations are likely regulated by top-down predation from harpy eagles and other top predators. The magnitude of cyclic changes in predator-prey interactions shown here potentially are even stronger in more seasonal tropical and subtropical forests experiencing cooler seasons, higher altitudes or prolonged flood pulses. Further studies on a diverse set of predator and prey assemblages in tropical forests elsewhere would help fill this knowledge gap.

3.7 Acknowledgements

We thank the many institutions and staff who have participated in The Peregrine Fund's Harpy Eagle Restoration Program. We also thank hack-site attendants for field assistance. Everton Miranda's logistical support was given by the Peugeot-ONF Carbon Sink Reforestation Project, based at the São Nicolau Farm in Cotriguaçu, Mato Grosso, Brazil. This Project is a Peugeot initiative to fulfil some of the Kyoto Protocol directions and is run by the ONF-Brasil enterprise. CTD is grateful to the University of KwaZulu-Natal (ZA) and the National Research Foundation (ZA) for funding. Marcus Canuto, Jose Vargas and Alexander Blanco provided useful discussions, improving a previous version of the manuscript. The Peregrine Fund Harpy Eagle Restoration Program complied with the laws of Panamá during the time in which the project was performed. We are grateful for the constructive comments of Mario Fernando Garces Restrepo and an anonymous reviewer.

3.8 References

Aguiar-Silva F, Sanaiotti T, Luz B. 2014. Food habits of the harpy eagle, a top predator from the Amazonian rainforest canopy. *Journal of Raptor Research* 48:24–45.

Beebe W. 1926. The three-toed sloth, *Bradypus cucullinger cucullinger* Wagler. *Zoologica* 7:1–67.

Birdlife International. 2017. *Harpia harpyja* (American Harpy Eagle, Harpy Eagle). *Available at http://datazone.birdlife.org/species/factsheet/22695998* (accessed February 13, 2018).

Bohlman SA. 2010. Landscape patterns and environmental controls of deciduousness in forests of central Panama. *Global Ecology and Biogeography* 19:376–385.

Campbell-Thompson E, Vargas FH, Watson RT, Muela A, Cáceres NC. 2012. Effect of sex and age at release on the independence of hacked harpy eagles. *Journal of Raptor Research* 46:158–167.

Caro T. 2005. *Antipredator defenses in birds and mammals*. Chicago, USA: University of Chicago Press.

Catzeflis F, J. P, Percequillo A, Bonvicino C, Weksler M. 2008.*Chaetomys subspinosus*. *Available at http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T4366A10812988.en*

Chiarello AG. 1998. Activity budgets and ranging patterns of the Atlantic forest maned sloth

Bradypus torquatus (Xenarthra: Bradypodidae). *Journal of Zoology* 246:1–10.
Cid B, Oliveira-Santos LGR, Mourão G. 2015. The relationship between external temperature and daily activity in a large rodent (*Dasyprocta azarae*) in the Brazilian Pantanal. *Journal of Tropical Ecology* 31:469–472.
Cozzi G, Broekhuis F, McNutt JW, Turnbull LA, Macdonald DW, Schmid B. 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology* 93:2590–2599.
Darimont CT, Reimchen TE. 2002. Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. *Canadian Journal of Zoology* 80:1638–1642.
Dill-McFarland KA, Weimer PJ, Pauli JN, Peery MZ, Suen G. 2016. Diet specialization selects for an unusual and simplified gut microbiota in two-and three-toed sloths. *Environmental Microbiology* 18:1391–1402.
Doody SJ, Sims RA, Letnic M. 2007. Environmental manipulation to avoid a unique predator: drinking hole excavation in the agile wallaby, *Macropus agilis*. *Ethology* 113:128–136.
Emmons L, Feer F. 1997. *Neotropical rainforest mammals: a field guide*. Chicago: University of Chicago Press.
Ferguson-Lees J, Christie D. 2001. *Raptors of the world*. New York, USA: Houghton Mifflin Harcourt.
Forsythe WC, Rykiel EJ, Stahl RS, Wu HI, Schoolfield RM. 1995. A model comparison for daylength as a function of latitude and day of year. *Ecological Modelling* 80:87–95.
Foster VC, Sarmento P, Sollmann R, Tôrres N, Jácomo ATA, Negrões N, Fonseca C, Silveira L. 2013. Jaguar and puma activity patterns and predator-prey interactions in four Brazilian Biomes. *Biotropica* 45:373–379.
Genovart M, Negre N, Tavecchia G, Bistuer A, Parpal L, Oro D. 2010. The young, the weak and the sick: evidence of natural selection by predation. *PloS One* 5:e9774.
Giné GAF, Cassano CR, de Almeida SS, Faria D. 2015. Activity budget, pattern and rhythm of maned sloths (*Bradypus torquatus*): Responses to variations in ambient temperature. *Mammalian Biology* 80:459–467.
Haugaasen T, Peres CA. 2009. Interspecific primate associations in Amazonian flooded and unflooded forests. *Primates* 50:239–251.
Lisney TJ, Stecyk K, Kolominsky J, Graves GR, Wylie DR, Iwaniuk AN. 2013. Comparison of eye morphology and retinal topography in two species of new world vultures (Aves: Cathartidae). *Anatomical Record* 296:1954–1970.
Mendoza I, Peres CA, Morellato LPC. 2016. Continental-scale patterns and climatic drivers of fruiting phenology: A quantitative Neotropical review. *Global and Planetary Change* 148:227–241.
Menezes JFS, Kotler BP, Mourão GM. 2014. Uniform predation risk in nature: common, inconspicuous, and a source of error to predation risk experiments. *Behavioral Ecology and Sociobiology* 68:1809–1818.
Menezes JF, Mourão GM, Kotler BP. 2017. Understory cover increases patch use in rodent *Thrichomys fosteri*. *Ethology Ecology & Evolution* 30:267-276.
Miranda EBP. 2015. Conservation implications of harpy eagle *Harpia harpyja* predation patterns. *Endangered Species Research* 29:69–79.
Miranda EBP. 2018. Prey composition of harpy eagles (*Harpia harpyja*) in Raleighvallen, Suriname. *Tropical Conservation Science* 11:1–8.
Miranda EBP, Menezes JFS, Farias CC, Munn C, Peres CA. 2019. Species distribution modelling

reveals strongholds and potential reintroduction areas for the world's largest eagle. *PloS One* 14:e0216323.

Miranda EBP, Menezes JFS, Rheingantz ML. 2016. Reptiles as principal prey? Adaptations for durophagy and prey selection by jaguar (*Panthera onca*). *Journal of Natural History* 50:2021–2035.

Moreira D de O, Leite GR, Siqueira MF de, Coutinho BR, Zanon MS, Mendes SL. 2014. The Distributional ecology of the maned sloth: environmental influences on its distribution and gaps in knowledge. *PLoS One* 9:e110929.

Muela A, Watson R, Mutch B, Heinrich W. 2003. *The Harpy Eagle: biology, restoration and hacking procedures*. Ciudad de Panamá.

Muñiz-López R. 2017. Harpy Eagle (*Harpia harpyja*) mortality in Ecuador. *Studies on Neotropical Fauna and Environment* 30:1–5.

Muñiz-López R, Limiñana R, Cortés GD, Urios V, Limiñana R, Cortés GD, Urios V. 2016. Movements of Harpy Eagles *Harpia harpyja* during their first two years after hatching. *Bird Study* 3657:509–514.

Pauli JN, Peery MZ, Fountain ED, Karasov WH. 2016. Arboreal folivores limit their energetic output, all the way to slothfulness. *American Naturalist* 188:196–204.

Peery MZ, Pauli JN. 2014. Shade-grown cacao supports a self-sustaining population of two-toed but not three-toed sloths. *Journal of Applied Ecology* 51:162–170.

Prugh LR, Golden CD. 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology* 83:504–514.

San-Jose LM, Séchaud R, Schalcher K, Judes C, Questiaux A, Oliveira-Xavier A, Gémard C, Almasi B, Béziers P, Kelber A, Amar A. 2019. Differential fitness effects of moonlight on plumage colour morphs in barn owls. *Nature Ecology & Evolution* 3:1331–1340.

Souza FM, Gandolfi S, Rodrigues RR. 2014. Deciduousness influences the understory community in a semideciduous tropical forest. *Biotropica* 46:512–515.

Sunquist ME, Montgomery GG. 1973. Activity patterns and rates of movement of two-toed and three-toed sloths (*Choloepus hoffmanni* and *Bradypus infuscatus*). *Journal of Mammalogy* 54:946–954.

Suscke P, Verderane M, de Oliveira RS, Delval I, Fernández-Bolaños M, Izar P. 2017. Predatory threat of harpy eagles for yellow-breasted capuchin monkeys in the Atlantic Forest. *Primates* 58:141-147.

Taube E, Keravec J, Vié JC, Duplantier JM. 2001. Reproductive biology and postnatal development in sloths, *Bradypus* and *Choloepus*: review with original data from the field (French Guiana) and from captivity. *Mammal Review* 31:173–188.

Terborgh J, Lopez L, Nunez P, Rao M, Shahabuddin G, Orihuela G, Riveros M, Ascanio F, Adler G, Lambert T, Balbas L. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294:1923–1926.

Touchton J, Hsu Y, Palleroni A. 2002. Foraging ecology of reintroduced captive-bred subadult harpy eagles (*Harpia harpyja*) on Barro Colorado Island, Panama. *Ornitología Neotropical* 13:365–379.

Urbani B, Bosque C. 2007. Feeding ecology and postural behaviour of the three-toed sloth (*Bradypus variegatus flaccidus*) in northern Venezuela. *Mammalian Biology* 72:321–329.

Vendl C, Frei S, Dittmann MT, Furrer S, Osmann C, Ortmann S, Munn A, Kreuzer M, Clauss M. 2016. Digestive physiology, metabolism and methane production of captive Linné's two-toed

sloths (*Choloepus didactylus*). *Journal of Animal Physiology and Animal Nutrition* 100:552–564.
Voirin B, Scriba MF, Martinez-Gonzalez D, Vyssotski AL, Wikelski M, Rattenborg NC. 2014. Ecology and neurophysiology of sleep in two wild sloth species. *Sleep* 37:753–761.
Watson RT, McClure CJW, Vargas FH, Jenny JP. 2016. Trial Restoration of the Harpy Eagle, a Large, Long-lived, Tropical Forest Raptor, in Panama and Belize. *Journal of Raptor Research* 50:3–22.
Wetzel R, Montgomery G. 1985. *The evolution and ecology of armadillos, sloths and vermilinguas*. Washington, USA: Smithsonian Institution.

CHAPTER 4

Landowners perceptions of livestock predation: implications for persecution of a keystone apex predator

Everton B. P. de Miranda*[1], Carlos A. Peres[2], Colleen T. Downs[1]

1 – Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, P/Bag X01, Pietermaritzburg, 3209, South Africa

2 – School of Environmental Sciences, University of East Anglia, Norwich NR47TJ, UK

***Corresponding author:** mirandaebp@gmail.com, phone +55 65 98153550

ORCID: https://orcid.org/0000-0003-2198-4742

Other emails and ORCIDs:

carlos.a.peres@gmail.com; ORCID: http://orcid.org/0000-0002-1588-8765

downs@ukzn.ac.za; ORCID: http://orcid.org/0000-0001-8334-1510

Running header: Harpy eagle persecution and livestock predation

Formatted for Animal Conservation (currently under review)

4.1 Abstract

Apex predators are threatened all over the world and considered a priority in the conservation biology agenda. The harpy eagle *Harpia harpyja* is an apex predator and is considered a flagship species in Neotropical conservation, being threatened by habitat loss and persecution. We investigated the roles of social, economic and environmental issues related to harpy eagle killing and suspected livestock predation by local communities. We conducted structured interviews of 184 local livestock owners who had admitted killing a combined total of 181 harpy eagles. We found that most of the harpy eagle killings were unrelated to suspected livestock predation, which accounted for 80% of eagles killed. None of the interviewees' perceptions related to the threat posed to livestock and humans by eagles, nor with the subjective norm, were relevant to the intentional killing of further harpy eagles. The single most important factor driving intentional killing of harpy eagles was an interviewee having suffered livestock predation in the past. Additionally, intention to kill eagles was negatively associated with landholding size. We found that livestock abundance and livestock husbandry were the best positive predictor of levels of suspected livestock predation by harpy eagles. Distance to forest had a positive but non-significant role. Domestic livestock suspected to be killed (192) were mainly chickens (47.9%), followed by goats (22.4%), pigs (18.2%) and sheep (8.3%), with pets representing only ~3% of kills. Killing of harpy eagles despite the lack of livestock predation seemed a result of futile curiosity, and many interviewees reported regretting their acts. Most of our interviewees were relatively large landowners, but they are outnumbered by smallholders who are more likely to persecute harpy eagles. Consequently, education, compensation and tourism activities should be directed to smallholders to inhibit unnecessary persecution and killing of harpy eagles.

Keywords: livestock predation; harpy eagle; *Harpia harpyja*; persecution; human-wildlife conflict; Arc of Deforestation; Likert scale; theory of planned behaviour.

4.2 Introduction

Apex predators are important species for the functioning of ecosystems (Terborgh et al., 2001; Humphries, Hill, & Downs, 2015; Cunningham, Johnson, & Jones, 2020). By keeping prey species populations in check, both by direct predation (Le Roux et al., 2019) and fear induction (Matthews et al., 2020), they play important roles in animal habitat and resource use (Menezes, Mourão, & Kotler, 2017). Because of these traits, combined with the requirements of typically large home-ranges (McBride & Thompson, 2018), habitat quality and prey (Lamichhane et al., 2018), they are often seen as important priority in the conservation biology agenda as umbrella and flagship species (Terborgh & Estes, 2013). Conversely, apex predators often pose risks to human lives (Khan, 2009; Murphy, 2020), are relatively expensive to study (Morato et al., 2018) and are frequently disliked by local communities (Bhattarai et al., 2019), all of which make apex predator conservation challenging (Ibanez et al., 2016).

The predation of domestic livestock has typically been one of the main reasons behind apex predator killing by affected livestock owners (Terborgh & Estes, 2013; Mondragón et al., 2017). This issue has been a component of apex predator research since the dawn of predator conservation (Leopold, 1949). However, most of this tradition focuses on the northern hemisphere (Bonnet, Shine, & Lourdais, 2002), especially mammalian carnivores that are typically the main apex predators of these ecosystems (Makarieva, Gorshkov, & Li, 2005). In addition, researchers in tropical regions mirror those efforts, focusing mostly on mammalian carnivores, with extensive research on the subject (Eklund et al., 2017; van Eeden et al., 2018). Tropical guilds of apex predators are, however, highly diverse (Glen & Dickman, 2014; Murphy, 2020). In tropical ecosystems, pythons (Goursi et al., 2012), anacondas (Miranda, Ribeiro-Jr., & Strüssmann, 2016), crocodilians (Corvera, Manalo, & Aquino, 2017) and large eagles (McPherson, Brown, & Downs, 2015; Restrepo-Cardona et al., 2020) prey on livestock—and pose conservation challenges similar to those of mammalian carnivores.

The harpy eagle *Harpia harpyja* (Fig. 4.1) is generally considered a livestock predator throughout its Neotropical distribution by local livestock owners (Sick, 1984; Trinca, Ferrari, & Lees, 2008; Curti & Valdez, 2009; Godoi et al., 2012). Harpy eagles are apex predators that prey on >100 species of arboreal vertebrates (Miranda, 2018). These prey are usually canopy species, especially sloths and primates, but also large birds such as cracids, and large reptiles such as iguanas (Miranda, 2015). Terrestrial vertebrates, in general, especially ungulates, are rarely consumed as prey (Miranda et al., 2017; Miranda, 2018). As many apex predators, harpy eagles occur at low densities of 8-12 breeding adults/100km^2 (Vargas-González & Vargas, 2011). Harpy eagles have undergone a 40% reduction in their distribution range (Miranda et al., 2019). This range contraction has not been incorporated into IUCN assessments as yet, and the species is still considered Near Threatened (Birdlife International, 2017). Although local communities frequently report that harpy eagles take domestic livestock as prey, this has been rarely documented in the literature, even though the diet of harpy eagles is one of the better-studied aspects of their biology.

Predators may include domestic prey in their diet as a response to habitat degradation or alteration (Odden, Nilsen, & Linnell, 2013; Mondragón et al., 2017). The Arc of Deforestation is an extensive section of the southern, south-eastern and eastern border of Amazonian Forests that have been intensely degraded (Roriz, Yanai, & Fearnside, 2017). The Amazon region comprises 93% of the harpy eagle's current distribution range (Miranda et al., 2019). State-sponsored migration programs and agrarian reform projects have been widely implemented in this region (Schneider & Peres, 2015). The natural forest is usually converted into cattle pastures, which are at times succeeded by grain croplands (Fearnside, 2005). In this region, several predators prey on domestic livestock (Michalski et al., 2006; Miranda, Ribeiro-Jr., & Strüssmann, 2016). Retaliatory or preventive killing of harpy eagles supposedly attacking livestock are reported across the region (Gusmão et al., 2016), but some of these killings appear to be unrelated to livestock predation (Trinca, Ferrari, & Lees, 2008). This is a serious concern for harpy eagles because their breeding cycle is extremely slow, taking 30-36 months to produce a single eaglet (Muñiz-López et al., 2012; Muñiz-López, 2017; Urios, Muñiz-López, & Vidal-Mateo, 2017).

Several frameworks have been proposed to promote conservation of large predators that prey on domestic livestock (Michalski et al., 2006; Cavalcanti & Gese, 2010; Miranda, Ribeiro-Jr., & Strüssmann, 2016; Restrepo-Cardona et al., 2020). The Theory of Planned Behaviour, which assumes that a person's attitude is formed by a subjective social norm and perception of behavioural control, can be applied to understand this problem (Marchini & Macdonald, 2012). For instance, the beliefs of pastoralists in Kenya lead to their attitudes regarding cattle management and lion (*Panthera leo*) predation (Perry et al., 2020). In this case, the subjective social norm is that those who properly manage cattle suffer less with lion predation. Still, the perception of behavioural control leads to variation in management since some pastoralists cannot perform certain livestock management practices because of logistic and economic limitations (Perry et al., 2020).

Regarding harpy eagles, some other elements must be brought to attention. For instance, it is known that perceived behavioural control increases in larger private landholdings (*e.g.* perceived lack of law enforcement), and consequently, so does predator killing (Marchini & Macdonald, 2012). On the other hand, livestock abundance, geographic traits (as proximity to forest) and livestock management techniques can also influence livestock predation rates (Michalski et al., 2006; Palmeira & Crawshaw, 2008). Knowing the social, environmental and psychological drivers that motivate killings of harpy eagles would be critical to predict and consequently prevent or reduce these events.

The knowledge of social and psychological drivers that motivate killings of harpy eagles could be used to predict, and consequently, prevent or reduce these events. Filling this information gap would allow a fine-tuning of conservation actions by the Government, Non-Governmental Organisations and the private sector, through practices such as paying compensations for livestock losses or environmental education. To enhance our understanding of the motivations behind local livestock owners killing harpy eagles and the extent of this behaviour, we explored the social, economic and environmental drivers of harpy eagle killings by local domestic livestock landowners. We tested the assumptions related to the Theory of Planned Behaviour, as well as hypotheses related to the livestock predation framework, as described below:

I. People who perceive that their livestock or human safety is threatened by harpy eagles are more likely to kill the eagles (Hypothesis I).

II. Taking into account factors that are unrelated to livestock depredation or human safety (*i.e.* subjective norm and perceived behavioural control), the theory of planned behaviour will provide a better model to explain harpy eagle killings, which is not strictly retaliatory or preventive (Hypothesis II, alternative to Hypothesis I).

III. Perceived behavioural control increases in larger private landholdings, and consequently so does harpy eagle killings (Hypothesis III).

IV. Harpy eagle predation on livestock will be positively affected by high livestock abundance, the proximity between the headquarters and the forest and poor livestock husbandry (Hypothesis IV).

Fig. 4.1 Harpy eagle preying on a rooster (*Gallus gallus*; A), a lamb (*Ovis aries*; B) and a domestic kitten (*Felis catus*; C). Although harpy eagles are recognised by local livestock owners as predators of domestic livestock, there were no formal studies on this topic. Photograph credits: Francisca do Carmo Firmo (B), Robson Silva e Silva (A and C).

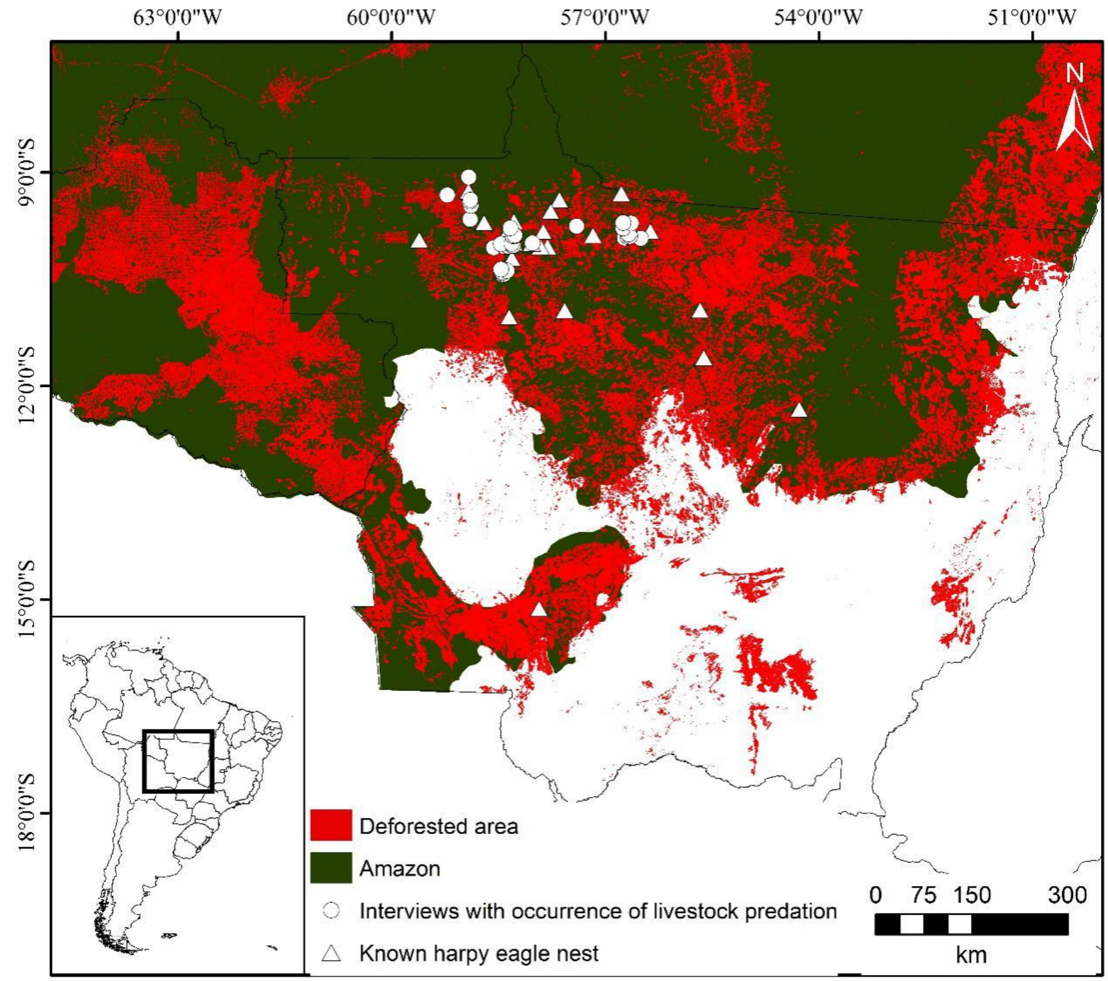

Fig. 4.2 Study landscape, showing the location where interviews reporting the occurrence of livestock predation and the location of harpy eagle nests monitored by our project.

4.3 Methods

Study area

This study was conducted in the Arc of Deforestation's southern portion, in the state of Mato Grosso, Brazil (Fig. 4.2). We conducted the interviews over ten counties that sum 149,394,000 km². Koeppen (1948) classifies the region's climate as "tropical wet climate" or Amazon (tropical monsoon) climate. Rainfall averages 2,350 mm, and ambient temperature averages 24.5°C, combined with a high relative air humidity (80–85%; Radam-Brasil 1983). This portion of the southern Amazon was originally inhabited by several indigenous tribes (Villas Boas & Villas Boas, 1994). Nowadays, the hyper-fragmented region is dominated by cattle ranching with smaller portions of land allocated to grain production (Junior & Lima, 2018) and forest remnants.

The Arc of Deforestation was created by state-sponsored migration programmes in the 1970s (Schneider & Peres, 2015). Population density is relatively low, and the ten counties studied by us support 241 thousand inhabitants (IBGE, n.d.). The land is occupied by: (1) relatively small properties (smallholdings, ~20-100 ha) often resulting from state-sponsored agrarian settlement programs (Wittman 2010); and (2) large holdings (500-150,000 thousand ha), often resulting from immigrated farmers and ranchers who sold their lands in southern Brazil and bought larger tracts of cheaper land in the Amazon. These private properties exist beside indigenous territories that sum 15 million ha on the Mato Grosso State (Begotti & Peres, 2020), and beside protected areas. Ranch headquarters in large holdings are typically surrounded by pasture and located far from forest (Michalski et al., 2006), but are frequently near riparian forests in smallholdings (Oliveira et al., 2013).

Although the main economic activity is cattle ranching (Fearnside, 2005; Schneider & Peres, 2015), small livestock is frequently raised on properties of all sizes. Of the domestic livestock kept by landowners, chickens *Gallus domesticus* are the most common (707,947 heads), but smallholders typically also keep pigs *Sus domesticus* (77,669 heads), sheep *Ovis aries* (37,268 heads), and goats *Capra* sp. (5,477 heads; IBGE, n.d.). In the ten counties where we conducted our interviews, they are used for food, commerce and barter (Gasques et al., 2012; Chávez, 2017). Small livestock are kept near the houses, so we assumed that predation detection is the same, independent of property size. Pet dogs *Canis familiaris* and cats *Felis catus* are also common, particularly around human habitation, but no statistics are available on them. Further details such as data per county are available on SI Table 4.1.

Migrant ranchers are mainly from southern Brazil (Schneider & Peres, 2015), and whereas they are as mixed with indigenous communities (Tavares et al., 2019), their culture has stronger European roots (De Majo & Relly, 2020). They do not enjoy eating wildlife other than ungulates and ungulate-like large rodents (Trinca & Ferrari, 2007). Poaching of canopy wildlife is limited to gamebirds (Michalski & Peres, 2017), and non-existent for other animals such as primates and sloths (Michalski & Peres, 2005; Trinca & Ferrari, 2007). Given the structural connectivity of the remaining fragments resulting from riparian corridor set-asides, as demanded by Brazilian forest legislation (Anonymous, 2012), vertebrate communities in the remaining forest canopy are relatively intact (Lees & Peres, 2008; Michalski, Metzger, & Peres, 2010; Zimbres, Machado, & Peres, 2018).

Table 4.1. The set of Planned Behaviour Theory subjects measured in the present study, with affirmations explicitly related to the perceptions of each interviewee in relation to harpy eagles (HEs). Affirmation rated as a 1-5 Likert scale by interviewees (1 would be highly agree the affirmation while 5 would be highly disagree the affirmation).

Theme	Affirmation rated as a 1-5 Likert scale by interviewees
Tourism	
	Do tourists want to see HEs?
	Do you have an interest in tourism?
Livestock predation	
	Would you implement methods for preventing livestock predation?
	Do you think there should be a monetary compensation for livestock losses?

The HE is a threat to livestock

The HE is a threat to humans

In this private landholding we cannot tolerate HE capturing livestock

Subjective norm

My neighbours approve the killing of HEs that attack livestock

My family approves killing HEs that attack livestock

My neighbours kill HEs that attack livestock

My neighbours are my friends

Perceived behavioural control

If I kill a HE on my property, it is my problem

The government must be held responsible for the HE problem

HE attacking livestock is an acceptable problem

Each property should solve this problem on its own

Conservation

I would be very happy if there were no HEs

HEs need to be protected

I would like help with resolving the HE issue

The Amazon is adequately protected

I consider myself aware of the conservation problems of the Amazon

Outcomes

I will kill the next HE that attacks my livestock

I will kill the next HE that appears on my property

Structured interviews

The process of interviewee selection was based on the premise that the interviewee had killed or attempted to kill a harpy eagle, regardless of their motivations. We found our interviewees during poster-fixing activities announcing a reward for anyone aware of a harpy eagle nest. Those posters were fixed in sport fishing stores, farmer shops, and Brazil nut collector associations (the latter is the category where most encounters happened). People normally approached us affirming they had shot 'this hawk' (locals in general do not label harpy eagle as an eagle, and have no specific name for it). Besides affirming that they had personally killed a harpy eagle, it was common for locals to declare that a friend, neighbour, relative or acquaintance had done so. On these occasions, we asked for the contact of such a person.

To confirm raptor species identification, we asked for photographs of killed individuals, and body parts. We also tested their harpy eagle call recognition using a playback. We presented a sheet of photographs including an adult harpy eagle together with other native and exotic eagle species of similar appearance asking the informant to identify which eagle species they had killed. In cases of livestock predation, playback of harpy eagle calls triggered predator-avoidance behaviour in livestock, helping to confirm predator identity (Dissegna, Turatto, & Chiandetti, 2018; Makin, Chamaillé-Jammes, & Shrader, 2019).

Harpy eagle persecution is illegal and can be a sensitive topic for landowners and their employees (Trinca, Ferrari, & Lees, 2008). Consequently, we took the following steps to avoid systematic biases during interviews: (1) all interviews were conducted by EBPM who was always accompanied by a local, well-known, familiar resident who first explained to the landowner that we had no relationship with law enforcement nor environmental authorities; (2) we affirmed that the information shared would remain strictly confidential and anonymous; and (3) informed interviewees that we were interested in designing solutions to their perceived harpy eagle problems. On several occasions, people offered to be interviewed—including offers of harpy eagle parts—after they were told by a neighbour who had been interviewed that we were trustworthy.

Interviews were usually conducted on the site where we met the landowner, with the exception of cases with livestock predation. In those cases, we booked a visit to the property so that we could collect data on landscape structure and livestock management. Interviews were conducted *ad libitum*, and the interviewees answered the questionnaire themselves while we stayed around to answer any questions. In cases on which interviewees were illiterate, partially literate, or had vision issues, we read the questions to them and were presented with a set of graphic 'smiles' that also ranged between 'highly agree' to 'highly disagree'. The questionnaire is available as supplementary information. We followed all standard ethics related to local interviews and followed ethical guidelines from the State of Mato Grosso University (CEP-Unemat, 25/2016).

Likert scale

We used a Likert scale for inferring perceptions about harpy eagle predation issues. The Likert scale is a psychometric scale frequently used in research that uses questionnaires (Bruskotter & Wilson, 2014). Likert scaling is a bipolar scaling method, measuring the positive, neutral or negative response to a statement, and therefore being useful for wildlife conflict issues (Marchini et al., 2019). We measured six components of the Planned Behaviour Theory, according to Moleón *et al.* (2011). Local perceptions were divided as follows: (1) Tourism, related to knowledge of harpy eagle as a species of touristic interest; (2) Perceived livestock predation, with a series of statements related to consumption of livestock by harpy eagles; (3) Subjective norm, on which we checked the subjacent issues and views about harpy eagles; (4) Perceived behavioural control, regarding personal views about law enforcement; (5) Conservation, on which we measured perceptions about common environmental issues; and (6) Outcomes, regarding the chances of further harpy eagle killings. A complete list of affirmatives related to each subject is presented in Table 4.1. The perception of each affirmative was recorded on a scale of 1-5 (highly agree to highly disagree, being 3 the neutral point).

Livestock predation

We built a domestic livestock husbandry index (LHI) based on the level of domestic livestock management implemented at each landholding where livestock predation was reported. This LHI was based on the degree to which shelter and food were available. In each case, we noted values of 0, 0.5 and 1 for absent, partial and permanent food or shelter. The value obtained for each domestic livestock species was then summed. We then divided this value by the number of domestic livestock raised and divided the resulting value by two (to account for food and shelter). The resulting value varies from 0 to 1. Therefore, the higher the grade obtained in the LHI, the higher the level of husbandry received by domestic animals within any property, with 1 representing all species having shelter and regular food. Pigs in large fenced areas that included sections of riparian forest and wetlands—but no sheltered pig housing—were defined as free-ranging. We added physical shelter to the odds of predation by harpy eagles because they lower predation risk if livestock could take shelter under any predation threat (Bickley et al., 2019; Mhlanga et al., 2019). Lack of regular food provision requires animals to expend more time foraging, and domestic animals typically exhibit low anti-predation vigilance rates while foraging (Brown & Kotler, 2007; Whelan & Schmidt, 2007). We calculated market prices per kg of live livestock body mass based on real transaction values in the study region, which were determined during each interview.

Statistical analyses

For all comparisons between persecution events preceded or not by reported livestock predation, we used a null-model approach. We chose this approach to avoid any bias in our results because of differences in sample sizes between farmers who killed harpy eagles in response to reported livestock predation and those who killed eagles for other reasons (Gotelli & Entsminger, 2006). Our null model was composed of the following steps: (1) bootstrapping one set of samples of landowners that suffered with livestock predation and another set of samples of those who did not; (2) calculating the median or the mean for each group; (3) creating a pairwise difference in medians or means between landowners who lost livestock and those who did not; and (4) determining if the difference in those medians or means found between landowners who lost livestock and those who did not was larger than expected by chance, by comparing differences between two randomly labelled bootstrapped sets of samples. While bootstrapping sets of samples for each simulation, we used the sample size of the smallest group (preceded by reported livestock predation). We carried out 1,000 iterations to calculate medians and means differences between different landowner groups, and an additional 1,000 were carried to see how far it was from random. We used the median of the Likert scale grade for all cases—since it is an ordinal value—except when comparing other traits for which the mean could be used (*e.g.* property size). Since we avoided finding a mean or standard deviation for ordinal data, we built our null models using medians and standard errors instead (Jamieson, 2004).

The effects of different independent variables related to the subjective norm or perceived behavioural control over the affirmative ‘I will kill the next harpy that appears on my property’ were tested using ordinal logistic regressions (OLRs). This approach allowed us to use the ordinal 1-5 Likert scale responses in a statistically meaningful way (Jamieson, 2004). We, therefore, ran the occurrence of reported livestock predation, and the perception of harpy eagles as a threat to livestock against the affirmative ‘I will kill the next harpy that appears on my property’ to test hypothesis I. We also ran the perceptions of family and neighbours’ opinions on harpy eagle killing, as well as the behavioural control perception of impunity against the outcome ‘I will kill the next harpy that appears on my property’ to test hypothesis II. We ran the property size in hectares against the statement ‘I will kill the next harpy that appears on my property’ to test hypothesis III. Finally, we ran livestock abundance (in heads), proximity to the nearest forest (in meters) and level of livestock management (see LHI) against the Likert grade of the statement ‘I will kill the next harpy that appears on my property’. Normal distributions for each test were derived from the original data. We used Akaike's Information Criterion (AIC) to inform hypothesis selection when comparing hypotheses I and II, since AIC estimates prediction error and consequently the quality of different statistical models for different sets of data (Gotelli & Ellison, 2013). In our case, those were our alternative hypotheses (I and II) for the same question, determining which was best-supported (Crawley, 2007). We conducted all analyses and produced all figures in the R coding environment, version 3.6.3 (R Core, 2020). R packages used were *FSA*, *plyr*, *foreign*, *ggplot2*, *MASS*, *Hmisc*, *reshape2*, *scales*, *RColorBrewer*, *dplyr*, *ggthemes* and *stringr* (Wickham, 2011, 2012; Ripley et al., 2013; Neuwirth, 2014; Wickham et al., 2015; Harrell Jr & Harrell Jr, 2015; Arnold, 2017; Ogle, 2017; Wickham & Wickham, 2020; Strong, 2019; Wickham & Wickham, 2019; Bivand et al., 2020).

4.4 Results

Local livestock owners

Collectively, a total of 181 harpy eagles were killed over a 2-year period by the 184 local livestock owners we interviewed, within a combined property area of 349,800 ha. This, therefore, represents a killing rate of 2.59 individuals/100km²/year. Only 19.5% (n = 36) of all killings or attempted killings were related to suspected (self-reported) livestock predation. Of those 36 events, five (13.8%) failed in killing the eagle, 29 (80.5%) killed one eagle, and two (5.5%) killed two eagles. Another 148 (80.5%) individual harpy eagle killings were entirely unrelated to livestock predation. The eagle carcass was consumed in only 4.4% of all occasions, and either discarded entirely or kept as souvenirs or relics (mostly talons) in 74.5% and 21.2% of occasions, respectively. Residents who killed harpy eagles were mostly migrant ranchers from southern Brazil, mainly from the state of Paraná (50.5%) and second-generation migrants from Rondonia (31.0%), with only 5.4% originally from Mato Grosso.

Ranchers who lost livestock to harpy eagle predation typically had smaller properties (1,062 ± 5,344 ha) compared with those who did not (2,104 ± 1,516 ha), but this difference was not significant (Null model, $P = 0.077$). However, after removing two outlier landholdings of 4,000 ha and 32,000 ha from the suspected livestock predation group because of peculiarities they shared, these differences increased (65 ± 81 ha vs. 2,104 ± 1,516 ha) rendering the null model significant ($P < 0.01$). Ranchers who reported having lost livestock to eagles, typically had their habitation and infrastructure (and consequently their small livestock) near forest edges (mean distance to the forest = 62 ± 74 m). All variables describing ranches that suffered harpy eagle predation are detailed in Table 4.2.

Table 4.2 Summary characteristics of the surveyed landholdings in terms of management and productivity of livestock.

Ranch characteristics	Mean	SD ±	Range	N
Ranch size (hectares)[1]	65.64	81.48	20 - 500	36
Residency years	16.1	6.48	2 - 30	36
Number of livestock attacked (~2014)	2.87	2.83	1 - 15	33
Number of livestock attacked (~2015)	3.23	2.67	1 - 12	30
Distance to the nearest forest (m)	62.16	74.39	0 - 400	36
Number of livestock head[2]	49	27.79	13 - 135	36
Number of pets	4	1.45	1 - 8	36

1 - two properties of 32,000 and 4,000 ha were excluded as outliers. 2 - cattle not included.

Table 4.3 Differences in a Likert scale (median ± SE) for people who had killed harpy eagles (HEs) with or without suspected livestock predation incidents, examined using null models. Values close to five indicate high disagreement with the statement, while values close to one indicate high agreement.

Statement	With livestock predation (n = 36)	Without livestock predation (n = 148)	***P* value**
The HE is a threat to livestock	2 ± 0.14	3 ± 0.12	0.331
The HE is a threat to humans	2 ± 0.26	4 ± 0.05	< 0.01

In this property we cannot tolerate HEs attacking livestock	3	-	-
My neighbours approve killing HEs attacking livestock	2 ± 0.26	4 ± 0.08	< 0.01
My family approves killing HEs attacking livestock	2 ± 0.21	3 ± 0.08	0.141
My neighbours kill HEs that attacks livestock	1 ± 0.11	4 ± 0.08	< 0.01
My neighbours are my friends	2 ± 0.12	4 ± 0.9	< 0.01
If I kill a harpy on my property it is my problem	2 ± 0.15	2 ± 0.07	1
I will kill the next HE that attacks my livestock	3	-	-
I will kill the next HE that appears on my property	2.78 ± 1.26	4.09 ± 1.18	< 0.01
HEs attacking livestock is an acceptable problem	1	-	-
I would be very happy if there were no HEs	3 ± 0.20	5 ± 0.05	< 0.01
HEs need to be protected	3 ± 0.16	5 ± 0.04	< 0.01
The government must be held responsible for the HE problem	3	-	-
Each property should solve it s own livestock predation problem	1	-	-
I would like help to solve the livestock predation issue	4	-	-
The Amazon is adequately protected	4 ± 0.10	4 ± 0.08	1
I consider myself aware of the conservation problems in the Amazon	3 ± 0.13	4 ± 0.08	0.305

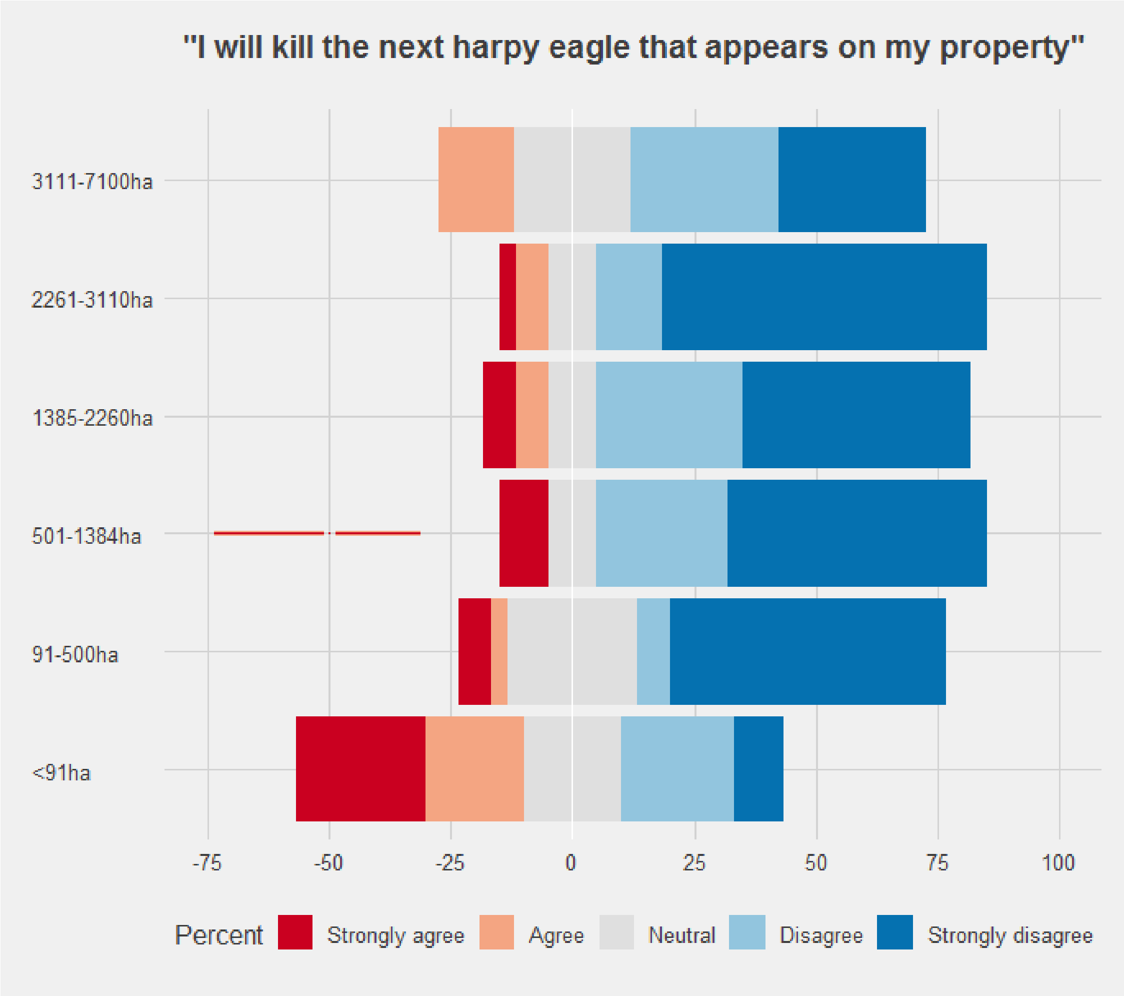

Fig. 4.3 Intention to kill harpy eagles along a gradient of property sizes. Each category has a sample size of ~30 properties. Intention to kill harpy eagles in the future were most prevalent among smallholders.

Likert scale

Several traits quantified by the Likert scale yielded significant differences between locals who killed harpy eagles because of suspected livestock predation and those who did not (Table 4.3). People who reported livestock predation were more likely to perceive that: a) harpy eagles were a threat to humans ($p < 0.01$); b) their neighbours also killed harpy eagles preying on livestock and approved of whom did so ($p < 0.01$); c) the neighbours were their friends ($p < 0.01$); d) planned to kill the next eagle that appeared on the property ($p < 0.01$); e) would be happier if there were no harpy eagles ($p < 0.01$); and f) perceived little need for harpy eagle protection ($p < 0.01$).

Regarding the likelihood of killing a harpy eagle again, perceptions regarding how much of a threat eagles represented to livestock or humans were irrelevant. The prior report of livestock predation was the single most important factor (OLR, $\chi^2 = 0.9942$, Residual Deviance: 505, AIC: 519, livestock predation $P = 0.006$, threat to livestock $P = 0.981$, threat to humans $P = 0.915$). We, therefore, rejected our Hypothesis I because those who perceived that livestock or humans were threatened by harpy eagles were less likely to kill them compared with those who previously lost livestock to harpy predation.

For our Hypothesis II, no variables related to the subjective norm (opinions of family and neighbours) and the perceived behavioural control (perception of impunity) had any relevance for the likelihood of someone killing harpy eagles (OLR, $\chi^2 = 0$, Residual Deviance: 501, AIC: 521, $P > 0.05$ for all variables). We, therefore, rejected our Hypothesis II as neither perceptions over subjective norm nor behavioural control were important in predicting harpy eagle killings.

Contrary to our Hypothesis III, property size exerted a strong negative effect on the intention to kill harpy eagles (OLR, $\chi^2 = 0.40624$, Residual Deviance: 519, $P < 0.01$). Consequently, smallholders had the most hostile profile regarding their intentions of potentially killing harpy eagles in the future, whereas large holders were most likely to spare eagles (Fig. 4.3).

Livestock predation

Livestock abundance, proximity to the nearest forest patch and less intensive livestock management had positive effects on domestic animal predation rates by harpy eagles. However, only livestock abundance and livestock management did so significantly (GLM, Residual deviance: 52.47, df = 32, $P < 0.01$ for livestock abundance and $P = 0.0157$ for livestock management). Distance to nearby forest (range: 0-400 m, $P = 0.10$) was of less importance (Fig. 4.4). Domestic livestock species perceived by interviewees as preyed on by harpy eagles are summarised in Table 4.4. Monetary losses resulting from harpy eagle predation were relatively low: the annual value of livestock kills across all 36 landholdings averaged USD438/year throughout our study region, and only a small number of livestock were taken from each property (3.05 head/property). This represented USD12.2/year per property or USD1.1/km²/year, considering the properties with attacks or USD0.1/km²/year if we consider our entire study region.

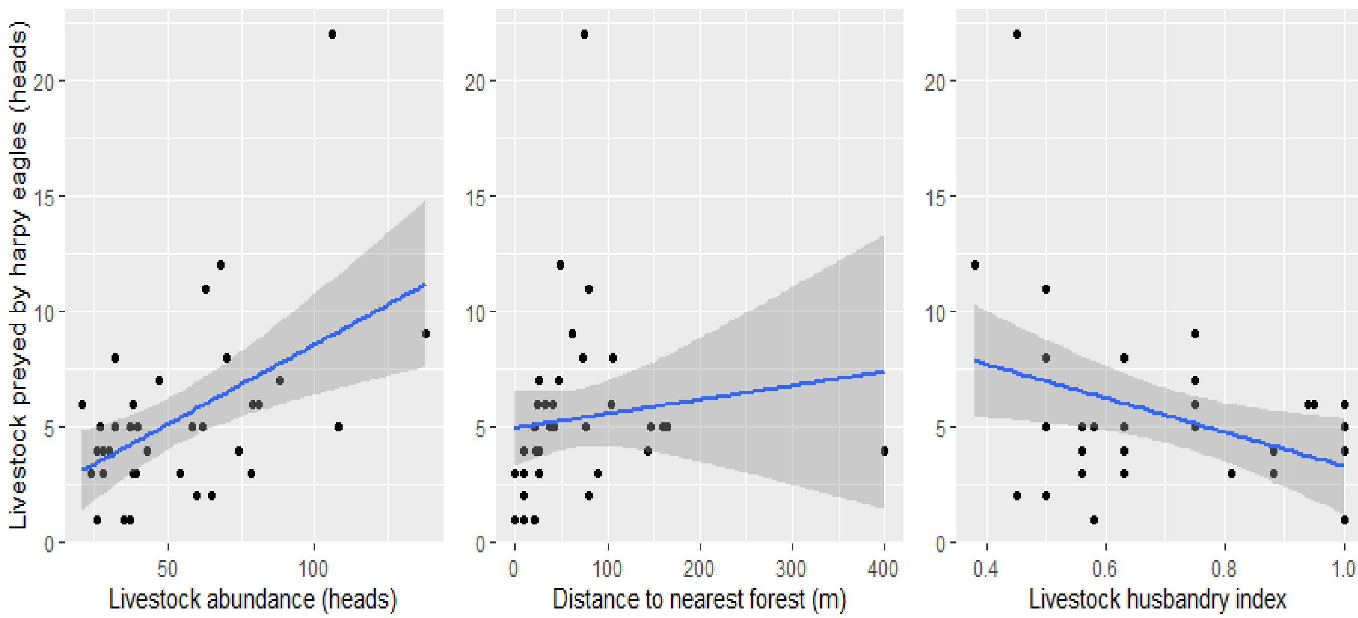

Fig. 4.4 Effects of livestock abundance, distance to the nearest forest patch area, and livestock husbandry index (LHI) over the number of individual livestock killed by harpy eagles. Although all of these relationships are positive, only livestock abundance had a statistically significant effect.

Table 4.4. Livestock species preyed on by harpy eagles in small ranches along the Arc of Deforestation of Brazilian Amazonia, as perceived by landowners in the present study. Values refer to two years of predation records, and monetary loss was calculated based on average losses per year.

Species	**%**	**N**	**Age class**			**Value (USD)**	**Observations**
			Newborn	**Young**	**Adult**		
Chicken (*Gallus gallus*)	47.9	92	0	0	100%	343.39	Preference for roosters
Goat (*Capra hircus*)	22.4	43	100%	0	0	380.08	
Pig (*Sus domesticus*)	18.2	35	100%	0	0	30.56	
Sheep (*Ovis aries*)	8.3	16	100%	0	0	121.73	
Dog (*Canis familiaris*)	2.1	4	50%	25%	25%	-	Small-sized sick adult
Cat (*Felis catus*)	1.0	2	0	0	100%	-	
						437.89	**Yearly total**

4.5 Discussion

Failing to consider local issues not only destabilises conservation efforts—and thus prevents or reduces meaningful impacts on conservation policy—but also erodes local community support for such conservation efforts (Widdows & Downs, 2018; Zuluaga et al., 2020). The extent and nature of harpy eagle killings must be central to apex predator conservation, since, even if local perceptions of livestock predation are exaggerated, the issue must be addressed proactively but based on evidence.

Here we showed that farmland reported livestock predation played a relatively small role in harpy eagle killings in the wider Amazonian countryside and was related to less than 20% of the cases interviewees reported. Most killings in our study region were typically out of curiosity, misconceptions or both. These were unrelated to the subjective norm nor the perceived behavioural control. Therefore, the Planned Behaviour Theory failed to explain our observations. Additionally, the intention to kill harpy eagles in the future appeared strongly associated with (a) smallholdings and (b) self-reported occurrence of livestock predation. This occurred independently of perceptions over the risk harpy eagles potentially present to humans or livestock. These findings are of crucial importance to continued harpy eagle conservation and ending unwarranted persecution.

Conservation opportunities and challenges for top predators within private landholdings are typically governed by the economies of scale of these properties, which is primarily a function of property area (Michalski et al., 2006; Silva et al., 2018). By rejecting our Hypotheses I and II, we established that compensation and education programs should focus on those who had lost livestock to harpy eagles. These were generally smallholders, who represented the single group that most consistently declared their intentions to kill further eagles because of a predation event in the past. We must also take into account that smallholdings largely exceed larger estates in numbers (Michalski, Metzger, & Peres, 2010; Godar et al., 2014). In contrast, large landowners frequently reported that they killed eagles out of curiosity and admiration, and generally declared regretting their actions. While our Likert scale was not designed to account for this perception, a large fraction of large holders declaring no plans to kill further harpy eagles confirmed this likelihood.

The rationale of killing an animal without purpose may sound strange—especially to foreigners—but the feeling of 'hand-experiencing' something is common and has even resulted in popular expression in Brazilian Portuguese: 'to see with the hands' (Rosumek, Schmiegelow, & de Sousa, 2018). Research shows that touching an object results in an increase in perceived ownership (Peck & Shu, 2009), and we believe this is one of the main issues behind many of the futile killings of harpy eagles. Furthermore, one must mind that countryside people in Brazil normally own illegal guns that are easy to obtain when compared with developed countries where people, even if incurring in the preventive killing of raptors, do so in a lesser and more considerate scale (Swan et al., 2020). Finally, a very unique trait of harpy eagles is that they remain perched for several hours in a single emergent tree, allowing a peasant the time to go home and grab his gun to 'investigate' the huge raptor. Therefore, initiatives for wildlife-based ecotourism (Tortato et al., 2017), compensation for lost livestock (Morehouse, Tigner, & Boyce, 2018) and environmental education (Curti & Valdez, 2009) will likely produce the best conservation results if conducted in collaboration with local landowners who have lost domestic livestock to harpy eagles in the past.

Searching for social cues to change behaviour and reduce harpy eagle killing seems a very straightforward consequence. We established a tourism initiative that relies on locals to (1) find nests; (2) build ecotourism towers and (3) act as a workforce for many tasks as paid jobs (Miranda et al., 2020), besides a share per tourist to each landowner. Perception of risks and benefits are primary factors regarding tolerance to apex predators (Bruskotter & Wilson, 2014), and we are introducing the benefits. Since people perceive mild risk in regards to harpy eagles (except between those who lost livestock), we made an effort to publicise the possible benefits of the species through tourism (Miranda et al., 2020). Furthermore, our initiative offers concrete economic benefits permeate the community through local restaurants, lodges, car rental companies and so on, as is typical for ecotourism (Kirkby et al., 2010). Further evidence of this is that five new nests were communicated to us after our publicity for nest finding was terminated in February (because of the pandemic), even without any recent advertising. This represents a successful case of conservation marketing (Wright et al., 2015).

The higher rates of harpy eagle suspected livestock predation on smallholdings were likely related to the fact that their habitation and homestead infrastructure were frequently located near the borders of forest patches. These riparian forests are legally required to be set-aside according to Brazil forestry law (Anonymous, 2012). Smallholders typically have their houses near perennial streams to facilitate access to the water table through wells, and the disposal of wastewater. Small livestock is consequently highly exposed to predators, not only harpy eagles but also other smaller-bodied raptors, mammalian carnivores and boid snakes. It is worth mentioning that the two estates mentioning suspected livestock predation that we removed as outliers (32,000 and 4,000 ha) were both dedicated to selective timber extraction, with their offices and habitation also on the forest border (pers. obs.). High rates of harpy eagle killings shown by rejecting Hypothesis III is further evidence to add to a myriad of environmental issues induced by small landholdings distributed by agrarian reform in the Amazon. This further results in higher levels of riparian forest degradation (Zimbres, Machado, & Peres, 2018) and higher proportions of forest property areas converted into pastures (Schneider & Peres, 2015) practised by smallholders. Although most killings of harpy eagles were carried out by large- and medium-sized landowners in our study, smallholdings outnumber larger estates at a ratio of 50:1 (Michalski, Metzger, & Peres, 2010; Godar et al., 2014).

In contrast to most large raptors, harpy eagles are typically poor long-distance fliers. Their wings are relatively short and round, making them highly adept at manoeuvring in closed forest canopies (Ferguson-Lees & Christie, 2001). They rarely cross non-forest areas wider than 500m (Aguiar-Silva, 2016). These dispersal limitations in traversing gap areas have already reduced their genetic diversity in the region (Banhos et al., 2016), and are further compounded by high deforestation rates since the early 1980s. This ‘sit-and-wait’ trait (Touchton, Hsu, & Palleroni, 2002) has led them to be restricted to attacking domestic livestock close to forest, but this habit appears to be limited to a relatively few nesting pairs. Our research project has monitored 14 harpy eagle nests intensively—some of which are close to human habitation—recording ~300 prey samples, but this has yielded no records of domestic livestock predation (EBPM, unpublished data). Miranda *et al.* (2017) showed that males prey five times more frequently on terrestrial prey compared with females (2 vs 11% of prey composition). Males are also are more generalist, and have a wider niche compared with females (Levin’s niche width of 6.0 vs 3.4). Those characteristics probably make livestock predation a typically male behaviour in harpy eagles. This could lead to biased mortality toward males, with severe consequences to the population demography since they are monogamous and exhibit high rates of paternal care in nest provisioning (Alvarez-Cordero, 1996).

Since the completion of these interviews in 2016, we have implemented a tourism initiative focused on harpy eagles in the region (Miranda et al., 2020). Our initiative offers USD20 per tourist per day to the landowner, a USD100 reward to anyone who can locate an harpy eagle nest, and created alternative employment on properties of all sizes, thereby changing local perceptions on this mega-raptor species. We suggest repeating our structured interviews in the future, to test whether the opinion profiles and the perceptions on the species documented here have changed over time. It may then be possible to explore new hypotheses and overcome the limitations of the sampling design we used, for which the main framework was derived from studies on mammalian carnivores (e.g., Marchini and Macdonald 2012). This points to the need to develop theoretical frameworks for other groups of predators such as reptiles and raptors. Since we have been addressing these issues, a second round of interviews would present a completion of the conservation planning cycle (Marchini et al., 2019).

Predator persecution in the complete absence of human-predator conflict is not unheard of (Knox et al., 2019). However, in these situations, the problem is usually the perceived threat posed to humans. Regarding harpy eagles, while many indigenous legends exist, local beliefs that they could prey on small children were typical, and perhaps understandably, held by those who lost livestock to eagles. Prevention of further predation events is difficult to consider because several different measures must be taken regarding different domestic livestock types. Animal husbandry had a significant effect on harpy eagle predation levels, in spite of livestock abundance being more likely to result in attacks (Hypothesis IV), is hard to consider implementing for all species in all contexts. Furthermore, the yearly value of killed livestock was relatively reduced and inexpensive in our study region (<USD500/year or USD12.2/year per property), and a small number of livestock heads were taken per property (<4 heads/property). In other words, this can be easily matched by a compensation program deriving from tourism, since Brazil is one of the few countries where there is no state-sponsored compensation system (Ravenelle & Nyhus, 2017). It is interesting to note that low levels of livestock predation—or even the lack of it—have been reported for other eagles, such as crowned solitary eagles (*Urubitinga coronata*) in Argentina (Sarasola, Santillán, & Galmes, 2010) or urban crowned eagles (*Stephanoaetus coronatus*) in South Africa (McPherson, Brown, & Downs, 2015). Comparatively, large felids in similar landscapes frequently make livestock their main prey (Cavalcanti & Gese, 2010; Jhala et al., 2019). In our study region, establishing concrete tourism income for small landowners can compensate for the monetary losses of minor livestock predation by harpy eagles, thereby boosting predator tolerance.

The overall killing rate of 2.59 harpy eagles per 100 km^2/year is an important finding. Published harpy eagle densities report 8-12 breeding adults/100km^2 in high-density areas (Vargas-González & Vargas, 2011), and each couple produces a single eaglet every 30-36 months (Muñiz-López et al., 2012; Muñiz-López, 2017). This eaglet will then take two years more to reach sexual maturity (Oliveira, 2019). Given their extremely slow life-history traits, harpy eagles cannot persist under sustained killing rates as high as those reported in this study. That, combined with the still ongoing extensive forest loss across the Amazonian Arc of Deforestation, makes conservation management of harpy eagles critical for their persistence throughout this region.

In conclusion, the patterns we showed here regarding harpy eagle killing profiles and landowner perceptions are important in designing, managing and funding conservation activities for this species as well as other Amazonian large predators. Livestock predation was typically uncommon, and killings were not normally related to mortality of domestic animals. Suspected livestock predation in the past was, however, a strong predictor of further intentions of harpy eagle killing. Smallholders were most likely to perform these killings, and because they are the dominant class of landowners, they must be the focus for education and compensation activities to address undesirable killings. Since admiration was commonly reported by larger landowners, they may also benefit from educational activities. Livestock abundance and animal husbandry had a positive effect on livestock predation by harpy eagles, while distance to the nearest forest areas had a weaker but positive effect. As a result, our determination of the profiles and drivers of landowners persecuting harpy eagles presented here provides important insights and a baseline to understand continued harpy eagle persecution, providing cues about where to start working to reduce it.

4.6 Acknowledgements

This research would not be possible without the endless support of Gilberto Araujo, who was our spearhead in the contact with local communities. CTD is grateful to the University of KwaZulu-Natal and the National Research Foundation (ZA) for funding. We greatly appreciate the generous financial support of the following donors: Rufford Small Grants Foundation (18743-1, 23022-2 and 31091-B), Rainforest Biodiversity Group, Idea Wild, The Mamont Scholars Program of the Explorer's Club Exploration Fund, Cleveland Metroparks Zoo, and the SouthWild.com Conservation Travel System. Logistical support was given by the Peugeot-ONF Carbon Sink Reforestation Project, based at the São Nicolau Farm in Cotriguaçu, Mato Grosso, Brazil. This project is a Peugeot initiative to fulfil some of the Kyoto Protocol directions and is run by the ONF-Brasil enterprise. We thank CEP-Unemat for providing the ethics permit 25/2016. Dr David L. Anderson greatly improved the manuscript through his detailed review. Finally, we thank ICMBio for authorising the project activities under the permit SISBIO 58533.

4.7 References

Aguiar-Silva, H. (2016). Uso e seleção de recursos por harpia em múltiplas escalas espaciais: persistência e vulnerabilidade. INPA.

Alvarez-Cordero, E. (1996). Biology and conservation of the harpy eagle in Venezuela and Panama. DSc Thesis. University of Florida, Florida, USA.

Anonymous. Novo Código Florestal, Lei 12.651 de 25 de maio de 2012, Dispõe sobre a proteção da vegetação nativa (2012). Brasília: Subchefia de assuntos jurídicos.

Arnold, J. B. (2017). "ggthemes" packages. CRAN Repository.

Banhos, A., Hrbek, T., Sanaiotti, T. M., & Farias, I. P. (2016). Reduction of genetic diversity of the harpy eagle in Brazilian Tropical Forests. *PLoS One* **11**, e0148902.

Begotti, R. A., & Peres, C. A. (2020). Rapidly escalating threats to the biodiversity and ethnocultural capital of Brazilian Indigenous Lands. *Land Use Policy* **96**, 104694.

Bhattarai, B. R., Wright, W., Morgan, D., Cook, S., & Baral, H. S. (2019). Managing human-tiger conflict: lessons from Bardia and Chitwan National Parks, Nepal. *Eur. J. Wildl. Res.* **65**, 34.

Bickley, S. M., Lemos, F. G., Gilmore, M. P., Azevedo, F. C., Freeman, E. W., & Songsasen, N.

(2019). Human perceptions of and interactions with wild canids on cattle ranches in central Brazil. *Oryx* **54**, 546-553.

Birdlife International. (2017). *Harpia harpyja* (American Harpy Eagle, Harpy Eagle). *Species factsheet: Harpia harpyja*.

Bivand, R., Carey, V. J., DebRoy, S., Eglen, S., Guha, R., Herbrandt, S., Lewin-Koh, N., Myatt, M., Nelson, M., & Pfaff, B. (2020). Package 'foreign.'

Bonnet, X., Shine, R., & Lourdais, O. (2002). Taxonomic chauvinism. *Trends Ecol. Evol.* **17**, 1–3.

Brown, J., & Kotler, B. (2007). Foraging and the ecology of fear. In D. Stephens, J. Brown, & R. Ydenberg (Eds.), *Foraging Behav. Ecol.* Chicago, USA: University of Chicago Press.

Bruskotter, J. T., & Wilson, R. S. (2014). Determining where the wild things will be: using psychological theory to find tolerance for large carnivores. *Conserv. Lett.* **7**, 158–165.

Cavalcanti, S., & Gese, E. (2010). Kill rates and predation patterns of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. *J. Mammal.* **91**, 722–736.

Chávez, M. A. (2017). It's Not Just About Us: Food as a Mechanism for Environmental and Social Justice in Mato Grosso, Brazil. In *Food Justice US Glob. Context.* pp. 51–66. Springer.

Corvera, M. D., Manalo, R. I., & Aquino, M. T. R. (2017). People and crocodiles sharing one environment: an analysis of local human-crocodile conflict management strategies in the Philippines. *J. Anim. Sci. Res.* **1**, 1–6.

Crawley, M. J. (2007). The R book. Second edi. Silwood Park: Imperial College London.

Cunningham, C. X., Johnson, C. N., & Jones, M. E. (2020). A native apex predator limits an invasive mesopredator and protects native prey: Tasmanian devils protecting bandicoots from cats. *Ecol. Lett.* **23**, 711–721.

Curti, M., & Valdez, U. (2009). Incorporating community education in the strategy for Harpy Eagle conservation in Panama. *J. Environ. Educ.* **40**, 3–16.

De Majo, C., & Relly, E. (2020). American vines, European potatoes: An evolutionary history of European migrations in Southern Brazil. *Int. Rev. Environ. Hist.* **6**, 5.

Dissegna, A., Turatto, M., & Chiandetti, C. (2018). Short-term memory in habituation and dishabituation of newborn chicks' freezing response. *J. Exp. Psychol. Anim. Learn. Cogn.* **44**, 441–446.

Eklund, A., López-Bao, J. V., Tourani, M., Chapron, G., & Frank, J. (2017). Limited evidence on the effectiveness of interventions to reduce livestock predation by large carnivores. *Sci. Rep.* **7**, 1–9.

Fearnside, P. M. (2005). Deforestation in Brazilian Amazonia: History, rates, and consequences. *Conserv. Biol.* **19**, 680–688.

Ferguson-Lees, J., & Christie, D. (2001). Raptors of the world. New York, USA: Houghton Mifflin Harcourt.

Gasques, J. G., Bastos, E. T., Valdes, C., & Bacchi, M. R. P. (2012). Productivity and structural transformation in Brazilian agriculture: analysis of Agricultural Census data. *Brazilian Agric. Dev. Chang.* Brasília.

Glen, A., & Dickman, C. (2014). Carnivores of Australia: Past, Present and Future. Sydney: CSIRO, Australia.

Godar, J., Gardner, T. A., Tizado, E. J., & Pacheco, P. (2014). Actor-specific contributions to the deforestation slowdown in the Brazilian Amazon. *Proc. Nat. Acad. Sci.* **111**, 15591–15596.

Godoi, M., Filho, J., Faxina, C., Modena, C., Pivatto, E., Castro, M., Granville, D. m, Bocchese, R., Teribele, R., R, A., Martins, R., & Stavis, v k. (2012). Aves de rapina raras no estado de

Mato Grosso do Sul, Brasil. *Atualidades Ornitológicas* **170**, 41–47.
Gotelli, N., & Entsminger, G. (2006). EcoSim: null models software for ecology. Jericho: Acquired Intelligence Inc. and Kesey-Bear.
Gotelli, Ni. J., & Ellison, A. m. (2013). A primer of ecological statistics. Sunderland: Sinauer Associates Inc.
Goursi, U., Awan, M., Minhas, R., Ali, U., Kabir, M., & Dar, N. (2012). Status and Conservation of Indian Rock Python (*Python molurus molurus*) in Deva Vatala National Park, Azad Jammu and Kashmir, Pakistan. *Pak. J. Zool.* **44**, 1507–1514.
Gusmão, A. C., Banhos, A., Aguiar-Silva, F. H., Souza, L. S. de, Sanaiotti, Tânia Margarete Silva, Adriano Martins da Costa, T. M., Oliveira, L. E., Morais, W. G. de, & Ferrari, S. F. (2016). Records of the occurrence, nesting, and hunting of the Harpy Eagle (*Harpia harpyja*) (Aves: Accipitridae) in Rondônia. *Atualidades Ornitológicas* **190**, 18–23.
Harrell Jr, F. E., & Harrell Jr, M. F. E. (2015). Package 'Hmisc.' CRAN Repository.
Humphries, B. D., Hill, T. R., & Downs, C. T. (2015). Landowners' perspectives of black-backed jackals (*Canis mesomelas*) on farmlands in KwaZulu-Natal, South Africa. *Afr. J. Ecol.* **53**, 540–549.
Ibanez, J., Sumaya, A. M., Tampos, G., & Salvador, D. (2016). Preventing Philippine Eagle hunting: what are we missing? *J. Threat. Taxa* **8**, 9505–9511.
IBGE, I. B. de G. e E. (n.d.). Cidades@ 2017-2018. *IBGE Cid.*
Jamieson, S. (2004). Likert scales: how to (ab) use them. *Med. Educ.* **38**, 1217–1218.
Jhala, Y. V., Banerjee, K., Chakrabarti, S., Basu, P., Singh, K., Dave, C., & Gogoi, K. (2019). Asiatic lion: ecology, economics and politics of conservation. *Front. Ecol. Evol.* **7**, 1–21.
Junior, C. S., & Lima, M. (2018). Soy Moratorium in Mato Grosso: deforestation undermines the agreement. *Land Use Policy* **71**, 540–542.
Khan, M. (2009). Can domestic dogs save humans from tigers *Panthera tigris*? *Oryx* **43**, 44–47.
Kirkby, C. A., Giudice-Granados, R., Day, B., Turner, K., Velarde-Andrade, L. M., Dueñas-Dueñas, A., Lara-Rivas, J. C., & Yu, D. W. (2010). The market triumph of ecotourism: an economic investigation of the private and social benefits of competing land uses in the Peruvian Amazon. *PLoS One* **5**, e13015.
Knox, J., Negrões, N., Marchini, S., Barboza, K., Guanacoma, G., Balhau, P., Tobler, M. W., & Glikman, J. A. (2019). Jaguar Persecution without "cowflict": insights from protected territories in the Bolivian Amazon. *Front. Ecol. Evol.* **7**, 494.
Koeppen, W. (1948). Climatologia: con un estudio de los climas de la tierra.
Lamichhane, B. R., Pokheral, C. P., Poudel, S., Adhikari, D., Giri, S. R., Bhattarai, S., Bhatta, T. R., Pickles, R., Amin, R., Acharya, K. P., Dhakal, M., Regmi, U. R., Ram, A. K., & Subedi, N. (2018). Rapid recovery of tigers *Panthera tigris* in Parsa Wildlife Reserve, Nepal. *Oryx* **52**, 16–24.
Le Roux, E., Marneweck, D. G., Clinning, G., Druce, D. J., Kerley, G. I., & Cromsigt, J. P. (2019). Top–down limits on prey populations may be more severe in larger prey species, despite having fewer predators. *Ecography* **42**, 1115–1123.
Lees, A. C., & Peres, C. A. (2008). Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. *Conserv. Biol.* **22**, 439–449.
Leopold, A. (1949). Thinking like a mountain. In *A sand Cty. Alm.* pp. 137–141. New York, USA: Oxford University Press.
Makarieva, A. M., Gorshkov, V. G., & Li, B.-L. (2005). Gigantism, temperature and metabolic rate in terrestrial poikilotherms. *Proc. R. Soc. B Biol. Sci.* **272**, 2325–8.

Makin, D. F., Chamaillé-Jammes, S., & Shrader, A. M. (2019). Alarm calls or predator calls: which elicit stronger responses in ungulate communities living with and without lions? *Oecologia* **190**, 25–35.
Marchini, S., & Macdonald, D. W. (2012). Predicting ranchers' intention to kill jaguars: case studies in Amazonia and Pantanal. *Biol. Conserv.* **147**, 213–221.
Marchini, Silvio, Ferraz, K. M. P., Zimmermann, Alexandra, Guimarães-Luiz, Thaís, Morato, R., Correa, P. L., & McDonald, D. W. (2019). Planning for coexistence in a complex human-dominated world. In B. Frank, J. A. Glikman, & S. Marchini (Eds.), *Human-Wildlife Interactions Turn Conflict into Coexistence*. Cambridge: Cambridge University Press, pp. 414–438.
Matthews, C. J., Breed, G. A., LeBlanc, B., & Ferguson, S. H. (2020). Killer whale presence drives bowhead whale selection for sea ice in Arctic seascapes of fear. *Proc. Nat. Acad. Sci.* **117**, 6590–6598.
McBride, R. T., & Thompson, J. J. (2018). Space use and movement of jaguar (*Panthera onca*) in western Paraguay. *Mammalia* **82**, 540–549.
McPherson, S. C., Brown, M., & Downs, C. T. (2015). Diet of the crowned eagle (*Stephanoaetus coronatus*) in an urban landscape: potential for human-wildlife conflict? *Urban Ecosyst.* 1–14.
Menezes, J. F., Mourão, G. M., & Kotler, B. P. (2017). Understory cover increases patch use in rodent *Thrichomys fosteri*. *Ethol. Ecol. Evol.* 1–10.
Mhlanga, M., Muranda, F. J., Ramesh, T., Ramesh, R., & Downs, C. T. (2019). Influence of settlement type and land use on public attitudes towards spotted hyaenas (*Crocuta crocuta*) in Zimbabwe. *Afr. J. Wildl. Res.* **49**, 142–154.
Michalski, F., Boulhosa, R. L. P., Faria, A., & Peres, C. A. (2006). Human-wildlife conflicts in a fragmented Amazonian Forest landscape: Determinants of large felid depredation on livestock. *Anim. Conserv.* **9**, 179–188.
Michalski, F., Metzger, J. P., & Peres, C. A. (2010). Rural property size drives patterns of upland and riparian forest retention in a tropical deforestation frontier. *Glob. Environ. Chang.* **20**, 705–712.
Michalski, F., & Peres, C. A. (2005). Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biol. Conserv.* **124**, 383–396.
Michalski, F., & Peres, C. A. (2017). Gamebird responses to anthropogenic forest fragmentation and degradation in a southern Amazonian landscape. *PeerJ* **5**, e3442.
Miranda, E. B. P. (2015). Conservation implications of harpy eagle *Harpia harpyja* predation patterns. *Endanger. Species Res.* **29**, 69–79.
Miranda, E. B. P. (2018). Prey composition of harpy eagles (*Harpia harpyja*) in Raleighvallen, Suriname. *Trop. Conserv. Sci.* **11**, 1–8.
Miranda, E. B. P., Campbell-Thompson, E., Muela, A., & Vargas, F. H. (2017). Sex and breeding status affect prey composition of Harpy Eagles *Harpia harpyja*. *J. Ornithol.* DOI 10.1007/s10336-017-1482-3
Miranda, E. B. P. de, Kenup, C. F., Munn, C. A., Huizinga, N., Lormand, N., & Downs, C. T. (2020). Harpy Eagle nest activity patterns: Potential ecotourism and conservation opportunities in the Amazon Forest. *Bird Conserv. Int.* **In press**, **-**.
Miranda, E. B. P., Menezes, J. F. S., Farias, C. C., Munn, C., & Peres, C. A. (2019). Species distribution modeling reveals strongholds and potential reintroduction areas for the world's

largest eagle. *PLoS One* **14**, e0216323.
Miranda, E. B. P., Ribeiro-Jr., R. P., & Strüssmann, C. (2016). The ecology of human-anaconda conflict: a study using internet videos. *Trop. Conserv. Sci.* **9**, 26–60.
Moleón, M., Sánchez-Zapata, J. A., Gil-Sánchez, J. M., Barea-Azcón, J. M., Ballesteros-Duperón, E., & Virgós, E. (2011). Laying the foundations for a human-predator conflict solution: assessing the impact of Bonelli's eagle on rabbits and partridges. *PLoS One* **6**, e22851.
Mondragón, J., Castillo, A., Hoogesteijn, A., & Meyer, H. (2017). Livestock predation by jaguars Panthera onca in south-eastern Mexico: the role of local peoples' practices. *Oryx* **51**, 254–262.
Morato, R. G., Thompson, J. J., Paviolo, A., Torre, de La, J.A., Lima, F., McBride Jr, R. T., Paula, R. C., Cullen Jr, L., Silveira, L., Kantek, D. L., & Ramalho, E. E. (2018). Jaguar movement database: a GPS-based movement dataset of an apex predator in the Neotropics. *Ecology* **99**, 1691–1691.
Morehouse, A. T., Tigner, J., & Boyce, M. S. (2018). Coexistence with large carnivores supported by a predator-compensation program. *Environ. Manage.* **61**, 719–731.
Muñiz-López, R, Limiñana, R., Cortés, G., & Urios, V. (2012). Movements of harpy eagles *Harpia harpyja* during their first two years after hatching. *Bird Study* **59**, 509–514.
Muñiz-López, Ruth. (2017). Harpy Eagle (*Harpia harpyja*) mortality in Ecuador. *Stud. Neotrop. Fauna Environ.* **30**, 1–5.
Murphy, J. C. (2020). Giant Snake-Human Relationships. In L. Angelici, Francesco Maria, Rossi (Ed.), *Problem Wildlife. II*. pp. 581–602. II: Springer.
Neuwirth, E. (2014). "ColorBrewer" package.
Odden, J., Nilsen, E. B., & Linnell, J. D. C. (2013). Density of wild prey modulates lynx kill rates on free-ranging domestic sheep. *PLoS One* **8**, e79261.
Ogle, D. (2017). Package 'FSA.' CRAN Repository.
Oliveira, E. C., dos Santos, E. S., Zeilhofer, P., Souza-Santos, R., & Atanaka-Santos, M. (2013). Geographic information systems and logistic regression for high-resolution malaria risk mapping in a rural settlement of the southern Brazilian Amazonia. *Malar. J.* **12**, 420.
Oliveira, M. J. (2019). Manejo reprodutivo de harpia em cativeiro no Brasil. Universidade Federal do Paraná.
Palmeira, F., & Crawshaw, P. (2008). Cattle depredation by puma (*Puma concolor*) and jaguar (*Panthera onca*) in central-western Brazil. *Biol. Conserv.* **141**, 118-125.
Peck, J., & Shu, S. B. (2009). The effect of mere touch on perceived ownership. *J. Consum. Res.* **36**, 434–447.
Perry, L. R., Moorhouse, T. P., Loveridge, A. J., & Macdonald, D. W. (2020). The role of psychology in determining human–predator conflict across southern Kenya. *Conserv. Biol.* **34**, 879–890.
R Core. (2020). R: A language and environment for statistical computing (No. Version 3.6.3). Vienna: R Fondation for Statistical Computing.
Radam-Brasil. (1983). Projeto Radam-Brasil: levantamento de recursos naturais. Rio de Janeiro.
Ravenelle, J., & Nyhus, P. J. (2017). Global patterns and trends in human–wildlife conflict compensation. *Conserv. Biol.* **31**, 1247–1256.
Restrepo-Cardona, J. S., Echeverry-Galvis, M. Á., Maya, D. L., Vargas, F. H., Tapasco, O., & Renjifo, L. M. (2020). Human-raptor conflict in rural settlements of Colombia. *PLoS One* **15**, e0227704.
Ripley, B., Venables, B., Bates, D. M., Hornik, K., Gebhardt, A., Firth, D., & Ripley, M. B. (2013).

Package MASS.
Roriz, P. A. C., Yanai, A. M., & Fearnside, P. M. (2017). Deforestation and Carbon Loss in Southwest Amazonia: Impact of Brazil's Revised Forest Code. *Environ. Manage.* **60**, 367-382.
Rosumek, G. B., Schmiegelow, S. S., & de Sousa, R. P. L. (2018). A exploração da sensorialidade na comunicação das marcas na mídia impressa. *Front. Midiáticos* **20**, 265–276.
Sarasola, J. H., Santillán, M. Á., & Galmes, M. A. (2010). Crowned eagles rarely prey on livestock in central Argentina: persecution is not justified. *Endanger. Species Res.* **11**, 207–213.
Schneider, M., & Peres, C. A. (2015). Environmental costs of government-sponsored agrarian settlements in Brazilian Amazonia. *PLoS One* **10**, e0134016.
Sick, H. (1984). Ornitologia brasileira, uma introdução. Brasília, Brasil: Universidade de Brasília.
Silva, M. A., Lima, M., Silva Junior, C. A., Costa, G. M., & Peres, C. A. (2018). Achieving low-carbon cattle ranching in the Amazon:'Pasture sudden death'as a window of opportunity. *L. Degrad. Dev.* **29**, 3535–3543.
Strong, H. (2019). Package 'scales.' CRAN Repository.
Swan, G. J., Redpath, S. M., Crowley, S. L., & McDonald, R. A. (2020). Understanding diverse approaches to predator management among gamekeepers in England. *People Nat.* **2**, 495–508.
Tavares, G. M., Reales, G., Bortolini, M. C., & Fagundes, N. J. (2019). Measuring the impact of European colonization on Native American populations in Southern Brazil and Uruguay: evidence from mtDNA. *Am. J. Hum. Biol.* **31**, e23243.
Terborgh, J., & Estes, J. (2013). Trophic cascades: predators, prey, and the changing dynamics of nature. Washington, USA: Island Press.
Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, F., Adler, G., Lambert, T., & Balbas, L. (2001). Ecological meltdown in predator-free forest fragments. *Science* **294**, 1923–1926.
Tortato, F. R., Izzo, T. J., Hoogesteijn, R., & Peres, C. A. (2017). The numbers of the beast: Valuation of jaguar (Panthera onca) tourism and cattle depredation in the Brazilian Pantanal. *Glob. Ecol. Conserv.* **11**, 106–114.
Touchton, J., Hsu, Y., & Palleroni, A. (2002). Foraging ecology of reintroduced captive-bred subadult harpy eagles (*Harpia harpyja*) on Barro Colorado Island, Panama. *Ornitol. Neotrop.* **13**, 365–379.
Trinca, C., Ferrari, S., & Lees, A. (2008). Curiosity killed the bird: arbitrary hunting of Harpy Eagles *Harpia harpyja* on an agricultural frontier in southern Brazilian Amazonia. *Cotinga* **30**, 12–15.
Trinca, C. T., & Ferrari, S. F. (2007). Game populations and hunting pressure on a rural frontier in Southern Brazilian Amazonia. *Biol. Geral e Exp.* **7**, 5–16.
Urios, V., Muñiz-López, R., & Vidal-Mateo, J. (2017). Juvenile dispersal of harpy eagles (*Harpia harpyja*) in Ecuador. *J. Raptor Res.* **51**, 439–445.
van Eeden, L. M., Eklund, A., Miller, J. R., Lopez-Bao, J. V., Chapron, G., Cejtin, M. R., Crowther, M. S., Dickman, C. R., Frank, J., Krofel, M., & Macdonald, D. W. (2018). Carnivore conservation needs evidence-based livestock protection. *PLoS Biol.* **16**, 1–8.
Vargas-González, J. de J., & Vargas, F. H. (2011). Nesting density of Harpy Eagles in Darien with population size estimates for Panama. *J. Raptor Res.* **43**, 199–210.
Villas Boas, O., & Villas Boas, C. (1994). A marcha para o oeste: a epopéia da expedição Roncador-Xingu. São Paulo: Globo.

Whelan, C., & Schmidt, K. (2007). Food acquisition, processing and digestion. In D. Stephens, J. Brown, & R. Ydenberg (Eds.), *Foraging Behavioural Ecology*. pp. 141–172. Chicago: University of Chicago Press.

Wickham, H. (2011). Package "ggplot2." *Wiley Interdiscip. Rev. Comput. Stat.* **3**, 180–185.

Wickham, H. (2012). reshape2: Flexibly reshape data: a reboot of the reshape package. CRAN Repository.

Wickham, H., Francois, R., Henry, L., & Müller, K. (2015). "dplyr" package. CRAN Repository.

Wickham, H., & Wickham, M. H. (2019). Package 'stringr.' CRAN.

Wickham, H., & Wickham, M. H. (2020). Package 'plyr.' CRAN Repository.

Widdows, C., & Downs, C. T. (2018). Genets in the city: community observations and perceptions of large-spotted genets (*Genetta tigrina*) in an urban environment. *Urban Ecosyst.* **21**, 357–367.

Wittman, H. (2010). Agrarian reform and the environment: fostering ecological citizenship in Mato Grosso, Brazil. *Can. J. Dev. Stud. Can. d'études du développement* **29**, 281–298.

Wright, A. J., Veríssimo, D., Pilfold, K., Parsons, E. C. M., Ventre, K., Cousins, J., Jefferson, R., Koldewey, H., Llewellyn, F., & McKinley, E. (2015). Competitive outreach in the 21st century: Why we need conservation marketing. *Ocean Coast. Manag.* **115**, 41–48.

Zimbres, B., Machado, R. B., & Peres, C. A. (2018). Anthropogenic drivers of headwater and riparian forest loss and degradation in a highly fragmented southern Amazonian landscape. *Land Use Policy* **72**, 354–363.

Zuluaga, S., Salom, A., Vargas, F. H., Coulson, J. O., Kohn, S., & Grande, J. M. (2020). Acknowledging Andean Condor predation on livestock, a first step in addressing the human-condor conflict: A commentary to Estrada Pacheco et al. (2020). *Biol. Conserv.* **247**, 108618.

CHAPTER 5

Harpy Eagle *Harpia harpyja* nest activity patterns: Potential ecotourism and conservation opportunities in the Amazon Forest

EVERTON B. P. MIRANDA, CAIO F. KENUP, CHARLES A. MUNN, NIKI HUIZINGA, NICKOLAS LORMAND, COLLEEN T. DOWNS

EVERTON B. P. MIRANDA Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, P/Bag X01. Pietermaritzburg, 3209, South Africa https://orcid.org/0000-0003-2198-4742 (mirandaebp@gmail.com)
CAIO F. KENUP Wildlife and Ecology Group, Massey University, Palmerston North, 4410, New Zealand (caio.kenup@gmail.com)
CHARLES A. MUNN SouthWild, Várzea Grande, Mato Grosso, 78125-048, Brazil (charles@southwild.com)
NIKI HUIZINGA HAS University, 90108 5200, Netherlands (n.huizinga@student.has.nl)
NICKOLAS LORMAND New Mexico Highlands University, New Mexico, 87701, United States (n.lorm17@gmail.com)
COLLEEN T. DOWNS (Corresponding author) Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, P/Bag X01. Pietermaritzburg, 3209, South Africa; http://orcid.org/0000-0001-8334-1510 (downs@ukzn.ac.za)

Running header: Harpy Eagle activity patterns and ecotourism

Accepted with modifications in Bird Conservation International. Formatted in accordance with Oryx rules, since the paper reached Bird Conservation International by transfer.

5.1 Abstract

Tourism can be a powerful tool for wildlife conservation if well controlled and responsibly managed. Apex predators constitute particularly attractive subjects for tourism, but simultaneously they may generate conflict with local communities. Harpy eagles are the largest eagle species and are highly sought-after by ecotourists. The last stronghold of the harpy eagle is the Amazon Forest, which is being deforested for cattle ranching. We tested methods for developing harpy eagle ecotourism as a potential tool to solve these issues. Using camera-traps, we collected data on the timing of harpy eagle visits to their nests, as well as on probabilities of viewing an eagle. Harpy eagles can only be seen predictably during the first 12 of the 30-36 months nest cycle. In nests with nestlings (up to 5-7 months), adults are visible on a daily basis, and this period lasts 16.6% of the nesting cycle, demanding 13, 17 and 26 nests for having at least one nest with nestling on 90%, 95% and 99% of the days. After this 5-7 months window, we found that 2 and 4.16 days spent at nests afforded high probabilities of sighting a fledgling or adult eagle, respectively. Harpy eagles were mainly active at the beginning and the end of the day. Activity core last 6.5 decimals hours for adults, peaking at 10h, and 7.45 decimal hours for fledged eagles, peaking at 15h. Our results demonstrate that harpy eagles fit several criteria for a viable wildlife attraction: predictability in activity and location, viewable, and diurnal, even though at the same time there are considered a rarity. In a broader perspective, harpy eagle tourism shows every indication of being a significant tool for more robust rainforest conservation.

Keywords: activity patterns; apex predator; Arc of Deforestation; canopy; conservation tourism; habituation; nesting; wildlife tourism.

5.2 Introduction

Wildlife tourism has mixed effects for nature conservation. When properly performed, it can generate resources to fund both conservation and research, engage local communities through economic incentives and encourage governments to manage nature better (Buckley, 2010; Ribeiro et al., 2018). Conversely, the literature is full of examples where tourism practices have negative outcomes for wildlife, including harm done through baiting and capture (D'Cruze et al., 2017). As nature conservation is mostly an unprofitable activity (Strand et al., 2018), tourism, especially conservation tourism (*sensu* Buckley, 2010), is one of the few profitable activities that can generate financing for conservation (Kirkby et al., 2010, 2011; Vianna et al., 2018). Therefore, even if initially imperfect, tourism for conservation should be improved and refined rather than prohibited (SEMA, 2018; Muntifering et al., 2019).

Wildlife tourism is an industry that creates millions of trips worldwide per year (UNWTO, 2015). In the Amazon Forest, South America, however, it is still restricted to relatively few locations. This 6,300,000 km² region (Goulding et al., 2003) has some world-class wildlife attractions (Burger & Gochfeld 2003; Lee et al. 2013; Vidal 2018). Collectively, locations connected with global tourism markets represent less than 0.01% of the Amazon region, which points to a clear need for expansion. The Amazon Forest is being incinerated at its southern and eastern margins to provide land for meat and grain production. This region is called the Arc of Deforestation (Fearnside & Figueiredo, 2015), and is virtually *terra incognita* regarding biodiversity, with new vertebrate species, including even new primates, being described every year (Boubli et al., 2019; Costa-Araújo et al., 2019). In Brazil, substantial reductions in conservation funding (Magnusson et al., 2018) increases the need for the private sector to take a larger role in conservation funding in the Amazon Forest. The region harbours several charismatic species that have potential to become important ecotourist attractions, one important one being the harpy eagle (*Harpia harpyja*; Plate 5.1).

Plate 5.1 A harpy eagle female arriving at nest with a woolly monkey (*Lagothrix cana*) as prey for her fledgling.

The harpy eagle is the world's largest eagle. They form long-term pair bonds, nesting in the same nest tree for decades and producing clutches of one or two eggs that take 55-57 days to hatch. Despite often having two-egg clutches, invariably only one nestling survives (Seymour et al., 2010). Harpy eagles produce one dispersing juvenile every 30-36 months. The eaglets fledge at 5-7 months, but parent harpy eagles continue to bring food to these dependent juveniles until they reach 30-36 months of age, at which point the offspring disperse (Muñiz-López et al., 2016; Urios et al., 2017). Harpy eagles are long-lived: one wild individual that was captured as an adult has been in captivity for 54 years, as reported in the last studbook update (Hall, 2011). Birders describe harpy eagles as the most prized species to spot (Pivatto et al., 2007).

During the 19th century, harpy eagle distribution ranged as far south as northern Argentina and as far north as southern Mexico. Their historical range distribution has suffered a 40% reduction, and nowadays, their core habitat and last stronghold are the Amazon Forest (Miranda et al., 2019). In the Atlantic Forest, their distribution is restricted to two populations—one in northern Argentina and another in north eastern Brazil—with fewer than ten known nests in each (Srbek-Araujo & Chiarello, 2006; Anfuso et al., 2008; Sánchez-Lalinde et al., 2011). Central American populations of harpy eagles appear to be in somewhat better shape, probably reaching a total of a few hundred nests (Vargas-González & Vargas, 2011; Watson et al., 2016). Research analysing microsatellites in harpy eagle feathers from the Arc of Deforestation have found their genetic diversity to be declining in fragmented forests (Banhos et al., 2016), where human settlers commonly kill them (Trinca et al., 2008; Freitas et al., 2014; Gusmão et al., 2016).

With the expansion of the Arc of Deforestation—and the economy of ranching in that region—new roads and airports have made the Arc accessible from the rest of Brazil (ZSEE, 2008; Carrero et al., 2020). An extensive network of roads for logging and trails used for Brazil nut (*Bertholletia excelsa*) extraction provide relatively easy access to dozens of harpy eagle nests (Cavalcante, Tuyama, & Mourthe, 2019; Miranda et al., 2019). These roads and trails make harpy eagles relatively visible in a highly-accessible landscape. The same state-sponsored migrants who created the Arc of Deforestation (Schneider & Peres, 2015) can provide important assistance in finding and providing access to harpy eagle nests. Harpy eagle tourism can help to generate concrete financial value for habitat conservation, as has happened with other predators (Macdonald et al., 2017; Tortato et al., 2017). Although practical protocols have been developed for better practices of wildlife tourism (Haskell et al., 2015), few have addressed Amazonian wildlife. Creating evidence-based visitation schedules and tailoring them to offer higher viewing probabilities can help jumpstart the region's potential.

Our present study was designed to fine-tune the relationships of the conservation-tourism alliance, aiming to provide the best opportunities to view nesting harpy eagles in the shortest time, with the harpy eagles remaining unharmed by human presence. Consequently, we describe how many nests are required to guarantee nests in the nestling phase, during which adults are most visible. Further, we used camera-trap data to describe the circadian activity pattern of harpy eagles and to characterise the daily activity patterns of the parent birds and their fledged eaglets. Finally, we calculated the number of days that a tourist needs to wait at a nest to spot an adult eagle. These factors can improve the outcomes of tourists visiting nest visitation and decrease the time tourists need to spend near harpy eagle nests. We predicted that (1) harpy eagles would be most active during the early morning and late afternoon, as is the case for most diurnal species of tropical vertebrates and that (2) nest visitation rates by parent eagles would decrease during the nesting cycle. By offering better-tailored schedules to tourists and using a policy-oriented management strategy, we aim to establish this apex predator as a tool for conservation of the Amazon Forest.

Study area

The Arc of Deforestation is the region of the Amazon Forest comprising the southern, south-eastern and eastern regions of the Amazon Basin. Since 2016 we have worked in the northern part of Mato Grosso State, Brazil (Fig. 5.1) with our main base at ONF-Brasil's São Nicolau reforestation project (9°51'20.7"S, 58°14'53.9"W). The high rate of forest loss in the Arc of Deforestation, including a startling 26% increase of forest loss in 2020 compared with 2019

(PRODES data; Anonymous, 2020), has a profound impact on biodiversity (Peres 2005; Schneider and Peres 2015). The climate is generally humid and hot, with mean temperatures of 24ºC, 80% humidity (Vourlitis et al., 2002), and annual rainfall averages 2,000 mm (Noronha et al., 2015). The region includes primary and secondary, open, ombrophilous Amazon Forest (Veloso et al., 1991; Siqueira et al., 2018). The succession of anthropogenic land-use change and economic activities in the region starts with selective logging, followed by forest incineration and planting of pasture for cattle (Junior & Lima, 2018; Eri et al., 2020). State-sponsored migrants from southern Brazil (where harpy eagles have been extinct for several decades) now inhabit this region (Schneider & Peres, 2015). These recent human settlers have relatively little knowledge of forest use or existence of harpy eagles (pers. obs.).

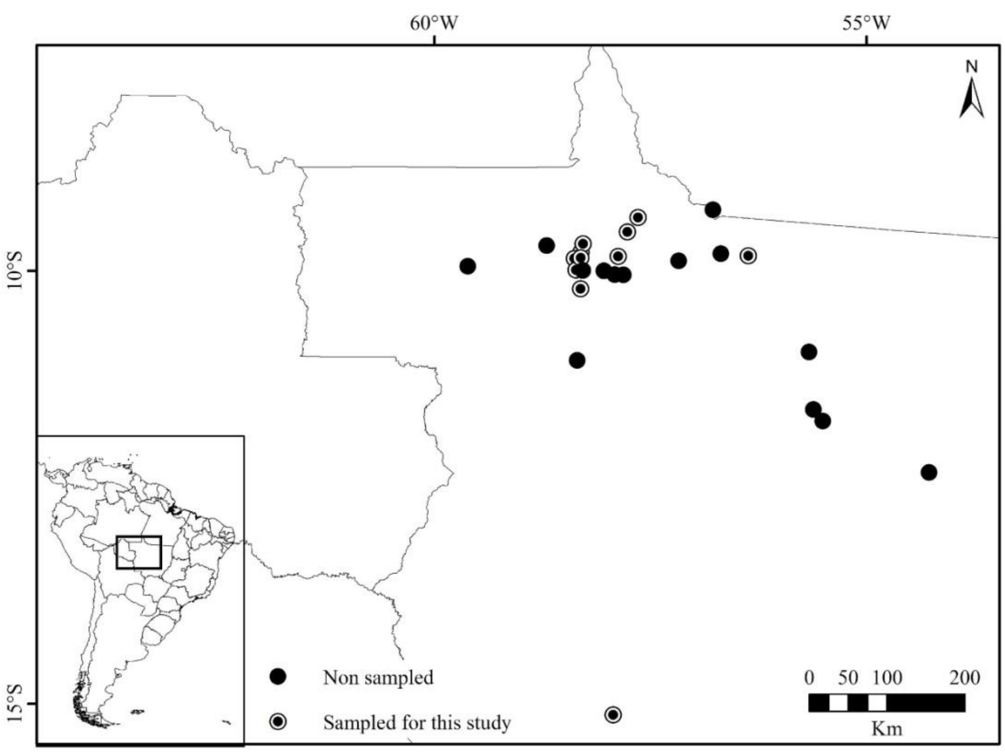

Fig. 5.1 Distribution of harpy eagle nests monitored in the present study throughout Mato Grosso state, Brazil (insert). Nests sampled using camera-traps for this study are represented by light circles.

5.3 Methods

Nest finding We offered a reward representing ~US$100 (BRL500), about 50% of the minimum monthly wage in Brazil, for each active harpy eagle nest that was communicated to us. This reward was widely publicised in posters and pamphlets that we disseminated in the study area among key groups of rural workers, particularly Brazil nut collectors. Most of the local population, including the nut collectors, are migrants or descendants of migrants from other parts of Brazil (Schneider and Peres 2015), and none of them hunts canopy vertebrates (Michalski & Peres, 2005; Trinca & Ferrari, 2007; Barbosa, 2012). This release from hunting pressure results in abundant, readily easily-seen canopy vertebrates that are attractive for tourism (Oliveira et al., 2019). The payment of nest rewards allowed us rapidly to discover harpy eagle nest locations.

Considering that finding enough nests is the main challenge to developing viable harpy eagle tourism, we calculated how many are necessary to have at least one in the brooding period for most of the time. The nestling phase—when adults can be seen all the time—lasts for at least five months, and each successful nesting cycle lasts a minimum of 30 months (Urios et al., 2017). The nestling phase thus represents only 16.6% or 1/6th of the nesting cycle. We, therefore, used a Bernoulli trial to calculate how many nests are required to have at least one in the brooding period:

$$1-(1-p)^{n}$$

In this case, "p" is the probability (1/6 or 16.6%,%) and *n* is the number of nests. We then calculated the probability of having at least one active nest for 90%, 95% and 99% of the time, assuming that breeding is aseasonal. We made this assumption of aseasonal reproduction based on published observations of egg-laying occurring in 10 months of the year (Watson et al., 2016). There is, however, limited evidence from captive individuals that harpy eagles are seasonal breeders (Blank et al., 2020), but that possible seasonality appears to be very modest, and all the data are from the southern limit of the species distribution. For the purposes of the present analyses, we assumed that this species as an aseasonal breeder, though we encourage researchers to collect more data to test this assumption further.

Tourism model Harpy eagle tourism originated as a cooperative venture between a conservation and research project and a private tour company, SouthWild. That company specialises in wildlife photography ecotourism that supports conservation action. SouthWild team install near harpy eagle nests mobile observation towers, with a maximum capacity of 12 persons. Tower construction at a nest would start at 15 or more days post-hatching and lasts 48-72 h depending on tower size (25-35 m) and model.

Our initiative required that the SouthWild pay ~US$20 (BRL80) per tourist per day to the landowner of the forest where the harpy eagle nest was located. In exchange, each landowner signed a legal contract stipulating that the landowner 1) would not damage or disturb the nest tree or the surrounding vegetation; 2) would not clear-cut any tracts of forest within a 1-km radius of the nest; c) would not hunt or allow hunting on the property; d) would not enlarge pastures by burning forest; e) would not carry out any legal or illegal logging within a 1-km radius of the nest. After careful confirmation that the parent birds were tolerant of human presence, SouthWild erected the viewing tower at 25-40 m from the nest tree. The tower always was tall enough to permit eye-level viewing of the nest and also ensured a green background to the nest. Local inhabitants earned money from the project by transporting and building the towers, as well by trail-cleaning, driving, cooking for tourists and staff, and other associated logistical services. To qualify for the operation, tourists needed to stay on the tower from sunrise until sunset hours for one, two, or three complete days, which thereby guaranteed the viewing of at least one adult bird or fledged eaglet. If any guest had not seen an adult bird after the waiting, they would have received a 100% refund of all jetport-to-jetport ground services.

Climbing, nest access and camera-trapping protocols For installing the camera-traps (several models from Bushnell, Kansas, USA) at nests, we work using the best-practices of accepted, published, raptor-specific rope climbing protocols (Pagel & Thorstrom, 2007; Rosenfield et al., 2007). We use an arborist slingshot to shoot a monofilament line over a branch near the nest, and then used this line to pull up a 4 mm line, which then pulled an 11 mm climbing rope so that an experienced rope climber could reach the vicinity of the nest. We then fastened two or three camera-traps on branches at 0.5-2 m from each nest, choosing camera angles that facilitated prey identification. We hammered between two to four 15-20-cm-long nails into a chosen branch and used flexible, 1.65-mm-diameter malleable wire to attach the camera-trap to the nails. We set the camera-traps to take one still photograph every 10 min. Some cameras reset configurations, taking photographs every few seconds. These data were used to calculate the time of adult permanence at nests. At nests, where we installed more than two camera-traps, we set one of them to video mode.

Nest access protocol for climbing was to produce minimal disturbance for the eagles while maximising the safety of the climber. We only installed cameras after the nestling was at least 15 days old. We avoided climbing nests during the first days after hatching because the nestling depends on the adults for thermoregulation and can suffer from excessive heat or excessive cold resulting from direct sun or rain, respectively (Collopy, 1984; Ellis & Schimitt, 2017). Adult harpy eagles, particularly the females, can be extremely aggressive during the first days after hatching, so going into nests should be avoided at this stage (Seymour et al., 2010). Taking these factors into consideration, we only climbed and installed cameras in the nest during periods that were safe for the nestling.

Statistical analyses The circadian activity pattern of fledgling eagles and adults delivering prey were analysed using data from the camera-traps. We did not include data from nestling phase (5-7 months old) because adults usually observe nestling eaglets at close range (or are inside the nest) and therefore are easy to sight and photograph. We used the circular Kernel method for analyses of activity data (Ridout & Linkie, 2009). The 95% isoline was utilised to describe the complete activity pattern for the nesting eagles, and the 50% isoline to represent the core activity range. The bandwidth parameter used was five, as recommended by Oliveira-Santos, Zucco, and Agostinelli (2013). A bootstrap of 10,000 samples with the original sample size, with replacement, as recommended by Ridout and Linkie (2009) was performed to calculate the confidence interval of the measures of presence duration. Records were considered independent if they occurred at an interval of more than 20 min. These criteria were used to be able to achieve a fine temporal resolution for circadian patterns, without oversampling moments where individuals (especially adults) triggered the camera repeated times during one quick visit.

To estimate the estimated time until detection of a harpy eagle, we ran an analysis in two steps. Firstly, we used generalised linear mixed models (GLMM) to estimate the probability of a camera-trap detecting fledglings and adults as a function of days passed from the start of sampling (i.e., the deployment of the camera-traps), since eagles visit their nest less often as a breeding cycle nears its end. We included a random effect of nest identity on the intercept, to account for the fact that deployment of cameras occurred at different times in the eaglet's development. Analyses were run using the binomial family and a logit link function (Ashe et al., 2010). We know that camera-traps may fail to detect adults when they visit the nest (from records of prey delivery without a visible adult), so we corrected the estimated detection probabilities using the false omission rate (FOR) of adults, by applying Bayes' theorem:

$$P(Detection|Presence) = \frac{P(Presence|Detection) \times P(Detection)}{P(Presence)}$$

Where $P(Detection|Presence)$ is the complement of the false omission rate (1-FOR), $P(Presence|Detection)$ is 1 (since there are no false omission errors), $P(Detection)$ is the estimated probability by the GLMM, and $P(Presence)$ is the focal value, the probability of an harpy actually visiting the nest. The second step consisted of the estimation of time until detection by tourists for both age classes using bootstrap analysis. We ran 10,000 simulations where we sampled a) the date since nest detection in which a nest is visited by a tourist, b) the estimated detection probability for that date onwards (as predicted from the GLMM, accounting for uncertainty). We then simulated Bernoulli trials over each day starting from the sampled date at a) and recorded the numbers of days sampled until first successful detection.

We split the nest visitation schedules by adults (from which males and females are separated by talon size) and eaglets into two main categories: 1) early nesting, composed of recently-fledged birds (from ~6 to 12 months of age) and 2) late nesting, composed of late fledglings from 12 to 20 months of age. Older fledglings sporadically visit nests seldomly to be useful for tourism, and during that stage of the nesting cycle, parent birds offer food at increasing distances from the nest to stimulate dispersion of the juveniles (Muñiz-López et al., 2016). The analyses were performed using the coding environment R version 4.0.2 (R Team, 2019), and are available at https://github.com/KenupCF/HarpyEagleTourism.

5.4 Results

We found 35 different nests in four years. Considering a 16.6% chance of a nest having a nestling, we estimate that 13, 17 and 26 nests are required for having at least one nest with nestling on 90%, 95% and 99% of the days. The camera-trap sampling resulted in 21,554 photographs and videos of 32 harpy eagles (21 adults and 10 eaglets), from 11 different nests. Furthermore, three nests sampled were excluded because forest fragmentation created food stress creating reduced visitation rates by adults. From the identified records, 3,650 independent records of adult and fledgling harpy eagles were obtained (Table 5.1).

The circadian pattern of harpy eagle adults nest visits was diurnal, and the mean of the total activity core duration (50% isoline) was 6 h 20 min for young and 7 h 20 min for adults. The core activity of adults was diurnal, and they were predominantly active from 8:30 to 14:00 and again 14:20 to 15:00. Fledglings visited the nests predominantly in the morning to the middle of the day, from 8:20-10:35 and again from 11:15 to 16:20. Fledgling harpy eagles differed from adults mainly by: 1) having less-pronounced activity peaks; 2) the second peak was more pronounced than the first; and 3) core activity was 12.75% longer (Fig. 5.2).

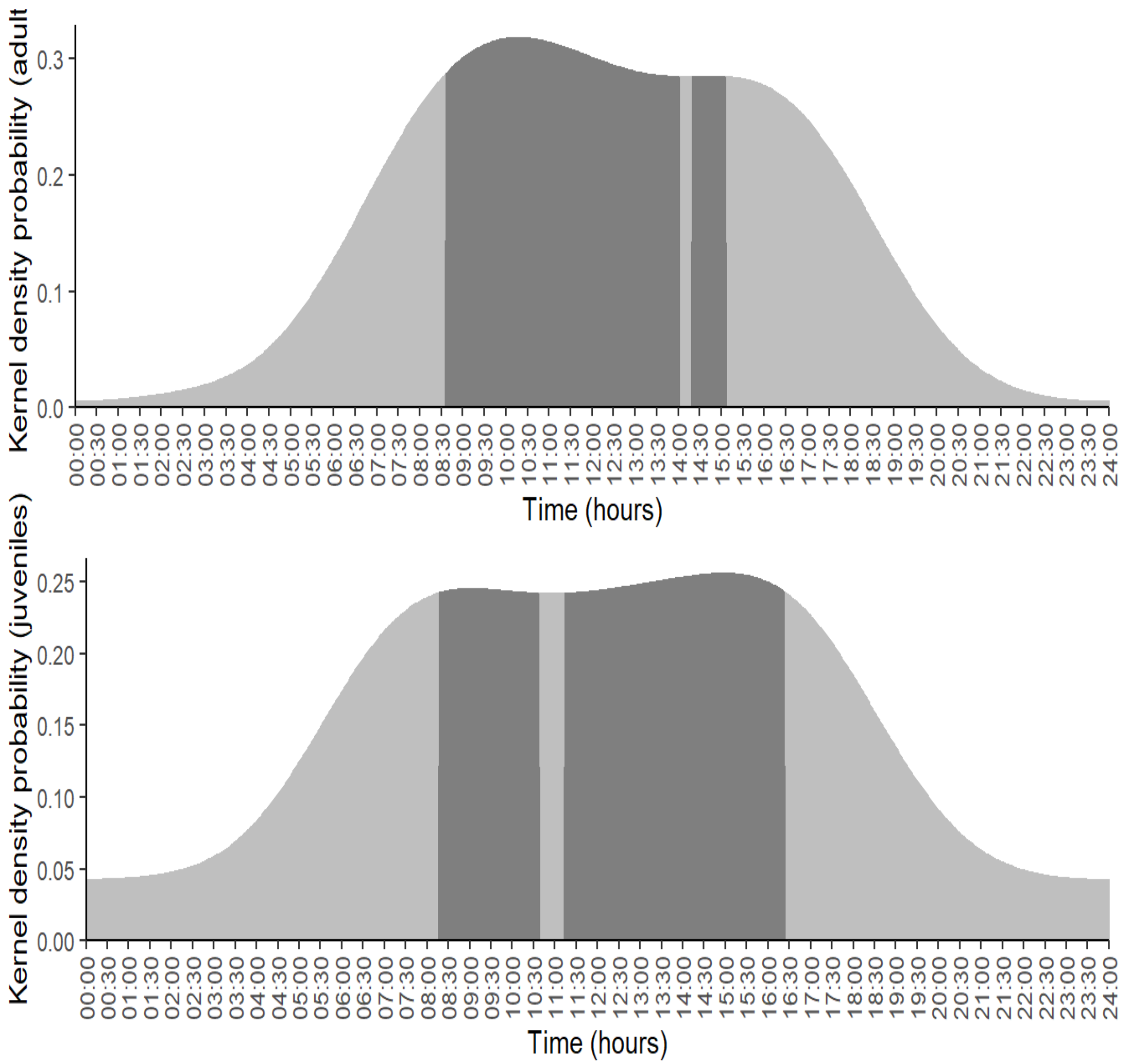

Fig. 5.2 Harpy eagle circadian patterns of nest visits for adults and fledged juveniles. (Dark grey shows the core activity 50% isoline). Core activity lasted 6.5 decimals hours for adults, peaking at 10h, and 7.45 decimal hours for fledged eagles, peaking at 15 h.

Table 5.1 List of nests monitored for the present study with respective geographical coordinates and number of independent photographs (>20 min, see methods for details) used in the analyses of the study. Total photographs refers to the sum of photographs with eagles and empty photographs.

Nest	Latitude	Longitude	Adult photographs	Fledgling photographs	Total photographs
Cotriguaçu II	-9.45620	-58.38038	28	545	1317
Apiacás I	-9.38385	-57.14427	1	3	846
Aripuanã I	-9.04596	-59.11002	14	399	794
Cotriguaçu IV	-9.49050	-58.36133	34	414	1451
Cotriguaçu I	-9.78344	-58.60232	29	165	586
Cotriguaçu III	-9.08732	-58.48032	61	0	1680
SdC I	-15.9274	-57.93090	24	183	1627
Cotriguaçu V	-9.85009	-58.60628	37	136	657
Cotriguaçu VI	-9.9938	-58.0806	27	744	3312
NB II	-10.9067	-58.30748	18	267	1188
Paranaíta I	-9.82669	-56.66821	29	492	8096

Each visit from an adult to its nest lasted on average 4.7 min. The required observation time for a tourist to sight a harpy eagle varied with age of the young bird and nest phase. At early nesting (meaning young eaglets from fledging at 5-7 to 12 months of age), it averaged 2 days for fledgling individuals and 4.16 days for adults. For a 95% probability of sighting of an adult-sized bird (either fledged bird or a parent bird), tourists must stay a minimum of 5 days for fledglings and 12 days for adults. At late nesting (12 to 20 months), the observation time required averaged 2.5 days for fledgling eagles and 5.2 days for adults. For a 95% sighting rate, tourists must stay 7 and 15 days for fledglings and adults, respectively. Further details on the odds can be seen in Table 5.2 and Fig. 5.3.

Table 5.2 Number of days necessary for at least one harpy eagle sightings at nests from platforms or towers. Values refer to percentages of tourists seeing an eagle on the different number of day's combinations, then averaged in the last column. Early nesting refers to the nest cycle from 5-7 to 12 months old, and late nesting to birds 12-20 months of age.

	Nest and age category	**Probability of sightings**			**Mean time spent**
		50%	**75%**	**95%**	**(days)**
Time spent (days)	Adult harpy eagles (early nesting)	3	5	12	4.16
	Fledged harpy eagle (early nesting)	1	2	5	2.06
	Adult harpy eagles (late nesting)	4	7	15	5.19
	Fledged harpy eagles (late nesting)	2	3	7	2.47

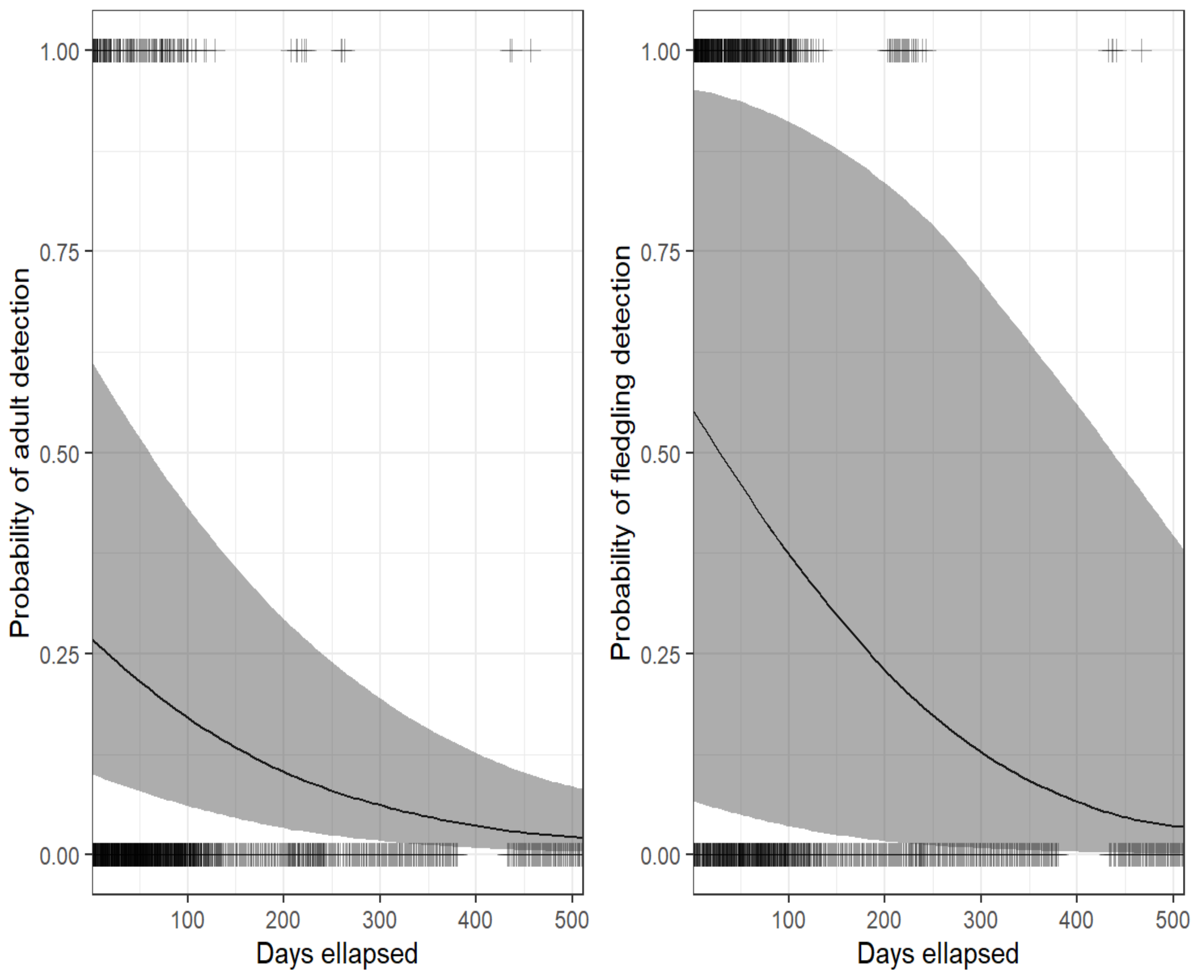

Fig. 5.3 Predictions of the probability of sighting an adult (left) and a fledgling (right) harpy eagle, according to generalised linear mixed model analyses and corrected for false omissions. The uncertainty for fledgling detection probability occurred because camera-trapping started at different stages in eaglet development at different nests.

As evidence of incidental habituation, 95.4% of fledged harpy eaglets remained in the nest tree or approached the climber during camera installation or removal (n = 44). The two occasions where the fledgling harpy eagles fled when we climbed the tree were from a nest in an indigenous reserve, where the tribesmen actively hunt harpy eagles, and a logging site where a tall tree next to the nest tree had dealt a major, glancing blow to the nest tree while being felled by loggers.

5.5 Discussion

Creating methods to manage the intricacies between tourism and harpy eagle conservation should be based on evidence, and those approaches should be evaluated using evidence from field tests such as presented in this study. Here we showed when harpy eagles could be found predictably at their nests, allowing tourists to enjoy reliable viewing. Besides making the first concrete analysis of adult and fledgling eaglet activity on nests, we describe the circadian patterns that allow us to identify the timing of eagle behaviours that tourists and media professionals desire—namely adults flying to the nest with prey. Finally, we offer tourism managers and stakeholders a tool to predict how to estimate the length of tourist stays to have high chances of seeing harpy eagles. Poorly conceived or ill-implemented wildlife-viewing practices that displace or harm wildlife can create further threats to the species, but our results can avoid those issues, thereby positively-effecting harpy eagle conservation.

South America's two long-running harpy research projects (one in Venezuela and the other in Brazil) have found around ~120 nests in 20-30 years of work (pers. obs.). This represents fewer than five nests per year, whereas relying on the assistance of local people, we found 35 nests in four-years (>8 nests/year). Harpy Eagle nests generally are extremely hard to locate, and finding even one is a highly-noteworthy event for ornithologists (Pereira & Salzo, 2006; Ubaid et al., 2011; Rotenberg et al., 2012). Therefore, counting on locals who work in the eagles was a highly cost-effective method for finding nests, and one that was capable of generating high-quality data reported in the only previous study that relied on a relatively large number of nests (Vargas-González & Vargas, 2011). Furthermore, it quickly provides a meaningful way of reaching nest numbers that allow reasonable chances of having at least one nestling available for year-round phototourism. The minimum number of 13 nests to have nestlings for 90% of days can be reached in 1.5-2 years.

Fledgling harpy eagles, being ~adult-size with a grey-white plumage are generally the most sought-after thing after adults themselves (pers. obs.). The detection of harpy eagles was estimated by camera-traps only, and therefore it represents a shortcoming regarding undetected adult and fledged eagle visits to the tree, but not to the nest itself. While our methods are statistically sound, our resulting requirements for staying at a nest and guaranteeing a sight represent a conservative approximation of the real requirements. Therefore, the number of days required for 50, 75 or 95% probability of sighting must be interpreted with caution. On the other hand, the average length of days required to see an eagle was consistent with what we observed on a day-to-day basis during our nest visits, and therefore represent robust estimates.

Regarding tourism, the seminal paper by Reynolds and Braithwaite (2001) stated that wildlife attractions must be: (1) predictable in their activity or location; (2) approachable; (3) readily viewable (open habitats); (4) tolerant of human intrusion; (5) possess elements of rarity or local super abundance; and (6) have a diurnal activity pattern. Fortunately, harpy eagles match all these traits, except for the fact that they inhabit the canopy (item 3), a problem that we overcome by using custom-designed, purpose-built observation towers and platforms. Predictability of nesting sites (item 1) is also a subject of concern because 16.6% of nesting pairs of eagles also have alternative nests (Vargas-González & Vargas, 2011), which may mean that in some years, they may be using the other, undiscovered nest tree. Our work contributes directly to the understanding of items 1 and 6. Those discoveries are of prime interest regarding harpy eagles as a wildlife attraction and the management of tourism that fits nest visitation schedules of eagles.

Responsible and controlled schedules for tourists viewing nests are particularly important for sensitive species with multi-decade life cycles, low breeding potential and high tourism value (Ashe et al., 2010; Haskell et al., 2015; Tortato et al., 2017). For harpy eagles, our data showed that both adults and fledglings were mainly active during the early and late hours of the day, with a higher peak in activity during the morning (10:15-10:45) for adults and at late afternoon (15:15 to 15:45) for fledgling, adult-sized eaglets. Nest visits by tourists can be planned to allow the incorporation of other wildlife attractions such as viewing toucans, macaws, or primates during times of low viewing chances for harpy eagles. Our present study provides evidence of ideal times for nest visits by tourists when an optimal photographic experience would be most likely.

One clear pattern emerging from our analyses was that later parts of the nesting cycle offered a relatively low potential for tourism. Tourism activities, therefore should then be focused on the first 12 months post-hatching, especially 0-5 months when the odds of viewing adults with the nestling are extremely high. Harpy eagle tourism trips are presently commercialised as 2-4 day excursions for the ~4,780 guests that annually visit Pantanal for jaguars (Tortato et al., 2017). Longer packages do not fit in the current model, so tourism must focus on early phases of harpy eagle breeding cycle, when eagles can be seen in shorter periods. It is therefore imperative to have agreements with the dozens of landowners so that visitation can alternate between many nests, thus increasing the chances that at least a few of the nests will be in the right phase for successful harpy eagle sightings and tourism development.

Poor tourism practices that could cause disruption of abandonment of nests would threaten both the eagles and the tourism business models, thus requiring yet more nests to be found. The operation of responsible, sustainable, profitable harpy nest phototourism is a laborious and expensive process, as towers must be moved and new agreements reached with landowners.

Besides threatening wildlife, poor management decisions would ultimately affect the attractions they were built on, compromising the sustainability of the business model (Haskell et al., 2015). Furthermore, having harpy eagle nests under a relatively constant watch could open the door to several avenues of conservation actions in the face of fairly heavy deforestation. For example, supplementary food could be offered to harpy eagles that are under food stress in severely fragmented landscapes. Nestlings that fall from nests while learning how to fly (the main cause of natural mortality for fledging harpy eagles; Muñiz-López, 2017) can be returned to their nests. Fledgling harpy eagles that are stranded in isolated forest patches and thus are unable to disperse could be translocated to other, larger forests, thus preventing the parents from killing the young that needs to disperse (Muñiz-López, 2017) and genetic diversity loss (Banhos et al., 2016). Finally, we emphasise that the same protocols used to install the camera-traps should be applied to tourism, and those terms addressed in contracts and permits. We emphasise that future research should test for breeding seasonality and compare prey delivery rates as well as activity patterns in nests with and without tourism. These two lines of research would produce important information helping guide more effective eagle conservation and tourism.

Habituation can be defined as the process of reducing an animal's instinct of escape in the presence of humans (Geffroy et al., 2015). In a tourism context, habituation is encouraged or desired to improve the guest experience and to reduce animal displacement and stress (Higham & Shelton, 2011). In our study region, 72% of the harpy nests were in Brazil nut trees (*Bertholletia excelsa*; n = 35, EBP Miranda, unpublished data). In the system described here, the presence of nut collectors working below nest trees for many years before the inception of the project, coincidently made harpy eagles accustomed to people; therefore, no formal, elaborate habituation was required.

On two occasions, one of which occurred before the inception of this project, camera-traps were installed during the nest-building process. In both cases, the harpy eagles abandoned the nest. Simultaneously, an old logging road passing 150 m from one nest was reopened. In the other case, the female harpy eagle was reportedly killed (she was never seen again) by members of a nearby community (pers. comm.). Although we cannot definitively attribute these two cases of abandonment to installing camera-traps during the nest-building phase, we nevertheless recommend that future researchers avoid disturbing nests before incubation is concluded. Other than the cases reported, no harpy eagles abandoned the nests, and several have already re-nested at the same nest sites during the present study.

By creating functional systemic and economic links between our conservation project, ecotourism investors, and stakeholders (including local people), we structured the system so that the ecotourism would gain momentum and spread in the region through similar initiatives, protecting more nests and more forest. As evidence of this momentum, five new nests were communicated to us after our publicity for nest finding was terminated in February 2020 (because of the COVID-19 pandemic and lockdown), even without any recent advertising. This represents a successful case of conservation marketing (Wright et al., 2015). Without continued management to promote tourism and other conservation strategies in the Arc of Deforestation, the harpy eagles will continue to face substantial distribution range loss or local extinction that made them almost totally disappear from the Atlantic Forest (Srbek-Araujo & Chiarello, 2006; Suscke et al., 2017).

Here we show in what parts of the nesting cycle can be visited safely, and for how long—for the benefit of both guests and harpy eagles. To succeed in the goal of harpy eagle conservation, evidence-based management actions must be in place. Tourism can be one of those actions, and maybe the only one that can generate funding to fuel other conservation activities. The appearance of the Arc of Deforestation is a double-edged weapon for harpy eagles. It created a fragmented landscape with high levels of habitat loss (Carrero et al., 2020), while also creating a landscape where harpy eagles are, for the first time, easily accessible thanks to a wide network of roads and airports. Approached under a policy-oriented strategy, harpy eagles will become a tool for conservation of the Amazon Forest.

5.6 Author contributions

Formulation and evolution of research ideas, goals and aims: EBPM; Management activities to annotate, scrub data and maintain research data. Conduction of research and investigation process and data collection: EBPM, NH, NL; Application of statistical and computational techniques to analyse study data. Development and design of methodology: EBPM, CFK. Acquisition of the financial support for the project leading to this manuscript: EBPM, CAM. Mentorship responsibility for the manuscript planning and execution. Preparation and presentation of the work after the original draft, critical review, commentary and revision: CAM, CTD.

5.7 Acknowledgements

We greatly appreciate the generous financial support of the following donors: the SouthWild.com Conservation Travel System, Rainforest Biodiversity Group, Idea Wild, The Mamont Scholars Program of the Explorer’s Club Exploration Fund, Cleveland Metroparks Zoo and the Rufford Small Grants Foundation (18743-1, 23022-2 and 31091-B). CTD is grateful to the University of KwaZulu-Natal and the National Research Foundation (ZA) for funding. Logistical support was given by the Peugeot-ONF Carbon Sink Reforestation Project, based at the São Nicolau Farm in Cotriguaçu, Mato Grosso, Brazil. This project is a Peugeot initiative to fulfil some of the Kyoto

Protocol directions and is run by the ONF-Brasil enterprise. We also thank the fieldwork help given by Dr Alexander Blanco, Gilberto Araujo, Lucas Buttura and Roberto Stofel. Finally, we thank ICMBio for authorising the project activities under the permit SISBIO 58533.

5.8 Conflicts of interest

None.

5.9 Ethical standards

This research involved no human subjects, no experimentation with animals and no collection of specimens and was done with minimally-invasive protocols.

5.10 References

ANFUSO, J., SUAREZ, M. & CHEBEZ, J. (2008) Nuevo Registro de Nidificación de la harpía (*Harpia harpyja*) en la provincia de Misiones, Argentina y Consideraciones sobre su conservación. *Nótulas Faunísticas*, 21, 1–13.

ANONYMOUS (2020) Monitoramento do Desmatamento da Floresta Amazônica Brasileira por Satélite. *PRODES report*. Http://www.obt.inpe.br/OBT/assuntos/programas/amazonia/prodes.

ASHE, E., NOREN, D.P. & WILLIAMS, R. (2010) Animal behaviour and marine protected areas: incorporating behavioural data into the selection of marine protected areas for an endangered killer whale population. *Animal Conservation*, 13, 196–203.

BANHOS, A., HRBEK, T., SANAIOTTI, T.M. & FARIAS, I.P. (2016) Reduction of Genetic Diversity of the Harpy Eagle in Brazilian Tropical Forests. *PloS One*, 11, e0148902.

BARBOSA, H. (2012) Estrutura de comunidades de mamíferos de médio e grande porte em fragmentos florestais da Amazônia Meridional. Unemat-Cáceres.

BLANK, M.H., OLIVEIRA, M.J., CUBAS, Z.S., MORAE, W., MOREIRA, N. & PEREIRA, R.J. (2020) Fecal sex steroids and reproductive behaviors in harpy eagles (*Harpia harpyja*). *Zoo Biology*, 1–10.

BOUBLI, J.P., BYRNE, H., DA SILVA, M.N., SILVA-JÚNIOR, J., ARAÚJO, R.C., BERTUOL, F., ET AL. (2019) On a new species of titi monkey (Primates: Plecturocebus Byrne et al., 2016), from Alta Floresta, southern Amazon, Brazil. *Molecular Phylogenetics and Evolution*, 132, 117–137.

BUCKLEY, R. (2010) Conservation tourism. CAB International, Wallingford.

BURGER, J., & GOCHFELD, M. (2003) Parrot behavior at a Rio Manu (Peru) clay lick: temporal

patterns, associations, and antipredator responses. *Acta Ethologica*, 6, 23–34.
CARRERO, G.C., FEARNSIDE, P.M., DO VALLE, D.R. & DE SOUZA ALVES, C. (2020) Deforestation Trajectories on a Development Frontier in the Brazilian Amazon: 35 Years of Settlement Colonization, Policy and Economic Shifts, and Land Accumulation. *Environmental Management*, 1–19.
CAVALCANTE, T., TUYAMA, C.A. & MOURTHE, I. (2019) Insights into the development of a juvenile harpy eagle's hunting skills. *Acta Amazonica*, 49, 114–117.
COLLOPY, M.W. (1984) Parental care and feeding ecology of Golden Eagle nestlings. *Auk*, 101, 753–760.
COSTA-ARAÚJO, R., MELO, F.R. DE, CANALE, G.R., HERNÁNDEZ-RANGEL, S.M., MESSIAS, M.R., ROSSI, R.V., ET AL. (2019) The Munduruku marmoset: a new monkey species from southern Amazonia. *PeerJ*, 7, e7019.
D'CRUZE, N., MACHADO, F.C., MATTHEWS, N., BALASKAS, M., CARDER, G., RICHARDSON, V. & VIETO, R. (2017) A review of wildlife ecotourism in Manaus, Brazil. *Nature Conservation*, 22, 1–16.
ELLIS, D.H. & SCHIMITT, N.J. (2017) Behavior of the golden eagle: an illustrated ethogram. Hancock House Publishers, Surrey.
ERI, M., JUNIOR, C.A. DA S., LIMA, M., JÚNIOR, N.L.S., OLIVEIRA-JÚNIOR, J.F. DE, TEODORO, P.E., ET AL. (2020) Capitalizing on opportunities provided by pasture sudden death to enhance livestock sustainable management in Brazilian Amazonia. *Environmental Development*, 4, 100499.
FEARNSIDE, P.M. & FIGUEIREDO, A.M. (2015) China's Influence on Deforestation in Brazilian Amazonia: A Growing Force in the State of Mato Grosso. In *BU Global Economic Governance Initiative Discussion Papers 2015-3* p. 229. Boston University, Boston.
FREITAS, M.A., LIMA, D.M. & GOMES, F.B. (2014) Registro de abate de gaviões-reais *Harpia harpyja* (Accipitridae) para consumo humano no Maranhão, Brasil. *Atualidades Ornitológicas*, 178, 12–15.
GEFFROY, B., SAMIA, D.S., BESSA, E. & BLUMSTEIN, D.T. (2015) How nature-based tourism might increase prey vulnerability to predators. *Trends in Ecology & Evolution*, 30, 755–765.
GOULDING, M., BARTHEM, R. & FERREIRA, E. (2003) The Smithsonian atlas of the Amazon, 1st edition. Smithsonian Books, Washington.
GUSMÃO, A.C., BANHOS, A., AGUIAR-SILVA, F.H., SOUZA, L.S. DE, SANAIOTTI, TÂNIA MARGARETE SILVA, ADRIANO MARTINS DA COSTA, T.M., OLIVEIRA, L.E., ET AL. (2016) Records of the occurrence, nesting, and hunting of the Harpy Eagle (*Harpia harpyja*) (Aves: Accipitridae) in Rondônia. *Atualidades Ornitológicas*, 190, 18–23.
HALL, C. (2011) Harpy Eagle Studbook *Harpia harpyja* North American Regional. San Diego.
HASKELL, P.J., MCGOWAN, A., WESTLING, A., MÉNDEZ-JIMÉNEZ, A., ROHNER, C.A., COLLINS, K., ET AL. (2015) Monitoring the effects of tourism on whale shark *Rhincodon typus* behaviour in Mozambique. *Oryx*, 49, 492–499.
HIGHAM, J.E.S. & SHELTON, E.J. (2011) Tourism and wildlife habituation: reduced population fitness or cessation of impact? *Tourism Management*, 32, 1290–1298.
JUNIOR, C.S. & LIMA, M. (2018) Soy Moratorium in Mato Grosso: deforestation undermines the agreement. *Land Use Policy*, 71, 540–542.
KIRKBY, C.A., GIUDICE-GRANADOS, R., DAY, B., TURNER, K., VELARDE-ANDRADE, L.M., DUEÑAS-DUEÑAS, A., ET AL. (2010) The market triumph of ecotourism: an economic investigation of the private and social benefits of competing land uses in the Peruvian

Amazon. *PloS One*, 5, e13015.

KIRKBY, C.A., GIUDICE, R., DAY, B., TURNER, K., SOARES-FILHO, B.S., OLIVEIRA-RODRIGUES, H. & YU, D.W. (2011) Closing the ecotourism-conservation loop in the Peruvian Amazon. *Environmental Conservation*, 38, 6–17.

LEES, A.C., ZIMMER, K.J., MARANTZ, C.A., WHITTAKER, A., DAVIS, B.J. & WHITNEY, B.M. (2013) Alta Floresta revisited: an updated review of the avifauna of the most intensively surveyed locality in south-central Amazonia. *Bulletin of the British Ornithologists' Club*, 133, 165–252.

MACDONALD, C., GALLAGHERB, A.J., BARNETTD, A., BRUNNSCHWEILERE, J., SHIFFMANF, D.S. & HAMMERSCHLAGA, N. (2017) Conservation potential of apex predator tourism. *Biological Conservation*, 215, 132–141.

MAGNUSSON, W.E., GRELLE, C.E., MARQUES, M., ROCHA, C.F.D., DIAS, B., G., O., ET AL. (2018) Effects of Brazil´s political crisis on biodiversity conservation. *Frontiers in Ecology and Evolution*, 6, 163.

MICHALSKI, F. & PERES, C.A. (2005) Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biological Conservation*, 124, 383–396.

MIRANDA, E.B.P., MENEZES, J.F.S., FARIAS, C.C., MUNN, C. & PERES, C.A. (2019) Species distribution modeling reveals strongholds and potential reintroduction areas for the world's largest eagle. *PloS One*, 14, e0216323.

MUÑIZ-LÓPEZ, R. (2017) Harpy Eagle (*Harpia harpyja*) mortality in Ecuador. *Studies on Neotropical Fauna and Environment*, 30, 1–5.

MUÑIZ-LÓPEZ, R., LIMIÑANA, R., CORTÉS, G.D., URIOS, V., LIMIÑANA, R., CORTÉS, G.D. & URIOS, V. (2016) Movements of Harpy Eagles *Harpia harpyja* during their first two years after hatching. *Bird Study*, 3657, 509–514.

MUNTIFERING, J.R., LINKLATER, W.L., NAIDOO, R., URIKHOB, S., PREEZ, P.D., BEYTELL, P., ET AL. (2019) Sustainable close encounters: integrating tourist and animal behaviour to improve rhinoceros viewing protocols. *Animal Conservation*, 22, 189–197.

NORONHA, J.C., LIMA, M.M., VELASQUEZ, C.L., ALMEIDA, E.J., BARROS, A.B. & RODRIGUES, D.J. (2015) Update das espécies de anuros da Fazenda São Nicolau, Mato Grosso, Brasil. *Scientific Electronic Archives*, 8, 15–25.

OLIVEIRA-SANTOS, L.G.R., ZUCCO, C.A. & AGOSTINELLI, C. (2013) Using conditional circular kernel density functions to test hypotheses on animal circadian activity. *Animal Behaviour*, 85, 2692–80.

OLIVEIRA, A.T.M., SÃO BERNARDO, C.S., MELO, F.R., SANTOS-FILHO, M., PERES, C.A. & CANALE, G.R. (2019) Primate and ungulate responses to teak agroforestry in a southern Amazonian landscape. *Mammalian Biology*, 96, 45–52.

PAGEL, J.E. & THORSTROM, R.K. (2007) Accessing nests. In *Raptor research and management techniques* (ed D.M. Bird), pp. 171–180. Hancock House Publishers, Blaine.

PEREIRA, A.D.M.M. & SALZO, I. (2006) Primeiro registro da nidificação de Harpia harpyja (Falconiformes, Accipitridae) na Serra da Bodoquena (Mato Grosso do Sul, Brasil). *Revista Brasileira de Ornitologia*, 14, 157–160.

PERES, C.A. (2005) Why we need megareserves in Amazonia. *Conservation Biology*, 19, 728–733.

PIVATTO, M.A.C., SABINO, J., FAVERO, S. & MICHELS, I.L. (2007) Perfil e viabilidade do turismo de observação de aves no Pantanal Sul e Planalto da Bodoquena (Mato Grosso do Sul) segundo interesse dos visitantes. *Revista Brasileira de Ornitologia*, 15, 520–529.

R Core (2020) R: A language and environment for statistical computing. R Fondation for Statistical Computing, Vienna.

Reynolds, P.C. & Braithwaite, D. (2001) Towards a conceptual framework for wildlife tourism. *Tourism Management*, 22, 31–42.

Ribeiro, S.M.C., Soares Filho, B., Costa, W.L., Bachi, L., de Oliveira, A.R., Bilotta, P. & Queiroz, L. (2018) Can multifunctional livelihoods including recreational ecosystem services (RES) and non timber forest products (NTFP) maintain biodiverse forests in the Brazilian Amazon? *Ecosystem Services*, 31, 517–526.

Ridout, M.S. & Linkie, M. (2009) Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14, 322–337.

Rosenfield, R.N., Grier, J.W. & Fyfe, R.W. (2007) Reducing Management and Research Disturbance. In *Raptor research and management techniques* (ed D.M. Bird), pp. 351–364. Hancock House Publishers, Blaine.

Rotenberg, J., Marlin, J., Pop, L. & Garcia, W. (2012) First record of a Harpy Eagle (*Harpia harpyja*) nest in Belize. *Wilson Journal of Ornithology*, 124, 292–297.

Sánchez-Lalinde, C., Silveira, L.F., Vélez-García, F., Cornélio, A.Ca. & Alvarez, M.R. (2011) Records of the Harpy Eagle (*Harpia harpyja*) in the Serra Bonita reserves complex, Camacan, Bahia, with evidence of breeding. *Revista Brasileira de Ornitologia*, 19, 436–438.

Schneider, M. & Peres, C.A. (2015) Environmental costs of government-sponsored agrarian settlements in Brazilian Amazonia. *PloS One*, 10, e0134016.

SEMA (2018) Instrução Normativa N° 28, 30 de janeiro de 2018. In pp. 17–18. Manaus.

Seymour, A., Hatherley, G., Contreras, F.J., Aldred, J. & Beeley, F. (2010) Hatching synchrony, green branch collecting, and prey use by nesting Harpy Eagles (*Harpia harpyja*). *Wilson Journal of Ornithology*, 122, 792–795.

Siqueira, A., Ricaurte, L.F., Borges, G.A., Nunes, G.M. & Wantzen, K.M. (2018) The role of private rural properties for conserving native vegetation in Brazilian Southern Amazonia. *Regional Environmental Change*, 18, 21–32.

Srbek-Araujo, A. & Chiarello, A. (2006) Registro recente de harpia, *Harpia harpyja* (Linnaeus)(Aves, Accipitridae), na Mata Atlântica da Reserva Natural Vale do Rio Doce, Linhares, Espírito Santo e. *Revista Brasileira de Zoologia*, 23, 1264–1267.

Strand, J., Soares-Filho, B., Costa, M.H., Oliveira, U., Ribeiro, S.C., Pires, G.F., et al. (2018) Spatially explicit valuation of the Brazilian Amazon Forest's Ecosystem Services. *Nature Sustainability*, 1, 657.

Suscke, P., Verderane, M., de Oliveira, R.S., Delval, I., Fernández-Bolaños, M. & Izar, P. (2017) Predatory threat of harpy eagles for yellow-breasted capuchin monkeys in the Atlantic Forest. *Primates*, 58, 141-147.

Tortato, F.R., Izzo, T.J., Hoogesteijn, R. & Peres, C.A. (2017) The numbers of the beast: Valuation of jaguar (*Panthera onca*) tourism and cattle depredation in the Brazilian Pantanal. *Global Ecology and Conservation*, 11, 106–114.

Trinca, C., Ferrari, S. & Lees, A. (2008) Curiosity killed the bird: arbitrary hunting of Harpy Eagles *Harpia harpyja* on an agricultural frontier in southern Brazilian Amazonia. *Cotinga*, 30, 12–15.

Trinca, C.T. & Ferrari, S.F. (2007) Game populations and hunting pressure on a rural frontier in Southern Brazilian Amazonia. *Biologia Geral e Experimental*, 7, 5–16.

Ubaid, F., Ferreira, L. & Antas, P. (2011) Primeiro registro de *Harpia harpyja* para o bioma Pantanal, com dados sobre atividade reprodutiva. *Revista Brasileira de*.

UNWTO (2015) Towards Measuring the Economic Value of Wildlife Watching Tourism in Africa. Madrid.

URIOS, V., MUÑIZ-LÓPEZ, R. & VIDAL-MATEO, J. (2017) Juvenile Dispersal of Harpy Eagles (*Harpia harpyja*) in Ecuador. *Journal of Raptor Research*, 51, 439–445.

VARGAS-GONZÁLEZ, J. DE J. & VARGAS, F.H. (2011) Nesting density of Harpy Eagles in Darien with population size estimates for Panama. *Journal of Raptor Research*, 43, 199–210.

VELOSO, H., RANGEL FILHO, A. & LIMA, J. (1991) Classificação da vegetação brasileira adaptada a um sistema universal. Rio de Janeiro.

VIANNA, G.M., MEEKAN, M.G., ROGERS, A.A., KRAGT, M.E., ALIN, J.M. & ZIMMERHACKEL, J.S. (2018) Shark-diving tourism as a financing mechanism for shark conservation strategies in Malaysia. *Marine Policy*, 94, 220–226.

VIDAL, M.D. (2018) Turismo interativo com botos (*Inia geoffrensis*) no baixo Rio Negro, Amazônia Central. Universidade Federal Do Amazonas.

VOURLITIS, G., FILHO, N., HAYASHI, M., NOGUEIRA, J., CASEIRO, F. & CAMPELO JR, J. (2002) Seasonal variations in the evapotranspiration of a transitional tropical forest of Mato Grosso, Brazil. *Water Resources*, 38, 11.

WATSON, R.T., MCCLURE, C.J.W., VARGAS, F.H. & JENNY, J.P. (2016) Trial Restoration of the Harpy Eagle, a Large, Long-lived, Tropical Forest Raptor, in Panama and Belize. *Journal of Raptor Research*, 50, 3–22.

WRIGHT, A.J., VERÍSSIMO, D., PILFOLD, K., PARSONS, E.C.M., VENTRE, K., COUSINS, J., ET AL. (2015) Competitive outreach in the 21st century: Why we need conservation marketing. *Ocean & Coastal Management*, 115, 41–48.

ZSEE (2008) Zoneamento Socioeconômico Ecológico do Estado de Mato Grosso.

CHAPTER 6

Harpy Eagle (*Harpia harpyja*) nest tree selection: Logging in Amazonian Forests threatens Earth's largest eagle

Everton B. P. Miranda*[1], Carlos A. Peres[2], Miguel Ângelo Marini[3], Colleen T. Downs[1]

1 - Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, P/Bag X01. Pietermaritzburg, 3209, South Africa

2 - School of Environmental Sciences, University of East Anglia, Norwich NR47TJ, UK.

3 - Departamento de Zoologia, IB, Universidade de Brasília, Brasília, Distrito Federal, Brazil.

*Corresponding author: mirandaebp@gmail.com, phone +55 65 98153550

Published in Biological Conservation. For the published version, please visit:

https://www.sciencedirect.com/science/article/abs/pii/S0006320720308120

6.1 Abstract

Characterising 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 characterise 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 <45º, 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 the unflooded forests 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.

Keywords: *Bertholletia excelsa*, breeding, *Ceiba pentandra*, emergent tree, habitat degradation, nest site selection, nest tree selection, raptor.

6.2 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 & Ponzoni, 2014) restricted the species to a few isolated pairs scattered across the largest remaining forest tracts (de Lucca, 1996; Suscke et al., 2017). 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. 6.1). 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.

Fig. 6.1 Mother and chick at the nest. Harpy Eagle nest at a Brazil-nut tree (*Bertholletia excelsa*) in southern Amazonia. (Photo: Roy Toft).

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.

6.3 Methods

Review and data standardisation

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 led to 17 published and three 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 the 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 pseudocontrols. The variables measured at nesting trees and the surrounding vegetation differed across studies (Table 6.1). 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.

Table 6.1 Checklist and description of the structure of 20 nest-tree species and predictor variables related to the surrounding vegetation explaining Harpy Eagle nest site colonisation of emergent trees. Sources: 1) Alvarez-Cordero 1996; 2) Granados 2005; 3) 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 0º. Estimated from the ground.	Nest tree	2
Number of emergents trees	Number of emergent trees in a plot of 25×40m 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 10cm of diameter at breast height in five plots of 25×40m around nest tree and around a control emergent tree.	Vegetation structure	2
Wood cover	Wood cover in the same plots, in m²/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 centre 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 >25cm of trunk diameter at breast height in a 60-m² plot around the nest tree.	Vegetation structure	3
Declivity	Mean declivity, measured with a clinometer, in six points in the 60-m² plot.	Vegetation structure	3

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$/m³ ~ 1 US$ = 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.

Statistical analyses

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 Generalised Additive Model (GAM). As semiparametric extensions of generalised 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 2,345 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 1,000 iterations of the means of randomly labelled groups (i.e. random categorisation 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 6.1 shows, a long list of variables were 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 6.1). By using both trees with nests and pseudocontrol samples we produced a binary response variable. Since Luz (2005) and Granados (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).

6.4 Results

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 6.2). These nests were located on the main fork (85.7%), primary branches (12.2%) and secondary branches (2%) of emergent trees (n = 98; Fig. 6.2). 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 6.3). 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$3.88/$m^3$), 15.4% were species with average commercial value (~US$7.74/$m^3$), 19.2% species were of high commercial value (~US$11.5/$m^3$) and 7.7% species were commercially very valuable (>US$20.4/$m^3$).

Table 6.2 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

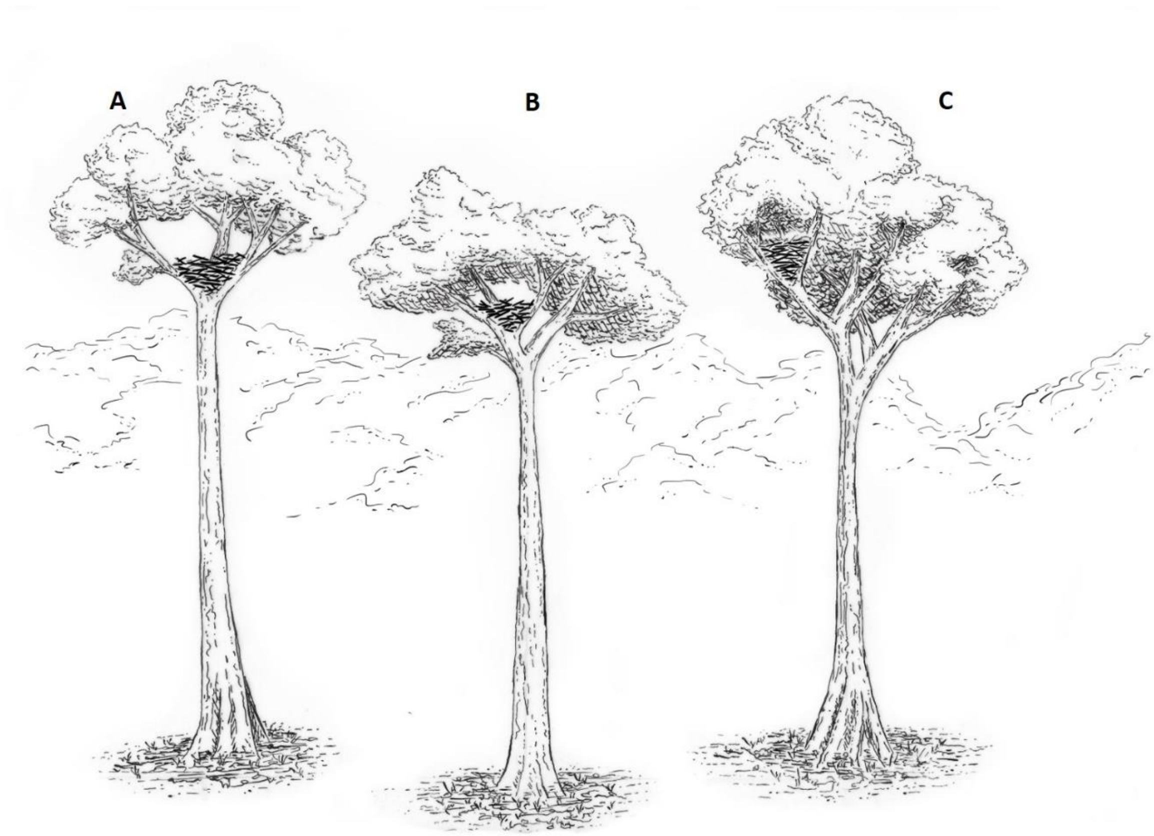

Fig. 6.2 Nest size and position. Harpy Eagle nests exhibited a mean width of 152 cm and a mean height of 99 cm. These nests were located at the main fork of nest trees (85.7%, A), primary branches (12.2%, B), and secondary branches (2%, C) of 28 species of emergent trees averaging 33.5 m in height at the main bifurcation (illustration: Paula Viana).

Table 6.3 Harpy Eagle nesting on a variety of emergent tree species shown as a frequency of occurrence. Tree families: [a] Malvaceae; [b] Lecythidaceae; [c] Fabaceae; [d] Chrysobalanaceae; [e] Anacardiaceae; [f] Combretaceae; [g] Myristicaceae; [h] Vochysiaceae; [i] Arecace. 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	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 Carvalho-Jr 2000, 8. Granados 2005, 9. Gusmão et al. 2016, 10. Kuniy et al. 2015, 11. Luz 2005, 12. Muñiz-López 2008, 13. Muniz-Lopez 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.

Spatial patterns of tree size

Regardless of forest type, Harpy Eagles always selected the largest available trees in which to build their nests (Fig. 6.3). 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 (Generalised Additive Model; $P < 0.05$ for all variables except for crown diameter; Fig. 6.4). In Amazonia, the total height of selected trees, nest height above ground, trunk diameter and crown diameter were all higher in upland unflooded forests compared with 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. 6.5).

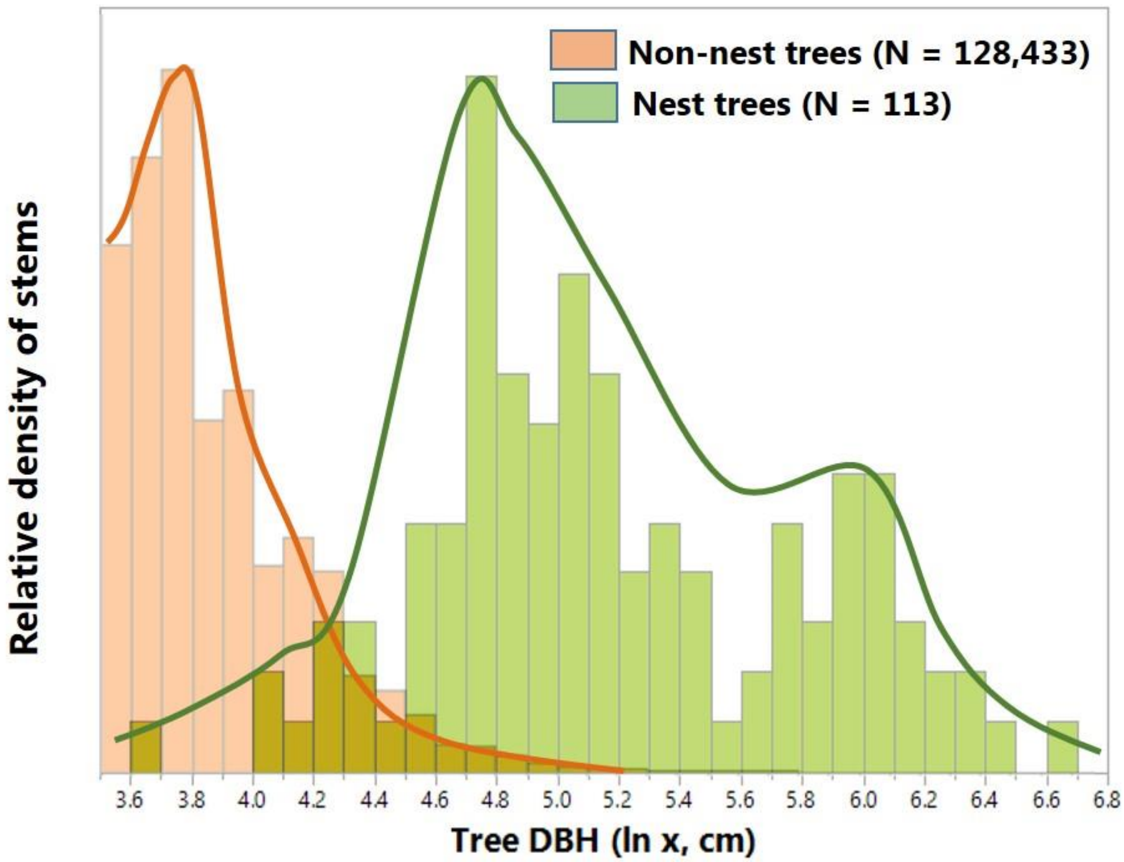

Fig. 6.3 Tree size. A double-histogram showing the tree size distribution (log of DBH, cm) of Harpy Eagle nest trees (green bars) across the Neotropics and non-nest trees (orange bars) across the Brazilian Amazon. Dark green bars show the overlap in tree sizes. Data for non-nest trees were sourced from the RADAMBRASIL floristic inventories (Peres et al. 2016).

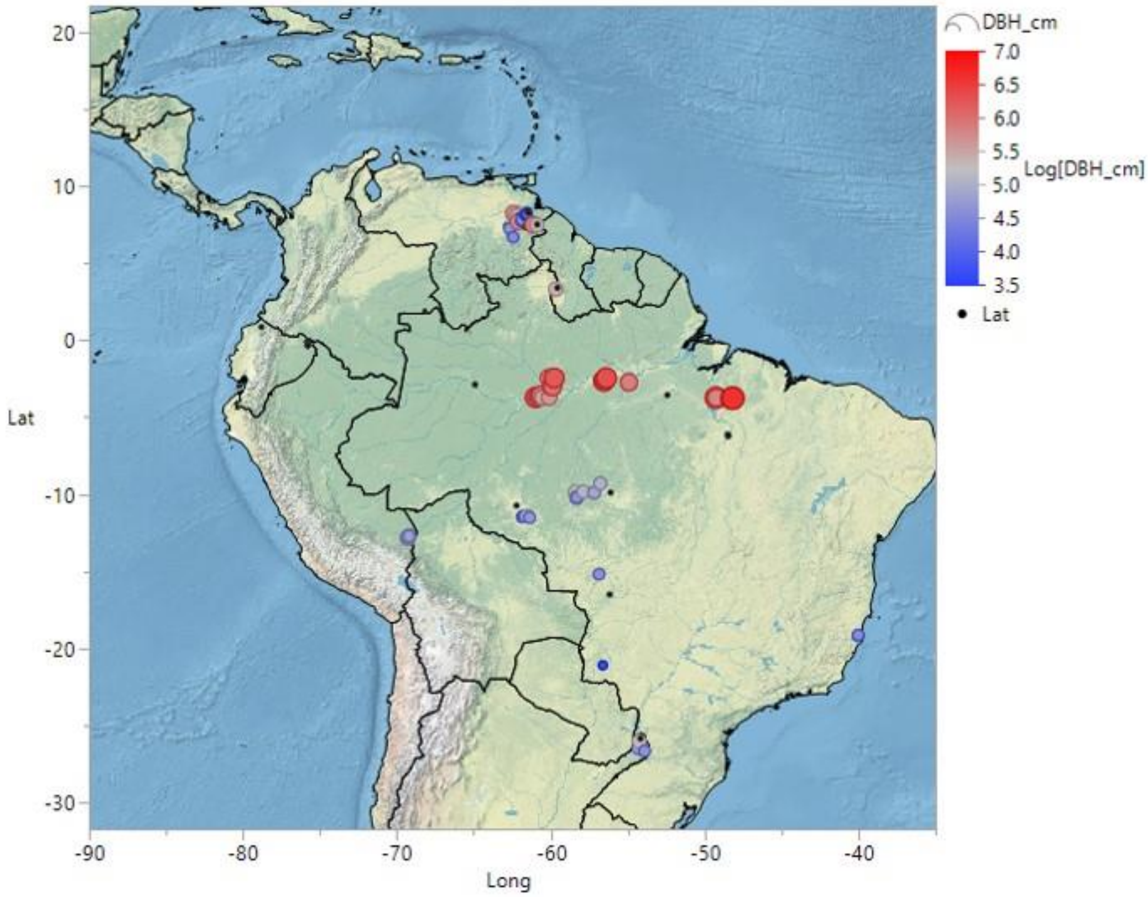

Fig. 6.4 Nest-tree size across South America. Wide variation in the size of observed nest-trees across the Harpy Eagle range distribution showing the spatial increase in tree diameter at breast height (DBH) towards the equator (GAM, R^2 0.0014, n = 52, $p > 0.05$). The same pattern of increase towards 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 represents nest-trees lacking any information on tree size.

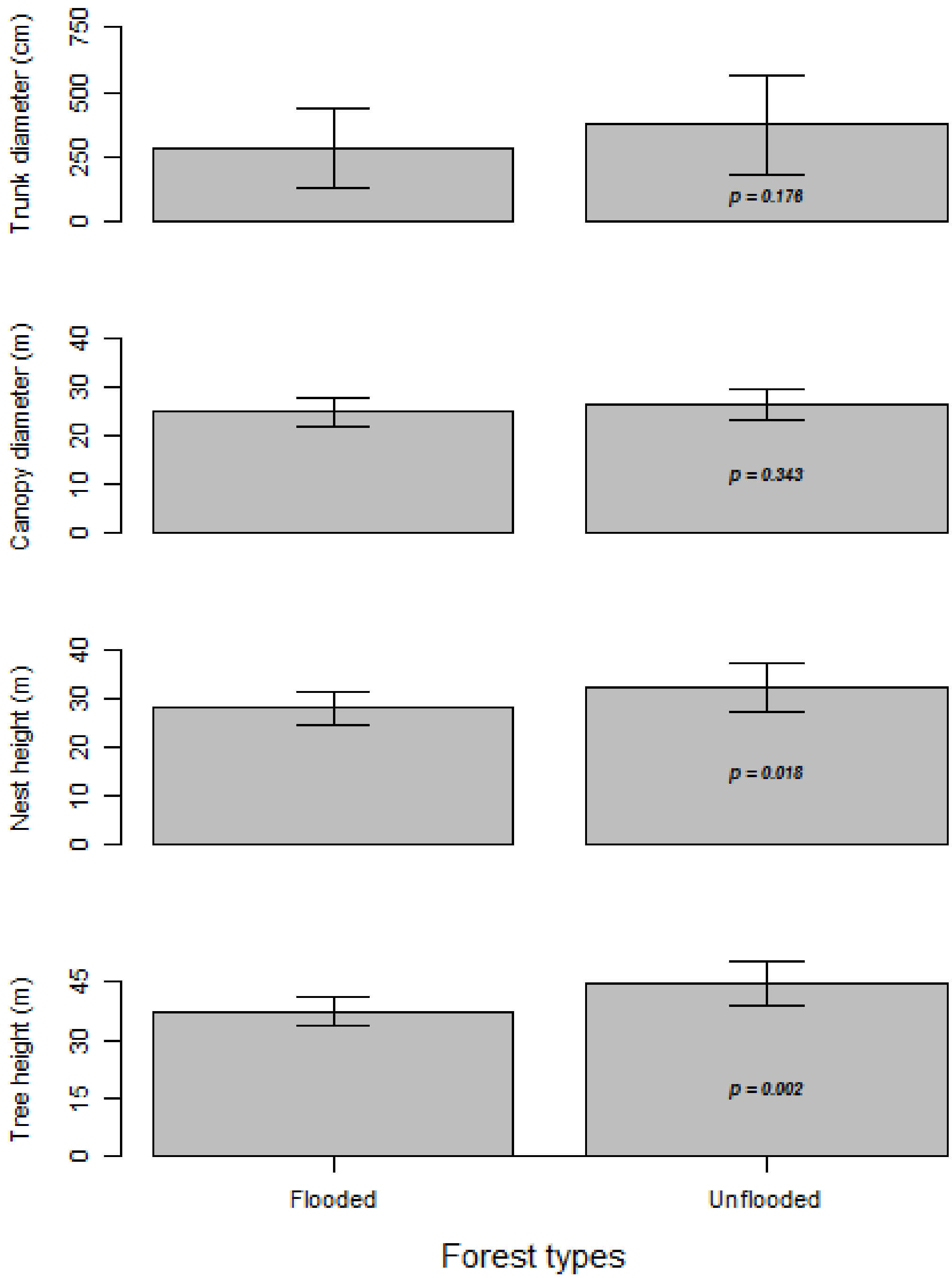

Fig. 6.5 Tree size in different forest types. Mean value for each variable and its standard deviation in flooded and unflooded Amazonian Forests for Harpy Eagles nest trees. Trees were lower-statured in the seasonally flooded forests, but this difference only held statistical significance for nest height and tree height.

Vegetation structure

The number of emergent trees, distance to the 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 colonisation 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, the 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).

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 the number of branches lower than 45° at the nest fork (3.56 *vs*. 2.67, 33.3% more <45º 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 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 (82.5º vs. 61.0º, 35% less inclined in selected trees) positively affected tree colonisation 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 the 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. 6.6).

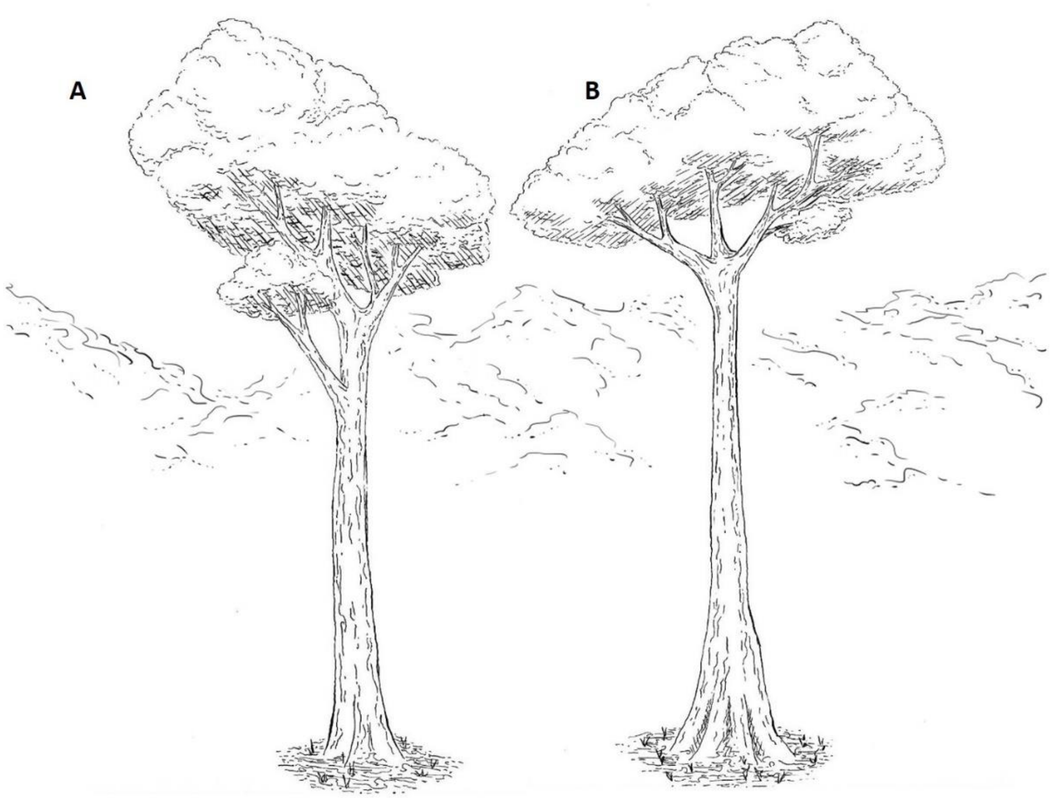

Fig. 6.6 Comparison of tree architecture. Pseudocontrol emergent trees (A) were 26.6% narrower in crown diameters, had 33.3% less <45º branches, were 19.6% shorter, and their branches were 35% steeper compared with selected Harpy Eagle nest-trees (B) (illustration: Paula Viana).

6.5 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 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 relatively 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, maybe 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. The topographic slope may be an effect of selection of nest-trees that are located at locally 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 with 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 6.2 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 a 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 to the extensive occurrence of buttressed trees in Amazonia (Parolin et al., 2016). The 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 trees 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 favour tailored planning before searching specific areas for climbing or installing an observation canopy tower.

While frequently used as Harpy Eagle nest-trees in the Amazon, Brazil-nut trees are 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 firma*) forests are related to these trees being frequently visited by Brazil-nut collectors. Any nest is more likely to come to the 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 emphasises 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 have been perceived as important to the processes that control tropical forest dynamics (Marklein et al., 2016). By concentrating nutrients underneath the crowns of nest-trees through long-term deposition of prey carcasses and faeces/ excreta over decades, Harpy Eagles may provide a key mutualistic relationship with the trees in which they nest. The impact of Harpy Eagle presence over that of seed predators and dispersers of nest trees, combined with the possibility of secondary seed dispersal from prey stomach contents (Nogales et al., 2002), maybe 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 emphasise 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 actually sustainable use, and that 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 improving the legislation of natural resources extraction by local communities in Panama to foster keeping 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. To make the problem worse, timber theft is extensive across Amazonia (Asner et al., 2006), including protected areas and indigenous reserves. 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-cut (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. comm.). These examples highlight the effects of forest governance over multiple countries covered by the Amazon Forest, suggesting extensive habitat degradation.

Forest governance on the ecological impacts of logging in other Amazonian countries is equally concerning. In Ecuador, there are five different timber extraction systems, each of which destined 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 timber volumes extracted. To make the problem worse, timber theft is extensive across Amazonia (Asner et al., 2006), including protected areas and indigenous reserves. The Environmental Ministry of Ecuador estimates that 40-50% of all timber in the Ecuadorian Amazon is illegally harvested (Orozco et al., 2014), and in Colombia, at least 42% of all timber harvest in natural forests is illegal (Orozco et al., 2014). While Peru and Bolivia have made improvements on forest governance laws to accommodate local communities and indigenous people demands (Cano et al., 2019), they also function under the minimum size paradigm (Piponiot-Laroche et al., 2019). In other words, it ignores mega-trees of value for Harpy Eagle nesting (although forbidding the felling of Brazil-nut trees; Nepstad et al., 1992). Venezuela current political turmoil has been terminating the governance over environmental resources, with entire timber concessions clear-cut (Pacheco-Angulo et al., 2017). On the other hand, the long-term conservation project in Venezuela entails loggers to pardon active Harpy Eagle nest-trees (Alexander Blanco, pers. comm.). These examples highlight the effects of forest governance over multiple countries covered by Amazon Forest, 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$3.88 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 emphasise 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 emphasise 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.

6.6 Acknowledgements

This study 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 and 23022-2), 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.

6.7 References

Aguiar-Silva, F.H., Jaudoin, O., Sanaiotti, T.M., Seixas, G.H.G., Duleba, S., Martins, F.D., 2017.

Camera trapping at active Harpy Eagle nests: interspecies interactions under predation risk. J. Raptor Res. 51, 72–29.
Aguiar-Silva, F.H., Sanaiotti, T.M., Jaudoin, O., Srbek-Araujo, A.C., Siqueira, G., Banhos, A., 2012. Harpy Eagle sightings, traces and nesting records at the “Reserva Natural Vale”, a Brazilian Atlantic Forest remnant in Espírito Santo, Brazil. Rev. Bras. Ornitol. 20, 148–155.
Alvarez-Cordero, E., 1996. Biology and conservation of the harpy eagle in Venezuela and Panama. DSc Thesis. University of Florida, Florida, USA.
Anfuso, J., Suarez, M., Chebez, J., 2008. Nuevo Registro de Nidificación de la harpía (*Harpia harpyja*) en la provincia de Misiones, Argentina y Consideraciones sobre su conservación. Nótulas Faunísticas 21, 1–13.
Asner, G., Knapp, D., Broadbent, E., Oliveira, P., Keller, M., Silva, J., 2006. Selective Logging in the Brazilian Amazon. Science 310, 483.
Barrientos, R., Arroyo, B., 2014. Nesting habitat selection of Mediterranean raptors in managed pinewoods: searching for common patterns to derive conservation recommendations. Bird Conserv. Int. 24, 138–151.
Birdlife International, 2017. *Harpia harpyja* (American Harpy Eagle, Harpy Eagle) [WWW Document]. Species factsheet: Harpia harpyja. URL http://datazone.birdlife.org/species/factsheet/22695998 (accessed 2.13.18).
Blaser, J., Sarre, A., Poore, D., Johnson, S., 2011. Status of tropical forest management. ITTO Tech. Ser. 38, 376–384.
Bonilla-Bedoya, S., Estrella-Bastidas, A., Ordoñez, M., Sánchez, A., Herrera, M.A., 2017. Patterns of timber harvesting and its relationship with sustainable forest management in the western Amazon, Ecuador case. J. Sustain. For. 26, 433–453.
Campos-Silva, J.V., Peres, C.A., 2016. Community-based management induces rapid recovery of a high-value tropical freshwater fishery. Sci. Rep. 6, 34745. https://doi.org/10.1038/srep34745
Cano, W., Van De Rijt, A., De Jong, W., Pacheco, P., 2019. Public innovation and changes in communal access to timber in the northern Bolivian Amazon. Int. For. Rev. 21, 432–445.
Chebez, J., Croome, M., Serret, A., Taborda, A., 1990. La nidificación de la Harpía (*Harpia harpyja*) en Argentina. Hornero 13, 155–158.
Crawley, M.J., 2007. The R book, Second edi. ed. Imperial College London, Silwood Park.
de Lucca, E.R., 1996. Observaciones de un nido exitoso de Harpia (*Harpia harpyja*) em Argentina. Hornero 14, 70–72.
Dobrovolski, R., Loyola, R.D., Guilhaumon, F., Gouveia, S.F., Diniz-Filho, J.A.F., 2013. Global agricultural expansion and carnivore conservation biogeography. Biol. Conserv. 165, 162–170.
DOEPA, 2010. N° 31.698. Anexo II lista de espécie e definição de categorias com seus respectivos preços individuais e preço médio por categoria. Belém.
Fearnside, P.M., 2005. Deforestation in Brazilian Amazonia: History, rates, and consequences. Conserv. Biol. 19, 680-688. https://doi.org/10.1111/j.1523-1739.2005.00697.x
Fernandez, F. dos S., Antunes, P., Macedo, L., Zucco, C.A., 2012. How sustainable is the use of natural resources in Brazil? Nat. Conserv. 10, 77–82.
Fowler, J., Cope, J., 1964. Notes on the Harpy Eagle in British Guiana. Auk 81, 257–273.
Freitas, M.A., Lima, D.M., Gomes, F.B., 2014. Registro de abate de gaviões-reais *Harpia harpyja* (Accipitridae) para consumo humano no Maranhão, Brasil. Atualidades Ornitológicas 178, 12–15.

Galetti, M., Carvalho-Jr, O. de, 2000. Sloths in the diet of a harpy eagle nestling in Eastern Amazon. Wilson Bull. 112, 535–536.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., A, C.J., Bradshaw, Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378.

Gil-da-Costa, R., 2007. Howler monkeys and harpy eagles: A communication arms race. In: Gursky, S.L., Nekaris, K.A.I. (Eds.), Primate Anti-Predator Strategies. Springer, Oxford, pp. 289–307.

Giudice, R., 2005. Arquitectura de árboles y estructura de la vegetación del bosque como factores determinantes en la anidación del Águila Arpía (*Harpia harpyja* Linnaeus 1878) en la cuenca baja del Río Tambopa. Universidad Nacional Agraria La Molina.

Giudice, R., Piana, R., Williams, M., 2007. Tree architecture as a determinant factor in nest-tree selection by Harpy Eagles. In: Bildstein, K.L., Barber, D.R., Zimmerman, A. (Eds.), Neotropical Raptors. Hawk Mountain Sanctuary, Orwigsburg, pp. 14–22.

Gorgens, E.B., Motta, A.Z., Assis, M., Nunes, M.H., Jackson, T., Coomes, D., Rosette, J., Aragão, L.E.O. e C., Ometto, J.P., 2019. The giant trees of the Amazon basin. Front. Ecol. Environ. 17, 373–374.

Grubb, T., Eakle, W., 1987. Comparative morphology of bald and golden eagle nests in Arizona. J. Wildl. Manage. 51, 744-748.

Gusmão, A.C., Banhos, A., Aguiar-Silva, F.H., Souza, L.S. de, Sanaiotti, Tânia Margarete Silva, Adriano Martins da Costa, T.M., Oliveira, L.E., Morais, W.G. de, Ferrari, S.F., 2016. Records of the occurrence, nesting, and hunting of the Harpy Eagle (*Harpia harpyja*) (Aves: Accipitridae) in Rondônia. Atualidades Ornitológicas 190, 18–23.

Hirota, M.M., Ponzoni, F.J., 2014. Atlas dos Remanescentes Florestais da Mata Atlântica: período 2012-2013. São Paulo.

Kuniy, A., Viana, M., Zahn, T., 2015. Translocation of harpy eagle (*Harpia harpyja*)(Linnaeus, 1758) nest. Brazilian J. Biol. 75, 1035–1036.

Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., Likens, G.E., Banks, S.C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., McBurney, L., Manning, A.D., Stein, J.A.R., 2014. New Policies for old trees: averting a global crisis in a keystone ecological structure. Conserv. Lett. 7, 61–69.

Logan, M., 2011. Biostatistical design and analysis using R: a practical guide.

Luz, B.B. da, 2005. Características de árvores emergentes utilizadas por Gavião-real (*Harpia harpyja*) para nidificação no centro e leste da Amazônia Brasileira.

Macdonald, C., Gallagherb, A.J., Barnettd, A., Brunnschweilere, J., Shiffmanf, D.S., Hammerschlaga, N., 2017. Conservation potential of apex predator tourism. Biol. Conserv. 215, 132–141.

Marklein, A.R., Winbourne, J.B., Enders, S.K., Gonzalez, D.J.X., van Huysen, T.L., Izquierdo, J.E., Light, D.R., Liptzin, D., Miller, K.E., Morford, S.L., Norton, R.A., Houlton, B.Z., 2016. Mineralization ratios of nitrogen and phosphorus from decomposing litter in temperate versus tropical forests. Glob. Ecol. Biogeogr. 25, 335–346.

Miranda, E.B.P., Menezes, J.F.S., Farias, C.C., Munn, C., Peres, C.A., 2019. Species distribution modeling reveals strongholds and potential reintroduction areas for the world's largest eagle. PLoS One 14, e0216323.

Moles, A.T., Warton, D.I., Warman, L., Swenson, N.G., Laffan, S.W., Zanne, A.E., Pitman, A., Hemmings, F.A., Leishman, M.R., 2009. Global patterns in plant height. J. Ecol. 97, 923–

932.
Monsalvo, J.A.B., Heming, N.M., Marini, M.Â., 2018. Breeding biology of Neotropical Accipitriformes: Current knowledge and research priorities. Rev. Bras. Ornitol. 26, 151–186.
Mori, S.A., Prance, G.T., 1990. Taxonomy, ecology, and economic botany of the Brazil nut (*Bertholletia excelsa* Humb. & Bonpl.: Lecythidaceae). Adv. Econ. Bot. 8, 130–150.
Muñiz-López, R., 2017. Harpy Eagle (*Harpia harpyja*) mortality in Ecuador. Stud. Neotrop. Fauna Environ. 30, 1–5.
Muñiz-López, R., 2008. Revisión de la situación del Águila Harpía *Harpia harpyja* en Ecuador. Cotinga 29, 42–47.
Muñiz-López, R., Criollo, O., Mendúa, A., 2007. Results of five years of the "Harpy Eagle (*Harpia harpyja*) Research Program" in the Ecuadorian tropical forest. In: Bildstein, K., Barber, D., Zimmerman, A. (Eds.), Neotropical Raptors. Hawk Mountain Sanctuary, Orwigsburg, USA, pp. 22–32.
Muñiz-López, R., Limiñana, R., Cortés, G., Urios, V., 2012. Movements of harpy eagles *Harpia harpyja* during their first two years after hatching. Bird Study 59, 509–514.
Muñiz-López, R., Limiñana, R., Cortés, G.D., Urios, V., Limiñana, R., Cortés, G.D., Urios, V., 2016. Movements of Harpy Eagles *Harpia harpyja* during their first two years after hatching. Bird Study 3657, 509–514.
Muñiz López, R., 2016. Biología y conservación del Águila Harpía (*Harpia harpyja*) en Ecuador. Universidad de Alicante.
Murawski, D.A., Hamrick, J.L., 1992. The mating system of *Cavanillesia platanifolia* under extremes of flowering-tree density: a test of predictions. Biotropica 24, 99–101.
Nellemann, C., 2012. Green carbon, black trade: illegal logging, tax fraud and laundering in the world's tropical forests. United Nations Environment Programme (UN Environment), INTERPOL Environmental Crime Programme.
Nepstad, D.C., Brown, I.F., Luz, L., Alechandre, A., Viana, V., 1992. Biotic impoverishment of Amazonian Forests by rubber tappers, loggers, and cattle ranchers. Adv. Econ. Bot. 9, 1–14.
Nogales, M., Quilis, V., Medina, F.M., Mora, J.L., Trigo, L.S., 2002. Are predatory birds effective secondary seed dispersers? Biol. J. Linn. Soc. 75, 345–352.
Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M.H.H., Oksanen, M.J., Suggests, M.A.S.S., 2007. The vegan package. Community Ecol. Packag.
Olmos, F., Pacheco, J.F.J., Silveira, L.L.F., 2006. Notas sobre aves de rapina (Cathartidae, Acciptridae e Falconidae) brasileiras. Rev. Bras. Ornitol. 14, 401–404.
Orozco, J.M., Mogrovejo, P., Jara, L.F., Sánchez, Á., Buendia, B., Dumet, R., Bohórquez, N., 2014. Tendencias de la Gobernanza Forestal en Colombia, Ecuador y Perú. Cambridge.
Pacheco-Angulo, C., Vilanova, E., Aguado, I., Monjardin, S., Martinez, S., 2017. Carbon emissions from deforestation and degradation in a forest reserve in Venezuela between 1990 and 2015. Forests 8, 1–22.
Parolin, P., Ferreira, L. V., Piedade, M.T.F., da Cunha, C.N., Wittmann, F., Arias, M.E., 2016. Flood tolerant trees in seasonally inundated lowland tropical floodplains. In: Tropical Tree Physiology. Springer, Cham, pp. 127–147.
Pereira, A.D.M.M., Salzo, I., 2006. Primeiro registro da nidificação de *Harpia harpyja* (Falconiformes, Accipitridae) na Serra da Bodoquena (Mato Grosso do Sul, Brasil). Rev. Bras. Ornitol. 14, 157–160.
Peres, C.A., Emilio, T., Schietti, J., Desmoulière, S.J., Levi, T., 2016. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian Forests. Proc. Nat. Acad. Sci. 113,

892–897.
Peres, C.A., Gardner, T.A., Barlow, J., Zuanon, J., Michalski, F., Lees, A.C., Vieira, I.C., Moreira, F.M., Feeley, K.J., 2010. Biodiversity conservation in human-modified Amazonian forest landscapes. Biol. Conserv. 143, 2314–2327.
Pinho, B.X., Peres, C.A., Leal, I.R., Tabarelli, M., 2020. Critical role and collapse of tropical mega-trees: A key global resource. Tropical Ecosystems in the 21st Century. In: Tropical Ecosystems in the 21st Century. p. 253.
Piponiot-Laroche, C., Rödig, E., Putz, F.E., Rutishauser, E., Sist, P., Ascarrunz, N., Blanc, L., Derroire, G., Descroix, L., Carneiro Guedes, M., Honorio Coronado, E.N., 2019. Can timber provision from Amazonian production forests be sustainable? Environ. Res. Lett. 14, 064014.
Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. For. Ecol. Manage. 327, 251–264.
Reina, R.E., Kensinger, K.M., 1991. The Gift of Birds: Featherworking of Native South American Peoples. University Museum of Archaeology & Anthropology, Pennsylvania.
Rettig, N., 1978. Breeding behavior of the harpy eagle (*Harpia harpyja*). Auk 95, 629–643.
Richardson, V.A., Peres, C.A., 2016. Temporal decay in timber species composition and value in Amazonian logging concessions. PLoS One 11, e0159035.
Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D., Ripley, M.B., 2013. Package MASS.
Rosa, J.M., 2010. Harpia. Editora Nitro, Belo Horizonte.
Rotenberg, J., Marlin, J., Pop, L., Garcia, W., 2012. First record of a Harpy Eagle (*Harpia harpyja*) nest in Belize. Wilson J. Ornith. 124, 292–297.
Sanaiotti, T., Junqueira, T., Palhares, V., Aguiar-Silva, F., Henriques, L., Oliveira, G., Guimarães, V., Castro, V., Mota, D., Trombin, D., Villar, D., Lara, K., Fernandes, D., Castilho, L., Yosheno, E., Alencar, R., Cesca, L., Dantas, S., Laranjeiras, T., Mathias, P., Mendonça, C., 2015. Abundance of Harpy and Crested Eagles from a reservoir-impact area in the Low- and Mid-Xingu River. Brazilian J. Biol. 75, 190–204.
Seymour, A., Hatherley, G., Contreras, F.J., Aldred, J., Beeley, F., 2010. Hatching synchrony, green branch collecting, and prey use by nesting Harpy Eagles (*Harpia harpyja*). Wilson J. Ornithol. 122, 792–795.
Sick, H., 1984. Ornitologia brasileira, uma introdução. Universidade de Brasília, Brasília, Brasil.
Sist, P., Mazzei, L., Blanc, L., Rutishauser, E., Mazzeib, L., Blanc, L., Rutishauserc, E., 2014. Large trees as key elements of carbon storage and dynamics after selective logging in the Eastern Amazon. For. Ecol. Manage. 318, 103–109.
Sousa, G.L., Oliveira, C., Procópio, J., Amaral, N., Brito, A.S., Aguiar-Silva, F.H., Jaudoin, O., 2015. Harpy Eagle (*Harpia harpyja*) monitoring project in São Geraldo do Araguaia, South-eastern Brazilian Amazon. Spizaetus 2, 2–11.
Suscke, P., Verderane, M., de Oliveira, R.S., Delval, I., Fernández-Bolaños, M., Izar, P., 2017. Predatory threat of harpy eagles for yellow-breasted capuchin monkeys in the Atlantic Forest. Primates 58, 141-147.
ter Steege, H., Mota de Oliveira, S., Pitman, N.C.A., Sabatier, D., Antonelli, A., Guevara Andino, J.E., Aymard, G.A., Salomão, R.P., 2019. Towards a dynamic list of Amazonian tree species. Sci. Rep. 9, 3501.
Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, F., Adler, G., Lambert, T., Balbas, L., 2001. Ecological meltdown in predator-free forest fragments. Science 294, 1923–1926.

Tobler, M.W., Anleu, R.G., Carrillo-Percastegui, S.E., Santizo, G.P., Polisar, J., Hartley, A.Z., Goldstein, I., 2018. Do responsibly managed logging concessions adequately protect jaguars and other large and medium-sized mammals? Two case studies from Guatemala and Peru 245-253. Biol. Conserv. 220, 245–253.

Trinca, C., Ferrari, S., Lees, A., 2008. Curiosity killed the bird: arbitrary hunting of Harpy Eagles *Harpia harpyja* on an agricultural frontier in southern Brazilian Amazonia. Cotinga 30, 12–15.

Ubaid, F.K., Ferreira, L.P., de Oliveira, S.B., Antas, P.D.T.Z., 2011. Primeiro registro de *Harpia harpyja* para o bioma Pantanal, com dados sobre atividade reprodutiva. Rev. Bras. Ornitol. 19, 88–92.

Urios, V., Muñiz-López, R., Vidal-Mateo, J., 2017. Juvenile dispersal of Harpy Eagles (*Harpia harpyja*) in Ecuador. J. Raptor Res. 51, 439–445.

Vargas-González, J. de J., Vargas, F.H., 2011. Nesting density of Harpy Eagles in Darien with population size estimates for Panama. J. Raptor Res. 43, 199–210.

Vargas-González, J. de J., Whitacre, D., Mosquera, R., Albuquerque, J., Piana, R., Thiollay, J.-M., Márquez, C., Sánchez, J.E., Lezama-López, M., Midence, S., Matola, S., Aguilar, S., Rettig, N., Sanaiotti, T.M., 2006. Estado y distribucion actual del aguila arpia (*Harpia harpyja*) en Centro y Sur America. Ornitol. Neotrop. 17, 39–55.

Vargas González, J. de J., Vargas, F.H., McClure, C., 2014. Características de la vegetación en sitios de anidación del águila arpía (*Harpia harpyja*) en Darién, Panamá. Ornitol. Neotrop. 25, 207–218.

Vargas González, J.D.J., McCabe, J.D., Anderson, D.L., Curtí, M., Cárdenas, D.C., Castillo, F.H.V., 2020. Breeding habitat suitability index for the harpy eagle in Panama: conservation implications. J. Raptor Res. in press.

Watson, J., 2010. The golden eagle. Bloomsbury Publishing, Poyser.

Wilcove, D.S., Giam, X., Edwards, D.P., Fisher, B., Koh, L.P., 2013. Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. Trends Ecol. Evol. 28, 531–540. https://doi.org/10.1016/j.tree.2013.04.005

Wood, S., Wood, M.S., 2007. The mgcv package.

Woodroffe, R., 2000. Predators and people: using human densities to interpret declines of large carnivores, in: Animal Conservation Forum. Cambridge University Press, Cambridge, pp. 165–173.

CHAPTER 7

Tropical deforestation induces thresholds of reproductive viability and habitat suitability for Earth's largest eagles

Everton B. P. Miranda*[1], Carlos A. Peres[2], Vitor Carvalho-Rocha[2,3], Bruna V. Miguel[4], Nickolas Lormand[5], Niki Huizinga[6], Charles A. Munn[7], Thiago B. F. Semedo[8], Thiago V. Ferreira[9], João B. Pinho[9], Vitor Q. Piacentini[10], Miguel Â. Marini[11], Colleen T. Downs[1]

1 – Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, P/Bag X01, Pietermaritzburg, 3209, South Africa
2 – School of Environmental Sciences, University of East Anglia, Norwich NR47TJ, UK
3 – Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, 88040-900, Santa Catarina, Brazil
4 – Medicina Veterinária, Universidade Federal de Mato Grosso, Sinop 78550-728, Brazil
5 – New Mexico Highlands University, New Mexico, 87701, United States
6 – HAS University, 90108, 5200 MA, Netherlands
7 – SouthWild, Várzea Grande, Mato Grosso, 78125-048, Brazil
8 – Instituto Nacional de Pesquisa do Pantanal (INPP), Museu Paraense Emílio Goeldi (MPEG) - Programa de Capacitação Institucional, Cuiabá, Mato Grosso, 78735-901, Brazil.
9 – Programa de Pós-graduação em Ecologia e Conservação da Biodiversidade, Instituto de Biociências, Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, 78735-901, Brazil
10 – Programa de Pós-graduação em Zoologia, Departamento de Biologia e Zoologia Instituto de Biociências, Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, 78735-901, Brazil
11 – Departamento de Zoologia, IB, Universidade de Brasília, Brasília, 70910-900, Distrito Federal, Brazil

***Corresponding author:** mirandaebp@gmail.com, phone +55 65 98153550
ORCID: https://orcid.org/0000-0003-2198-4742
Other emails and ORCIDs:
c.peres@uea.ac.uk; ORCID: http://orcid.org/0000-0002-1588-8765 downs@ukzn.ac.za; ORCID: http://orcid.org/0000-0001-8334-1510
marini@unb.br; ORCID: http://orcid.org/0000-0002-7300-7321

Running header: Harpy eagle feeding ecology and landscape degradation

Formatted for Nature Scientific Reports

7.1 Abstract

Apex predators are threatened globally, and their local extinctions are often driven by sustained failures in prey acquisition under contexts of severe prey scarcity or human retaliation against livestock predation. The harpy eagle *Harpia harpyja* is one of Earth's largest raptors and the apex aerial predator of Amazonian Forests, but no previous study has examined the impact of forest loss on their demography. We monitored 14 harpy eagle nests embedded within landscapes that had experienced 0% to 85% of forest loss and identified 306 prey items. Harpy eagles were unable to switch to open-habitat prey in deforested habitats and retained a diet primarily based on forest canopy vertebrates even in highly fragmented forest landscapes. However, prey delivery rates decreased with forest loss, with two fledged individuals dying of starvation in landscapes that had been deforested by 50-70%. Because landscapes >70% forest loss supported no nests, and eaglets could not be raised within landscapes >50% forest loss, we established 50% forest cover threshold for the reproductive viability of harpy eagle pairs. We, therefore, estimated that 35% of the entire study region in the Mato Grosso portion of the Amazonian Arc of Deforestation is already unsuitable for breeding harpy eagle populations. Our results suggest that restoring harpy eagle population viability within highly fragmented forest landscapes critically depends on forest conservation actions.

Keywords: *Harpia harpyja*; *Choloepus*; food stress; Arc of Deforestation; canopy; nest.

7.2 Introduction

Finding food is a biological imperative that drives fundamental elements of an organism's life such as mating[1], risk assessment[2], survival[3] and even the entire species distribution[4]. Consequently, the study of feeding ecology has become central to population ecology[3]. These studies have shown how food abundance is related to consumer density[5] and why some species can persist in human-dominated ecosystems[6–8], while others cannot[9–11]. Apex predators are particularly sensitive to changes in food abundance because of their high ecological requirements[12], which depend on healthy prey populations to fuel daily survival and breeding[13].

Anthropogenic habitat degradation and prey scarcity caused by poaching forces predators to adapt to feeding on alternative prey species to meet basic metabolic rates. Countless examples of prey switching include jaguars (*Panthera onca*) feeding mostly on armadillo (Cingulata) prey in defaunated habitats[14], and golden eagles (*Aquila chrysaetus*) extensively feeding on mesopredators at sites that lack their usual lagomorph prey[15]. Some natural predators may switch to feed on domestic livestock[8,16–18], but once exacerbated by habitat loss, these problems often extirpate apex predators at a landscape scale[9,10]. Predators can adjust to these changes and thrive in anthropogenic landscapes as long as prey remains abundant, and humans show tolerance[19–21]. The threshold of minimum food availability that can still ensure the persistence of apex predators has therefore been extensively investigated[22–24], as this threshold can be used to predict the population viability of any predator species within degraded landscapes.

Fig. 7.1 Harpy eagle (*Harpia harpyja*) arriving with a capuchin monkey at a nest (Photo: Jiang Chunsheng).

The harpy eagle (*Harpia harpyja*; Fig. 7.1) is an apex predator that feeds primarily on forest canopy vertebrates [25,26]. Being one of the Earth's largest eagles (averaging 5.9 and 7.3 kg for males and females, respectively), they have differing feeding habits depending on sex when floaters. Harpy eagles have stringent ecological requirements that include 0.8 kg of food per day for adults[27] and emergent nest trees taller than 40-45 m[28]. Harpy eagles have a 30-36-month-long breeding cycle, during which they fledge only a single eaglet despite the fact that they lay two eggs [29–32]. Harpy eagles are typically long-lived; a wild individual caught as an adult was still alive 54 years later at the publication of the latest studbook[33]. They usually nest in the same specific nest trees for several consecutive decades[34,35]. Studies of their breeding biology are still considered a high research priority[32]. They generally breed in T-shaped emergent trees that are of interest to the logging industry[28,36]. Their global distribution has contracted by 41% since the 19th century, and currently, 93% of their distribution range is within Amazonian Forests, their last stronghold[10]. Leading causes for their decline are habitat loss[10], and shooting by inquisitive settlers and, to a lesser extent, reprisal for killing livestock[37].

Harpy eagles take a heavy toll on prey populations, which therefore are under strong top-down control[27,38]. The literature widely describes sloths as the main prey taxon, followed by primates[26]. Large reptiles (notably green iguanas *Iguana iguana*) and large birds (such as guans and curassows; Aves: Cracidae) are less important prey species for harpy eagles[26]. Ungulates such as deer (Cervidae) and peccaries (Tayassuidae) are even less frequent in their diet [25]. Studying how landscape degradation affects the feeding ecology of harpies can shed light on how they deal with habitat loss. While diet is the main aspect studied in harpy eagle ecology, with >1000 prey records available in the literature[25], there is little information on the impacts of landscape-scale primary habitat conversion on harpy eagle feeding ecology. Yet harpy eagles' ecological limits regarding habitat loss and prey scarcity are key to understanding their extirpation thresholds in human-modified landscapes.

To understand the impacts of forest loss on harpy eagle feeding ecology, our aims were fourfold:

(1) Examine the effects of harpy eagle sexual dimorphism on their feeding ecology. We predicted that the larger females would prey on larger-bodied and less diverse prey than would the smaller males.

(2) Test the effects of landscape degradation on their predation of non-forest and disturbance-tolerant species. We predicted that pairs nesting in highly deforested sites would be feeding on these species, and sustain a more diverse diet.

(3) Test the effects of landscape degradation over prey delivery rates and biomass delivered to eaglets. We predicted that in degraded landscapes, eaglets would face lower prey delivery rates at longer intervals, resulting in lower prey biomass delivered.

(4) Determine the tolerance threshold of harpy eagles to deforestation levels and associated prey scarcity.

By exploring the above, we will be able to estimate the consequences of extensive Amazon deforestation on the persistence of breeding pairs of harpy eagles. Finding and capturing prey is the key issue for the survival of such an apex predator. Their persistence in human-modified landscapes, therefore depends on their tolerance threshold to food stress, which is presently unknown.

7.3 Methods

Study area

Amazonian Forests have been degraded, particularly along a large a deforestation frontier known as the Arc of Deforestation[39,40]. This study was conducted in the southern portion of the Arc of Deforestation in the northern state of Mato Grosso, Brazil (Fig. 7.2). The main agricultural land uses in this region are cattle ranching and soybean farming[41–43]. Brazil forestry law requires that a proportion of any private property (varying per ecoregion, but 80% in Amazon Forests), as well as riparian forests and hilly terrains, be spared from deforestation[44]. Human occupation thus generates a hyperfragmented landscape mosaic with varying levels of habitat loss and structural connectivity[45,46]. Koeppen (1948) classifies the region's climate as "tropical wet climate" or Amazonian (tropical monsoon) climate. Annual rainfall averages 2,350 mm, and annual ambient temperature averages 24.5°C, with 80–85% relative air humidity (Radam-Brasil 1983). The wet season occurs from October through March, amounting to ~80% of the annual precipitation, while the dry season spans from April through September. Arboreal folivores such as howler monkeys (*Alouatta* spp.) and green iguanas are locally rare in forest areas[49–51], while the three-toed sloth (*Bradypus* sp.) is absent[51]. These prey species are important elsewhere as reported by most previous studies of harpy diets[52]. This portion of the southern Amazonia was originally inhabited by several indigenous groups[53], but they have been largely displaced since the 1970s by southern Brazilian ranchers who joined a government-sponsored transmigration program[40]. Our study region is currently dominated by cattle-ranches, with the largest forest remnants offset aside as forest reserves and indigenous lands, while most small forest fragments are within private landholdings[44].

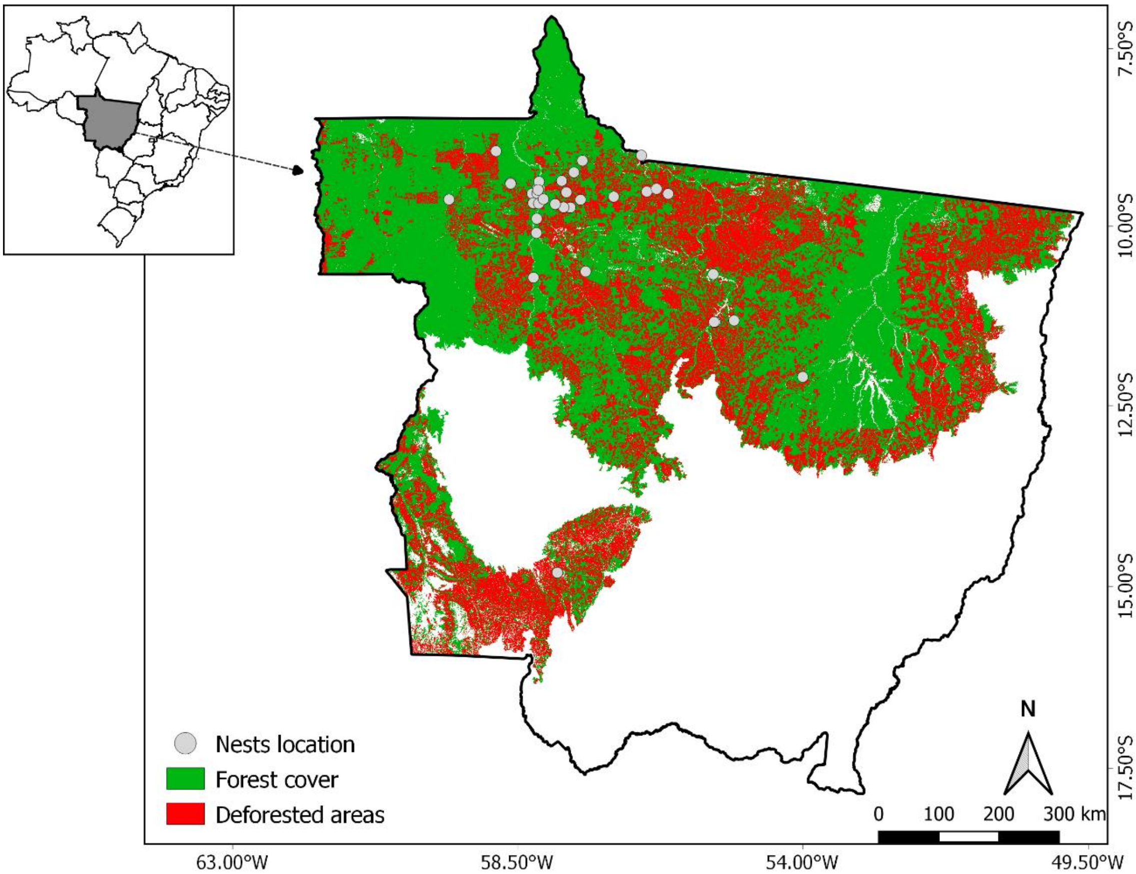

Fig. 7.2 The state of Mato Grosso in Brazil, showing the studied harpy eagle nests (grey circles) on the state region originally covered by Amazon Forest. Natural forest areas and deforested areas are depicted in green and red respectively and are based on 2019 MapBiomas collection.

Nest finding

We openly offered a reward amounting to ~USD100 or BRL500 (about 50% of the minimum Brazilian monthly wage) for positional information on each active harpy eagle nest reported to us. The reward was widely-publicised in posters and pamphlets that were disseminated among key groups of rural workers, indigenous groups, timber industry workers and especially Brazil-nut collectors. This reward payment allowed us to 'discover' harpy eagle nest locations at a rapid rate, unconstrained by biases related to forest location, as Brazil-nut collectors and indigenous people range widely within forest areas, while other informants were largely urban dwellers. Once we identified a nest location, we proceeded to reach contractual agreements with the landowners and then installed camera-traps up in primary branches near the nests. These contracts included formal agreements to ensure access to scientific research and low-disturbance ecotourism, that included an attractive share of local financial benefits to the landowner[54].

Climbing and camera-trapping protocols

We climbed harpy eagle nests using published, raptor-specific tree-climbing protocols[55,56]. We first determined eaglet age class using binoculars or climbed a neighbouring tree when binoculars did not allow observations. We did not climb trees with nests containing either eggs or nestlings younger than 15 days-old, as young eaglets depend on adults for thermoregulation[57]. When climbing nests that contained older nestlings, we planned our climbing approach to avoid subjecting nestlings to any rain or excessive heat. Our climbing protocol involved using a professional arborist slingshot to shoot a monofilament nylon fishing line over a well-positioned branch above the nest. This line was then used to pull a 4 mm rope that then pulled a 11 mm semi-static rope. A team member then ascended this final rope to install camera-traps (several models of Bushnell camera-traps). Cameras were installed 0.5-2 m from nests, and fixed using 15-cm-long nails and malleable, 1.65-mm-thick wire. Camera-traps (containing ≥16 Gb memory cards and lithium batteries) were programmed to take one photograph every 10 min for 24 h a day, over several months. We used 2 or 3 camera-traps per nest so as to allow multiple angles to view the prey items delivered by adult eagles as well as minimise data loss from camera-trap failures. Two static cameras per nest allowed us to sex the adult eagles and even large nestlings by comparing talon thickness, as female harpies have much larger feet and talons. As nests are on average 1.5 m in diameter but can reach up to 2.4 m[28], different camera-traps allowed us to see different parts of the upper nest platform. We removed camera-traps after they had photographed a nest for at least 90 days (aiming at least 12,960 photographs/nest).

Effects of forest loss on the feeding ecology

To define landscape buffers around each nest—as proxies for the home range of each harpy eagle pair—we estimated the nest density using the maximum packaged nest density method (MNPD). The MNPD is based on demarcating a circle around each nest, for which the radius is defined according to half the mean distance to the nearest neighbouring nest in a cluster of nests[58]. A constant is then added to fill the interstitial spaces between circles using the equation $A = \pi \times r^2 \times 1.158$. We used two clusters of nests, with six and five nests, respectively, at two study subregions in which our project had comprehensively surveyed the forest (by the reward system) over many years, so we believe all nests in those two areas had been detected.

We estimated the percentage of forest area lost within each of those buffers using land cover data available from the MapBiomas Project (collection 5; year 2019; http://mapbiomas.org/). MapBiomas classified rasters have a georeferenced, 30-m pixel resolution and a general classification accuracy of 97.3% for the Amazon biome. We used the Google Earth's Engine cloud computing platform (https://code.earthengine.google.com/) to access MapBiomas 2019 collection and extract the pixels corresponding to natural forest formation (ID code 3). We then summed the area of the corresponding forest pixels within each buffer and divided it by the respective buffer area to obtain the percentage of forest area remaining. The proportion of forest loss was then calculated by subtracting the proportion of forest area remaining. We further assessed and added by hand any new data about recent deforestation that was revealed in recent images from Google Earth®.

Within the buffers described above, we analysed the effects of habitat loss on prey species composition. In addition to the amount of forest cover, we added distance in meters to the nearest pasture areas as a covariate, because even pairs of harpy eagles nesting within forest territories could access open-habitat prey at nearby pastures. We identified prey species from photographs using reference information in the zoological literature[59,60], and reference collections at the Federal University of Mato Grosso (UFMT), Brazil. We also identified to species level whenever possible any prey skeletal material collected both underneath and inside nests.

We defined prey biomass delivery rates by estimating the mass of prey delivered to each nest (using prey data exclusively from camera-traps). Harpy eagles frequently prey on subadult individuals and reduce the size of large-sized prey carcasses to reduce drag during flight[52]. Eagles reduce flight loads (i.e. prey mass) by both by consuming large parts of carcasses and also by discarding prey parts that they had stripped of meat. We, therefore, used a series of estimated reductions. Subadult prey were estimated to represent 66% of adult body mass. For very young prey (because ungulates taken by the eagles were almost exclusively newborns[26]), we estimated that they represented 20% of adult body mass. Sloths received a further 33% reduction, because of a large amount of foliage consumed, which represents ~30% of the body mass of living sloths[61]. Soon after killing sloths, eagles discarded all the foliage inside the carcasses. For dismembered prey, we used the following approximate body mass reductions: 10% (head or viscera), 20% (reduced per member missing or added per single-member delivered), 50% (lower or upper body missing), and 90% (prehensile tails of Atelinae primates from the genera *Ateles*, *Lagothrix* and *Alouatta*; tails of porcupines, Rodentia:

Erethizontidae) of the total carcass mass[7]. Body masses of these prey species were obtained from the literature[59,62]. When calculating the general reduction in body mass for analyses related to the feeding ecology purposes (rather than biomass delivered to nests), we only reduced the body mass to account for subadults, not performing the body part reduction. For the latter, we were, therefore, able to consider the mass of prey parts consumed by adults before carcass delivery at the nest.

We used the forest habitat amount remaining (or lost) around each nest to determine how much forest loss harpy eagles could tolerate while still exhibiting clear evidence of successful breeding. We defined a hexagonal cell area that represents a harpy eagle pair using the mean distance to the nearest neighbouring nest. The deforestation levels around known active nests surrounded by the highest levels of forest loss—but still successfully raising eaglets—were then used to identify hex-cells containing sufficient amounts of forest cover to be suitable for harpy eagles, while those below this threshold were defined as unsuitable. We then extended this rationale for the entire 428,800-km^2 area of the northern portion of the state of Mato Grosso, and calculated the amount of regional scale habitat suitability both for the first (1985) and last year (2019) of the land-use time series.

Statistical analyses

We ran the prey comparisons between sexes using null models[63], for several traits like prey size and Levin's niche breadth index. Levin's index is $B_{sta} = B - 1 / (n - 1)$, where B is Levin's index ($B = 1 / \Sigma p_j^2$), p_j is the frequency of occurrence of each group of prey species, and n is the total number of prey species[64]. Our null model was composed of the following steps: (1) bootstrapping one sample of 25 prey records of males and another sample of 25 prey records of females; (2) calculating niche breadth (or other differences between sexes) for each sex using a niche breadth measure; (3) creating a pairwise difference in niche breadth between males and females; and (4) determining if the difference in niche width found between breeders and floaters was larger than expected by chance by comparing differences between two randomly labelled bootstrapped samples (n = 25). We carried out 1,000 iterations to calculate niche width differences between sexes and see how far it was from random. We chose 25 as a sample size after previous work showed this sample to be large enough to adequately represent all prey species with frequencies >5% at a harpy eagle nest[26]. Alpha levels were defined as 5%.

We tested if the amount of forest loss in each nest buffer nest affected prey composition using a non-metrical multidimensional scaling (NMDS). We chose the NMDS with the goal of collapsing information from multiple dimensions (in our case from multiple harpy eagle nest sites with multiple prey species) into a few axes so that they could be interpreted. To understand the effects of forest loss on harpy eagle feeding ecology, we used the amount of lost forest as well as the linear distance to the nearest pasture (in meters). The first may limit the access of harpy eagles to canopy prey such as sloths and monkeys, while the second may increase the access to ground-dwelling prey such as armadillos.

We also tested the effect that forest loss (as a predictor variable) within the buffer had on prey species richness and Levin's niche breadth index (as response variables) per harpy eagle nest. We then ran both against the forest loss and the distance to the nearest pasture as covariates using a generalised linear model (GLM). We ran the analyses using the Gaussian family and a logit link function[65].

For determining the impact of forest loss on harpy eagle feeding ecology, we ran the amount of habitat loss (as a predictor variable) for each nest against the responsible variables interval between prey deliveries (feeding frequency) and biomass delivery rates (prey mass delivered). For these analyses, we also used a GLM with a Gaussian family and a logit link function. We defined feeding rates as the interval in days between prey deliveries by adults, in which 0 represents two prey deliveries made on the same day. We added the nesting phase (nestling, fledgling and dependent juvenile) as covariates factors since interval slowly decreases from 1.8 to 5.12 days per prey from the nestling to dependent juvenile phases, respectively[66]. We, therefore, assumed each nest phase per nest to be an independent replica. Analyses were performed using R coding environment, version 4.0.2[67].

Table 7.1 Harpy eagle prey species general composition from bones and camera-trap data. Percentage (%) describes prey composition regarding all samples. Camera and Bones show the raw sample size from camera traps and prey bone collection. Prey brought by harpy eagle males (M) and females (F) from 14 nests in Southern Amazonia is from camera-trap only. Biomass and sexes are in percentages.

Species	%	Camera	Bones	Biomass	M	F
Two-toed sloth *Choloepus hoffmanni*	23.9	47	26	18.8	10.14	25.00
Capuchin monkey *Sapajus apella*	18.3	52	4	15.5	31.88	19.05
Woolly monkey *Lagothrix cana*	7.5	21	2	15.7	1.45	15.48
Brazilian porcupine *Coendou prehensilis*	6.2	17	2	7.3	4.35	7.14
Spider monkey *Ateles chamek*	5.6	13	4	13.8	0.00	5.95
Black vulture *Coragyps atratus*	3.3	3	7	0.7	1.45	0.00
Coati *Nasua nasua*	2.9	9	0	3.1	4.35	0.00
Red-nosed saki *Chiropotes albinasus*	2.6	8	0	2.8	1.45	4.76
Lesser anteater *Tamandua tetradactyla*	2.6	7	1	3.9	2.90	3.57
Opossum *Didelphis* spp.	2.9	7	2	0.9	0.00	2.38
Titi monkey *Plecturocebus* spp.	2.3	6	1	1.0	1.45	0.00
Golden-and-blue macaw *Ara ararauna*	2.3	6	1	0.6	7.25	0.00
Peccaries[1] *Tayssuidae* spp.	2.0	6	0	5.2	1.45	1.19
Squirrel monkey *Saimiri ustus*	2.3	7	0	0.9	4.35	2.38
Olingo *Potos flavus*	1.6	5	0	1.0	1.45	1.19
Woolly opossum[2] *Caluromys* spp.	2.0	6	0	0.2	7.25	0.00
Crested curassow *Crax fasciolata*	1.0	3	0	1.1	2.90	2.38
Howler monkey *Alouatta* spp.	1.0	3	0	2.4	4.35	0.00
Parrot *Amazona* spp.	1.0	2	1	0.2	1.45	0.00

Guan *Penelope jacquacu*	1.0	3	0	0.6	1.45	1.19
Pygmy anteater *Cyclopes xinguensis*	1.0	3	0	0.1	0.00	3.57
Marmosets *Mico* spp.	1.0	3	0	0.1		
Common armadillo *Dasypus septemcinctus*	1.3	3	1	0.3	0.00	1.19
Trumpeter *Psophia viridis*	0.3	1	0	0.2	1.45	0.00
Dwarf porcupine *Coendou roosmalenorum*	0.3	1	0	0.1	0.00	1.19
Black porcupine *Coendou nycthemera*	0.3	1	0	0.1	1.45	0.00
Red-and-green macaw *Ara chloropterus*	0.3	1	0	0.3	1.45	0.00
Night monkey *Aotus azarae*	0.3	1	0	0.1	1.45	0.00
Brocket deer *Mazama* spp.	0.3	1	0	0.4		
Cocoi heron *Ardea cocoi*	0.3	1	0	0.5		
Razor-billed curassow *Pauxi tuberosa*	0.3	1	0	0.4	0.00	1.19
Green iguana *Iguana iguana*	0.3	1	0	0.3		
Tayra *Eira barbara*	0.3	1	0	0.4	0.00	1.19
Crab-eating fox *Cerdocyon thous*	0.3	1	0	0.2	1.45	0.00
Channel-billed toucan *Ramphastus vitellinus*	0.3	1	0	0.0	1.45	0.00
Green ibis *Mesembrinibis cayennensis*	0.3	1	0	0.1		
Agouti *Dasyprocta* spp.	0.3	0	1	0.4		
Unidentified vertebrates		26	23			
Total		355				

1 – One individual could be identified as *Tayassu pecari*, all other were too young to classify as either *Tayassu pecari* or *Pecari tajacu*.

2 – One individual was a *Caluromys lanatus*, all others could not be classified below genus.

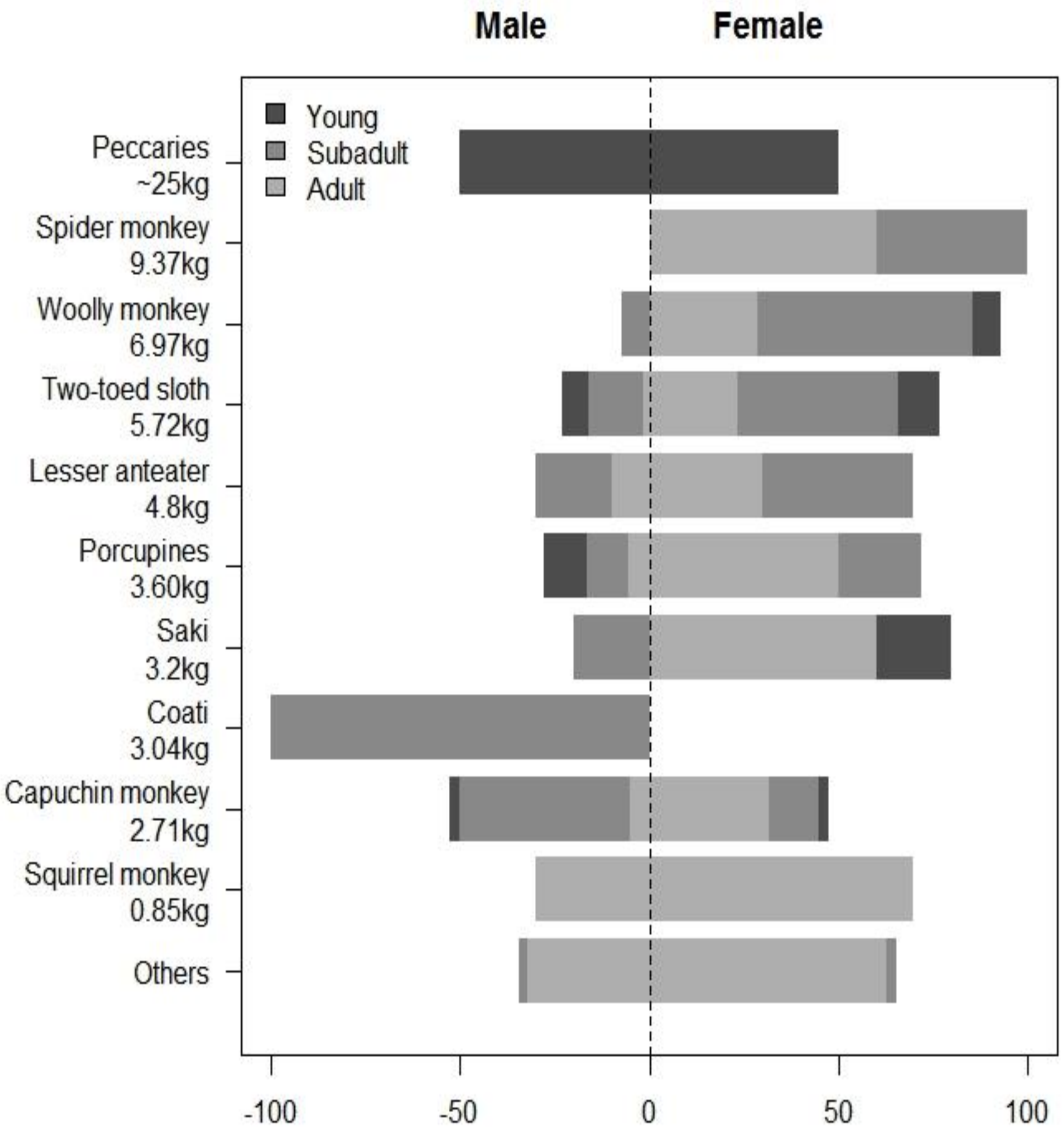

Fig. 7.3 Prey age classes consumed by male and female harpy eagles. The ten most important prey (>80% of total) are ordered by adult body mass, and divided between male and female harpy eagles, per prey age class. Male harpy eagles are less likely to tackle adult prey.

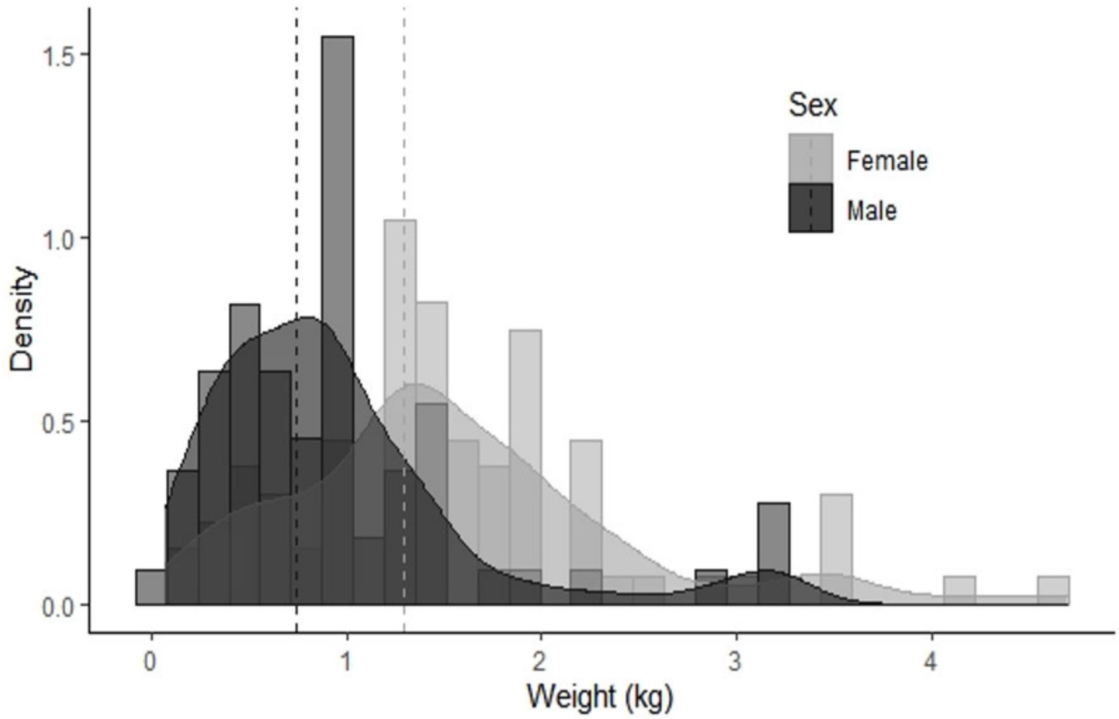

Fig. 7.4 Prey body mass brought by male (n = 75) and female (n = 92) harpy eagles. Male prey averaged 0.74kg, while female prey was 57.3% heavier, averaging 1.29kg (hatched lines). The largest individual prey brought to the nest was a ~4.7 kg lower body of a howler monkey brought by a male.

7.4 Results

Prey profiles

From a total of 279 prey deliveries recorded by camera-traps, 253 (89.7%) were identified from 16 different harpy eagle nests. We complemented camera-trap data with analysis of prey bones collected under and in nests. We found bones of 76 different prey individuals, of which 53 (69.7%) we could identify. We recorded 92 prey deliveries to nests by female eagles and 75 by male eagles (♀♀ 34.5 *vs*. ♂♂ 27.2%). An additional 74 (26.9%) of prey items seen in nests could not be linked to delivery by an adult eagle. These additional prey deliveries of unknown origin were either the eaglet hunting its prey or the camera-traps failing to record the adult's arrival. In the remaining 34 prey deliveries (12.3%), we could not identify the sex of the adult bird because its talons were not visible in the camera-trap images. All prey deliveries, together with bone identification analysis, yielded 306 prey samples that included 37 vertebrate species (Table 7.1). Canopy-dwelling mammals dominated the diet: two-toed sloths (*Choloepus didactylus*, 23.9%), brown capuchin monkeys (*Sapajus apella*, 18.3%) and grey woolly monkeys (*Lagothrix cana*, 7.5%).

Females and males preyed on similar percentages of arboreal prey (♀♀ 75.8 *vs*. ♂♂ 70.6%, null model, P = 0.756). The same applied for scansorial prey (♀♀ 17.5 *vs*. ♂♂ 16.0%, null model, P = 0.611) and terrestrial prey (♀♀ 4.4 *vs*. ♂♂ 6.6%, null model P = 0.283). Females preyed mostly on adult prey, while males preferred young and subadult prey (Fig. 7.3). This preference for different age classes led to a significantly-different prey mass between the sexes. Male prey averaged 0.74 ± 0.69 kg (geometric mean ± SD), while female prey were 57.3% heavier, averaging 1.29 ± 0.88 kg (null model, P <0.001, Fig. 7.4). The largest individual prey brought to the nest by a female was a ~4.7-kg, lower body section of a spider monkey, while for a male it was a ~3.2 kg lower body section of a howler monkey. One adult not identified to sex arrived at a nest carrying simultaneously the lower body of an opossum (*Didelphis* spp.) and the lower body of a juvenile spider monkey (totalling ~3.6kg). Levin's niche width analysis yielded similar values for the sexes: 7.20 for females and 7.42 for males (n = 84 ♀♀, 69 ♂♂). After bootstrapping using a null model, however, the niche width fell to 2.40 for females and 4.62 for males, and this was significant (P < 0.001). Problems caused by bad photographic angles or faulty functioning of camera-traps (rendering 29% of cameras inoperant) can be seen in Supplementary information Table S7.1.

Nest density and buffer definition

Using the maximum packed nest density method, we found the distance to the nearest harpy eagle neighbouring nest to average 2.99 km in nest cluster A (n = 6 nests) and 5.90 km in cluster B (n = 5). Cluster A had 195 km^2 with 124 km^2 of remaining forest cover, while cluster B had 633 km^2 with 254 km^2 of remaining forest cover. These data translated into a density of 1.97-4.84 nests/100 km^2 of forest habitat, or 0.79-3.07 nests/100 km^2 if we also include the degraded terrain (Fig. 7.5). We, therefore, used 3- and 6-km radii as buffers for landscape analyses, and the midpoint between both (4 km, or 50 km^2) as a rough approximation of breeding territory size, and therefore the hexagon cell size for the habitat loss analyses.

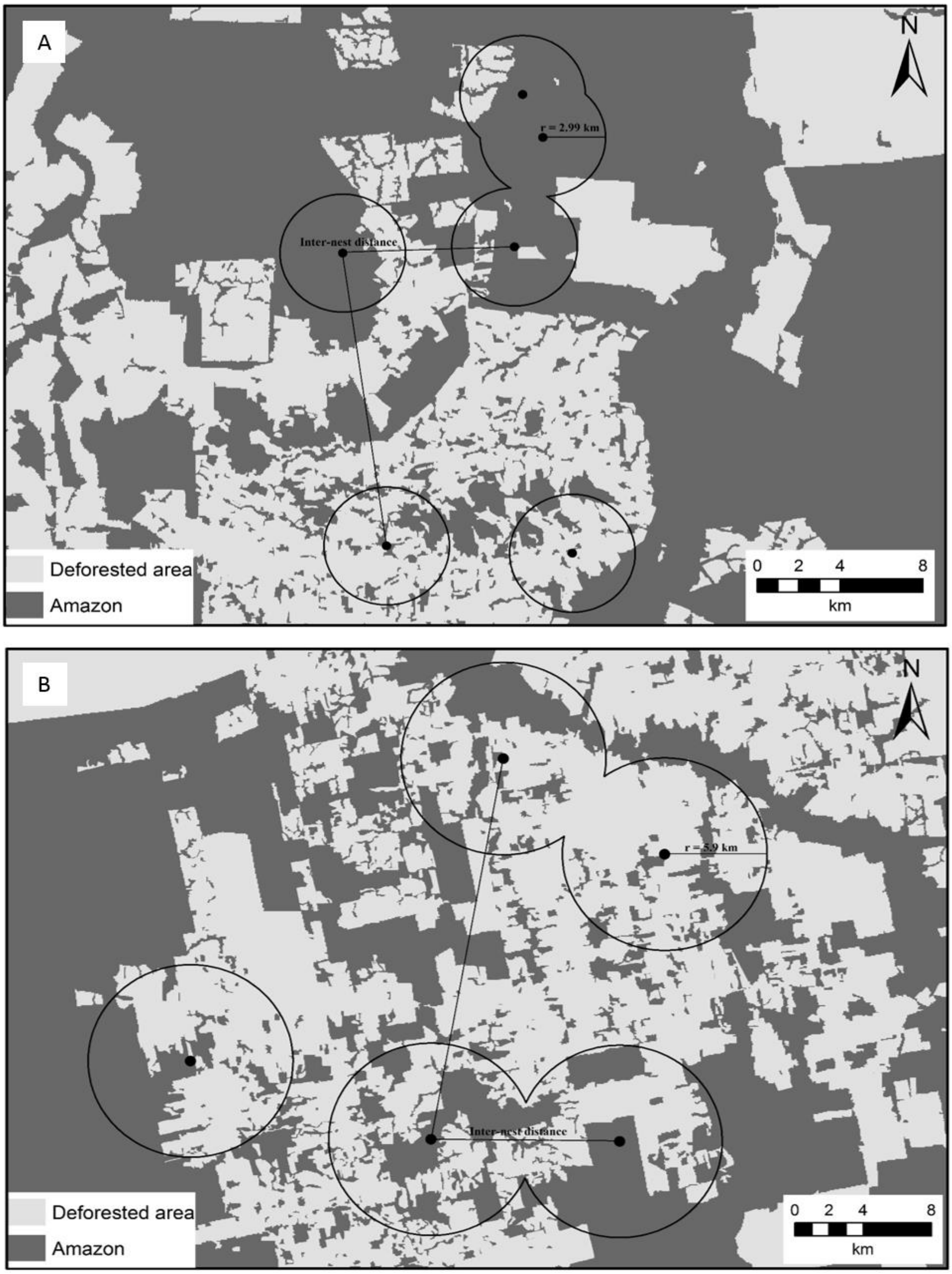

Fig. 7.5 Nest density calculated by maximum packed nest density method. Distances to the nearest neighbour were 2.99 km in cluster A and 5.90 km in cluster B, and we, therefore, used 3 and 6 km to calculate landscape buffers.

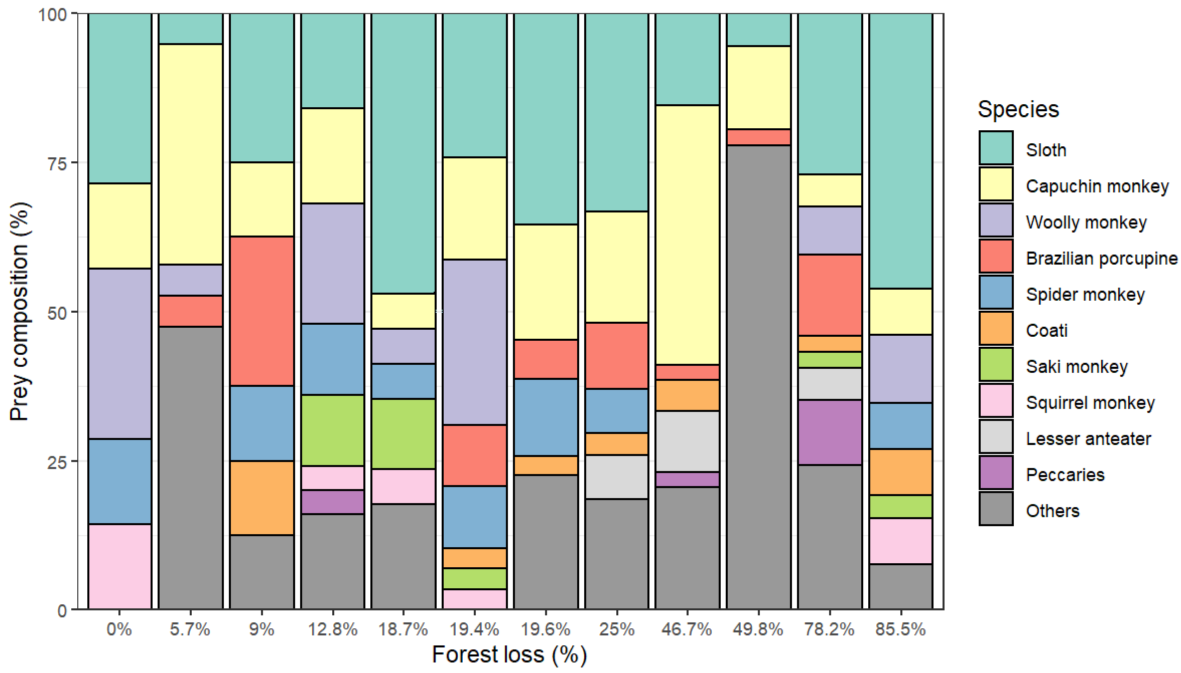

Fig. 7.6 Prey composition on harpy eagle nests. Main prey species are in order of abundance. Each column represents a nest, ordered by the lowest to the largest level of forest loss in a 3 km buffer around the nest site. Harpy eagles continue to depend on canopy prey even when in degraded landscapes and are unable to adapt to non-forest prey species.

Landscape degradation effects on prey composition

Harpy eagle nests had a mean Levin's trophic niche width of 5.50 and received an average of 9.5 prey species. Deforestation did not cause significant changes in prey composition of harpy eagles (Fig. 7.6), nor did distance to pasture (range: 0-6300 m, $\bar{X}$ = 1159 ± 1703 m) nor did forest cover at 3-km radius (range: 14-100%, $\bar{X}$ = 69 ± 28%; NMDS, 999 permutations, stress = 0.1335, P = 0.332 for forest loss and 0.079 for distance to pasture, n = 12 nests). Even when nesting in sites with severe forest loss, the eagles continued to capture sloths and primates as their main prey. The forest loss did not affect Levin's index for niche breadth nor prey species richness (GLM, residual deviance: 152.59 on 10 DF, P = 0.23), showing that even in highly-degraded landscapes, harpy eagles relied mostly on sloths and primates and barely switched at all to open landscape vertebrates (Fig. 7.7).

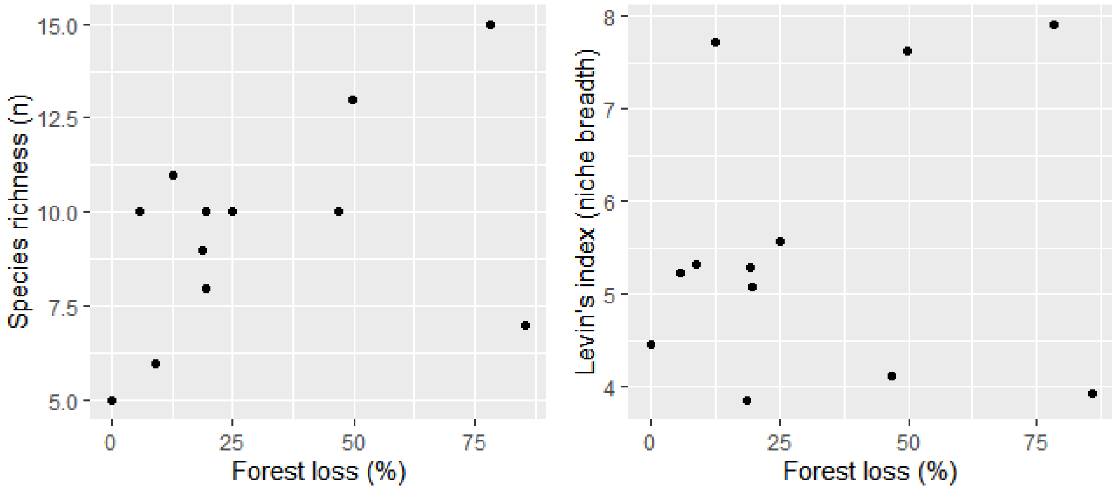

Fig. 7.7 Effects of forest loss (3 km buffer) on the feeding ecology of harpy eagles. Eagles nesting over degraded landscapes had prey diversity and niche breadth values that are similar to the ones in more continuous forests, with sloths and primates as main prey.

The effect of landscape degradation on prey delivery and prey biomass

For these analyses, we excluded the two nests that were located in riparian forests within deforested landscapes, which had high prey delivery and biomass rates, equivalent to fully-forested breeding territories, as they represented atypical outliers. The overall interval between deliveries averaged 4.20 ± 1.97 days (range: 1.0-7.67 days, referring to the mean for nestling and dependent juvenile phases, respectively). Prey biomass delivery rates averaged 0.37 ± 0.27 kg/day (range: 0.10-0.65 kg/day). Details on prey body parts brought to the nest are shown in Table 7.2.

Data from 16 nest-phases and 189 prey deliveries showed that habitat loss caused food stress on nesting harpy eagles (Fig. 7.8). Habitat loss caused an increase of the interval between prey deliveries for both 3-km (GLM, Residual deviance: 0.68924 on 14 DF, P = 0.01387) and 6-km buffers (GLM, Residual deviance: 33.293 on 14 DF, P = 0.030308). Habitat loss also resulted in decreased biomass delivery rates, which was significant for both 3-km (GLM, Residual deviance: 0.68157 on 14 DF, P = 0.012734) and 6-km buffers (GLM, Residual deviance: 0.68924 on 14 DF, P = 0.01387). There were no effects of nesting phase (nestling, fledged and dependent juvenile) on the interval between prey deliveries nor biomass delivered.

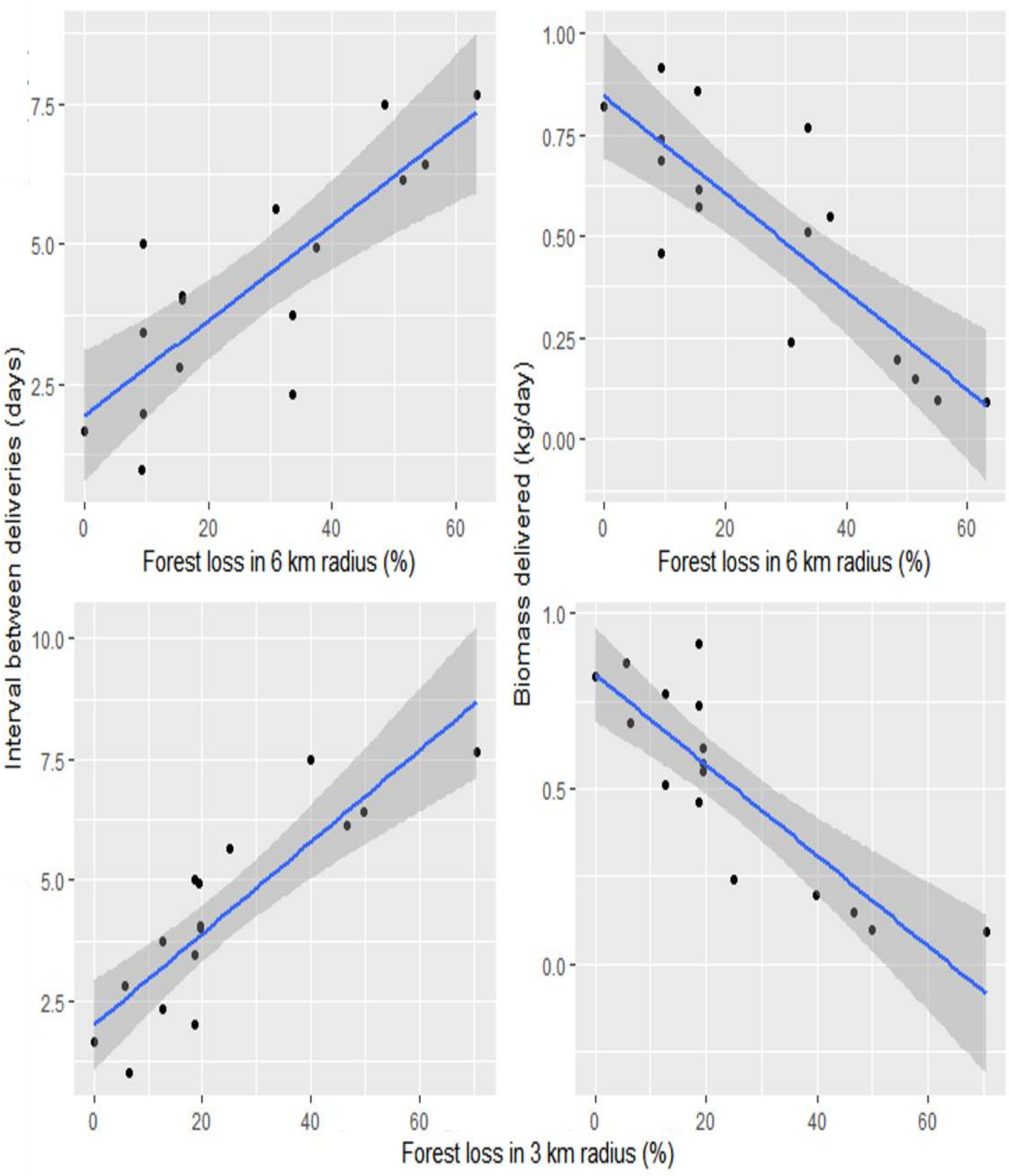

Fig. 7.8 Effects of habitat loss on harpy eagle feeding ecology. On the right, habitat loss lowered feeding frequency (right) as well as biomass delivered to the nest (left), which is significant for all cases.

Table 7.2 Body parts brought to nest for the ten most common prey species. This table represents the species of >80% of total prey species. Each column represent the body part brought to the nest. For most prey, only the lower body is brought to the nest, except for sloths, for which harpy eagles bring more frequently the upper body. All prey are represented in percentages of individuals (for which sample sizes are shown in column N).

Prey species	**N**	**Full body***	**Beheaded**	**Upper body**	**Member**	**Single member**	**Lower body**	**Tail**
Capuchin monkeys (*Sapajus apella*)	46	6.5	2.2	0.0	8.7	2.2	80.4	0.0
Two-toed sloth (*Choloepus hoffmanni*)	41	2.4	0.0	85.4	7.3	0.0	2.4	0.0
Woolly monkey (*Lagothrix cana*)	20	5.0	5.0	0.0	0.0	0.0	80.0	10.0
Porcupines (*Coendou* spp.)	17	0.0	0.0	0.0	5.9	0.0	58.8	35.3
Spider monkey (*Ateles chamek*)	9	0.0	0.0	0.0	0.0	0.0	77.8	22.2
Coati (*Nasua nasua*)	9	22.2	11.1	0.0	0.0	0.0	66.7	0.0
Saki (*Chiropotes albinasus*)	8	11.1	0.0	0.0	0.0	0.0	77.8	0.0
Squirrel monkey (*Saimiri ustus*)	7	28.6	0.0	0.0	0.0	0.0	71.4	0.0
Lesser anteater (*Tamandua tetradactyla*)	6	33.3	0.0	16.7	0.0	0.0	33.3	16.7
Peccaries (*Tayssuidae* spp.)	6	33.3	0.0	0.0	0.0	16.7	50.0	0.0

*except squirrel monkeys, all prey brought in full body condition were small young.

Food stress threshold

Considering that we found no nests in landscapes with more than 70% forest loss (n = 33, excluding the nests in riparian corridors as mentioned above), we determined the threshold to which harpy eagles can tolerate deforestation. Even so, harpy eagle pairs nesting within landscapes with 50-70% forest cover were unable to feed fledged eaglets even up to the dependent juvenile phase. We witnessed two fledged eaglets dying of starvation at our monitored nest in this 30-50% level of landscape degradation. We, therefore, consider 50% of forest habitat loss to be the lower limit for harpy eagles to successful raise nestlings. Habitat loss has therefore extirpated harpy eagles from 35% of their original range distribution in the forests of northern Mato Grosso (Fig. 7.9), with a concerning 28.7% lost during the last 35 years. We estimated that this represents the loss of ~3,256 harpy eagle pairs.

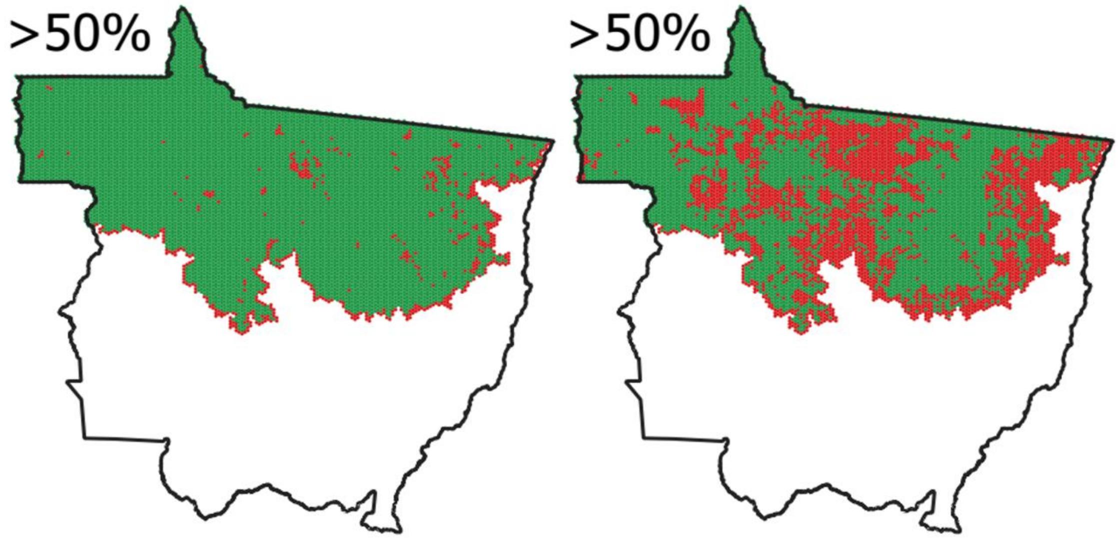

Fig. 7.9 Comparison of cells with more than 50% of forest loss (unsuitable) in 1985 and in 2019 on the northern region of Mato Grosso originally covered by Amazon Forest. White area are other ecoregions and sections of Amazon we did no sample. No harpy eagle nests have been found in landscapes with <30% of forest cover, and pairs on 50-30% forest cover margin were unable to feed nestlings/fledglings into the dependent juvenile phase (see results for exceptions). We, therefore, consider 50% to be harpy eagle limit regarding habitat and prey loss. Lost harpy eagle ranges—with more the 50% of forest loss—now represent 35% of Mato Grosso’s section of the Arc of Deforestation.

7.5 Discussion

We showed that forest loss is associated with severe reductions in food delivered by adult harpy eagles to their eaglets. On the other hand, harpy eagle prey composition changed little in habitats with varying deforestation. These data are evidence that harpy eagles depend upon canopy vertebrates as prey, and showed their limited ability to feed on ground-living vertebrates that inhabit pastures. These traits make them unable to continue to use any nest with more than 70% forest loss in the vicinity, and they are unable to feed young until they reach the dependent juvenile phase in the nests with 50-70% forest loss. These results provide the basis to predictively understand the persistence of harpy eagles within fragmented forest landscapes.

The feeding ecology of harpy eagle in northern Mato Grosso was somewhat atypical, with sloths comprising a quarter of total prey items, while they are normally two thirds or more[26]. Importantly, three-toed sloths (*Bradypus* spp.), which normally are important components of harpy diets, are not present at our study site, while elsewhere they represent the bulk of harpy prey items[26,52]. The lack of three-toed sloths in southern Amazonia[51] probably is related to relatively-drier conditions, which may make trees increase defence of foliage by augmenting the amount of secondary compounds in foliage. Differences between the age and size of prey taken by male and female harpy eagles were similar to previously-published literature, but the habits of prey (as terrestrial and scansorial), the difference were lower than what is typical for floater (not paired) individuals[68]. Another surprising fact emerging from our study is the lack of livestock in the harpy diet in our study area. Other apex predators in this fragmented landscape, such as jaguars[18], are known to prey on cattle. We conducted prior research in the region to focus on understanding the retaliatory killing of harpy eagles. While the reported livestock predation prevalence was relatively low in harpy eagle killings (<20% of 184 interviewees reported such losses[37]), we expected eagles to kill livestock, especially eagles nesting near houses. Perhaps livestock predation is a trait of floater individuals and therefore was not recorded in nests where mated pairs did almost all of the hunting.

Another important fact was that in the present study, harpy eagles took a large number of relatively large-sized Atelinae primates (namely spider and woolly monkeys). Previously, researchers considered such large monkeys to be unlikely prey as they live and travel in vigilant groups, and are aggressive. The rarity of past records of harpy eagles preying on these large primates has led primatologists to consider such harpy predation on these large monkeys as "isolated" predation events. We suspect that the reason that past research lists these large monkeys as very rare harpy prey is that our study site is unique in harpy eagle research in that it is the only site to date in which there is no hunting of Atelinae primates. As a result, our study area boasts with high population densities of these large monkeys[50,51]. In northern Mato Grosso State, illegal hunting of canopy wildlife is limited to game birds such as guans and curassows[69]. The reason for that is that settlers in that part of the Amazon are European-Brazilian mixed-bloods from southern Brazil[40], and those people have cultural objections to hunting and eating monkeys and sloths[70–72]. Harpy eagles in our study region regularly killed Atelinae primates. Grey woolly monkeys were highly represented in harpy diets in our study area, particularly considering that they only occur in roughly half of our study area, namely in the forests west of the Juruena River[73]. The high abundance of Atelinae primates, however, is a rare phenomenon in most parts of Amazonia[74–76], where fragmentation and poaching may have a synergistic effect on prey loss. In such areas, harpy eagles may not be able to persist at the percentages of forest loss that the eagles can tolerate in our area.

In our study, the predation by harpy eagles on non-forest, open-country prey species was relatively minor, as evidenced by the very few armadillos, opossums and other open-country prey in their diet. The Levin's index for trophic niche breadth of harpy eagles was, however, much greater than the figures given in the literature[52], which usually is only 0.309-1. We believe this higher trophic breadth index is caused by the use of camera-traps to monitor the nests. Specifically, our camera-traps added 14 species to the previous total of 102 known prey species taken by harpy eagles. Many prey species would have gone unidentified if we had relied exclusively on bones to identify prey species (Table 7.1). As Table 7.2 shows, the butchering carried out by the eagles to reduce drag during flight may leave few identifiable parts of some prey. Figure 7.2 showed how the eagles carry whole prey in specific orientations that reduce aerodynamic drag. Further evidence of the importance of camera-traps is that our prey composition, if it were based exclusively on bones recovered in and under nests, would show "the usual suspects" of harpy eagle prey species, with the notable exception of Atelinae primates. We therefore highly recommend the use of camera-traps in further feeding ecology studies of rainforest eagles. Given the problems we encountered with some of the camera-traps, however, precautions will need to be taken to reduce camera failure to the bare minimum (Supplementary information Table S7.1).

An additional detail of prey choice that is unclear is why harpy eagles in other significantly-fragmented forest areas prey heavily on armadillos (A. Blanco, C. Tuyama, pers. comm.). At one much more southerly harpy nest that we excluded from the current analysis, we observed the adult birds bringing to the nest almost exclusively armadillos. This nest lies 800 km south of the 14 nests included in the current analysis, laying at the very southernmost edge of Amazonia in a much drier location that entirely lacks sloths. Due to this atypical location, which features different habitat and availability of prey species, we excluded it from the analyses in this paper. In the nests described here in this paper, parent birds occasionally delivered dead armadillos to juveniles in nests. As the armadillos were delivered belly-down, the young birds did not turn the armadillos over to get to their fleshy underside, and the armadillos went uneaten. The two eagles, however, that fledged from that sloth-free outlier nest were extremely proficient at removing meat from armadillos brought to them by their parents. It is worth studying how these two young eagles both knew how do eat armadillos while the young from our other nests do not.

Harpy eagle prey delivery rates and delivered biomass decreased with habitat loss. On two occasions, both involving recently-fledged eagles, delivery rates were so low that the fledglings died of starvation. One of those nests was monitored by camera-traps, where prey delivery intervals were consistently greater than 15 days. The usual interval for recently-fledged eaglets is ~2.5 days. In the other case in which the fledgling survives, the desperate parents tried to fall back on a diet of forest birds. That pair of adult eagles was responsible for all the predation reported here on blue-and-gold macaws (*Ara ararauna*) and crested curassows (*Crax fasciolata*). In this case, the dependent, juvenile male eagle quickly learned to hunt black vultures (*Coragyps atratus*) and was responsible for nine of the ten records presented here of harpy predation on them. Hunting by recently-fledged harpy eaglets is not unheard of[77] and is especially common for fledged male harpy eagles[78,79]. We emphasise that a harpy eagle requires 0.8kg of prey/day[80], and this is an impossible goal to meet if relying on only a diet of forest birds. In all other cases, adults continued bringing sloths and primates to the nests, and the impact of this on the populations of these prey species in fragmented sites deserves further study, as harpy eagles exert top-down pressure on some prey species[27,38]. The decreasing rates of food delivery to offspring were somewhat consistent with those observed in places that have no deforestation (5.12 days between deliveries for fledged, dependent juveniles, Chapter 8). The relatively modest increase—7.67 days for dependent juveniles—suggests that harpy eagles may abandon territories where they are not able to hunt sufficient food to feed their fledglings.

By establishing the ecological limits of deforestation that harpy eagles can tolerate, we also are now able to state what percentage of the Amazonian section of Mato Grosso State probably has lost all of its harpy eagles. The current, extensive forest cover of northern Mato Grosso now stands at 64.9%, which to a naïve observer might sound impressive and would be the cause for some optimism regarding the survival of harpies. Much of the remaining, intact forest habitat, however, lies inside indigenous lands[81]. The vast majority of those Amazonian tribes hunt harpy eagles without any limits, and the tribes actively hunt these eagles to use the eagles' large wing and tail feathers in headdresses and for fletching arrows[53,82,83]. To make matters worse, these indigenous people often illegally sell headdresses to non-indigenous people, a practice that is prohibited even for tribal peoples[84]. Furthermore, indigenous people also frequently capture harpy eagle nestlings, which they keep as caged pets in indigenous communities[53] and sometimes sell illegally into the black market wildlife trade (EBPM, pers. obs.). All the indigenous lands in Mato Grosso State sum up to 15 million ha in Mato Grosso State. Proactive wildlife management[90,91] with and for tribal peoples must take place to prevent the extirpation on indigenous lands of harpy eagles and other species with long life-cycles and low breeding potential. [92].

We support the traditional rights of indigenous communities to use harpy eagle for cultural but not commercial purposes and are in agreement with their land rights. Indigenous populations coexisted with harpy eagles for millennia, and range reduction for the harpy only really started with the arrival of European colonists[10]. When indigenous communities that are connected to nationwide and even international market systems start to hunt harpy eagles to sell headdresses and live eagles, and when these tribes have given up many or most of their traditional ways of life (*e.g.* nomadism and use bows instead of fire guns), scientifically-sound bag-limits must be put in place and enforced. Considering that besides the levels of anthropogenic habitat loss caused by cattle ranching and soybean farming[93], harpy eagles also face hunting pressure in indigenous lands, which represent a large fraction of their remaining forest habitat, makes conservation prospects worrisome. The threat from indigenous people hunting harpy eagles changes little in the larger picture because nearly half of the Brazilian Amazon is within indigenous lands[81].

We observed that in two riparian forest nests, harpy eagles were feeding well despite forest loss above 70%. These promising observations will certainly show that some of our predictions are wrong, since some cells in our maps may be riparian sites well connected to larger fragments. Another possible limitation is that forest fragments patchiness may also influence harpy eagle feeding ecology. Riparian forests that successfully support harpy eagle reproduction must have links to larger fragments or continuous forests, a situation that is uncommon. About half of riparian forests corridors in the region have degraded sections[45,94,95] that hinder locomotion by canopy wildlife such as woolly monkeys and sloths. Furthermore, logging is widespread in those riparian forests[45] and removes the exact same trees that harpies need for nesting[28,45]. Their last nest tree option—the Brazil nut tree *Bertholetia excelsa* (that is forbidden to cut[96])—seldom occurs within riparian sites, growing most commonly in higher terrain[97].

Our results contribute to understanding how harpy eagle feeding ecology is impacted by anthropogenic land-use change, with prey availability frequently the main constraint for the conservation of this apex predator. Determining the threshold of deforestation that they can tolerate is of prime interest for conservation actions such as adding value to forest habitat through ecotourism and carrying out eagle reintroduction or translocation. These techniques can protect this species and their forest environments. Finally, it is likely that some harpy eagles nesting in the hyperfragmented landscapes of the Atlantic Forest and the (recently) degraded Arc of Deforestation are stranded in relatively small fragments. To persist, these stranded eagles may be dependent on conservation techniques that could include translocation of juveniles and food supplementation to eaglets.

7.6 Acknowledgements

This research would not be possible without the contribution of Roberto Stofel, Carlos Tuyama, Guilherme R.R. Brito, Guilherme S. T. Garbino and Alexander Blanco. CTD is grateful to the University of KwaZulu-Natal (ZA) and the National Research Foundation (ZA) for funding. We greatly appreciate the financial support of the following donors: SouthWild.com Conservation Travel System, Rainforest Biodiversity Group, Idea Wild, The Mamont Scholars Program of the Explorer's Club Exploration Fund, Cleveland Metroparks Zoo, and the Rufford Small Grants Foundation (18743-1, 23022-2 and 31091-B). Logistical support was given by the Peugeot-ONF Carbon Sink Reforestation Project, based at the São Nicolau Farm in Cotriguaçu, Mato Grosso, Brazil. This project is a Peugeot initiative to fulfill some of the Kyoto Protocol directions and is run by the ONF-Brasil enterprise. Finally, we thank ICMBio for authorising the project activities under the permit SISBIO 58533.

7.7 References

1. McQueen, A. *et al.* Evolutionary drivers of seasonal plumage colours: colour change by moult correlates with sexual selection, predation risk and seasonality across passerines. *Ecol. Lett.* **22**, 1838–1849 (2019).
2. Menezes, J. F., Kotler, B. P. & Dixon, A. K. Risk pump in *Gerbillus pyramidum*: quality of poor habitats increases with more conspecifics. *Ethol. Ecol. Evol.* **31**, 140–154 (2019).
3. Stephens, D., Brown, J. & Ydenberg, R. *Foraging: behavior and ecology*. (University of Chicago Press, 2007).
4. Schweiger, A., Fünfstück, H.-J. & Beierkuhnlein, C. Availability of optimal-sized prey affects global distribution patterns of the golden eagle *Aquila chrysaetos*. *J. Avian Biol.* **46**, 81–88 (2015).
5. Carbone, C. & Gittleman, J. L. A common rule for the scaling of carnivore density. *Science* **295**, 2273–2276 (2002).
6. Athreya, V., Odden, M. & Linnell, J. A cat among the dogs: leopard *Panthera pardus* diet in a human-dominated landscape in western Maharashtra, India. *Oryx* 1–7 (2014). doi:10.1017/s0030605314000106
7. Van der Meer, T., McPherson, S. & Downs, C. Temporal changes in prey composition and biomass delivery to African Crowned Eagle nestlings in urban areas of KwaZulu-Natal, South Africa. *Ostrich* **83**, 241–250 (2018).
8. Miranda, E. B. P., Ribeiro-Jr., R. P. & Strüssmann, C. The ecology of human-anaconda conflict: a study using internet videos. *Trop. Conserv. Sci.* **9**, 26–60 (2016).
9. Paviolo, A. *et al.* A biodiversity hotspot losing its top predator: The challenge of jaguar conservation in the Atlantic Forest of South America. *Sci. Rep.* **6**, 37147 (2016).
10. Miranda, E. B. P., Menezes, J. F. S., Farias, C. C., Munn, C. & Peres, C. A. Species distribution modeling reveals strongholds and potential reintroduction areas for the world's largest eagle. *PLoS One* **14**, e0216323 (2019).
11. Marshall, B. M. *et al.* Hits close to home: repeated persecution of King Cobras (*Ophiophagus hannah*) in Northeastern Thailand. *Trop. Conserv. Sci.* **11**, 1–14 (2018).
12. Carbone, C., Pettorelli, N. & Stephens, P. A. The bigger they come, the harder they fall:

body size and prey abundance influence predator-prey ratios. *Biol. Lett.* **7**, 312–315 (2011).
13. Garcia-Heras, M. S., Mougeot, F., Simmons, R. E. & Arroyo, B. Regional and temporal variation in diet and provisioning rates suggest weather limits prey availability for an endangered raptor. *Ibis (Lond. 1859).* **159**, 567–579 (2017).
14. Miranda, E. B., Jácomo, A. T. D. A., Tôrres, N. M., Alves, G. B. & Silveira, L. What are jaguars eating in a half-empty forest? Insights from diet in an overhunted Caatinga reserve. *J. Mammal.* **99**, 724–731 (2018).
15. Ellis, D. H. & Gombobaatar, S. Ecology of the Golden Eagle in Mongolia, Part 2: Prey. *J. Raptor Res.* **54**, 30–37 (2020).
16. Zuluaga, S. & Echeverry-Galvis, M. Á. Domestic fowl in the diet of the Black-and-chestnut Eagle (*Spizaetus isidori*) in the Eastern Andes of Colombia: a potential conflict with humans. *Ornitol. Neotrop.* **27**, 113–120 (2016).
17. McPherson, S. C., Brown, M. & Downs, C. T. Diet of the crowned eagle (*Stephanoaetus coronatus*) in an urban landscape: potential for human-wildlife conflict? *Urban Ecosyst.* 1–14 (2015). doi:10.1007/s11252-015-0500-6
18. Michalski, F., Boulhosa, R. L. P., Faria, A. & Peres, C. A. Human-wildlife conflicts in a fragmented Amazonian Forest landscape: Determinants of large felid depredation on livestock. *Anim. Conserv.* **9**, 179–188 (2006).
19. Lamichhane, B. R. *et al.* Rapid recovery of tigers *Panthera tigris* in Parsa Wildlife Reserve, Nepal. *Oryx* **52**, 16–24 (2018).
20. Tortato, F. R., Izzo, T. J., Hoogesteijn, R. & Peres, C. A. The numbers of the beast: Valuation of jaguar (*Panthera onca*) tourism and cattle depredation in the Brazilian Pantanal. *Glob. Ecol. Conserv.* **11**, 106–114 (2017).
21. Macdonald, C. *et al.* Conservation potential of apex predator tourism. *Biol. Conserv.* **215**, 132–141 (2017).
22. Karanth, K. U., Kumar, N. S., Nichols, J. D., Link, W. A. & Hines, J. E. Tigers and their prey: Predicting carnivore densities from prey abundance. *Proc. Nat. Acad. Sci. U. S. A.* **101**, 4854–4858 (2004).
23. Nelson, A. A. *et al.* Native prey distribution and migration mediates wolf (*Canis lupus*) predation on domestic livestock in the Greater Yellowstone Ecosystem 94(4), . *Can. J. Zool.* **94**, 291–299 (2016).
24. Terborgh, J. & Estes, J. *Trophic cascades: predators, prey, and the changing dynamics of nature*. (Island Press, 2013).
25. Miranda, E. B. P. Prey composition of harpy eagles (*Harpia harpyja*) in Raleighvallen, Suriname. *Trop. Conserv. Sci.* **11**, 1–8 (2018).
26. Miranda, E. B. P. Conservation implications of harpy eagle *Harpia harpyja* predation patterns. *Endanger. Species Res.* **29**, 69–79 (2015).
27. Touchton, J., Hsu, Y. & Palleroni, A. Foraging ecology of reintroduced captive-bred subadult harpy eagles (*Harpia harpyja*) on Barro Colorado Island, Panama. *Ornitol. Neotrop.* **13**, 365–379 (2002).
28. Miranda, E. B. P., Peres, C. A., Marini, M. Â. & Downs, C. T. Harpy Eagle (*Harpia harpyja*) nest tree selection: Logging in Amazonian Forests threatens Earth's largest eagle. *Biol. Conserv.* ******, ** (2020).
29. Muñiz-López, R. *et al.* Movements of Harpy Eagles Harpia harpyja during their first two years after hatching Movements of Harpy Eagles *Harpia harpyja* during their first two years after hatching. *Bird Study* **3657**, 509–514 (2016).
30. Muñiz-López, R. Harpy Eagle (*Harpia harpyja*) mortality in Ecuador. *Stud. Neotrop. Fauna Environ.* **30**, 1–5 (2017).
31. Urios, V., Muñiz-López, R. & Vidal-Mateo, J. Juvenile Dispersal of Harpy Eagles

(*Harpia harpyja*) in Ecuador. *J. Raptor Res.* **51**, 439–445 (2017).
32. Monsalvo, J. A. B., Heming, N. M. & Marini, M. Â. Breeding biology of Neotropical Accipitriformes: Current knowledge and research priorities. *Rev. Bras. Ornitol.* **26**, 151–186 (2018).
33. Hall, C. *Harpy Eagle Studbook Harpia harpyja North American Regional*. (2011).
34. Alvarez-Cordero, E. Biology and conservation of the harpy eagle in Venezuela and Panama. DSc Thesis. (University of Florida, Florida, USA, 1996).
35. Rettig, N. Breeding behavior of the harpy eagle (*Harpia harpyja*). *Auk* **95**, 629–643 (1978).
36. Giudice, R., Piana, R. & Williams, M. Tree architecture as a determinant factor in nest-tree selection by Harpy Eagles. in *Neotropical raptors* (eds. Bildstein, K. L., Barber, D. R. & Zimmerman, A.) 14–22 (Hawk Mountain Sanctuary, 2007).
37. Miranda, E. B. P. de, Peres, C. A. & Downs, C. T. Perceptions of livestock predation (or the lack of it) drive the persecution of Earth's largest eagle. *Anim. Conserv*. **Press**, (2020).
38. Terborgh, J. *et al.* Ecological meltdown in predator-free forest fragments. *Science* **294**, 1923–1926 (2001).
39. Fearnside, P. M. Deforestation in Brazilian Amazonia: History, rates, and consequences. *Conservation Biology* **19**, 680–688 (2005).
40. Schneider, M. & Peres, C. A. Environmental costs of government-sponsored agrarian settlements in Brazilian Amazonia. *PLoS One* **10**, e0134016 (2015).
41. Junior, C. S. & Lima, M. Soy Moratorium in Mato Grosso: deforestation undermines the agreement. Land use policy. **71**, 540–542 (2018).
42. Lima, M. *et al.* The paradoxical situation of the white-lipped peccary (*Tayassu pecari*) in the state of Mato Grosso, Brazil. *Perspect. Ecol. Conserv.* **17**, 36–39 (2019).
43. Eri, M. *et al.* Capitalizing on opportunities provided by pasture sudden death to enhance livestock sustainable management in Brazilian Amazonia. *Environ. Dev*. **4**, 100499 (2020).
44. Anonymous. *Novo Código Florestal, Lei 12.651 de 25 de maio de 2012, Dispõe sobre a proteção da vegetação nativa*. (Subchefia de assuntos jurídicos, 2012).
45. Zimbres, B., Machado, R. B. & Peres, C. A. Anthropogenic drivers of headwater and riparian forest loss and degradation in a highly fragmented southern Amazonian landscape. *Land use policy* **72**, 354–363 (2018).
46. Zimbres, B., Peres, C. A. & Machado, R. B. Terrestrial mammal responses to habitat structure and quality of remnant riparian forests in an Amazonian cattle-ranching landscape. *Biol. Conserv.* **206**, 283–292 (2017).
47. Koeppen, W. *Climatologia: con un estudio de los climas de la tierra.* (1948).
48. Radam-Brasil. *Projeto Radam-Brasil: levantamento de recursos naturais*. (1983).
49. Ayres, J. M. Observações sobre a ecologia e o comportamento dos cuxiús (*Chiropotes albinasus* e *Chiropotes satanas*, Cebidae: Primates). (1981).
50. Oliveira, A. T. M. *et al.* Primate and ungulate responses to teak agroforestry in a southern Amazonian landscape. *Mamm. Biol.* **96**, 45–52 (2019).
51. Silva, D. A. Comunidade de mamíferos de médio e grande porte em fragmentos florestais da amazônia meridional. (Unemat - Nova Xavantina, 2016).
52. Aguiar-Silva, F., Sanaiotti, T. & Luz, B. Food habits of the Harpy Eagle, a top predator from the Amazonian rainforest canopy. *J. Raptor Res.* **48**, 24–45 (2014).
53. Villas Boas, O. & Villas Boas, C. *A marcha para o oeste: a epopéia da expedição Roncador-Xingu*. (Globo, 1994).
54. Miranda, E. B. P. de *et al.* Harpy Eagle nest activity patterns: Potential ecotourism and conservation opportunities in the Amazon Forest. *Bird Conserv. Int.* **In press**, **-**

(2020).
55. Rosenfield, R. N., Grier, J. W. & Fyfe, R. W. Reducing Management and Research Disturbance. in *Raptor research and management techniques* (ed. Bird, D. M.) 351–364 (Hancock House Publishers, 2007).
56. Pagel, J. E. & Thorstrom, R. K. Accessing nests. in *Raptor research and management techniques* (ed. Bird, D. M.) 171–180 (Hancock House Publishers, 2007).
57. Ellis, D. H. & Schimitt, N. J. *Behavior of the golden eagle: an illustrated ethogram*. (Hancock House Publishers, 2017).
58. Brown, D. A test of randomness of nest spacing. *Wildfowl* **26**, 102–103 (1975).
59. Emmons, L. & Feer, F. *Neotropical rainforest mammals: a field guide*. (University of Chicago Press, 1997).
60. Sick, H. *Ornitologia brasileira, uma introdução*. (Universidade de Brasília, 1984).
61. Goffart, M. *Function and Form in the Sloth*. (Pergamon Press, 1971).
62. Dunning, J. Handbook of Avian Body Masses. *CRC, London* (1993).
63. Gotelli, N. & Aaron, M. *A primer of ecological statistics*. (Sinauer Associates, 2005).
64. Krebs, C. *Ecological methodology*. (Benjamin/Cummings, 1999).
65. Ashe, E., Noren, D. P. & Williams, R. Animal behaviour and marine protected areas: incorporating behavioural data into the selection of marine protected areas for an endangered killer whale population. *Anim. Conserv.* **13**, 196–203 (2010).
66. Miranda, E. B. P., Peres, C. A. & Downs, C. T. Changes in soil fertility mosaics in the Amazon Forest induced by an apex predator. *Press* (2020).
67. R Core. *R: A language and environment for statistical computing*. (R Fondation for Statistical Computing, 2020).
68. Miranda, E. B. P., Campbell-Thompson, E., Muela, A. & Vargas, F. H. Sex and breeding status affect prey composition of Harpy Eagles *Harpia harpyja*. *J. Ornithol.* (2017).
69. Michalski, F. & Peres, C. A. Gamebird responses to anthropogenic forest fragmentation and degradation in a southern Amazonian landscape. *PeerJ* **5**, e3442 (2017).
70. Barbosa, H. Estrutura de comunidades de mamíferos de médio e grande porte em fragmentos florestais da Amazônia Meridional. (Unemat - Cáceres, 2012).
71. Michalski, F. & Peres, C. A. Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biol. Conserv.* **124**, 383–396 (2005).
72. Trinca, C. T. & Ferrari, S. F. *Caça em assentamento rural na amazônia matogrossense. Diálogos em ambiente e sociedade no Brasil*. (2006).
73. Cavalcante, T. *et al.* Niche overlap between two sympatric frugivorous Neotropical primates: improving ecological niche models using closely-related taxa. *Biodivers. Conserv.* **29**, 2749–2763 (2020).
74. Endo, W. *et al.* Game vertebrate densities in hunted and nonhunted forest sites in Manu National Park, Peru. *Biotropica* **42**, 251–261 (2010).
75. Peres, C. A. Effects of hunting on western Amazonian primate communities. *Biol. Conserv.* **54**, 47–59 (1990).
76. Zimmerman, B., Peres, C. A., Malcolm, J. R. & Turner, T. Conservation and development alliances with the Kayapó of south-eastern Amazonia, a tropical forest indigenous people. *Environ. Conserv.* **28**, Pagination missing-please provide (2001).
77. Cavalcante, T., Tuyama, C. A. & Mourthe, I. Insights into the development of a juvenile harpy eagle's hunting skills. *Acta Amaz.* **49**, 114–117 (2019).
78. Campbell-Thompson, E., Vargas, F. H., Watson, R. T., Muela, A. & Cáceres, N. C. Effect of Sex and Age at Release on the Independence of Hacked Harpy Eagles. *J. Raptor Res.* **46**, 158–167 (2012).
79. Watson, R. T., McClure, C. J. W., Vargas, F. H. & Jenny, J. P. Trial Restoration of the

Harpy Eagle, a Large, Long-lived, Tropical Forest Raptor, in Panama and Belize. *J. Raptor Res.* **50**, 3–22 (2016).
80. Touchton, J. The Harpy Eagle. in *The eagle watchers: Observing and conserving raptors around the world* (eds. Tingay, R. & Katzner, T.) 264 (Cornell University Press, 2010).
81. Crisostomo, A. C., Alencar, A., Mesquita, I., Silva, I. & Dourado, M. *Terras Indígenas Na Amazônia Brasileira: reservas de carbono e barreiras ao desmatamento*. (2015).
82. Tufiño, P. *Cunsi Pindo: The Mistress of the Monkeys*. (Simbioe, 2007).
83. Reina, R. E. & Kensinger, K. M. *The Gift of Birds: Featherworking of Native South American Peoples*. (University Museum of Archaeology & Anthropology, 1991).
84. Anonymous. *Lei de Proteção à Fauna, Lei 5.197, de 03 de janeiro de 1967*. (1967).
85. de Oliveira, C., de Carvalho Pacagnella, R. & da Glória Chiarello, M. Projeto Huka Katu: a FORP-USP no Parque Indígena do Xingu. *ABENO* **1**, 135–139 (2001).
86. Poz, J. D. Homens, animais e inimigos: simetrias entre mito e rito nos Cinta Larga. *Rev. Antropol.* 177–206 (1994).
87. Sobral, C. A., Amendoeira, M. R. R., Teva, A., Patel, B. N. & Klein, C. H. Seroprevalence of infection with Toxoplasma gondii in indigenous Brazilian populations. *Am. J. Trop. Med. Hyg.* **72**, 37–41 (2005).
88. Dario, F. R. Conhecimento tradicional da avifauna pelos indígenas Kayabi, Amazônia meridional, Brasil. *Rev. Geotemas* **8**, 140–160 (2018).
89. Pires, P. W. D. L. Rikbaktsa: um estudo de parentesco e organização social. (Universidade de São Paulo, 2009).
90. Campos-Silva, J. V. & Peres, C. A. Community-based management induces rapid recovery of a high-value tropical freshwater fishery. *Sci. Rep.* **6**, 34745 (2016).
91. Antunes, A.P., Rebêlo, G.H., Pezzuti, J.C.B., de Mattos Vieira, M.A.R., Constantino, P. D. A. L. *et al.* Antunes, A. P., Rebêlo, G. Subsistence hunting rights in the Brazilian Amazon. *Land use policy* **84**, 1–11 (2019).
92. Aleixo, A. & Galetti, M. The conservation of the avifauna in a lowland Atlantic forest in south-east Brazil. *Bird Conserv. Int.* **7**, 235–261 (1997).
93. Griffiths, P., Jakimow, B. & Hostert, P. Reconstructing long term annual deforestation dynamics in Pará and Mato Grosso using the Landsat archive. *Remote Sens. Environ.* **216**, 497–513 (2018).
94. Lees, A. C. & Peres, C. A. Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. *Conserv. Biol.* **22**, 439–449 (2008).
95. Michalski, F., Metzger, J. P. & Peres, C. A. Rural property size drives patterns of upland and riparian forest retention in a tropical deforestation frontier. *Glob. Environ. Chang.* **20**, 705–712 (2010).
96. Nepstad, D. C., Brown, I. F., Luz, L., Alechandre, A. & Viana, V. Biotic impoverishment of Amazonian Forests by rubber tappers, loggers, and cattle ranchers. *Adv. Econ. Bot.* **9**, 1–14 (1992).
97. Mori, S. A. & Prance, G. T. Taxonomy, ecology, and economic botany of the Brazil nut (*Bertholletia excelsa* Humb. & Bonpl.: Lecythidaceae). *Adv. Econ. Bot.* **8**, 130–150 (1990).

7.8 Supplementary information

Supplementary information Table S7.1. General problems faced with camera trap use in nests. The 37 camera-traps installed at harpy eagle nests had several issues. Configurations reset in 8.1% of cameras, producing photographs every couple of seconds with the wrong dating and timing. Epiphytic foliage grew in front of 5.4% of camera-traps, obscuring prey view and causing the camera-traps to trigger without the presence of a harpy eagle. Poor positioning occurred in 16.2% of all camera-traps and created issues for prey identification. The nest section being monitored by a camera-trap fell naturally in 5.4% of nests. Nails hammered shallowly in the bark caused the camera-trap to dislodge losing the view of the nest, or even to fall, in 8.1% of camera-traps. Finally, camera-traps completely failed in 29.7% of all occasions, which was a high toll considering that none of the other issues are necessarily fatal to sampling. All camera-traps suffered minor damage from eaglets playing with them, but on no occasion, was it an issue for sampling prey. No adults were seen interacting with the camera-traps. First column shows nests, the second shows the camera-trap number (2-3 per nest), CD column has the camera-days, and photos represent the number of photographs per camera-trap.

Nest	Cam	CD	Photos	Configurations	Epiphytic leaves	Bad positioning	Nest section fell	Nails	Camera failed
1	I	75	318						
	II	75	76			x		x	
	I	79	190						
	II	1	4						x
2	I	52	3365	x			x		
	II	134	498						
3	I	107	267						
	II	76	1006						
4	I	92	6987		x				
	II	101	1106						
5	I	5	956			x			
	II	1	2						x
	III	10	1116			x			
	I	1	7						x
	II	5	45						x
6	I	4	44			x			x
	II	2	2			x			x

	I	166	778			x			
	II	-	-						x
7	I	104	864						
	II	104	1230					x	
8	I	119	793						
	II	-	-						x
9	I	27	438						
	II	98	1012				x		
10	I	53	209						
	II	-	-						x
	I	11	92						x
	II	39	354						
11	I	81	391						
	II	79	389						
12	I	109	1558						
	II	73	1753						
13	I	52	1187	x	x				
	II	-	-						x
14	I	31	331					x	
	II	26	10059	x					

CHAPTER 8

Long-term concentration of tropical forest nutrient hotspots are generated by a central-place apex predator

Everton B. P. de Miranda*[1], Carlos A. Peres[2], Luiz Gustavo Rodrigues Oliveira-Santos[3], Colleen T. Downs[1]

1 – Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, P/Bag X01, Pietermaritzburg, 3209, South Africa

2 – School of Environmental Sciences, University of East Anglia, Norwich NR47TJ, UK

3 - Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal de Mato Grosso do Sul, Av. Costa e Silva, 79070-900 Campo Grande, MS, Brazil

***Corresponding author:** mirandaebp@gmail.com, phone +55 65 98153550

ORCID: https://orcid.org/0000-0003-2198-4742

Other emails and ORCIDs:

carlos.a.peres@gmail.com; ORCID: http://orcid.org/0000-0002-1588-8765

downs@ukzn.ac.za; ORCID: http://orcid.org/0000-0001-8334-1510

Running header: Tropical forest fertilization by an apex predator

Formatted for *PNAS*

8.1 Abstract

Apex predators typically affect the distribution of key nutrients for soil and vegetation through the heterogeneous deposition of prey carcasses and excreta. These effects can be in the form of nutrient concentration in a hotspot or nutrient spread against a natural gradient. Examples of nutrient transport have been restricted to mammalian apex predators in temperate ecosystems. The exact role of central place foragers such as tropical raptors in nutrient deposition and cycling is not yet known. We investigated whether harpy eagles (*Harpia harpyja*) in Amazonian Forests — a typically low soil fertility ecosystem where phosphorus is a limiting nutrient — affect soil nutrient profiles and phytochemistry around their nest-trees through cumulative deposition of prey carcasses and excreta. Nest-trees occurred in densities of 1.5-5.0/100 km^2, and each nest received ~102.3 kg of undressed carcasses each year. Effects of nests were surprisingly negative over local soil nutrient profiles, with soil underneath nest-trees showing reductions of 50% for phosphorus, 32% for calcium, 21% for magnesium, and 50% for aluminium compared with controls. These effects were presumably negative because the canopy surrounding nest-trees intercepts nutrients through foliar uptake, in the form of excreta, allowing increased removal of nutrients from soil because those limiting nutrients are abundantly available. Leaves from the canopy around nests showed significant 99.0%, 154.0% and 50.8% increases in nitrogen, phosphorus and potassium, respectively. Effects on understorey vegetation underneath nest-trees were positive for potassium only, with increases of 16%. This form of carrion deposition is by no means an exception since several large central-place raptors have similar habits. Since harpy eagles have experienced a 41% decline in their distribution range, and many raptor species are becoming locally extirpated, this is a general example of disruption in biogeochemical cycles and nutrient heterogeneity caused by apex predator population declines. This further poses the question of how far the downstream effects

triggered by a central-place predator can spread over animal and plant communities in tropical forest ecosystems.

Keywords: Amazon phosphorus; *Bertholletia excelsa*; biogeochemical cycles; carrion ecology; *Harpia harpyja*; nutrient cycling; raptor; vegetation quality.

8.2 Introduction

In his seminal work Animal Ecology (1927), Charles Elton states: "It is usual to speak of an animal as living in a certain physical and chemical environment, but it should always be remembered that strictly speaking we cannot say exactly where the animal ends and the environment begins". Elton meant that animals could only be interpreted if their ecological interactions are considered. This was followed by a profusion of ecological research built around this idea in the 20th century (2, 3). Elton then continued: "unless it is dead, in which case it has ceased to be a proper animal at all". In the 21st century, however, ecologists have explored in detail the notion that even after death, animals continue to influence their physical and chemical environments, sometimes at unexpected spatial scales (4, 5). Nothing exerts a stronger connection between life and death, the two conditions discussed by Elton, than an apex predator (6). In particular, the rapacious behaviour of apex predators renders them inextricably intertwined with their chemical and physical environments.

Animals can influence biogeochemical cycles via two main processes: concentration into hotspots (7) and diffusion against natural gradients (8). Since large-bodied carnivores are rare (9, 10), concentration into hotspots is the main pathway through which many terrestrial apex predators influence biogeochemical cycles. Polis, Anderson, and Holt (1997) provided the first definition of these nutrient subsidies affecting biogeochemical cycles as a donor-controlled resource from one habitat to a recipient (such as a plant) in a habitat which increases productivity (as population or body growth) of the recipient, with potential to alter consumer–

resource relationship in the recipient ecosystem. For apex predators, those resources are usually prey items (carcasses) or prey-derived detritus (scats or excreta) that are locally concentrated because of landscape traits (7, 12).

Amazonian forest soils are particularly sensitive to changes in the distribution of key nutrients because they are usually nutrient-poor (13), with most nutrients concentrated in the aboveground biomass. Even modest changes in soil nutrient profiles can have profound effects on biodiversity. Examples of key nutrient concentrations in the Amazon Basin include mineral licks used by geophagous vertebrates in search of sodium (14, 15). Good apex predator candidates for the role of nutrient concentrators in the megadiverse Amazonian ecosystem, however, are hard to predict. Multiple species of apex predators may coexist including black caiman (*Melanosuchus niger*), green anaconda (*Eunectes murinus*), puma (*Puma concolor*), jaguar (*Panthera onca*) and harpy eagle (*Harpia harpyja*), all of which play critical apex predator roles (16). Therefore, single-species effects over any phenomena should be rare or non-existent as predicted by ecological theory applied to tropical ecosystems (17).

Fig. 8.1 Harpy eagle female protecting a chick at her nest in an emergent kapok tree (*Ceiba pentandra*, Bombacaceae; Photo: David Bates).

Harpy eagles (Fig. 8.1) are particularly interesting in their potential role of nutrient concentrators. Being long-lived—at least 54 years in captivity (18)—they typically nest in the same giant emergent tree for decades (19). The harpy eagle breeding cycle is the longest of all birds, during which they bring prey to their eaglets for 30-36 months (20–22). They feed extensively on medium-sized canopy vertebrates (23). Prey skeletal material on the ground underneath their nests is often abundant, and consequently, the dietary ecology of harpy eagles is the best-known of any Neotropical raptor (24). Bird excreta is often very rich in limiting nutrients, and harpy eagle excreta often taint the surrounding canopy foliage and branches of the nest-tree (12, 25). These traits render them an ideal model to test the nutrient concentration hypothesis in Amazonian Forests. Most notably, harpy eagles are relatively small compared with other lesser phylopatric apex predators that redistribute nutrients across the landscape in a more diffuse manner. Although harpies are one of Earth's largest eagles (26), averaging 5.9-7.3 kg for males and females, they are surpassed by other candidates for such roles—such as wolves and bears— by one or two orders of magnitude (27). Contrary to those predators, however, harpy eagles do not rely on landscape traits to increase prey kill rate, and are obligatory central-place foragers once they reach breeding age. This raises the question: can harpy eagles influence soil chemistry and therefore nutrient cycling in the ecosystem?

Our objectives were to test the hypothesis that harpy eagles serve as accumulation agents of macro- and micro-nutrients, by concentrating decaying remains of prey items at nest sites over decades, thereby biomagnifying soil and foliage nutrients in the undergrowth, nest-tree and canopy vegetation (Fig. 8.2). We predicted that nutrient profiles of both soils and foliage would be positively affected by harpy eagles at long-term nest sites. In providing these ecosystem-level insights, we attempt to show how local extinctions of this apex predator may result in disruptions in biogeochemical cycles that modulate soil and vegetation nutrient heterogeneity across the Amazon Basin.

8.3 Methods

Study area

Our study was conducted in the southern portion of Amazonia's Arc of Deforestation, in the northern state of Mato Grosso, Brazil (Fig. 8.3). Koeppen (1948) classifies the regional climate as "tropical wet climate" or Amazonian (tropical monsoon climate). Rainfall averages 2,350 mm/yr, and the ambient temperature averages 24.5°C, combined with a high relative air humidity of 80–85% (29).

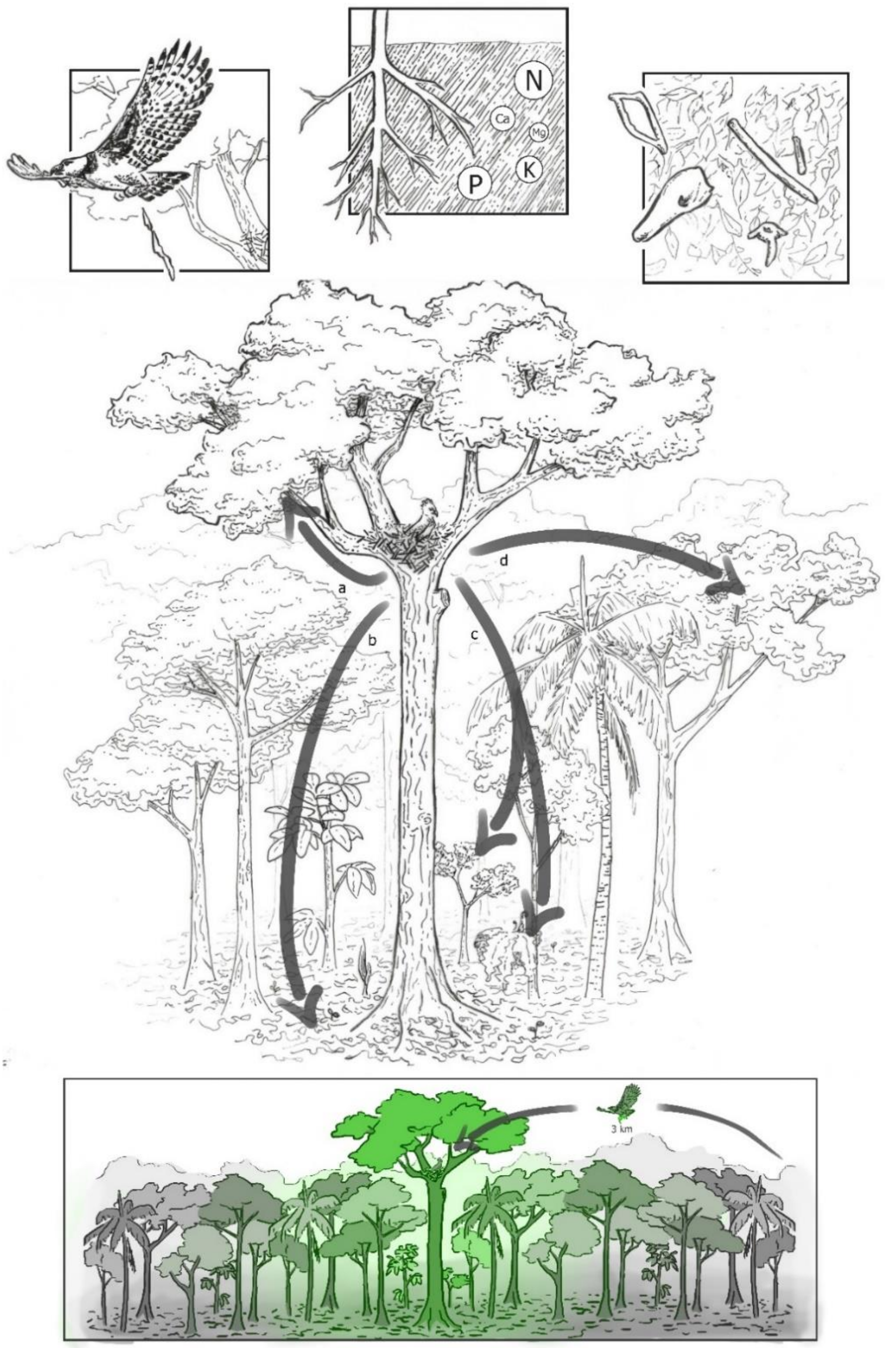

Fig. 8.2 Schematic representation of the nutrient concentration role of nesting harpy eagles through central-place prey carcass and excreta deposition on different vegetation strata, including the canopy and understorey foliage and soils (arrows). The lower panel represents the landscape-scale dynamic of nutrient concentration from commuting distances of up to 3 km from the nest. The magnitude of nutrient concentration is indicated by increasingly brighter green colours (Illustration: Paula Viana).

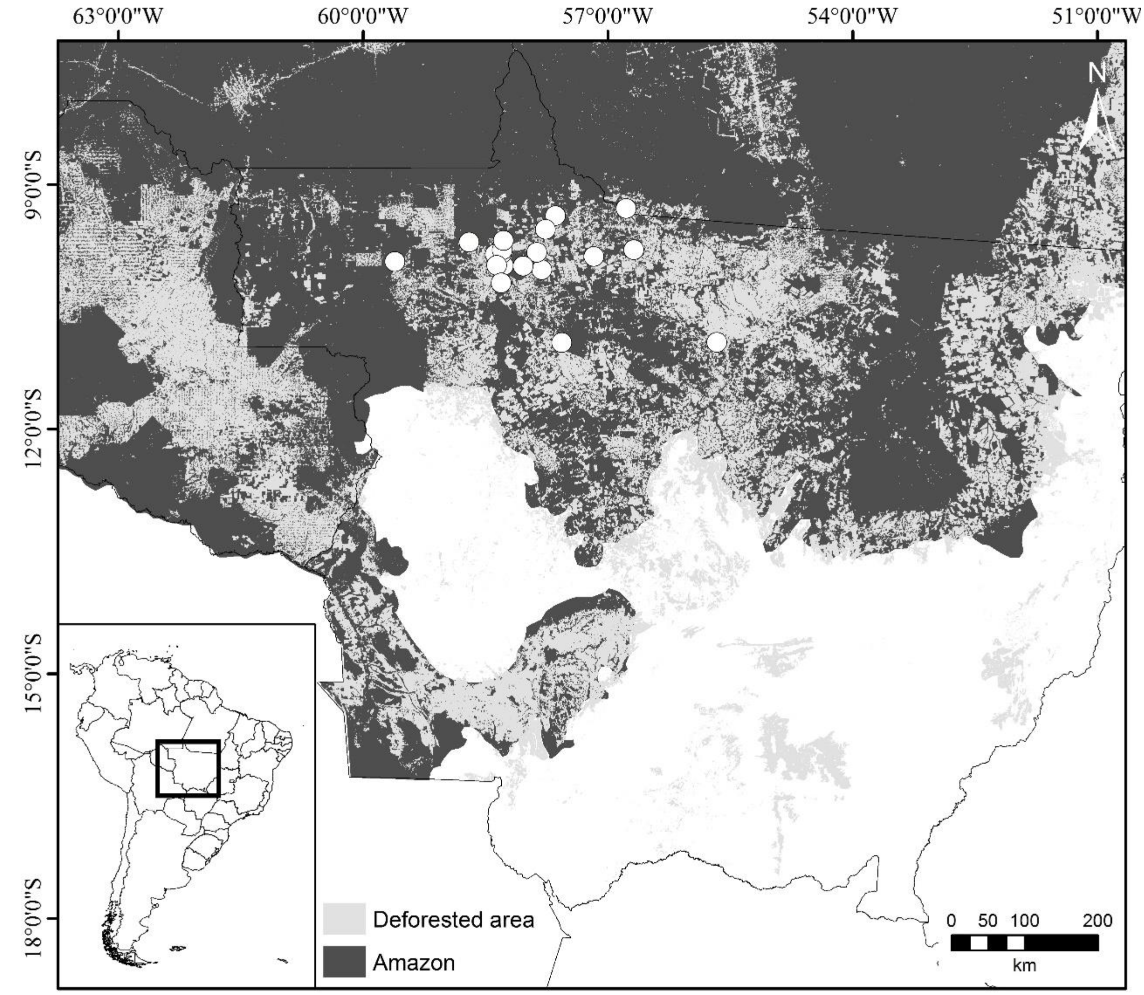

Fig. 8.3 Map showing the geographic location of all 20 harpy eagle nests (white circles) sampled in terms of soil and plant chemistry within our southern Amazonian study region in northern Mato Grosso. Prey composition and delivery rates were also monitored at all occupied nests for up to 24 months. Background map shows forest cover (dark grey) and deforestation areas (light grey).

As in most of the Amazon Basin, soils in our study region are highly acidic, which becomes more intensive in unflooded upland areas of *terra firma* forests (13). Levels of phosphorus, potassium, calcium, and magnesium are generally low while aluminium and H + Al are generally high to the point of toxicity. Phosphorus limitation is particularly severe, like in most of the lowland Amazon (8). Currently, the hyper-fragmented region of the 'Arc of

Deforestation' is mainly occupied by cattle ranches and smaller areas of cropland allocated to grain production (30). The remaining forest cover is typically comprised of forest fragments connected by riparian forests strips as required by Brazilian forest legislation (31).

Biomass input and timing

We installed 2 or 3 camera-traps at each nest site to sample harpy eagle food delivery rates, thereby enabling estimates of nutrient input into the soil underneath the nests from remains of prey carcasses (see Miranda et al., 2020 for details on camera-trapping methodology). To do so, we used nests without signs of food stress resulting from habitat fragmentation (i.e. no nests located at sites with more than 20% of deforestation within a 3-km radius, unless they were within forest corridors). Since prey delivery rates decreased with eaglet development, we defined four categories of prey delivery rates: 0-6 months (unfledged), 7-12 months (recently fledged eaglets), 13-24 months (late-fledged eaglets) and 25-36 months (individuals at the onset of dispersal). We inferred eaglet age from known hatchling dates, or feather colours and nest degradation status when hatchling date was unknown (19, 33). We defined unoccupied nests as those in disuse because the heterosexual pair was occupied at an alternative nest and the ones with eaglets above 25-36 months.

We estimated prey biomass delivered per nest based on the average body size described for each species (e.g., 26, 34). Subadult prey were attributed two-thirds of the adult body mass. For infant or juvenile prey (such as ungulates that were killed almost exclusively as newborns; 24), we attributed one-fifth of the adult body mass. Sloths received a further reduction of one-third, because of the large amount of foliage representing ~30% of the body mass in living sloths (35) that is readily discarded by harpy eagles soon after kills. As prey items are usually dismembered when delivered to nests, we applied approximate reductions in body mass as follows: 10% (head or viscera), 20% (per member missing or single-member delivered), 50%

(lower or upper body missing), and 90% (tail of Atelinae primates, porcupines) of the total prey body mass (36).

We also calculated harpy eagle nest density to infer nutrient input rates at the landscape scale. We found harpy eagle nests by occupied distributing brochures advertising a reward of USD100 (BRL500) to anyone who could locate a harpy eagle nest, especially among Brazil nut (*Bertholletia excelsa*) collectors. We found a total of 35 nests over four years. After excluding alternative nests (around 16.6% of harpy eagle pairs have alternative nests; 37), we calculated occupied nest density using two methods: maximum packed nest density (MPND), and the polygon method. We selected these methods to maximise comparability with previous studies (37). The MPND (38) is calculated as:

$$A = \pi r^2 * 1.158$$

where A is defined as half the distance to the nearest neighbouring nest in a cluster of nests. This distance is then considered as the radius for a circular breeding territory, centred at the nest. The 1.158 is a constant designed to fill the interstitial space between breeding territory circumferences. The polygon method uses half the average distance to the nearest neighbouring nest to establish a polygon around all nests within a cluster, from which we estimated the total cluster area. We calculated the two density estimates for our study area based on two known clusters of nests (with five and six nests each) located at sites with different levels of fragmentation. This project has concentrated the most intensive sampling effort at those clusters over the last four years, thereby deriving a high nest detection rate. We then divided the values resulting from both estimates by 100km² of available forest habitat to derive a nest density estimate.

Soil sampling

We collected five standard soil samples underneath the harpy eagle nest-tree at 5-15 cm depth using a mechanical auger. We sampled soil cores randomly at 1-10 m distance from the nest tree, where harpy eagle excreta and prey carcasses or bones typically fall. We paired each nest-tree to three comparable control sites, although local environmental idiosyncrasies made only one or two trees to be available in some locations. Control sites (1-3 conspecific tress according to local availability) for each nest-tree were centred at conspecific trees that lacked harpy eagle nests but exhibited very similar emergent-sized stature and girth. We performed the same soil collection procedure at control sites. This phylogenetic control was done to ensure that any nutrient effects were related to harpy eagle nesting activity, rather than tree species identity. We measured tree circumference at breast height and added this to the models. This warranted that the effects were not from the mega-trees since they can outlive a harpy eagle by timespans of one or two orders of magnitude (39), and alter soil composition through the continuous deposition of leaves, bark and branches. In selecting control sites, we also excluded any emergent trees frequently used as perches by adults and fledged eaglets.

We quantified soil aluminium, calcium and magnesium using the 1 M KCl extraction methods (40). Concentrations of these nutrients were determined by atomic absorption spectrometry. Phosphorus was extracted using the Mehlich 1 solution (41), and phosphorus concentrations were determined by spectrophotometry at 725 nm (40).

Vegetation sampling

At each nest-tree and non-nest control tree site, we collected undergrowth vegetation samples randomly at 1 to 10 m from the focal tree bole. We selected foliage from mature branches of three healthy stems of up to 1 m in height and active growth that were free from direct signs of harpy eagle excreta. We did not select foliage from any particular plant species but sampled stems according to their local abundance. Samples were stored in paper envelopes and dehydrated naturally. We also collected foliage samples from ~25m high three branches of canopy-height trees at 5-15 m from the nest, where harpy eagle excreta typically falls, as well as foliage from three branches from nest-trees, using a rope chainsaw (or hand-collection during climbing for camera installation in a few cases).

We rinsed vegetation samples in distilled water to remove any detrital material and dehydrated them subsequently over 72 h in a dry oven. We then ground these samples to the point of homogenisation. Finally, we analysed the nitrogen, phosphorus and potassium content of each sample using methods described by Embrapa (2009). Nitrogen was extracted using sulphuric acid (total Kjeldahl N). Nitricperchloric extract was used for the other elements: phosphorus (colorimetry), potassium and sodium (flame photometry), which were subsequently determined by spectrophotometry at 725 nm (40).

Statistical analyses

We used General Linear Mixed Models to test the effect of nest presence and nest activity, as well as their interaction, on nutrient profiles in the soil and across the vertical stratification of foliage. We ran a model for each nutrient in each stratum (five nutrients for soil, and three nutrients for each forest stratum: foliage in the undergrowth, canopy trees around the nest-tree, and the nest-tree). Because we strictly adopted a case-control design—*i.e*. nest-tree samples were paired to nearby non-nest tree samples—we included the identity of each case-control pair as a random intercept. In our case, including this random intercept aimed to mimic a repeated measure analysis. We also included the circumference at breast height of each tree as a covariate to account for uncontrolled trait differences between the nest-tree and non-nest tree, even though all paired trees were emergents belonging to the same tree species. Models were run using the NLME package (42) available in R (43), assuming a Gaussian residual distribution. Each model residuals were visually checked for normality and homoscedasticity.

8.4 Results

We collected soil and vegetation samples from 20 harpy eagle nests; 10 occupied, 10 unoccupied, plus one nest that we sampled while both occupied and unoccupied. Those 21 samples were paired with 47 conspecific control trees at which we collected comparable soil and vegetation samples. Nest-tree species included 16 Brazil nut trees (*Bertholletia excelsa*), the largest emergent tree in the study area, one *Ficus* spp., one *Astronium lecointei*, one *Cariniana* spp. and one *Apuleia leiocarpa*. Although we selected the largest available emergent individuals for non-nest trees, tree diameter was larger in nest trees (mean ± SD, 148.3 ± 25.5 cm) than in control trees (1.34 ± 0.25 cm; $\beta = 0.62$, $t = 5.94$, $p < 0.01$).

Biomass input

Using camera-traps to monitor ten harpy eagle nests (or 20 adult eagles), we recorded 212 prey items amounting to an estimated 411 kg of prey delivered per nest per nesting cycle (Table 8.1). Although adults continue to deliver prey to their nests after 24 months, eaglets usually consumed these elsewhere, in addition to hunting alone. We, therefore, labelled nesting cycles older than 24 months as “nutrient-inactive” and excluded these data from our carcass biomass input estimates. This resulted in a total of 307 kg delivered per nesting cycle (36 months), or approximately 102.3 kg/nest per year.

Using the maximum packed nest density, we estimated 1.97-4.84 nests/100km^2 in our study area (Table 8.2, Fig. 8.4). The polygon method produced densities of 1.55-3.30 nests/100km^2. Consequently, as a central-place hunter, harpy eagles concentrated 102.3 kg/year of prey captured over 20-64 km² into a single carcass hotspot, over an approximate density of 1.5-5.0 carcass hotspots per 100 km².

Table 8.1 Prey delivery rates of harpy eagles per nesting phase. The four phases each represent a different stage on which eaglets (and adult females, in case of early-unfledged chicks) receive prey on the nest. Since eagles >24 months frequently eat prey out of the nest, and hunt independently, those where removed from input calculations. Prey delivery rates (day/prey) and biomass delivery rates (kg/day) are shown in mean ± SD. The range represents the number of days between prey deliveries, with 0 representing two deliveries on a single day (i.e. less than a day of interval between deliveries).

Nesting phase (months)	Day/prey	Range	Prey mass (kg)	kg/day	Prey deliveries	Adult eagles
Unfledged (0-6)	1.8 ± 0.92	0-3	1.11 ± 1.06	0.62	11	6
Early fledged (7-12)	2.5 ± 1.71	0-8	1.33 ± 1.18	0.53	87	6
Late fledged (13-24)	4.17 ± 3.02	0-15	1.16 ± 0.86	0.28	36	4
Dispersing (25-36)	5.12 ± 4.90	0-21	1.49 ± 0.89	0.29	78	10
Whole cycle				411.52kg		
Last year excluded				306.95kg		

Table 8.2 Nest density calculate by maximum packed nest density (MPND) and polygon method, for two nest clusters in the study site.

Site	Nests	Total area (km²)	Forest area (km²)	Density (nests/100km²)
MPND				
A	5	632.85	253.66	1.97
B	6	195.12	123.9	4.84
Polygon				
A	5	742.3	322.63	1.55
B	6	271.62	181.63	3.30

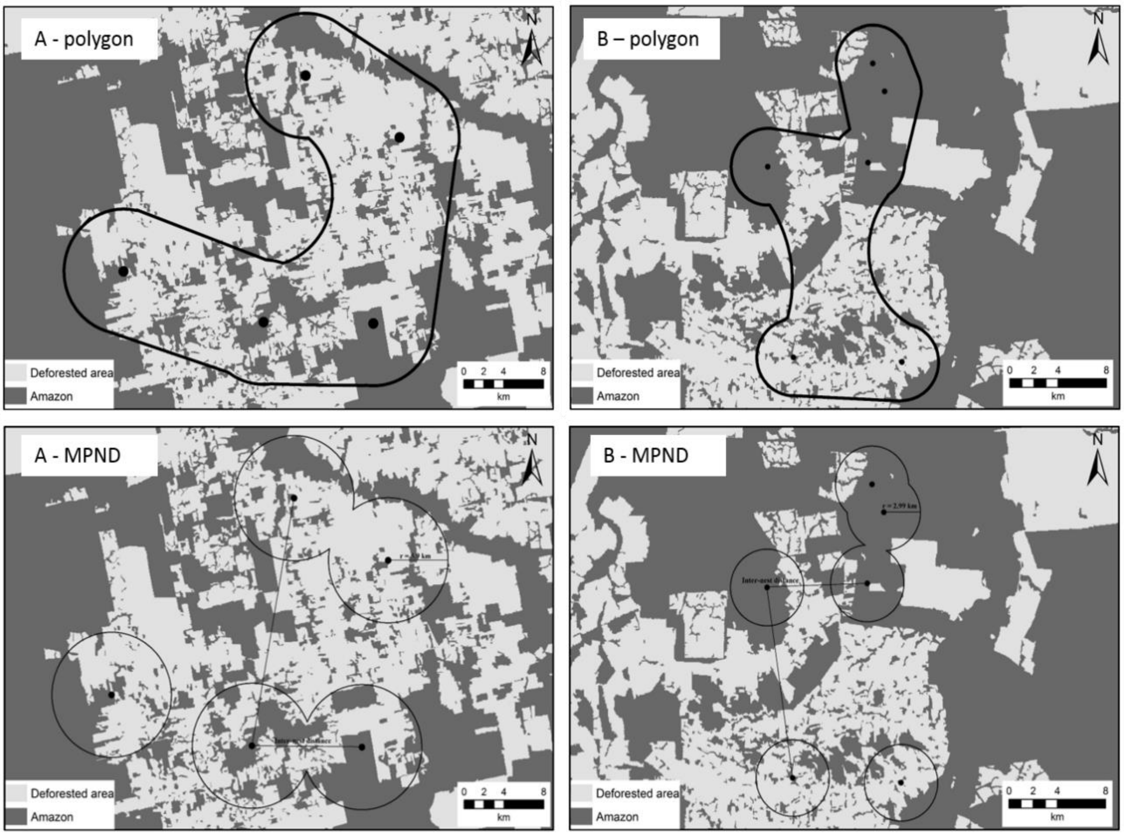

Fig. 8.4 Nest sites used to calculate nest density using both the polygon method and the maximum packed nest density method (MNPD). Nest densities were estimated at 1.55-3.30 nests/100 km² of forest in panel A, and 1.97-4.84 nests/100 km² of forest in panel B.

Soil nutrients

Contrary to our expectations (Supplementary information Table S8.1: soil stratum; Fig. 8.4: soil panel), soils underneath nest trees had a lower nutrient profile compared with controls for phosphorus (50% reduction; $\beta = -0.11$, $t = -2.29$, $p < 0.03$), calcium (32% reduction; $\beta = -0.42$, $t = -3.07$, $p < 0.01$), magnesium (21% reduction; $\beta = -0.11$, $t = -2.71$, $p < 0.01$), and aluminium (50% reduction; $\beta = -0.08$, $t = -2.29$, $p < 0.03$), but not for potassium ($\beta = -2.65$, $t = -0.67$, $p = 0.50$). We did not detect any main effect of nest activity for any nutrient type ($p > 0.05$; *i.e*. effects of nest were detected irrespective of activity), nor any interaction between nest presence and nest activity ($p > 0.05$). Positive effects of tree size (i.e. diameter at breast height) was important as a covariate for phosphorus ($\beta = 0.13$, $t = 1.83$, $p < 0.01$), potassium ($\beta = 3.68$, $t = 2.27$, $p < 0.03$) and aluminium ($\beta = 0.06$, $t = 2.62$, $p < 0.01$), but not for the other nutrients ($p > 0.05$).

Understory vegetation

We detected the effect of eagle nest presence only for potassium concentration (16% increases; $\beta = 2.15$, $t = 2.22$, $p < 0.03$) in the foliage samples in undergrowth vegetation (Supplementary information Table S8.1: undergrowth stratum, Fig. 8.4: undergrowth panel). Nitrogen ($\beta = 2.03$, $t = 1.23$, $p = 0.22$) and phosphorous ($\beta = 0.03$, $t = 1.35$, $p = 0.17$) concentrations were unaffected by nest presence. We did not find an effect of nest activity on any nutrient concentration ($p > 0.05$), or the interaction between nest presence and nest activity ($p > 0.05$; Table S8.1), with the exception of potassium. In the case of potassium concentration, a positive effect of nest presence occurred in occupied nests, but not in unoccupied nests (interaction term; $\beta = -3.17$, $t = -2.29$, $p < 0.03$). Tree girth (DBH) was also unimportant in determining nutrient concentrations ($p > 0.05$).

Canopy trees around nest-trees

Nest presence had a positive effect on foliage nutrient concentration of canopy trees adjacent to nest-trees for nitrogen (87% increases; $\beta = 16.95$, 13.03, $p < 0.01$), phosphorus (142% increases; $\beta = 0.31$, $t = 12.24$, $p < 0.01$), and potassium (79% increases; $\beta = 10.11$, $t = 8.32$, $p < 0.01$) (Supplementary information Table S81: surrounding canopy trees, Fig. 8.4: canopy panel). However, although we failed to detect a main effect of nest activity per se ($p > 0.05$), nest activity magnified the positive effect of nests on the concentration of nitrogen (interaction term; $\beta = 4.20$ $t = 1.95$, $p < 0.04$) and potassium (interaction term; $\beta = 7.50$, $t = 4.09$, $p < 0.01$), but not phosphorous (interaction term; $\beta = -0.01$, $t = -0.31$, $p = 0.75$). Nest activity also magnified by 24% and 74% the positive effect of nests on the canopy foliage for nitrogen and phosphorus, respectively, as observed for potassium. Tree size (DBH) was again unrelated to any of the nutrients ($p < 0.05$).

Nest-trees

Presence of harpy eagles at the nest exerted a strong positive effect on nutrient concentrations of nitrogen (80% increase; $\beta = 5.60$, $t = 9.73$, $p < 0.01$), phosphorus (25% increase; $\beta = 0.14$, $t = 23.54$, $p < 0.01$), and potassium (47% increase; $\beta = 3.04$, $t = 12.44$, $p < 0.01$) of nest-tree foliage (Table S8.1: nest tree; Fig. 8.4: nest-tree panel). However, we did not detect a main effect of nest activity ($p > 0.05$) on nutrient concentrations, nor the interaction between nest presence and nest activity ($p > 0.05$), with the exception for potassium concentration. For potassium, nest activity amplified the positive effect of nest presence by 50% (interaction term; $\beta = 1.51$, $t = 4.13$, $p < 0.01$). There were no effects of tree girth on any of the nutrient levels ($p < 0.05$).

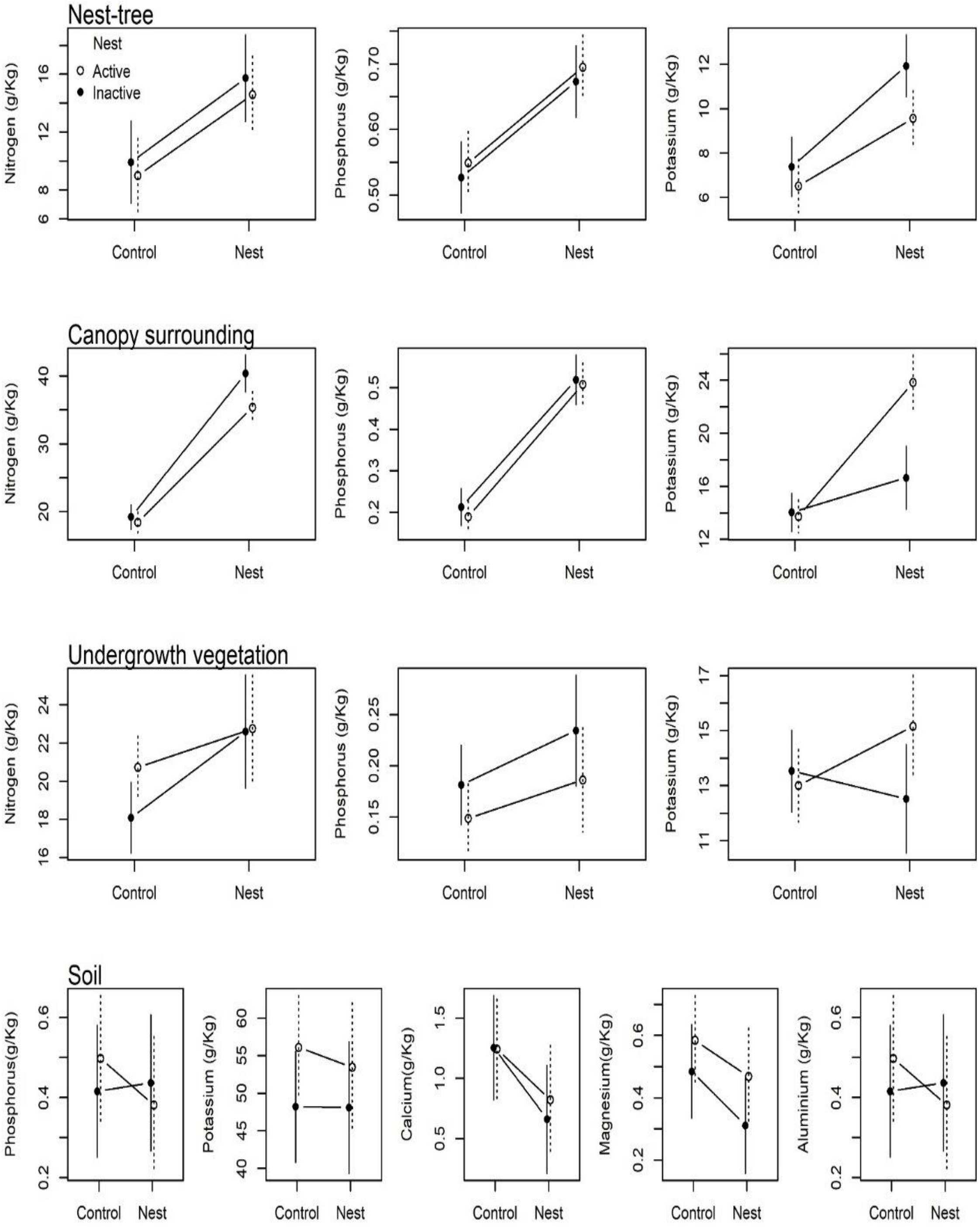

Fig. 8.5 Predicted effects of the long-term presence of harpy eagle nests on the nutrient profile in both the soils and across the vertical forest stratification depending on nest activity. (Note: White circles indicate occupied and black circles indicate unoccupied).

8.5 Discussion

Apex predators exert decisive effects on prey distribution, demography and behaviour (16, 44), but whether these extend to the bottom of food-webs remains uncertain. Here, we have shown that a rare apex predator affects soil nutrient mosaics and enhances nutrient availability for local plant communities in Amazonian forests. These findings are of prime interest to food web and carrion ecology. Our study highlights a new mechanism through which an apex predator exhibiting long-term site-fidelity can affect soil heterogeneity and vegetation phytochemistry through the cumulative deposition of carrion and excreta that is neither ephemeral nor constrained by landscape traits. While these trophic connections may now be obvious, they are hitherto unexpected because raptor and plant ecology represent opposite extremes of food webs and may appear to be hardly intertwined.

Our estimates of harpy eagle nest densities of 1.5-5.0 nests/100 km² suggest that these effects can be important at a landscape scale, generating a heterogeneous nutrient pump that affects the local fertility of otherwise oligotrophic Amazonian forest soils. Subalusky and Post (2019) highlighted that carcass input rates are one of the frequent missing links in carcass subsidies studies. In the case of direct and sustained nutrient inputs by harpy eagles at nest-trees—roughly 102.3 kg per year—challenges one of the central notions in carcass ecology: that animal carcasses are an 'ephemeral resource patch' (46). Here we have shown a mechanism by which carcasses are regularly deposited at roughly the same spot for periods that may extend for decades. Furthermore, this deposition is conditional on the harpy eagle reproductive phenology, fluctuating throughout the breeding cycles, which alters the dynamics of carcass disposition over time. The incidental consequences of this breeding cycle can be seen in differences in soil and vegetation nutrient profiles between occupied and unoccupied nests. Nests that were not occupied resulted in 24% and 74% increase of nitrogen and phosphorus in canopy foliage around the nest-tree, and a 50% increase in potassium for the nest-tree itself. This is consistent with the continuous uptake of soil nutrients by the nest-tree, which appears to be nutrient-unlimited by the continuous access to phosphorus and other nutrients directly through the nest. The "rare and unpredictable" availability of large vertebrate carrion is therefore challenged by this study, as seen in the consistent deposition through space and time of an otherwise limited resource.

Carrion is known to result in intense inter- and intraspecific competition, and this form of interaction has been shown to occur at harpy eagle nests (47), but not at the ground level. This mechanism of carrion deposition is, however, widespread in raptors even if the magnitude of localised small-carcass deposition by small-bodied raptors is far more modest. Several large-bodied raptors that habitually exercise a high degree of site-fidelity are known to exhibit similar habits, including crowned (*Stephanoaetus coronatus*), martial (*Polemaetus bellicosus*), golden (*Aquila chrysaetos*), Philippine (*Pithecophaga jefferyii*), and New Guinea (*Harpyopsis novaeguineae*) eagles (36, 48–51). This poses the question as to how these species affect nutrient mosaics of soils that range from oligotrophic to eutrophic (52, 53), but the relative importance of local nutrient inputs was clearly greater in nutrient-poor systems (54, 55).

The amount, quality and duration of carcass input is influenced by how this takes place. Prey remains underneath harpy eagle nests are mostly skeletal material, with few or no soft body parts. Bones exhibit the slowest decomposition rate of all carcass parts, taking 170 times longer than muscle to decompose in large mammal carcasses (56). On the other hand, bones provide the highest phosphorus content (>95%) of any body part (45). However, the relative proportions of muscle and skeletal mass change in large vertebrates, leading to an increase in phosphorus compared with carbon and nitrogen in larger-bodied animals, mostly because of the higher phosphorus content of bones and teeth (57). Harpy eagles, however, primarily prey on medium-sized vertebrates, and termite nests often cover skeletal remains within hours after they fall to the ground, thereby likely accelerating assimilation rates (EPBM, pers. obs.), consequently providing relatively little opportunity for nutrient diffusion into the topsoil. On the other hand, harpy eagles provide highly soluble nutrient-rich excreta, which are easily assimilated by vegetation (58), making excreta a high-quality resource.

Nevertheless, we found that occupied harpy eagle nests exerted a puzzling effect on soil quality even though nutrient subsidies resulted in lower nutrient availability in soils. Except for potassium, soil nutrients decreased in soil samples underneath nest-tree crowns (on average, by -50% for phosphorus, -32% for calcium, -21% for magnesium, and -50% for aluminium). In contrast, other cases of clumped deposition of faecal material typically boost soil nutrients. For instance, manganese and potassium concentrations are elevated in soils underneath latrines of frugivorous spider monkeys (*Ateles* spp.) in Central America (59). Howler monkeys (*Alouatta* spp.)—which are folivore-frugivores—also upgrade soil nutrient profiles, with phosphorus content increasing by 3.8-6.0 times in latrines compared with control sites in the Orinoco Basin, Venezuela (60). Since foliage and fruit pulp are clearly poorer than carcasses in nitrogen and phosphorus (61), how can these species produce a positive effect on soil nutrients while those of harpy eagles are negative?

The strong and consistent response of canopy foliage chemistry to deposition of harpy eagle excreta (i.e. 99%, 154% and 51% increases in nitrogen, phosphorus and potassium, respectively) suggests that the apparent soil nutrient sink observed here is a consequence of canopy trees shortcutting access to excreta nutrients through direct leaf uptake, rather than from the soil *per se*. Excreta from adults and eaglets usually smear much of the canopy foliage underneath the nest-tree, which is not the case of most detrital resources in a tropical forest (as primate faeces) that are deposited directly on the ground. By breaching a highly bioavailable limiting nutrient—phosphorus—before it reaches the ground, canopy trees putatively absorb other nutrients in greater amounts, including phosphorus. In a classic case of Liebig's Law of the minimum (62), nest trees fill the “barrel gap” with an abundance of nutrients that may exert limited soil availability, thereby promoting the uptake of nutrients before they become available to competition at the root level, consequently reducing soil nutrient profiles.

Nest trees also showed the effects of prolonged harpy eagle nesting activity. While those effects may be moderate when compared with the canopy, nest-trees may also remove nutrients from soils underneath their crowns by shortcutting the phosphorus uptake pathway. Some nutrient absorption likely occurs through the bark itself (the typical nest position at the primary crown bifurcation rarely allows excreta to reach terminal foliage; 58), but bark nutrient uptake is at best poorly understood (64). This is likely the reason for the weaker and inconsistent increase in the nest-tree foliage nutrient profile compared with the surrounding canopy. Harpy eagle nests are large structures averaging 152 × 99 cm that can reach up to 240 cm in diameter (63). This large platform of piled dead branches accumulates much of the carcass and skeletal remains while adults keep adding new green branches (23). Perhaps this accumulated nutrient source—a metaphorical carrion-enriched compost pile—becomes directly available to the nest tree through bark absorption, particularly given the frequent runoff of nutrients dissolved in rainwater through >30 m boles (or an average of 143.2 m^2 of bark on nest-tree trunks) before reaching the ground. While non-distilled water absorption through bark has been shown in several large conifers (65, 66), the degree to which this occurs in tropical trees remains unknown. Nevertheless, this is the single most likely mechanism increasing the foliar nutrient profiles of nest-trees observed here, thereby enabling a sustained physicochemical mutualism between harpy eagles and their long-term nest-trees. To what degree this may increase individual tree fitness or tree longevity, thereby ensuring a long-term nest platform, remains unclear.

These findings, therefore, suggest non-obligatory reciprocal benefits between harpy eagles and their nest-trees. Harpy eagles require a set of particular morphological traits of emergent trees to be selected as suitable nest-trees, particularly exceptionally high crown stature and a T-shaped primary branching (63). Trees with this crown structure may, in turn, benefit from nesting harpy eagles through a significant, long-term contribution of limiting nutrients. These effects may also feedback to influence the donor ecosystem: while we initially considered harpy eagles to be transferring nutrients from the canopy to the soil, direct nutrient augmentation in the canopy may affect the canopy ecology and primary tree productivity via increased foliage and fruit/seed production. Given the extremely low density of large raptors throughout Neotropical forests (37), this also creates a patchy mosaic of rare but sustained nutrient hotspots in a forest landscape otherwise dominated by nutrient-poor soils. That nest trees are direct beneficiaries of harpy eagle nests may extend well beyond their lifetimes as the decomposition of any nutrient-rich nest-tree can trigger further ecological interactions with fungi and other decomposers. Since heterogeneity is one of the main spatial correlates of landscape-scale plant and animal diversity, this could represent a mechanism by which the understorey in the vicinities of harpy eagle nests show higher floristic diversity (67).

The undergrowth vegetation underneath harpy eagle nest trees had higher potassium content even in more nutrient-poor soils. Significant increases of 16% for potassium have also likely resulted from direct deposition of harpy eagle excreta on leaves, ensuring direct nutrient absorption while circumventing below-ground root uptake. While we always selected foliage that lacked clear signs of excreta staining, the frequent downpours during the wet season likely induced detritus runoff, leaving no evidence of recent animal excreta. Foliar absorption is a well-known phenomenon that occurs in >85% of all plant species tested (68, 69), and the time-lag required for 50% absorption of phosphorus is estimated at 7-15 days, which is a plausible interval between consecutive rains during the transition between the dry and wet seasons and in the dry season itself. Harpy eagles show little breeding seasonality (70), with egg-laying spread over 10 months of the year (71); therefore, foliage smearing can extensively happen on the dry season. Other nutrients have a much shorter absorption time, estimated at 1-24 h for nitrogen and 1-4 days for potassium (68). This may elevate root nutrient uptake, given that this is frequently induced by foliar fertilization in several plant species (72). It is noteworthy that foliage phosphorus content in both control and nest-trees (19.57 vs. 22.71 g/kg) were much lower than those typically found in Amazonian *terra firma* forest sites (55 g/kg; 8), which may be an effect of the geochemistry and higher elevation of our study site.

Despite considerable progress in terrestrial food web ecology, the degree to which animal nutrient transport affects tropical vegetation chemistry remains contentious. Here, we provide clear evidence of the indirect effects of apex predators on forest phytochemistry. Our results are, therefore, at odds with previous conjectures that nest-tree selection by harpy eagles is driven by elevated floristic diversity underneath nest trees (37). Rather, this is most likely a by-product of prolonged site fidelity of many nesting cycles, which consistently provides direct detrital nutrient input to canopy foliage, inducing soil nutrient heterogeneity through increased root uptake.

Large hypercarnivores are rare and becoming even rarer worldwide (73, 74), so the degree to which local extinctions disrupt ecosystem processes should be explored in detail (75). Harpy eagles have succumbed to a 41% decline in their distribution range (76), and have been extirpated over vast landscapes of the Brazilian Atlantic Forest and Mesoamerica, which now lack this apex predator and its long-term forest nutrient transport and aggregation, and downstream bottom-up effects on vegetation. The markedly philopatric nature of large birds of prey suggests that other declining raptor species can also perform similar functions. We can only speculate on the magnitude of nutrient hotspots generated by the now extinct mega-raptors that once hunted many of the World’s large islands. Species such as the Cuban terrestrial owl (*Ornimegalonyx oteroi)* and New Zealand’s Haast eagle (*Hieraaetus moorei*) were much larger than harpy eagles and likely performed similar central-place nutrient inputs into soils and vegetation. Both of these species were extirpated after humans colonised their insular habitats

(77–79). This is yet another example of how historical and ongoing large vertebrate extinctions can sever nutrient transport systems, severely affecting biogeochemical cycles and nutrient redistribution (8, 80, 81).

In conclusion, we suggest that harpy eagles impact soil and vegetation nutrient heterogeneity by the continuous deposition of excreta and carrion from their nests over decades. This not only enhances our understanding of the role of carrion in sustaining nutrient cycles but also elucidates the role of large raptors in ecosystem processes. Finally, our findings pose further questions of how far the effects triggered by multi-annual site-specific prey delivery by large raptors reverberate over animal and vegetation communities in tropical forests and the degree to which trophic downgrading results from widespread apex-predator extinctions.

8.6 Acknowledgements

EM would like to thank Prof Vinicius Farjalla, for the inspiring ecosystem ecology classes during undergrad school where he had the insight that led to this research. CTD is grateful to the University of KwaZulu-Natal and the National Research Foundation (ZA) for funding. We greatly appreciate the generous financial support of the following donors: Rufford Small Grants Foundation (18743-1, 23022-2 and 31091-B), Rainforest Biodiversity Group, Idea Wild, The Mamont Scholars Program of the Explorer's Club Exploration Fund, Cleveland Metroparks Zoo, and the SouthWild.com Conservation Travel System. Logistical support was given by the Peugeot-ONF Carbon Sink Reforestation Project, based at the São Nicolau Farm in Cotriguaçu, Mato Grosso, Brazil. This project is a Peugeot initiative to fulfil some of the Kyoto Protocol directions and is run by the ONF-Brasil enterprise. We thank the Laboratory of Soil Analysis at Unemat – Alta Floresta, in the figure of Gustavo Caione, for timely performing the analysis. Finally, we thank ICMBio for authorising the project activities under the permit SISBIO 58533.

8.7 References

1. C. Elton, *Animal ecology* (Sidgwick & Jackson, 1927) (August 15, 2015).
2. D. H. Janzen, The deflowering of central America. *Nat. Hist.* **21**, 620–637 (1974).
3. J. S. Brown, J. W. Laundre, M. Gurung, The ecology of fear: Optimal foraging, game theory, and trophic interactions. *J. Mammal.* **80**, 385–399 (1999).
4. J. M. Helfield, R. J. Naiman, Keystone interactions: Salmon and bear in riparian forests of Alaska. *Ecosystems* **9**, 167–180 (2006).
5. W. C. Turner, *et al.*, Fatal attraction: vegetation responses to nutrient inputs attract herbivores to infectious anthrax carcass sites. *Proc. R. Soc. B Biol. Sci.* **281**, 20141785 (2014).
6. J. Terborgh, J. Estes, *Trophic cascades: predators, prey, and the changing dynamics of nature* (Island Press, 2013) (February 22, 2015).
7. G. Holtgrieve, D. Schindler, P. Jewett, Large predators and biogeochemical hotspots: brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils. *Ecol. Res.*, 1–11 (2009).
8. C. E. Doughty, A. Wolf, Y. Malhi, The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia. *Nat. Geosci.* **6**, 761–764 (2013).
9. P. A. Colinvaux, *Why big fierce animals are rare: an ecologist's perspective* (Princeton University Press, 1979).
10. C. Carbone, J. L. Gittleman, A common rule for the scaling of carnivore density. *Science* **295**, 2273–2276 (2002).
11. G. A. Polis, W. B. Anderson, R. D. Holt, Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Ann. Rev. Ecol. Syst.* **28**, 289–316 (1997).
12. J. K. Bump, R. O. Peterson, J. A. Vucetich, Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. *Ecology* **90**, 3159–3167 (2009).
13. A. Moreira, N. K. Fageria, Soil chemical attributes of Amazonas state, Brazil. *Commun. Soil Sci. Plant Anal.* **40**, 2912–2925 (2009).
14. E. Molina, T. E. León, D. Armenteras, Characteristics of natural salt licks located in the Colombian Amazon foothills. *Environ. Geochem. Health* **36**, 117–129 (2014).
15. L. L. Powell, T. U. Powell, G. V. Powell, D. J. Brightsmith, Parrots take it with a grain of salt: available sodium content may drive collpa (clay lick) selection in southeastern Peru. *Biotropica*, 279–282 (2009).
16. J. Terborgh, *et al.*, Ecological meltdown in predator-free forest fragments. *Science* **294**, 1923–1926 (2001).
17. E. P. Odum, G. W. Barrett, *Fundamentals of ecology* (Saunders, 1971).
18. C. Hall, "Harpy Eagle Studbook *Harpia harpyja* North American Regional" (2011).
19. E. Alvarez-Cordero, "Biology and conservation of the harpy eagle in Venezuela and Panama" DSc Thesis. University of Florida, Florida, USA. (1996).
20. V. Urios, R. Muñiz-López, J. Vidal-Mateo, Juvenile Dispersal of Harpy Eagles (*Harpia harpyja*) in Ecuador. *J. Raptor Res.* **51**, 439–445 (2017).
21. R. Muñiz-López, R. Limiñana, G. Cortés, V. Urios, Movements of harpy eagles *Harpia harpyja* during their first two years after hatching. *Bird Study* **59**, 509–514 (2012).
22. R. Muñiz-López, *et al.*, Movements of Harpy Eagles *Harpia harpyja* during their first two years after hatching. *Bird Study* **3657**, 509–514 (2016).
23. F. Aguiar-Silva, T. Sanaiotti, B. Luz, Food habits of the Harpy Eagle, a top predator from the Amazonian rainforest canopy. *J. Raptor Res.* **48**, 24–45 (2014).

24. E. B. P. Miranda, Prey composition of harpy eagles (*Harpia harpyja*) in Raleighvallen, Suriname. *Trop. Conserv. Sci.* **11**, 1–8 (2018).
25. C. H. Sekercioglu, Increasing awareness of avian ecological function. *Trends Ecol. Evol.* **21**, 464–471 (2006).
26. J. Dunning, Handbook of Avian Body Masses. *CRC, London* (1993) (September 6, 2015).
27. E. P. Walker, *Walker's Mammals of the world* (Johns Hopkins University Press, 1991).
28. W. Koeppen, *Climatologia: con un estudio de los climas de la tierra.* (1948).
29. Radam-Brasil, "Projeto Radam-Brasil: levantamento de recursos naturais" (1983).
30. C. S. Junior, M. Lima, Soy Moratorium in Mato Grosso: deforestation undermines the agreement. Land use policy. **71**, 540–542 (2018).
31. Anonymous, Novo Código Florestal, Lei 12.651 de 25 de maio de 2012, Dispõe sobre a proteção da vegetação nativa (Subchefia de assuntos jurídicos, 2012).
32. E. B. P. de Miranda, *et al.*, Harpy Eagle nest activity patterns: Potential ecotourism and conservation opportunities in the Amazon Forest. *Bird Conserv. Int.* **In press**, **-** (2020).
33. N. Rettig, Breeding behavior of the harpy eagle (*Harpia harpyja*). *Auk* **95**, 629–643 (1978).
34. L. Emmons, F. Feer, *Neotropical rainforest mammals: a field guide* (University of Chicago Press, 1997) (January 22, 2015).
35. M. Goffart, *Function and Form in the Sloth* (Pergamon Press, 1971) (February 16, 2015).
36. T. Van der Meer, S. McPherson, C. Downs, Temporal changes in prey composition and biomass delivery to African Crowned Eagle nestlings in urban areas of KwaZulu-Natal, South Africa. *Ostrich* **83**, 241–250 (2018).
37. J. de J. Vargas-González, F. H. Vargas, Nesting density of Harpy Eagles in Darien with population size estimates for Panama. *J. Raptor Res.* **43**, 199–210 (2011).
38. D. Brown, A test of randomness of nest spacing. *Wildfowl* **26**, 102–103 (1975).
39. J. Schöngart, R. Gribel, S. Ferreira da Fonseca-Junior, T. Haugaasen, Age and growth patterns of Brazil nut trees (*Bertholletia excelsa* Bonpl.) in Amazonia, Brazil. *Biotropica* **47**, 550–558 (2015).
40. Embrapa, *Manual de análises químicas de solos, plantas e fertilizantes*, F. C. S. Silva, Ed., Vol. 627 (Embrapa Informação Tecnológica, 2009).
41. A. Mehlich, "Determination of P, Ca, Mg, K, Na and NH4" (1953).
42. J. Pinheiro, *et al.*, Package 'nlme'. Linear and nonlinear mixed effects models, version, 3(1). 336 (2017).
43. R Core, "R: A language and environment for statistical computing" (R Fondation for Statistical Computing, 2020).
44. R. Gil-da-Costa, A. Palleroni, M. D. Hauser, J. Touchton, J. P. Kelley, Rapid acquisition of an alarm response by a neotropical primate to a newly introduced avian predator. *Proc. Biol. Sci.* **270**, 605–610 (2003).
45. A. L. Subalusky, D. M. Post, Context dependency of animal resource subsidies. *Biol. Rev.* **94**, 517–538 (2019).
46. P. S. Barton, J. K. Bump, "Carrion decomposition" in *Carrion Ecology and Management*, P. Olea, P. Mateo-Tomás, J. Sánchez-Zapata, Eds. (Springer, 2019), pp. 101–124.
47. F. H. Aguiar-Silva, *et al.*, Camera trapping at active Harpy Eagle nests: interspecies interactions under predation risk. *J. Raptor Res.* **51**, 72–29 (2017).
48. T. R. C. Abaño, D. J. Salvador, J. C. Ibañez, First nesting record of Philippine Eagle Pithecophaga jefferyi from Luzon, Philippines, with notes on diet and breeding biology.

Forktail **32**, 86–88 (2016).
49. S. T. Killengreen, E. Strømseng, N. G. Yoccoz, R. A. Ims, How ecological neighbourhoods influence the structure of the scavenger guild in low arctic tundra. *Divers. Distrib.* **18**, 563–574 (2012).
50. R. van Eeden, D. P. Whitfield, A. Botha, A. Amar, Ranging behaviour and habitat preferences of the Martial Eagle: Implications for the conservation of a declining apex predator. *PLoS One* **12**, e0173956 (2017).
51. L. A. T. Legra, "Nest-site selection and behavioural biology of the New Guinea Harpy Eagle *Harpyopsis novaeguineae*" University of Papua New Guinea. (2005).
52. F. Marshall, *et al.*, Ancient herders enriched and restructured African grasslands. *Nature* **561**, 387–390 (2018).
53. A. D. Palanog, *et al.*, Zinc and iron nutrition status in the Philippines population and local soils: A review. *Front. Nutr.* **6**, 0–81 (2019).
54. A. M. Panichev, *et al.*, Geological nature of mineral licks and the reasons for geophagy among animals. *Biogeosciences* **14**, 27–67 (2017).
55. C. T. Downs, I. P. Bredin, P. D. Wragg, More than eating dirt: a review of avian geophagy. *Afr. Zool.* **54**, 1–19 (2019).
56. A. L. Subalusky, C. L. Dutton, E. J. Rosi, D. M. Post, Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proc. Nat. Acad. Sci. U. S. A.* **114**, 7647–7652 (2017).
57. J. J. Elser, D. R. Dobberfuhl, N. A. MacKay, J. H. Schampel, Organism size, life history, and N: P stoichiometry: toward a unified view of cellular and ecosystem processes. *Bioscience* **46**, 674–684 (1996).
58. M. J. Vanni, Nutrient cycling by animals in freshwater ecosystems. *Ann. Rev. Ecol. Syst.* **33**, 341–370 (2002).
59. A. Whitworth, *et al.*, Spider Monkeys Rule the Roost: Ateline Sleeping Sites Influence Rainforest Heterogeneity. *Animals* **9**, 0–16 (2019).
60. K. Feeley, The role of clumped defecation in the spatial distribution of soil nutrients and the availability of nutrients for plant uptake. *J. Trop. Ecol.* **21**, 99–102 (2005).
61. C. D'Alessandro, G. B. Piccoli, A. Cupisti, The "phosphorus pyramid": a visual tool for dietary phosphate management in dialysis and CKD patients. *BMC Nephrol.* **16**, 1–6 (2015).
62. J. von Liebig, *Principles of agricultural chemistry with special reference to the late researches made in England*, W. Gregory, Ed. (Walton & Maberly, 1855).
63. E. B. P. Miranda, C. A. Peres, M. Â. Marini, C. T. Downs, Harpy Eagle (*Harpia harpyja*) nest tree selection: Logging in Amazonian Forests threatens Earth's largest eagle. *Biol. Conserv.* ******, ** (2020).
64. D. P. Aubrey, "Relevance of Precipitation Partitioning to the Tree Water and Nutrient Balance" in *Precipitation Partitioning by Vegetation*, (Springer, 2020), pp. 147–162.
65. S. Mayr, *et al.*, Uptake of water via branches helps timberline conifers refill embolized xylem in late winter. *Plant Physiol.* **164**, 1731–1740 (2014).
66. J. Mason Earles, *et al.*, Bark water uptake promotes localized hydraulic recovery in coastal redwood crown. *Plant. Cell Environ.* **39**, 320–328 (2016).
67. J. de J. Vargas González, F. H. Vargas, C. McClure, Características de la vegetación en sitios de anidación del águila arpía (*Harpia harpyja*) en Darién, Panamá. *Ornitol. Neotrop.* **25**, 207–218 (2014).
68. S. H. Wittwer, F. G. Teubner, Foliar absorption of mineral nutrients. *Ann. Rev. Plant Physiol.* **10**, 13–30 (1959).
69. G. R. Goldsmith, N. J. Matzke, T. E. Dawson, The incidence and implications of clouds for cloud forest plant water relations. *Ecol. Lett.* **16**, 307–314 (2013).

70. M. H. Blank, *et al.*, Fecal sex steroids and reproductive behaviors in harpy eagles (*Harpia harpyja*). *Zoo Biol.*, 1–10 (2020).
71. R. T. Watson, C. J. W. McClure, F. H. Vargas, J. P. Jenny, Trial Restoration of the Harpy Eagle, a Large, Long-lived, Tropical Forest Raptor, in Panama and Belize. *J. Raptor Res.* **50**, 3–22 (2016).
72. A. Geetah, "Physiology of Foliar Spray Uptake and Its Importance in Some of the Commercial Crops" in *Advances in Agriculture Sciences*, R. K. Naresh, Ed. (AkiNik Publications, 2019), pp. 01–28.
73. C. J. McClure, *et al.*, State of the world's raptors: Distributions, threats, and conservation recommendations. *Biol. Conserv.* **227**, 390–402 (2018).
74. J. A. Estes, *et al.*, Trophic downgrading of planet Earth. *Science* **333**, 301–306 (2011).
75. C. X. Cunningham, *et al.*, Top carnivore decline has cascading effects on scavengers and carrion persistence. *Proc. R. Soc. B* **285**, 20181582 (2018).
76. E. B. P. Miranda, J. F. S. Menezes, C. C. Farias, C. Munn, C. A. Peres, Species distribution modeling reveals strongholds and potential reintroduction areas for the world's largest eagle. *PLoS One* **14**, e0216323 (2019).
77. J. Orihuela, An annotated list of Late Quaternary extinct birds of Cuba. *Ornitol. Neotrop.* **30**, 57–67 (2019).
78. R. Scofield, K. Ashwell, Rapid somatic expansion causes the brain to lag behind: the case of the brain and behavior of New Zealand's Haast's Eagle (*Harpagornis moorei*). *J. Vertebr. Paleontol.* **29**, 637–649 (2009).
79. S. B. Cooke, L. M. Dávalos, A. M. Mychajliw, S. T. Turvey, N. S. Upham, Anthropogenic extinction dominates Holocene declines of West Indian mammals. *Ann. Rev. Ecol. Evol. Syst.* **48**, 301–327 (2017).
80. Y. Malhia, *et al.*, Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proc. Nat. Acad. Sci.* **113**, 838–846 (2016).
81. C. E. Doughty, *et al.*, Global nutrient transport in a world of giants. *Proc. Nat. Acad. Sci. U. S. A.* **113**, 868–873 (2015).

8.8 Supplementary information

Supplementary information Table S8.1. Summary statistics of models ran for different nutrients in different stratum. Parameters of the model (parameter column), coefficient estimation (coefficient), lower and upper 95% interval confidence (lower and upper), degrees of freedom (df), t statistic (t-value) and probability associate (p-value).

Stratum	**Nutrient**	**Parameter**	**Coefficient**	**Lower**	**Upper**	**df**	**t-value**	**p-value**
Soil	Phosphorous	Intercept	3.18	1.796	4.563	347	4.52	<0.001
		Nest	-0.928	-1.503	-0.353	347	-3.175	0.002
		Unoccupied	-0.594	-1.532	0.344	347	-1.246	0.214
		Circumference	0.093	-0.164	0.35	347	0.71	0.478
		Nest:unoccupied	0.189	-0.65	1.028	347	0.444	0.657
	Potassium	Intercept	40.22	24.137	56.304	347	4.918	<0.001
		Nest	-2.586	-10.406	5.234	347	-0.65	0.516
		Unoccupied	-7.916	-17.931	2.1	347	-1.555	0.121
		Circumference	3.638	0.400	6.875	347	2.21	0.028
		Nest:unoccupied	2.456	-8.929	13.84	347	0.424	0.672
	Calcium	Intercept	40.22	24.137	56.304	347	4.918	<0.001
		Nest	-2.586	-10.406	5.234	347	-0.65	0.516
		Unoccupied	-7.916	-17.931	2.1	347	-1.555	0.121
		Circumference	3.638	0.400	6.875	347	2.21	0.028
		Nest:unoccupied	2.456	-8.929	13.84	347	0.424	0.672
	Magnesium	Intercept	40.22	24.137	56.304	347	4.918	<0.001
		Nest	-2.586	-10.406	5.234	347	-0.65	0.516
		Unoccupied	-7.916	-17.931	2.1	347	-1.555	0.121
		Circumference	3.638	0.400	6.875	347	2.21	0.028
		Nest:unoccupied	2.456	-8.929	13.84	347	0.424	0.672
	Alumniu m	Intercept	40.22	24.137	56.304	347	4.918	<0.001
		Nest	-2.586	-10.406	5.234	347	-0.65	0.516

		Unoccupied	-7.916	-17.931	2.1	347	-1.555	0.121
		Circumference	3.638	0.4	6.875	347	2.21	0.028
		Nest:unoccupied	2.456	-8.929	13.84	347	0.424	0.672
Undergrowth	Nitrogen	Intercept	19.911	13.662	26.16	48	6.407	<0.001
		Nest	2.033	-1.415	5.481	48	1.186	0.242
		Unoccupied	-2.643	-5.39	0.104	18	-2.021	0.058
		Circumference	0.19	-1.233	1.612	48	0.268	0.79
		Nest:unoccupied	2.489	-2.569	7.546	48	0.989	0.327
	Phosphorous	Intercept	0.173	0.038	0.308	48	2.569	0.013
		Nest	0.037	-0.02	0.094	48	1.31	0.196
		Unoccupied	0.034	-0.025	0.092	18	1.212	0.241
		Circumference	-0.006	-0.036	0.025	48	-0.374	0.71
		Nest:unoccupied	0.015	-0.069	0.098	48	0.355	0.724
	Potassium	Intercept	13.031	7.871	18.19	48	5.078	<0.001
		Nest	2.151	0.209	4.093	48	2.227	0.031
		Unoccupied	0.533	-1.733	2.8	18	0.494	0.627
		Circumference	-0.007	-1.162	1.148	48	-0.012	0.99
		Nest:unoccupied	-3.172	-6.027	-0.318	48	-2.234	0.03
Nest-tree	Nitrogen	Intercept	19.911	13.662	26.16	48	6.407	<0.001
		Nest	2.033	-1.415	5.481	48	1.186	0.242
		Unoccupied	-2.643	-5.39	0.104	18	-2.021	0.058
		Circumference	0.19	-1.233	1.612	48	0.268	0.79
		Nest:unoccupied	2.489	-2.569	7.546	48	0.989	0.327
	Phosphorous	Intercept	0.173	0.038	0.308	48	2.569	0.013
		Nest	0.037	-0.02	0.094	48	1.31	0.196
		Unoccupied	0.034	-0.025	0.092	18	1.212	0.241
		Circumference	-0.006	-0.036	0.025	48	-0.374	0.71

		Nest:unoccupied	0.015	-0.069	0.098	48	0.355	0.724
	Potassium	Intercept	13.031	7.871	18.19	48	5.078	<0.001
		Nest	2.151	0.209	4.093	48	2.227	0.031
		Unoccupied	0.533	-1.733	2.8	18	0.494	0.627
		Circumference	-0.007	-1.162	1.148	48	-0.012	0.99
		Nest:unoccupied	-3.172	-6.027	-0.318	48	-2.234	0.03
Canopy surrounding	Nitrogen	Intercept	19.365	15.062	23.668	194	8.877	<0.001
		Nest	16.95	14.385	19.515	194	13.033	<0.001
		Unoccupied	0.79	-1.732	3.313	18	0.658	0.519
		Circumference	-0.213	-1.159	0.733	194	-0.444	0.657
		Nest:unoccupied	4.197	0.335	8.059	194	2.143	0.033
	Phosphorous	Intercept	0.225	0.127	0.322	194	4.561	<0.001
		Nest	0.319	0.268	0.371	194	12.241	<0.001
		Unoccupied	0.023	-0.039	0.086	18	0.787	0.442
		Circumference	-0.008	-0.029	0.013	194	-0.78	0.437
		Nest:unoccupied	-0.012	-0.09	0.065	194	-0.312	0.755
	Potassium	Intercept	12.808	9.209	16.408	194	7.018	<0.001
		Nest	10.116	7.717	12.515	194	8.316	<0.001
		Unoccupied	0.303	-1.715	2.322	18	0.316	0.756
		Circumference	0.213	-0.583	1.01	194	0.528	0.598
		Nest:unoccupied	-7.498	-11.115	-3.881	194	-4.089	<0.001

CHAPTER 9

CONCLUDING REMARKS

9.1 Background

The conservation of the Amazon Forest has been perceived as a central issue for maintaining the balance of Earth's climate and protecting biodiversity. Current public management of this region is characterized by poor law enforcement, while the land grabbing, followed by timber extraction, forest fires and establishment of cattle pasture is increasing (Carrero et al., 2020). In the hyperfragmented landscape created by deforestation, there are valuable forest patches and corridors (Zimbres et al., 2018) as required by Brazilian forestry law (Anonymous, 2012). Many large vertebrates remain within the fragmented landscape (Zimbres et al., 2017; Lima et al., 2019), and some—such as the harpy eagle (*Harpia harpyja*)—are dependent of proper land stewardship and conservation action.

9.2 Synthesis

Harpy eagle populations throughout the range of this species have declined mainly because of habitat loss and direct persecution. Through this thesis, I have been able to establish objective assessments of both of these drivers, which also account for the main threats affecting 32,000 species of vulnerable, endangered and critically endangered organisms (IUCN, 2020). Harpy eagles have sustained a 41% human-induced contraction of their original range, and nowadays their last stronghold is lowland Amazonia, which currently comprises 93% of the species distribution (Miranda et al., 2019; Chapter 2). Although anthropogenic drivers of biodiversity loss in the Amazon are complex (Peres et al., 2010), southern Amazonian Forests have succumbed to intentional or accidental fires as a product of an ever-expanding cattle ranching frontier, the Arc of Deforestation (Carrero et al., 2020). Extensive habitat degradation of the remaining forest tracts proceeds as a result of timber extraction, which removes many nest trees

(Miranda et al., 2020; Chapter 6). The protection of Brazil nut trees (Nepstad et al., 1992) has just about ensured the reproductive viability of harpy eagles within logged *terra firma* Amazon Forest landscapes (Giudice et al., 2007). Patterns of persecution presented here, on the other hand, uncovered a surprising outcome: curiosity is mentioned as an important factor justifying harpy eagle shootings (Miranda et al., 2020a; Chapter 4). While the main reason widely reported for predator elimination is livestock predation (Zuluaga & Echeverry-Galvis, 2016) or threat against humans (Knox et al., 2019), both issues exerted a minor role regarding harpy eagles (Miranda et al., 2020a; Chapter 4).

Regarding its feeding habits, harpy eagles have been shown to use key environmental cues—such as moonlight and temperature—to increase capture rates of their main prey species, sloths (Miranda et al., 2020; Chapter 3). Earlier research efforts demonstrated that the prey preferences of male and female floaters strongly differs (Miranda et al., 2018), but those differences are modest for nesting individuals (Miranda et al., 2020; Chapter 7). As a highly philopatric central-place forager after reaching sexual maturity (Muñiz López, 2016), harpy eagles are vulnerable to forest degradation around their nest-trees (Miranda et al., 2020; Chapter 7). Harpy eagle pairs nesting within fragmented landscapes incurred fitness costs such as food stress where deforested areas around their nests were >30% of the overall landscape and breeding pairs were unable to raise eaglets if with the surrounding forest loss ranged from 30 to 50% (Miranda et al., 2020; Chapter 7). Food stress was caused by harpy eagle being unable to consolidate a diet comprised of open-habitat mammals, as they still rely on canopy quarry even under extreme deforestation contexts (Miranda et al., 2020; Chapter 7). The strong philopatry, however, rendered excreta and prey carcasses deposited by harpy eagles on the same nesting site for decades, creating somewhat circumcentric nutrient hotspots that can easily be described as a plant-animal mutualism. Leaf uptake caused foliage around and within harpy eagle nest trees to be richer in nutrients, which in turn likely allowed those plants to remove soil nutrients at higher rates, rendering them more nutrient-poor (Miranda et al., 2020; Chapter 8). These novel findings are of prime interest for the conservation and management of harpy eagles and their forest habitats.

9.3 Limitations and scope for future research

Some clear multifaceted limitations prevent further strides for harpy eagle ecology and conservation. For example, methodological, temporal, financial and logistical constraints have affected several aspects of harpy eagle biology and conservation in this study. I present some future research issues below:

(1) Understanding where and how harpy eagle populations can persist outside rainforest ecoregions, and if there are any extant populations present. Forest enclaves in savannah landscapes such as Bodoquena National Park and riparian forests in the Araguaia Basin are among sites with the greatest potential for harpy eagle persistence (Pereira & Salzo, 2006; Sousa et al., 2015);

(2) Understanding how moonlight, leaf shedding and rainfall may affect harpy eagle foraging in forest landscapes subjected to strong seasonality, like southern Amazonia, seasonally flooded forests of central Amazonia (Olmos et al., 2006), subtropical sections of the Atlantic Forest (Meller & Guadagnin, 2016) and dry transitional forests (Pereira & Salzo, 2006). All of these environments have the potential to show strong seasonally controlled predator-prey relationships;

(3) Producing a better framework to understand local perceptions and behavioural changes regarding harpy eagle killings (Wright et al., 2015). Repeating the interviews at locations where ecotourism has been implemented would help understand the project impacts on the behaviour of local stakeholders regarding harpy eagles (Miranda et al.,

2020; Chapter 5). Furthermore, this would support an understanding of tourism initiative shortcomings, and allowing opportunities to fix them;

(4) Increasing the reach of tourism co-benefits over a larger section of the Arc of Deforestation would help protect harpy eagles while providing concrete economic benefits for local people (Kirkby et al., 2010, 2011). Developing a strategy prone to replication by publishing it as a business plan and financial viability evaluation would help other initiatives to establish successful harpy eagle tourism operations across the region.

(5) Investigate how forestry laws across Amazonian Forests—harpy eagle's last stronghold—can be modified to include a widespread 'no-take' policy protecting mega-trees (Miranda et al., 2020). This can protect harpy eagles and have widespread effects over biodiversity and carbon stocks (Pinho et al., 2020). Protecting these trees as presently enforced for Brazil nut trees (*Bertholletia excelsa*) over most of the Amazon (Nepstad et al., 1992) can help build a more robust safety net for forest protection. Increasing the knowledge of harpy eagle nest tree selection in selectively logged forest landscapes is also necessary. For instance, to establish if these mega raptors select 'poorer' tree forks—in the sense that these are unsafe for chicks during the branch hoping phase—or if they are able to find proper nesting platforms on large emergent trees that are spared from logging (such as Brazil nut trees). Analyses of nutrient profiles on tree rings may help establish if harpy eagle individuals in logged landscapes have recently switched to new nest trees after the original nest trees were felled since the dendrochronology of nest trees is most likely affected by the presence of active harpy eagle nests;

(6) Understanding how logging impacts the harpy eagle prey base, and which prey species undergo meaningful increases or declines in abundance or vulnerability to predation. Learning about foraging of eagles nesting in fragmented forests will help understand if

logging affects their feeding ecology. While estimating prey population sizes will remain challenging because of the low detectability of sloths (Laufer et al., 2012), comparing multiple breeding pairs in logged landscapes with those nesting in primary forests would provide useful insights. Finally, it is necessary to investigate why some harpy eagle pairs feed nearly exclusively on armadillos (Cingulata) in degraded landscapes to understand if this is either a local trait or learned behaviour.

(7) Comprehending how far nutrient hotspots created by harpy eagles are diffused into the neighbouring ecosystem, in terms of the soil fauna, ground level and canopy, as well as the overall floristic composition of the forest. Another promising research avenue would be to understand this impact on the life history of the nest tree itself, which is at the same time a beneficiary of the presence of key nutrients, but also incur more intensive attacks by termites and other insects.

Finally, a comprehensive effort to understand the harpy eagle use of space across the landscape would be important to define several aspects of its life history. The items 2, 4, 5 and 6 would be greatly improved if a large number of adult eagles can be simultaneously telemetered. It is surprising how three decades of research on harpy eagles have failed to produce a single major piece of work regarding their movement ecology and, to date, even very elementary questions on the ranging ecology of this species, such as the operational size of adult home ranges during and outside the nesting season, remain unanswered. While only occasional efforts to equip juveniles with radios have been made so far, these studies remain highly limited by small sample sizes. Therefore, pushing forward a major research effort focused on monitoring the movement ecology of multiple adults simultaneously, learning about habitat use and other wide-open questions about harpy eagle life history must be the next step in this large raptor research.

9.4 Management implications

Harpy eagles in degraded landscapes are dependent on conservation actions. Nests located in recently fragmented and degraded landscapes are vulnerable to being abandoned or failing to produce any eaglets because of food stress. Worse still, adult individuals in those landscapes may prey on domestic livestock and subsequently be killed in retaliation. Those issues are especially problematic if we consider that harpy eagles have long life cycles, long breeding cycles and a high degree of parental care that depends on both sexes.

Food supplementation may be a palliative measure, ensuring the survival of harpy eagle eaglets in nests within degraded landscapes where food stress may threaten their survival. In deciding to supplement chicks, some issues must be observed to avoid conditioning the animals to be fed by people. One of these is to place food on the main nest branches at night—when harpy eagles are unoccupied (Miranda et al., 2020)—so that eaglets cannot associate food with humans (Muela et al., 2003). Another issue that must be closely observed is that meat cannot come from domestic animals that eagles are able to find locally, thereby avoiding search image conditioning that will cause later problems with predation of domestic animals (Watson et al., 2016). While palliative, this measure can buy precious time to provide connectivity between forest fragments so that adults can adequate feed eaglets and give them the best possible chance of future dispersal.

Another issue is that harpy eagle eaglets stranded in isolated fragments may be unable to disperse. Preliminary evidence shows that adults hardly cross gap distances between forest patches farther than 500 m (Aguiar-Silva, 2016), such as cattle pasture or soybean fields. Eaglets probably are even less able to cross such distances. There is evidence that eaglets unable to disperse from natal territories are killed by their parents (Muñiz-López, 2017). Translocation management of chicks that should be starting to disperse (~30 months; Urios et al., 2017) in those cases is mandatory. While this does not solve the problems brought about by habitat fragmentation, it will help retain functional populations and avoid loss of genetic diversity that already occurs in harpy eagles in southern Amazonia (Banhos et al., 2016). Meanwhile, forest corridors connecting nests within fragments and larger forest paths can be implemented (see Lees & Peres, 2008)

Without the implementation of a better legal framework for timber extraction—a framework that can actually acknowledge the intrinsic value mega-trees have for biodiversity (Pinho et al., 2020)—logging will remain the primary form of habitat degradation for harpy eagles and Neotropical biodiversity in general (Richardson & Peres, 2016). While our ecotourism initiative has several times been able to break deals with large timber estates for protecting harpy eagle nest trees (as the profits from tourism are more attractive), this is an unrealistic proposal for the whole of the Amazon, even if this can be scalable to a much larger region then where it is operational at present. Therefore, putting better forestry law in place and simply sparing a large number of mega-trees altogether may provide long-lasting solutions for this issue.

Conservation in the Amazon—and therefore harpy eagle conservation—can be summarized as a clash between two worldviews for the economical use of the region. One view is integrating the forest into regional and global markets through destructive uses, like forest incineration for cattle ranching and soybean farming (Schneider & Peres, 2015; Carrero et al., 2020). The other view claims that it is possible to make the economic integration through initiatives that do not destroy the forest, such as sustainable "reduced-impact" logging (Richardson & Peres, 2016), sustainable freshwater fisheries (Campos-Silva & Peres, 2016), Brazil nut extraction (Guariguata et al., 2017) and ecotourism (Kirkby et al., 2010, 2011). Up to now, the single prevailing view that has been widely implemented is large scale forest conversion and degradation. While I was able to establish a small ecotourism alliance in the region, creating functionally systemic and economic links between the investor and local stakeholders, structuring a framework that gains its momentum will continue independently of this thesis, many challenges lie ahead. Millions of people in the Amazon aspire to more prosperous livelihoods, while few already wealthy large holders understand no other means of returning a profit other than the destructive liquidation of the natural capital. The means by which the rural poor will achieve prosperous lives and the wealthy will conduct ecologically sound land stewardship, will determine the baseline conditions of future Amazonian Forests across private lands and as of yet undesignated public lands. The region has potential to benefit from viable harpy eagle populations—and many other traits—such as an ecotourism asset of the Amazon Forest, providing a visible and tangible financial value for its preservation (Miranda et al., 2020; Chapter 5). However, creating a widespread sense of identity and ownership for biodiversity while positively incorporating this same biodiversity into local and global markets will require much greater effort and dedication.

9.5 References

AGUIAR-SILVA, H. (2016) Uso e seleção de recursos por harpia em múltiplas escalas espaciais: persistência e vulnerabilidade. INPA.

ANONYMOUS (2012) Novo Código Florestal, Lei 12.651 de 25 de maio de 2012, Dispõe sobre a proteção da vegetação nativa. Subchefia de assuntos jurídicos, Brasília.

BANHOS, A., HRBEK, T., SANAIOTTI, T.M. & FARIAS, I.P. (2016) Reduction of genetic diversity of the harpy eagle in brazilian tropical forests. *PloS One*, 11, e0148902.

CAMPOS-SILVA, J.V. & PERES, C.A. (2016) Community-based management induces rapid recovery of a high-value tropical freshwater fishery. *Scientific Reports*, 6, 34745.

CARRERO, G.C., FEARNSIDE, P.M., DO VALLE, D.R. & DE SOUZA ALVES, C. (2020) Deforestation Trajectories on a Development Frontier in the Brazilian Amazon: 35 Years of Settlement Colonization, Policy and Economic Shifts, and Land Accumulation. *Environmental Management*, 1–19.

GIUDICE, R., PIANA, R. & WILLIAMS, M. (2007) Tree architecture as a determinant factor in nest-tree selection by Harpy Eagles. In *Neotropical raptors* (eds K.L. Bildstein, D.R. Barber & A. Zimmerman), pp. 14–22. Hawk Mountain Sanctuary, Orwigsburg.

GUARIGUATA, M.R., CRONKLETON, P., DUCHELLE, A.E. & ZUIDEMA, P.A. (2017) Revisiting the 'cornerstone of Amazonian conservation': a socioecological assessment of Brazil nut exploitation. *Biodiversity and Conservation*, 26, 2007–2027.

IUCN (2020) Background & History. *Red List*. Https://www.iucnredlist.org/about/background-history [accessed 29 October 2020].

KIRKBY, C.A., GIUDICE-GRANADOS, R., DAY, B., TURNER, K., VELARDE-ANDRADE, L.M., Dueñas-Dueñas, A., et al. (2010) The market triumph of ecotourism: An economic investigation of the private and social benefits of competing land uses in the Peruvian Amazon. *PLoS One*, 5, e13015.

Kirkby, C.A., Giudice, R., Day, B., Turner, K., Soares-Filho, B.S., Oliveira-Rodrigues, H. & Yu, D.W. (2011) Closing the ecotourism-conservation loop in the Peruvian Amazon. *Environmental Conservation*, 38, 6–17.

Knox, J., Negrões, N., Marchini, S., Barboza, K., Guanacoma, G., Balhau, P., et al. (2019) Jaguar persecution without "cowflict": insights from protected territories in the Bolivian Amazon. *Frontiers in Ecology and Evolution*, 7, 494.

Laufer, J., Amador, J.A., Conceição, P.C., Norris, D. & Michalski, F. (2012) Use of boat surveys to provide complementary data on the ecology of *Bradypus tridactylus* (Pilosa: Bradypodidae) from Northern Amazonia. *Edentata*, 13, 56–60.

Lees, A.C. & Peres, C.A. (2008) Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. *Conservation Biology*, 22, 439–449.

Lima, M., Peres, C.A., Abrahams, M.I., da Silva Junior, C.A., de Medeiros Costa, G. & dos Santos, R.C. (2019) The paradoxical situation of the white-lipped peccary (*Tayassu pecari*) in the state of Mato Grosso, Brazil. *Perspectives in Ecology and Conservation*, 17, 36–39.

Meller, D.A. & Guadagnin, D.L. (2016) Rediscovery of the Harpy Eagle *Harpia harpyja* (Accipitriformes: Accipitridae) for Rio Grande do Sul state, Brazil. *Brazilian Journal of Ornithology*, 24, 53–57.

Miranda, E.B.P., Campbell-Thompson, E., Muela, A. & Vargas, F.H. (2018) Sex and breeding status affect prey composition of Harpy Eagles *Harpia harpyja*. *Journal of Ornithology* 159, 141–150.

Miranda, E. B. P. de, Kenup, C.F., Munn, C.A., Huizinga, N., Lormand, N. & Downs, C.T. (2020) Harpy Eagle nest activity patterns: Potential ecotourism and conservation opportunities in the Amazon Forest. *Bird Conservation International*, In press, **-**.

Miranda, E. B. P, Kenup, C.F., Campbell-Thompson, E., Vargas, F.H., Muela, A., Watson, R., et al. (2020) High moon brightness and low ambient temperatures affect sloth predation by harpy eagles. *PeerJ*, 8, e9756.

Miranda, E.B.P., Menezes, J.F.S., Farias, C.C., Munn, C. & Peres, C.A. (2019) Species distribution modeling reveals strongholds and potential reintroduction areas for the world's largest eagle. *PloS One*, 14, e0216323.

Miranda, E.B.P., Peres, C.A., Carvalho-Rocha, V., Miguel, B.V., Lormand, N., Huizinga, N., et al. (2020) Tropical deforestation induces thresholds of reproductive viability and habitat suitability in Earth's largest eagles. *submitted*, **-**.

Miranda, E.B.P., Peres, C.A. & Downs, C.T. (2020a) Perceptions of livestock predation (or the lack of it) and the persecution of harpy eagles. *Animal Conservation*, submitted, **.

Miranda, E. B. P., Peres, C.A. & Downs, C.T. (2020b) Changes in soil fertility mosaics in the Amazon Forest induced by an apex predator. *in press*.

Miranda, E.B.P., Peres, C.A., Marini, M.Â. & Downs, C.T. (2020) Harpy Eagle (*Harpia harpyja*) nest tree selection: Logging in Amazonian Forests threatens Earth's largest eagle. *Biological Conservation*, **, **.

Muela, A., Watson, R., Mutch, B. & Heinrich, W. (2003) The Harpy Eagle: biology, restoration and hacking procedures. In *Fondo Peregrino-Panamá* p. . Ciudad de Panamá.

Muñiz-López, R. (2017) Harpy Eagle (*Harpia harpyja*) mortality in Ecuador. *Studies on Neotropical Fauna and Environment*, 30, 1–5.

Muñiz López, R. (2016) Biología y conservación del Águila Harpía (*Harpia harpyja*) en Ecuador. Universidad de Alicante.

Nepstad, D.C., Brown, I.F., Luz, L., Alechandre, A. & Viana, V. (1992) Biotic impoverishment of Amazonian Forests by rubber tappers, loggers, and cattle ranchers. *Advances in Economic Botany*, 9, 1–14.

OLMOS, F., PACHECO, J.F.J. & SILVEIRA, L.L.F. (2006) Notas sobre aves de rapina (Cathartidae, Acciptridae e Falconidae) brasileiras. *Revista Brasileira de Ornitologia*, 14, 401–404.

PEREIRA, A.D.M.M. & SALZO, I. (2006) Primeiro registro da nidificação de *Harpia harpyja* (Falconiformes, Accipitridae) na Serra da Bodoquena (Mato Grosso do Sul, Brasil). *Revista Brasileira de Ornitologia*, 14, 157–160.

PERES, C.A., GARDNER, T.A., BARLOW, J., ZUANON, J., MICHALSKI, F., LEES, A.C., ET AL. (2010) Biodiversity conservation in human-modified Amazonian Forest landscapes. *Biological Conservation*, 143, 2314–2327.

PINHO, B.X., PERES, C.A., LEAL, I.R. & TABARELLI, M. (2020) Critical role and collapse of tropical mega-trees: A key global resource. Tropical Ecosystems in the 21st Century. In *Tropical Ecosystems in the 21st Century* p. 253.

RICHARDSON, V.A. & PERES, C.A. (2016) Temporal Decay in Timber Species Composition and Value in Amazonian Logging Concessions. *PLOS One*, 11, e0159035.

SCHNEIDER, M. & PERES, C.A. (2015) Environmental costs of government-sponsored agrarian settlements in Brazilian Amazonia. *PloS One*, 10, e0134016.

SOUSA, G.L., OLIVEIRA, C., PROCÓPIO, J., AMARAL, N., BRITO, A.S., AGUIAR-SILVA, F.H. & JAUDOIN, O. (2015) Harpy Eagle (*Harpia harpyja*) monitoring project in São Geraldo do Araguaia, South-eastern Brazilian Amazon. *Spizaetus*, 2, 2–11.

URIOS, V., MUÑIZ-LÓPEZ, R. & VIDAL-MATEO, J. (2017) Juvenile dispersal of harpy eagles (*Harpia harpyja*) in Ecuador. *Journal of Raptor Research*, 51, 439–445.

WATSON, R.T., MCCLURE, C.J.W., VARGAS, F.H. & JENNY, J.P. (2016) Trial restoration of the harpy eagle, a large, long-lived, tropical forest raptor, in Panama and Belize. *Journal of Raptor Research*, 50, 3–22.

WRIGHT, A.J., VERÍSSIMO, D., PILFOLD, K., PARSONS, E.C.M., VENTRE, K., COUSINS, J., ET AL. (2015) Competitive outreach in the 21st century: Why we need conservation marketing. *Ocean & Coastal Management*, 115, 41–48.

ZIMBRES, B., MACHADO, R.B. & PERES, C.A. (2018) Anthropogenic drivers of headwater and riparian forest loss and degradation in a highly fragmented southern Amazonian landscape. *Land Use Policy*, 72, 354–363.

ZIMBRES, B., PERES, C.A. & MACHADO, R.B. (2017) Terrestrial mammal responses to habitat structure and quality of remnant riparian forests in an Amazonian cattle-ranching landscape. *Biological Conservation*, 206, 283–292.

ZULUAGA, S. & ECHEVERRY-GALVIS, M.Á. (2016) Domestic fowl in the diet of the Black-and-chestnut Eagle (*Spizaetus isidori*) in the Eastern Andes of Colombia: a potential conflict with humans. *Ornitología Neotropical*, 27, 113–120.