CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Agrobiology, Food and Natural Resources

Department of Animal Husbandry and Ethology

Foraging ecology and predator avoidance in selected Neotropical Primates

DOCTORAL THESIS

Doktorand: Ing. Pavel Tománek

Supervisor: Dr. Adrian Ashton Barnett

Adm. Consultant: Doc. Ing. Helena Chaloupková, Ph.D.

Prague 2021

DECLARATION

I declare that I have prepared this thesis by myself using the cited literature. I agree to the use of included information on condition of the correct citation. Neither this Ph.D. thesis, or any substantial part of it, has been submitted to gain another or the same academic title.

Prague, …… 2021 ____________________________

ACKNOWLEDGMENTS

I would like to thank Dr. A. A. Barnett for his professional guidance, support and factual comments he provided me during the elaboration of this dissertation. Many thanks also go to all my collaborators who participated in the creation of published articles mentioned in this thesis.

Note: This doctoral thesis that follows consists of a review of the literature pertaining to the ecology of the Neotropical primate genus *Cacajao*, one published paper on which I am first author, and four other published papers on which I worked and where I appear as a co-author. The studies published in this thesis mainly concerned two genera in the Piteciindae sub-family of the Neotropical Primate family Pitheciidae, *Cacajao and Chiropotes*. However, they also include studies of species in two genera in another Neotropical primate family, the Atelidae (*Alouatta* and *Ateles*). For *Cacajao* studies focused on one member of the genus, *Cacajao ouakary* (Golden-backed uacari). However, future research will include fieldwork on the behavioral ecology of *Cacajao calvus rubicundus*, which is one of the least studied South American primates.

CONTENTS

1 INTRODUCTION

The study of primate ecology and behaviour has been key in developing strategies for their effective conservation (Fortes & Bicca-Marques 2005). These are required because of the high rate of habitat destruction that threatens the survival of these animals over much of their natural range (Estrada et al. 2017). Given this, it is clearly essential to understand the ecological and behavioural strategies that enable primates to survive in natural habitats, as well as cope with different types and intensities of environmental change (Fortes & Bicca-Marques 2005).

The life of any living organism is a constant series of trade-offs, between opposing demands on time and energy expenditure, and the need to meet physiological demands as well as to maximize inclusive fitness (Ellison 2003; Kramer & Ellison 2010;). Nowhere is this more acute than the trade-offs between feeding and predator avoidance (Caro 2005; Studd et al. 2015). Feeding is often risky as an animal may be distracted by the exegencies of food ietm selection and/or processing, and so be temporarily less vigilent (Clark & Dukas 1994). Thus, any means that maximize energetic gain from foraged items and minimize time spent in this potentially risky activity should, overall, be selected for (Caro 2005). Commensurately, animals should adjust their behaviors in relation not only to the risk of predation, but also to the type of predator, since the various forms of potential attack can make some elements of a behavioral repertoire more dangerous than others (Bateson 2002; Davies et al. 2012). Thus, animals might be expected to adjust their foraging and sleeping patterns depending on the form of predation most likely in a given site or situation (Davies et al. 2012). In addition, responses are likely to be weigted by the ´´dinner-life´´ principle, where is it is better to miss a meal, than be eaten (Dawkins & Krebs 1979). This leads to the concept of ´´pseudo-predators´´, innocuous species who´se physical appearance is suffeciently close to predators for their avoidance to be a viable survival trait.

However, avoidance of predators (and pseudopredators) needs to be circumscribed, since other biological needs must be met. How this is achieved is the subject of this thesis, which uses a series of species of Neotropical primates to test aspects of diet-item and sleeping-site selection, as well as responses to predators and pseudopredators to illustrate the dynamism and subtelties of everyday neotropical primate behavioral ecology.

2 LITERATURE REVIEW: Ecology of *Cacajao* (Pitheciidae), with reference to other large-bodied neotropical primates

2.1 TAXONOMY OF THE NEWWORLD PRIMATES (PLATYRRHINI)

The modern taxonomy of the Infraorder Platyrrhini is deeply influenced by the numerous publications of the late Philip Hershkovitz (1909–1997). This has meant that in many aspects platyrrhine taxonomy has been extraordinarily stable over the last decades, while his work has at the same time provided the wherewithal for considerable refinement and adjustments (Rylands & Mittermeier 2009).

It may well be that his legacy is the cause of there currently being more species and subspecies of primates in the New World than in Africa or Asia, providing as he did the capacity to compare findings with what is known, both in terms of the physiognomy of the primates under scrutiny and their supposed distributions. The latest taxonomies of the non-human primates indicate approximately 657 species and subspecies in 71 genera and 16 families (Rylands & Mittermeier 2009).

Two further tendencies deserve mention. The first is associated with the desce to conserve the full diversity of primates, an aspect that drags taxonomy from the realm of cataloging and academic pursuit into the applied sciences. It is of paramount importance that the full diversity of primates be recognized and mapped. The second is related to our increased knowledge of the geography of the phenotypes we observe in situ that has made it increasingly difficult to accept single definitions or dichotomies of species and subspecies. This and the new insights resulting from molecular genetics and chromosome, studies have promoted the adoption of the Phylogenetic Species Concept, and the gradual rejection of the often arbitrary interpretations of variation using the category of subspecies - see Groves 2001 (Rylands & Mittermeier 2009).

New World primates (NWPs) of tropical forests from Central to South America belong to the parvorder Platyrrhini. To shed light on their phylogeny and evolution, NWPs have been studied extensively via morphological, biogeographical, behavioral, and molecular analyses. Over the last few decades, contrasting hypotheses have been proposed, presumably due to different markers and the presence of variation and polymorphism in the characteres analysed. Agreement on the main clades of NWPs has been reached by use of different approaches, revealing a Unixe phylogenetic arrangement of Platyrrhini, with three monophyletic families: Pitheciidae, Atelidae, and Cebidae (James et al. 2018) Fig.1. Nevertheless, the exact nature of the relationships between them continues to be debated (Rosenberger 2020). Through the analysis of intergeneric and intrageneric relationships, intrafamily relationships have also been studied in depth (James et al. 2018). By incorporating all the available data, major advances have been made, and many taxonomic controversies have been clarified. Therefore, the Pitheciidae family is composed of the genera *Callicebus*, *Pithecia*, *Chiropotes*, and *Cacajao*, the Atelidae family of *Alouatta*, *Ateles*, *Brachyteles*, and *Lagothrix*, and the Cebidae family of *Cebuella*, *Mico*, *Callithrix*, *Callimico*, *Saguinus*, *Leontopithecus*, *Saimiri*, *Cebus*, *Sapajus*, and *Aotus*. However, relationships between or within some subfamilies and/or genera remain under discussion (James et al. 2018).

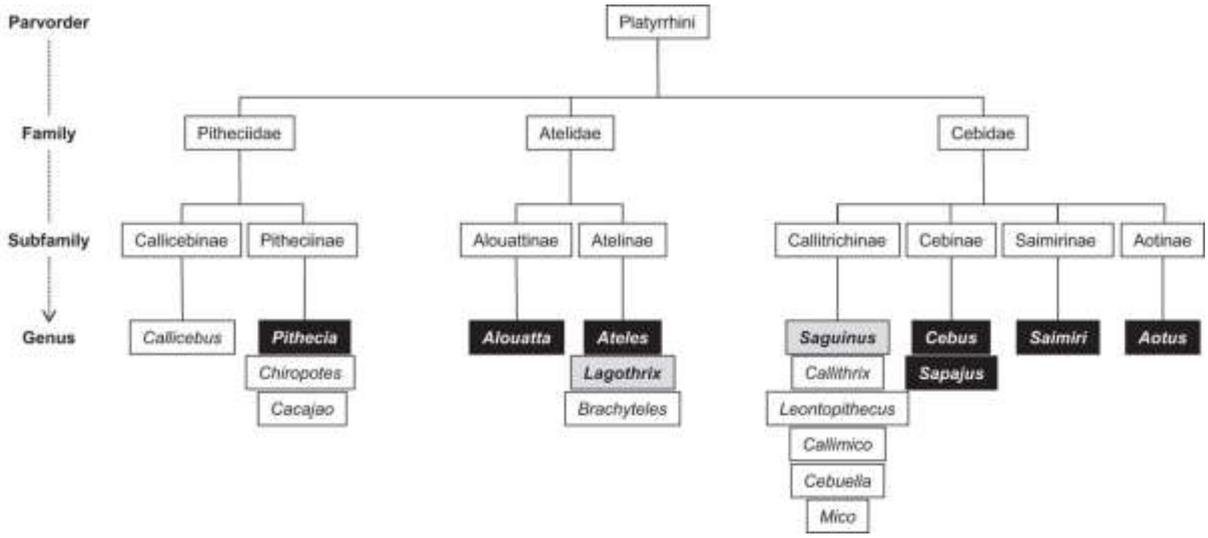


Figure 1. Diagramatic representation of Platyrrhini taxa in descending order ~~down~~ to genus level. Black and gray boxes represent New World Primate (NWP0 genera tested for CMVs (cytomegaloviruses). Black boxes correspond to NWP genera from which CMV sequences have been characterized, while gray boxes represent NWP genera from which no CMV sequence was obtained in the present study (after James et al. 2018).

Note: Now is more common to follow Bryne et al´s revision - owing to the great diversity found across titi monkey species, a new genus-level taxonomy was recently proposed that recognises three genera within the subfamily Callicebinae; *Cheracebus*, *Plecturocebus* and *Callicebus sensu stricto*.

Taxonomy of genus *Cacajao*

The *Cacajao* genus is divided into two groups, those with a naked read head (bald uacaris), and those with a furred head with black-facial skin (black-headed uacaris). There two clades of the genus *Cacajao*, are reported to have differentiated during the Pleistocene due to the fragmentation of the Amazon forest and the isolation of populations in these forest fragments or refuges (Boubli & Ditchfield 2000). There are four taxa in the former group: all considered subspecies of *Cacajao c. calvus*: *C. c. rubicundus*; *C. c. novaesi* and *C. c. ucayalii* (Figueiredo-Ready et al. 2013) (distribution see in Fig 3). The taxonomy and nomenclature of the black-headed group has been less clear-cut. Following an earlier recommendation by Hershkovitz (1987) proposed two sub-species (*Cacajao m. melanocephalus* – the black-backed uacari, and *C. m. ouakary*, the golden-backed uacari). Boubli et al. (2008) proposed that golden-back black uacari be called *Cacajao melanocephalus*, erected the name *Cacajao hosomi* for the black-backed uacari (for which they suggested the non-descriptive name ‘Neblina uacari’), and described a new species, Ayres black-backed uacari (*Cacajao ayresi*). Ferrari et al. (2014) showed that there was no reason to rename the taxa which Hershkovitz (1987) had called *C. m. melanocephalus*, and pointed out that “ouakary” remained the correct name for the black headed uacaris with golden backs south of the Rio Negro. They therefore proposed the two taxa be called *Cacajao ouakary* (Golden-backed uacari) and *Cacajao melanocephalus* (Black-backed uacari).

2.2 THE STUDY ANIMALS

In published articles, which form the main content of the dissertation, feeding behavior is mainly described in primates of the genus *Cacajao*, which is a specialist in seed consumer. For this reason, the following section provides a brief description of the morphological adaptation to diet processing, focused on in species and subspecies of the genus *Cacajao*, as well as their distribution and the nature of their habitats.

Like other members of the sub-family Pitheciinae, *Cacajao* species have morphological adaptations of the mandibular, and associated musculature, and the dentition that faciliate the predation of immature seeds located within hard-shelled fruits (Ayres 1986, 1989; Kinzey & Norconk 1990, 1993; Norconk et al. 2013). Seeds and fruits are the main food items in the diet of *C. c. calvus*, so that is is considered a frugivore specialised in immature seeds (Ayres 1986), and a habitat-specialist of the seasonally-flooded forests (Barnett et al. 2012b; Vieira et al. 2008). Figs 2 and 3.

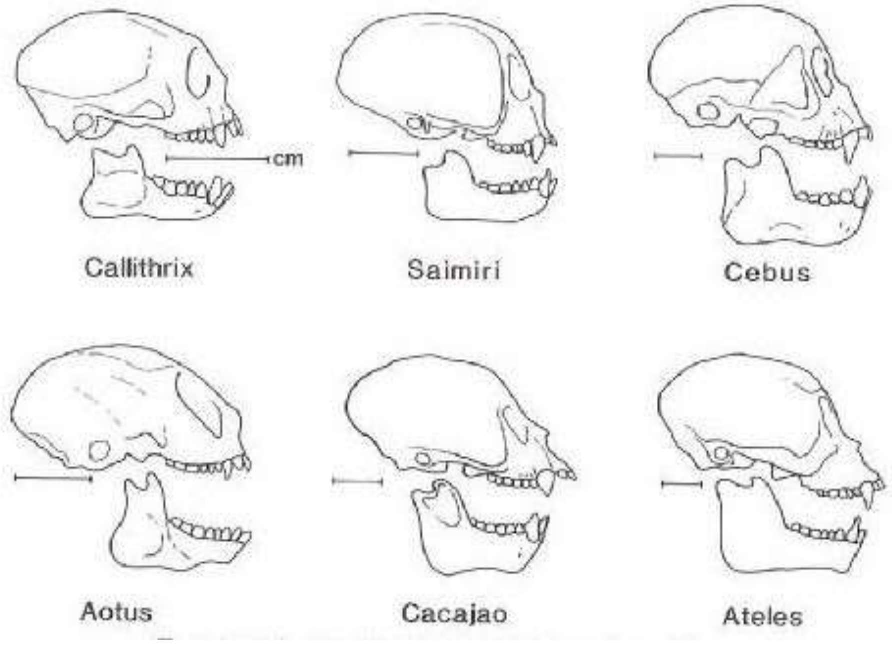


Figure 2. Skulls of several extant platyrrhines (Fleagle 1998)

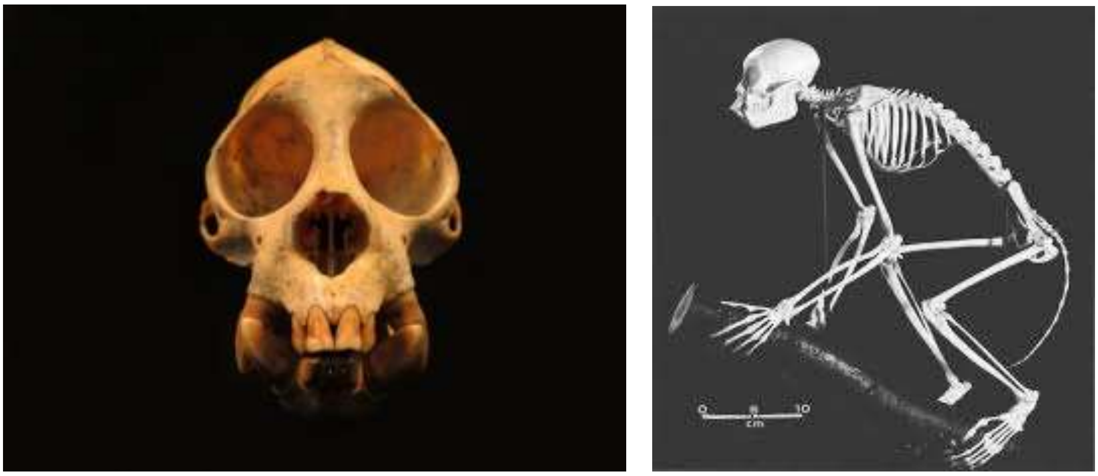


Figure 3. *Cacajao* skull and skeleton: showing (left) hypertrophied canines and procumbent incisors, and (right) the robust mandible, as well as the short tail characteristic of the genus

The white uacari, *Cacajao c. calvus* was studied by Ayres (1986), but the conspecific Solimões Red uacari, *Cacajao c. rubicundus* has received little attention. The white uacari was considered a subspecies endemic to the SDR Mamirauá flooded forests. However, more recent sightings have extended its distribution (Vieira et al. 2008, Cardoso et al. 2014) - see Fig 4.

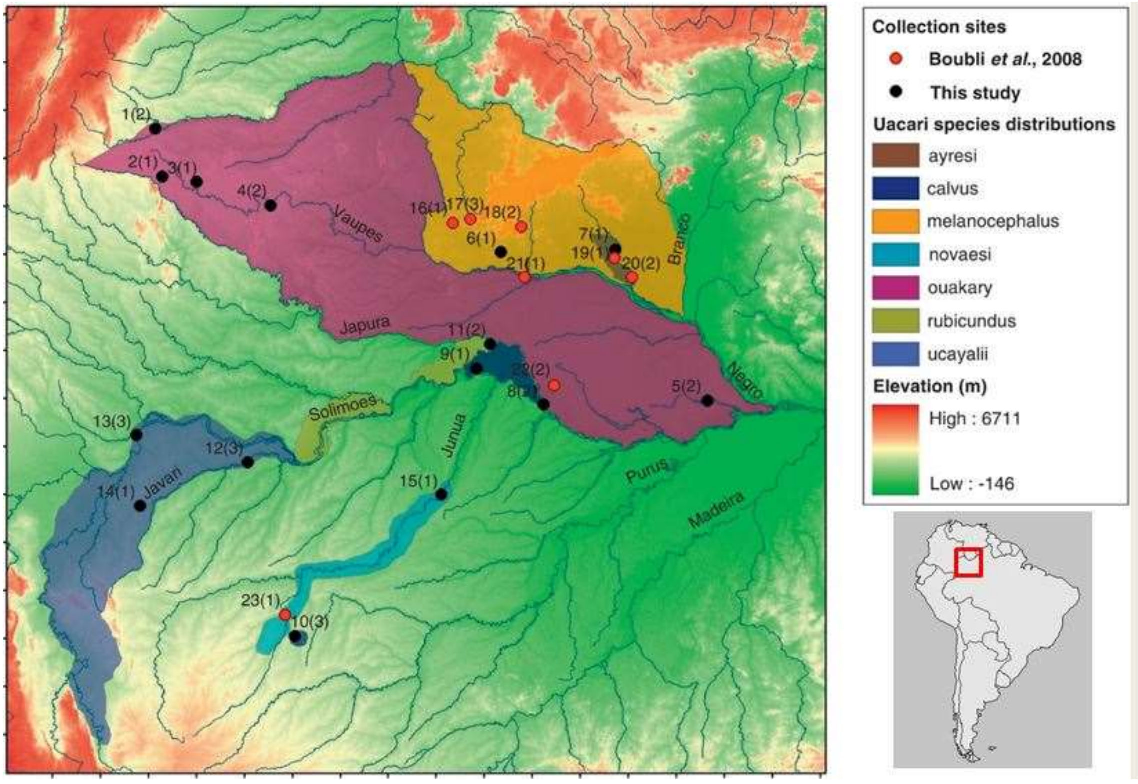


Figure 4. Distribution map of the various *Cacajao* taxa (main map), with a locator insert.

Another important aspect is the occurrence of sympatric primates considered essentially frugivorous on the left bank of the Solimões River, in the flooded forests of SDR Mamirauá. In the area in which this study has been proposed, for example, the area has *Pithecia cazuzai, Pithecia chrysocephala, Pithecia hirsuta* (Marsh 2014), *Ateles chamek, Saimiri boliviensis, Cebus albifrons and Sapajus macrocephalus* in addition to *C. c. rubicundus*. The genus *Pithecia* is also gramnivorous and specialised in seed predation (Kinzey & Norconk 1993; Norconk & Setz 2013; Cunningham & Janson 2006, Palminteri et al. 2012), while *Ateles* is a frugivore specialised on ripe fruit (Di Fiore et al. 2008).

2.3 FEEDING STRATEGY

The sympatry between potential primate competitors can result in different foraging strategies that optimise the use of resources (Vogel et al. 2017). Kinzey & Norconk (1990), in a comparative study, have developed a method for testing the fruit resistance to puncture and the seed resistance to crushing, using these parameters as criteria for food choice in *Chiropotes satanas* and *Ateles paniscus*. Both fed on the same fruits, but at different stages of ripeness. According to these authors, being able to puncture the hard shells of unripe fruit, *Chiropotes* has access to nutritive seeds with a smaller amount of toxic compounds. Reporting on data from Peru, Bowler & Bodmer (2011) ranked qualitatively the fruits of 6 of the 10 species most consumed by *C. c. ucayalii* as being "hard" or "very hard", which supports the hypothesis that uacaris feed selectively on harder fruit, instead of using such items only when ripe fruit are unavailable.

Uacaris appear to avoid foods with relatively large amounts of condensed tannins, total phenols and fiber. The extent to which seeds were used, appears to be linked to their fat content (Ayres 1986). There is considerable variation between months in the amount of food, rank in the monthly diet, and selection ratios within the same species. These changes could be due to several factors, including the chemical changes that occur as fruit matures.

For example, Ayres (1986) analysed immature and mature fruits of *Brosimum lactescens* (Moraceae), a species ranked number two in the annual diet of *Cacajao c. calvus*. Fruits were collected at the same time, then separated according to maturation stage. He found that ripe mesocarps were preferred to unripe ones which are discarded, while seeds in both maturation stages were eaten. Ripe and unripe seeds were preferred to ripe mesocarps. There were cases, however, where ripe mesocarps were preferred over seeds. *Apeiba* cf. *butchelli* (Malvaceae) has a relatively large fruit (up to 20 grams). Fruits from this species accounted for 10.5% of the diet of *Cacajao c. calvus* in some months. Both pulp and seeds from mature fruits lacked condensed tannins and total phenolics, and had very similar fibre contents. Seeds had 3.7 times more protein, but mesocarps had 3.04 more fats. Ayres found that uacaris threw away the seeds, eating only the ripe mesocarp which contained a very conspicuous yellow oil. Despite the relative lower fat content of the seeds, they were apparently of high nutritive value compared to most other foods.

In addition, age-sex differences in the capacity to open hard fruits have recorded in *Cacajao* spp. There are no records of juveniles of *C. melanocephalus* and *C. c. ucayalii* opening the fruits of greater hardness, which the adults often use in their diet (Boubli 1999; Bowler & Bodmer 2011). Likewise, male adult of *C. c. ucayalii* consume fruits of greater hardness than adult females. The sexual dimorphism in teeth and jaw, with the canines proportionately greater in adult males, is responsible for this difference in diet (Bowler & Bodmer 2011). Given the sympatry between frugivorous primates, the hardness of fruit can be considered an important variable in resource partitioning and a guideline to interspecific interactions.

In this regard, the classical model of foraging shows that, while individuals will focus their diet on just a few items during periods of high resource availability, the range of the diet increases when there is an overall decrease in the availability of those resources which the animals are best morphologically and physiologically adapted to exploit (MacArthur & Levins 1967). Cunningham & Janson (2006), in a study the diet of *Pithecia pithecia*, found that a single species (*Licania discolour*, Chrysobalenaceae) was the most abundant resource in the three sampling periods due to its high fruit productivity. *Pithecia pithecia* consumed *Licania* seeds, which were an important source of calories and nutrients. Consequently, the seasonal decrease in fruit production of this tree was responsible for the decrease in the consumption of this item in the third observation period (in May), when there was an increase in the consumption of leaves, flowers and insects (Cunningham & Janson 2006). Seasonal increases in non-fruit vegetable items, such as insects, have also been recorded for *C. ouakary* (Barnett 2010; Barnett et al., 2013) and *Chiropotes albinasus* (Pinto et al., 2018).

Similarly, Bowler & Bodmer (2011) demonstrated that the main item food in the diet of *C. c. ucayalii* changed during the dry seed to ripe fruit, mainly due to the presence of fruiting *Mauritia flexuosa* palms. The proportion in the consumption of fruit with ripe pulp was negatively correlated with its availability in the area used by the group, indicating an adjustment in the diet due to the distribution of this seasonal item (Bowler & Bodmer, 2011).

Studies of primate diet and food choice are common, but those involving optimal foraging are rare. Dias da Silva et al. (2020) studied optimality in foraging behavior of the golden-backed uacari, a specialist Amazonian seed-eating primate. Results showed biggest is not always best, because large fruit are hard to handle and take a long time to peel. Consequently, overall energy yield is less than that obtainable from medium-sized fruit, especially those the same length as the uacaris hand. Size of the fruit, thickness of the pericarp and relative weight/volume of seed/fruit are so selection criteria for the species *Cacajao ouakary* during the foraging of large fruits of *Aldina latifolia* - Fig.5. In addition, results suggest that the anatomy of the animal may be a limiting potential in the choice of fruits (Dias da Silva et al. 2020).

Figure 5. *Aldina latifolia* fruits, showing variation in size (left), and the thickness of the husk (right) (photos A.A. Barnett)

2.4 MORPHOLOGICAL FORAGING ADAPTATION OF PITHECIIN MONKEYS

Pitheciines (*Pithecia*, *Chiropotes*, and *Cacajao*) are a specialized clade of Neotropical seed predators that exhibit postcanine teeth with low and rounded cusps and highly crenulated occlusal surface enamel (Ledogar et al. 2013).

These genera exhibit a suite of cranial, mandibular, and dental morphologies hypothesized to be adaptations for feeding on mechanically challenging unripe fruits and seeds, yet pitheciines (*Pithecia*, *Chiropotes*, and *Cacajao*) exhibit significantly low molar shearing potential, occlusal surface relief, and overall surface curvature. Large canines and procumbent incisors (Fig. 6) allow pitheciines to extract nutrient-rich seeds from inside unripe fruits before being processed by the postcanine dentition, a process termed ´´sclerocarpic foraging´´ by Kinzey (1992) .

Figure 6. Skull of *Chiropotes satanas*. Note the large and robust canines, procumbent incisors, and deep mandible.

These findings concur with previous comparative analyses, and support the hypothesis that pitheciine molars are adapted to a specialized diet of unripe seeds that are both tough and crush- resistant (Kinzey 1992, Ledogar et al. 2013).

Pitheciine crania are well-suited to generate and withstand forceful canine and molar biting, with the prediction that they generate bite forces more efficiently and better resist masticatory strains than the closely-related *Callicebus*, which does not specialize on unripe fruits and/or seeds (Ledogar et al. 2018). *Pithecia*, *Chiropotes*, and *Cacajao* share a similar topographic pattern, suggesting adaptation to foods with similar structural and/or mechanical properties. However, *Cacajao* differs in surface complexity, which reflects some variation in its feeding ecology. *Cacajao* exhibits a less complex occlusal surface compared with *Pithecia* and *Chiropotes*, which could reflect some difference in the fracture properties of seeds in the *Cacajao* diet and/or their decreased reliance on leaf material compared with other pitheciines (Ledogar et al. 2013). This reduced competition allows uacaris to choose from a wider variety of fruits at various stages of ripeness (Ledogar et al. 2018). It is also worth mentioning in this context that both *Cacajao* and *Chiropotes* bite selectively at areas of fruit that are naturally weak either because they are sutures or the thinnest parts of a fruit´s husk (Barnett et al. 2017; AA Barnett, unpublished data, respectively). This both economizes on energetoc expenditure and reduces the chance of dental breakage.

2.5 CONSEQUENCES OF DIET TYPE

Most animals need to actively search for food to meet energetic requirements and live in heterogeneous environments where food resources have complex spatio-temporal patterns of availability. Consequently, foraging animals need to find a balance between effort and resource allocation while accounting for intrinsic and extrinsic factors, which are often overlooked when modelling foraging behaviour (Plante et al. 2014).

The foraging strategy adopted by an animal is the reset of complex interactions between its internal requirements and its environment (Stephens, Brown & Ydenberg 2007; Nathan et al. 2008). For black howler monkeys, it appears that both intrinsic (hunger and food preferences) and extrinsic factors (spatial distribution of preferred species, food items and high-quality patches) drive their foraging movements. Food preference emerges as the main driver of the black howlers' foraging, by directing movements and by inducing considerable use of highquality patches (Plante et al. 2014).

Neotropical monkeys are mostly highly arboreal, spending most of their time feeding and traveling in the upper canopy. They may be the terrestrial of the platyrrhines too (Barnett et al. 2012a), when engage in this behavior in response to the particular ecological contexts, for example retrieval of specific high-yield resources, such as insects or germinating seeds (Barnett et al. 2012b). Uacaris are unique among the platyrrhines in their degree of preference for flooded forests and most references to their terrestrial use are related to seasonal shortages of arboreal foods (e.g. Ayres, 1986). However, the rate and persistence of this activity appears to differ greatly among populations and species (Barnett et al. 2012c), with some populations undergoing seasonal mingrations to non-flooded forests (Barnett et al. 2013), which may occasionally be quite extensive (Defler 2001).

The foraging behaviour in social animals like primates is an important mechanism to offset the effect of seasonality in resource provision through organisation into subgroups or subunits for foraging (Garber 1987). The mechanism of fission-fusion (Aureli et al. 2008) has been interpreted as a strategy that allows some primate species to optimise the use of resources, especially fruits, during seasonal variations in their availability (Di Fiore et al. 2008). The formation of groups with large subunits operating in a fission-fusion system is a characteristic of the genus *Cacajao* (Ayres 1986; Bowler & Bodmer 2009).

2.6 INFLUENCE OF PREDATION ON THE BEHAVIOR OF NEOTROPICAL PRIMATES

One of the characteristic manifestations of primate behavior is their arboreal lifestyle, especially in New World monkeys (Platyrrhini). The absence of land thus raises questions about the ecological pressures that limit the occurrence of platyrrhins in terrestrial niches (Monteza-Moreno 2020).

The advantage of a treetop lifestyle is a reduction in the risk of predation. However, mobility in treetops means increased costs for primates to avoid moving on the ground if the risk of predation is low. In such situations, they are offered rich food sources on the forest floor, which can be an alternative in the absence of sufficient food on the trees (Monteza-Moreno 2020).

A great influence on the daily behavior of primates is their threat from predators, not only during the search for and consumption of food, but also during rest or night's sleep. Both large and small neotropical primates are preyed upon by several animals. Predators include constricting and venomous snakes, tayras, felids, domestic animals, and even other monkeys (Fernández-Duque et al. 2012). Primates often have to travel long distances to find suitable food (Schaffer 2013), often at a high energy price (Grove 2012; Markham & Gesquiere 2017). It is believed that species with large daily ranges should minimize wasteful time or energy expenditure in order to optimize their time and energy budgets (Pontzer et al. 2014). Primates thus issue various alarm calls that distinguish between types of predators, thereby inducing behavior suitable for preventing predatory activity (Arnold & Zuberbühler 2006). Primates also exhibit various behaviors against predators, including avoiding sites of possible assault (Barnett et al., 2012b).

One such manifestation is the choice of place to sleep, which is considered an example of such an adaptive response (Anderson, 2000). This can be influenced by various factors, including: suitability to escape from predators (Albert et al., 2011); minimizing predator detection (Ellison et al., 2019); and, conversely, maximizing the detectability of predators (Barnett et al., 2012b), and their complicated approach to prey (Matsuda et al., 2008a).

2.7 THE STUDY HABITAT

Amazon flooded forests

Amazonia is characterized by a wide range of vegetation types that affect the ecological distribution of the regional biota (Haugaasen & Peres 2005). While some species exploit a variety of habitats, others are primarily or entirely restricted to particular vegetation types. However, while the main determinants of the variation in primate species richness between sites are currently under debate (Eeley & Lawes, 1999; Peres & Janson, 1999). Peres (1997) found that on a local scale, habitat heterogeneity within and between different sites (α-diversity and β-diversity, respectively) is the best determinant of primate species richness (Haugaasen & Peres 2005).

The two most widespread forest environments in Amazonia are unflooded forests (hereafter termed ‘‘terra firme’’) and seasonally flooded forests, which represent the main difference in terrestrial macrohabitats across the region. Terra firme forests account for 83% of the central Amazon basin and are situated on land that never floods (Hess et al., 2003). Consequently, these unflooded forests are situated on well drained soil that tends to be heavily leached and nutrient-poor because it has long been deprived of alluvial sediments. The remaining 17% of the central Amazon basin consists of wetlands, 70% of which is seasonally flooded forest (Hess et al., 2003, Haugaasen & Peres 2005).

There are two principle types of flooded forests in Amazonia: várzea, Holocene floodplains or paleo-Pleistocene floodplains on white-water rivers (Junk et al. 2012), and the forests of igapó, on clear- and black-water rivers. These are classified according to hydrochemical (Sioli 1956) riverine (Sioli 1956), and floristic characteristics (Prance 1979). The formation of várzea and igapó is closely related to sea level fluctuations during the Pleistocene times is therefore a direct result of past global climatic changes (Junk 2013).

The Holocene is the geological epoch that began approximately 9,700 BCE following the end of the Pleistocene, itself the geological epoch which lasted from about 2,588,000 to 11,700 years ago, and which spanned the world's most recent period of repeated glaciations.

Due to Andean headwaters, Amazonian white-water rivers have a high sediment load and deposit some of this on broad floodplains which are nutrient-rich and highly productive. Clear- and black-water rivers, in contrast, are nutrient poor, as are the soils associated with their floodplains. Fed by large volumes of sediments, várzea-covered floodplains are wide (up to 10km), while igapó floodplains rarely exceed 100m (Barnett 2010; Haugaasen & Peres 2005; Melack & Hess 2010) - Fig.7.

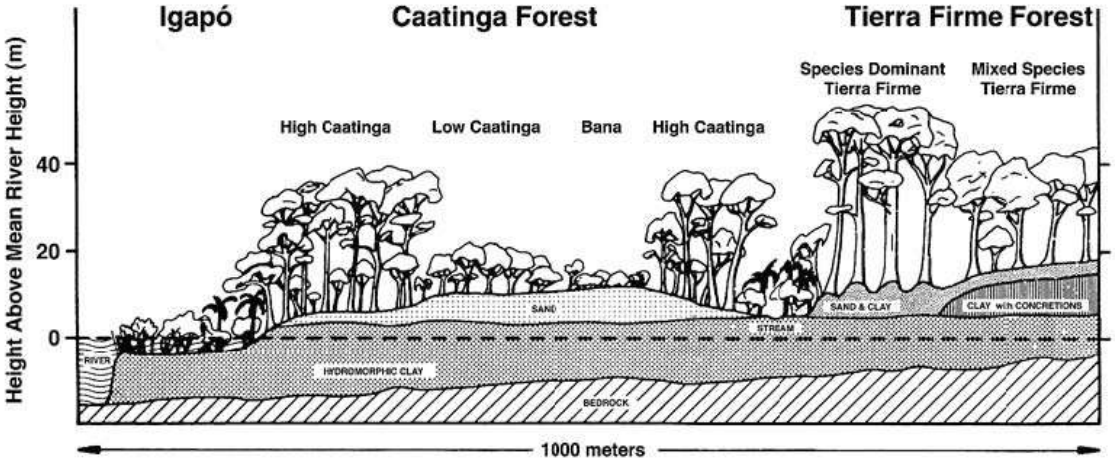


Figure 7. Idealized transect along a gradient from river to lateritic uplands. The igapo forest on the banks of the Rio Negro on the left is flooded for part of the year. Where coarse sand has been deposited, *caatinga* forest occurs where the water table is shallow, and *bana* occurs in areas with a deeper water table (after Jordan et al. 2013).

In both floodplain types, flooding may occur for up to 8 months and floodwater may reach 8m and hypoxia or anoxia occurs. Thus, many várzea and igapó plant species have a suite of adaptations to this annual inundation pulse (Ayres 2006), these include: morphological and physiological adaptations (Parolin 2001; Parolin et al. 2003), as well as fruiting and leaf-flush phenology, which is synchronized with river flood pulses (Correa & Winemiller 2014). Many várzea species are water-or fish-dispersed (Correa et al. 2007).

As a result, the Amazon flooded forests present a unique opportunity to understand how a biota adapts to seasonal environmental variations (Fig.8).

Figure 8. Floating seeds in flooded igapó forest (arrowed, left), and (right) *Cebus albifrons* about to visit a seed patch in non-flooded igapó (photos A. Barnett)

This is made more complex by the heterogenity of environment, a result of the deposition/erosion balance of water–born sediments, which provide different inundation and drainage regimes for associated vegetation. As a result, in várzeas, there are three main vegetation types: a) High Restinga-a forest plant assemblage occupying higher land where water column depth ranged from 1 to 2.5 m (flooded, <3 months/year); b) Low Restinga – a forest assemblage occupying lower-lying land where the seasonal maximum inundation depth ranges between 2.5 and 5 m(flooded, >3 months/year) and; c) Chavascal – a vegetation assemblage of dense shrubs and small trees occurring in areas where the water column depth ranged between 5 and 7 m (Ayres 2006; Junk et al. 2012; Ferreira-Ferreira 2015) - Fig 9.

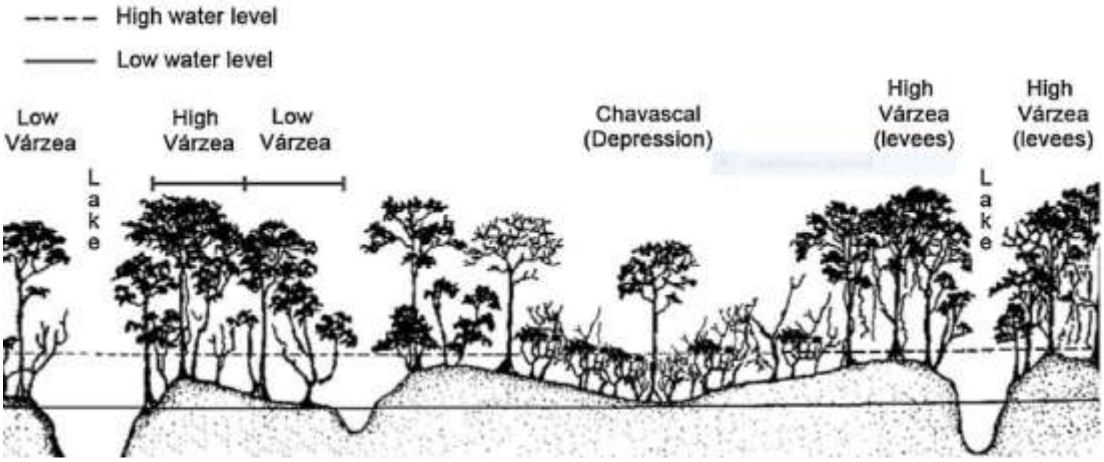


Figure 9. Conceptual cross-section diagram showing the three main forest types present in Mamirauá Sustainable Development Reserve (Central Amazon, Brazil) (after Ferreira-Ferreira 2015).

2.8 FLOODING AND PRIMATES

This flooding process and the annual variation in water level are also considered key reasons for várzea's very low faunal diversity (Ayres 1986; Haugaasen & Peres 2005; Adis et al. 2010). According to Ayres (1986), the processes of vertical and horizontal migration are very important for fauna to avoid unfavourable conditions arising from the variation in water level. Large rivers can be significant ecological barriers to terrestrial fauna and impede horizontal migration. This may be responsible for reducing species diversity in the flooded forest (várzea) compared to the adjacent to the Terra Firme (never-flooded) forest. The richness of mammal species for example in Mamirauá's flooded forests is lower compared with the forests of the Terra Firme on the opposite bank of these two rivers and only arboreal mammals or good swimmers can survive in the seasonal variation imposed by this habitat (Alvarenga et al. 2018; Ayres 1986).

On the other hand, the lower species diversity of such arboreal mammals as primates may be related to other factors, such as lower habitat quality in terms of abundance, diversity and distribution of resources (Ayres 1986; Haugaasen & Peres 2005). Haugaasen & Peres (2005) undertook a comparative study in the lower Purus River and found 12 primate species in Terra Firme forest, while in flooded areas there were just 8 species. Only three species occurred exclusively in flooded habitats. According to these authors, this difference shows that few species can survive exclusively in the floodplain forests, while most species found in lowland adjacent to Terra Firme ecosystems require both forest types to meet their metabolic needs throughout the year (Barnett & Jucá 2018, Barnett 2019). The availability of fruits in some periods of the year seems to be responsible for the seasonal presence of some Terra Firme species (e.g. *Ateles chamek*, *Cebus albifrons*, and *Lagothrix lagotricha*) in flooded forest (Haugaasen & Peres 2005).

Similarly, Ayres (1986), in a pioneering study with *Cacajao c. calvus* in the Holocene várzea between the Solimões and Japurá rivers (focal area of Mamirauá DSR), recorded just 4 species of sympatric primate, but, in flooded forests located west of the Paraná do Aranapú (subsidiary area of Mamirauá DSR), where the várzea is richer and of Pleistocene origin, there were at least six primate species in sympatry. One of the study questions of Ayres (1986) was: Why is the genus *Cacajao* the only one frugivore among the Neotropical primates able to live in Japurá/Solimões Holocene flooded forest (Ayres 2006), and why does it not occur in Terra Firme? The specialisation in seed predation on fruits at different levels of ripeness was seen as an essential factor in the survival of this species in this ecosystem (Ayres 1986).

2.9 EFFECT OF SEASONALITY

The effect of seasonality on the availability of resources, and in the social organisation of primates, may also require adjustments to their activity patterns. Consequently, it would be expected that larger groups would allocate more effort in feeding and movement, and less in resting and socialising than smaller groups. Group size and home range will be influenced by the pattern of spatial-temporal distribution of food resources (Terborgh & Janson 1986).

Uacaris and cuxuis have among the largest home and day ranges of any neotropical primates (Barnett et al. 2013). Total home range size and core areas used are smaller during the short dry season (September through December), when resource abundance is lowest (Shaffer 2012). In the study by Ayres (1986), the average activity of *C. c. calvus* each month was strongly associated with the distance travelled daily, with the water level and with the availability of ripe fruit. Also, during the wet season the time spent in "Movement" was significantly higher and lower in "Resting".

For uacaris, between-site variation has been recorded for some key ecological aspects. For example, in the extent of movement between habitats it appears different between places; in Jaú studies using transects on the mainland have never recorded *C. ouakary* more than 500m away from the igapó, but in Caparú on the Rio Apaprois, Colombia, the species is know to travel for many kilometers inside terra firme (Barnett et al. 2018a).

The weather in the tropics is dominated by the tropical rain belt, which moves from the northern to the southern tropics and back over the course of the year. The tropical rain belt lies in the southern hemisphere roughly from October to March; during that time the northern tropics have a dry season with lower precipitation, and days are typically sunny throughout. From April to September, the rain belt lies in the northern hemisphere, and the southern tropics have their dry season. Under the Köppen climate classification, for tropical climates, a dry season month is defined as a month when average precipitation is below 60 millimetres (Peel et al. 2007).

As a result, Amazonian floodplains are subjected to annual water level fluctuations of up to 14 m, which result in annual flood periods of up to 210 days in the forested wetlands (Ferreira & Parolin 2007). Average maximum flooding depths can reach up to 16 m in Western Amazonia, 10 m in Central Amazonia, and 6 m in Eastern Amazonia, and local flooding extent and duration depends on the interaction between precipitation, river discharge and topography. The flood pulse is the main ecological driver in the floodplain, controlling the occurrence and distribution of plants and animals, life-history traits, primary and secondary production, and also influencing carbon respiration, decomposition and nutrient cycles in water and soils (Junk 2013, Ferreira-Ferreira 2015). Ayres (2006) described different várzea forest types according to the mean inundation depth along the lower Japurá River (see Section 2.5 above).

In such forests, duration and predictability of the river level fluctuation and flooding have strong effects on the reproductive phenology of trees (Parolin 2001). Trees in Amazonian floodplains appear to have evolved the timing of their flowering and fruiting period to maximize vegetative competitive ability of individuals, and to maximize use of pollinating and dispersal agents in relation to the flooding periodicity (Ferreira & Parolin 2007). Fruit maturation occurs mainly at high water levels, when water and fish enhance seed dispersal, but the onset of flowering and fruiting may vary between species and along the flooding gradient (Ferreira & Parolin 2007).

The topography of the home range is likely to be an important factor to explain the daily distance travelled. This is because, as for the *C. c. calvus* studied by Ayres (1986), the habitat consists of long, narrow strips of restinga vegetation, interspersed with wide swathes of lower chavascal - Fig. 10.

Figure 10: Amazon Basin Floodplain types: várzea (up) in the flooding season, showing the complex topography and width of the floodplain; flooded igapó (down) occurs on a much narrower and topographically simple floodplain (photos M. Roggo)

Using the nomenclature used by the local population, Ayres classified the forests as *chavascal* (mean inundation of 5.0–7.0 m), *restinga baixa* (2.5–5.0 m), and *restinga alta* (1.0–2.5 m) (this is now the standard nomenclature for these associations: see Junk et al. 2010).

Ayres (1986) showed how this pattern resulted in extensive movement by *C. c. calvus* groups in order to reach different feeding sites. Once again, the selection of fruits or seeds of high caloric value was considered to be related to the extensive home range and to the long distances covered to access these resources. Home range size is also explained by the rate of resource renewal at feeding sites (Boubli et al. 2008). If a particular resource has a low renewal rate, and if this is a common feature of the habitat, then it is expected that a group will travel across a large area, visiting several such resources in sequence before returning to the first, since this by now should have had a chance to renew the resources to a level of availability that makes its exploitation energetically viable (Boubli 2008).

Note: Following the above described aspects of the environment and their influence on the behavioral strategies of Neotropical Pitheciidae primates, the following aspects were considered in this dissertation:

- diet composition
- foraging
- seed dispersal
- defense strategies - places to sleep and rest and the reasons for their choice, contact with predators

3 PUBLISHED STUDIES

Note: The following paper deals with the behavioral ecology of the golden-backed uacari, specifically the topics of food, foraging, seed dispersal, sleeping sites and predation. The text was originally published in Portuguese.

3.1 THE ECOLOGY OF THE GOLDEN-BACKED UACARI (*CACAJAO OUAKARY*) (PITHECIIDAE) IN AMAZONIAN BRAZIL

ADRIAN A. BARNETT[1,2], **PAVEL TOMÁNEK**[3] & LUCY M. TODD[1]

[1]Centre for Research in Evolutionary and Environmental Anthropology, Roehampton University, London, England

[2]Amazon Mammal Research Group, *and* Flooded Habitats Study Group, Institutio Nacional de Pequisas da Amazonia, Manaus, Brasil.

[3] Department of Animal Behaviour, Czech University of Life Sciences, Prague, Czech Republic.

Published in:

Urbani B, Kowalewski M, Cunha RGT, de la Torre S & L Cortés-Ortis (eds.) *La primatologia en Latinoamérica 2- A primatologia na America Latina 2. Tomo I Argentina – Colombia.* Idiciones IVIC. Instituto Venezolano de Investigaciones Cientificas (IVIC). Caracas, Venezuela. 2018. Pp. 219-228. ISBN 9789-8026-1185-0

ABSTRACT

The golden-backed uacari, *Cacajao ouakary*, is a medium-sized primate from western Amazonia. It was originally considered highly specialized in habitat (*igapó*) and diet (immature seeds of hard-husked fruits). However, more recent research has shown that, while *igapó* is its prime habitat and such seeds its principle food, it uses other habitats when food is scare in *igapó*. Morever, it also eats leaves and insects, and may act as a seed disperser in some instances. It also shows subtleties in food choice and processing, biting at the weakest points, and choosing larvae-infested fruits of some species.

Choice of sleeping trees is also very specific and may be related to avoiding predation, as may its patterns of site choice when foraging terrestrial. Further research is needed on factors influencing diet choice, habitat use and the resilience of the species to human-mediated change.

KEY WORDS: igapó, neotropics, primates

INTRODUCTION

The golden-backed uacari is a medium-sized Neotropical primate (adult weight, 3-4 kg) in the Pitheciidae, a family that also includes *Callicebus* (titis), *Chiropotes* (the cuxius) and *Pithecia* (sakis) (Groves 2001). The tail is remarkably short and the hair on the flanks and shoulders is long (Figure 1). Until the latter part of the 1980s, there were no dedicated field studies of *C. ouakary*. Since then, there have been studies in both Brazil and Colombia (Barnett et al. 2013). This chapter provides a description of the current knowledge status of *C. ouakary*, based mainly on studies carried out in the Jaú National Park, Amazonas state, Brazil. Because clear taxonomic definitions are important for ecological and conservation studies (Rylands & Mittermeier 2009), the history of the current Latin name of the golden-backed uacari is also discussed briefly. The anatomical characteristics of *C. ouakary* and the studies that link morphological and anatomical aspects with ecology and theoretical considerations are discussed in Barnett (2010), and are not mentioned here.

Figure 1. The golden-backed uacari, *Cacajao ouakary* (Photo: Gareth Jones)

BRIEF PORTRAIT OF NOMENCLATURAL HISTORY OF UACARI OF GOLDEN BACK.

The *Cacajao* genus has two major divisions: the red-headed uacari (the subspecies of *Cacajao calvus*) and the black-headed uacari (Barnett 2005). The golden-backed uacari is a member of the second group.

The golden-backed uacari was originally described (as *Brachyurus ouakary*) by the German naturalist explorer Johann Baptist von Spix in 1823, based on a specimen collected in February 1820 when he was visiting the lower Rio Negro as part of his scientific exploration in Brazilian Amazon made between 1819 and 1820 (Hershkovitz 1987). Subsequent changes were described by Barnett (2005). Up to this stage there were two black-headed uacari, the black-backed uacari (*Cacajao m. melanocephalus*) and the golden-backed uacari (*C. m. ouakary*).

After a genetic analysis, de Figueiredo (2006) raised these two rates to the species level. Boubli et al. (2008) followed Figueiredo (2006), considering the two current rates of being true species, while adding a third species, *C. ayresi*, based on three specimens collected in the foothills of the Pico da Neblina mountain range, northwestern Brazil. They considered *C. ouakary* to be a junior synonym for *C. melanocephalus*. Confusingly, they chose to rename the nominal subspecies, not the junior synonym. Under this arrangement, the new name for *C. ouakary* (*sensu* Figueredo) became *C. melanocephalus*, while *C. melanocephalus* (*sensu* Figueredo) was renamed *C. honsomi*. Studies by Ferreri et al. (2014) showed that 1) *C. ouakary* is the valid name for populations of black-headed uacaris with golden backs, 2) *C. melanocephalus* is the most appropriate name for populations north of Rio Negro, and 3) currently, there is insufficient evidence to consider ayresi a full and valid species, and the taxa can be considered, at most, as a subspecies of C. *melanocephalus*, *C. m. ayresi*. Subsequently, Bertuol (2015a) showed that there is an insufficient genetic distance between 'ayresi' and other members of the genus *Cacajao* for taxa to be considered a species. Therefore, Bertuol (2015b) considered that there is a form of genetic structure between the two black-backed uacaris, supporting the subspecies division of Ferrari et al. (2014). Subsequently, other authors (e.g. dos Reis et al. 2015) have used *C. ouakary* as the name for the golden-backed uacari, and this arrangement is followed here.

FIELD STUDIES

For *C. ouakary*, long-term studies were conducted in three locations: the Jaú National Park and the Amanã Sustainable Development Reserve (both at the interfluvium between the Solimões and Negro rivers in the western Brazilian Amazon) and Caparú, on the Apaporis River, Eastern Colombian Amazon (Figure 2). In addition, some short-term studies were carried out in the Jaú River area (Rylands 1992; Barnett et al. 2000, 2002, 2005), along the lower Rio Negro (Mittermeier & Coimbra-Filho 1977), and in tributaries of the upper Rio Negro (the Curicuriari and Uaupés rivers: da Cunha & Barnett 1990; Barnett & da Cunha 1991).

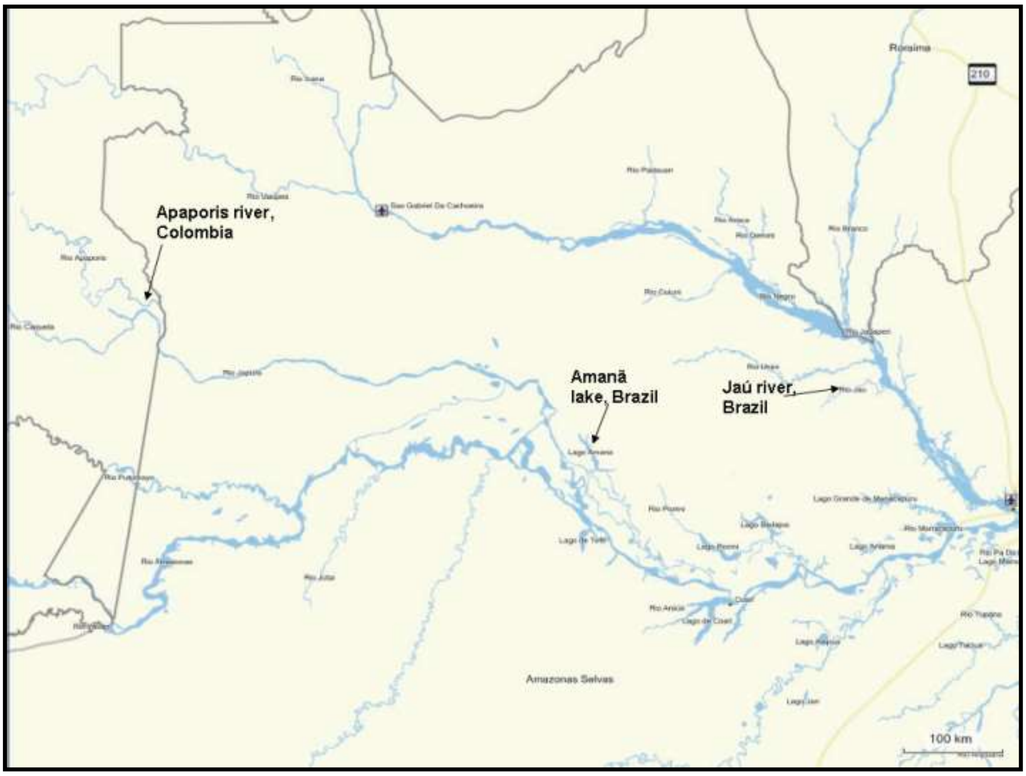


Figure 2. Locations of the three field work sites mentioned in the text

In each place, the groups studied were observed mainly in igapó, one of the two main types of seasonally flooded forests on the banks of rivers in the Amazon basin. Igapó occurs on the banks of black water rivers (Prance 1979). In comparison to terra firma (never-flooded) forest, the igapó has fewer tree species (212 vs. 89 per ha, in Jaú: Barnett 2010), but a greater equatability (in igapó the six most common species contributed 49%, but only 13% on dry land). In igapó plots, less than 10% of species were represented by a single individual, but on dry land 65.9% of species were like this: Barnett 2010). Black water rivers are poor in suspended sediments, and the floodplain is narrow, with a steep slope. As a result, the duration of annual floods can vary from 30 to 210 days. For this reason, most species in igapó will occupy only part of the plain, based on their physiological tolerance to flooding (Parolin 2002). However, even if its width is generally less than 100m, the igapó is complex, with vegetation in diffuse bands and with distinct composition and discrete distances between the shore of the mainland and the open water (Ferreria 1997; Barnett 2010). The other largest type of seasonally flooded forest is várzea, which occurs on the broad floodplains along the banks of whitewater rivers. Because of the high levels of sediment in the waters, the plains may be many kilometers wide and, because of their lower general inclination, they are mainly structured by a system of channels and levees (elevated areas) (Ayres 2006).

Patterns of production of leaves and fruits in igapó are linked with the pulses of seasonal flooding (Parolin et al. 2002). With more or less 60% of the trees in igapó are dispersed by fish or water (Correa et al. 2007), the fruit production happens mainly during the periods when riverwater levels are highest. Production of new leaves usually takes place after the fruiting season is finished (Haugaasen &

Peres 2006). The result is an extreme seasonal skew in fruit availability, with (in Jaú) 80% of species fruiting during the flooding period. In addition, species that do not bear fruit in the maximum flood season are generally small and rare (e.g., in Jaú - *Mouriri guianensis*, Melastomataceae; *Caraipa grandifolia*, Calophyllaceae). When upland and flooded forest phenologies were studied quantitatively, it was revealed that both have peak asynchronism in flower and fruit production (e.g. Haugaasen & Peres 2006; Barnett 2010). Consequently, there is a seasonal movement of mammals and birds between the two types of forests, as the species follow seasonal fluxes in food availability. This happens with primates (Haugaasen & Peres 2005), other arboreal mammals (e.g. Haugaasen & Peres 2007), and bats (Bobrowiec et al. 2014). However, the movements and peaks do not match perfectly; in Jaú, for example, golden-backed uacaris stay in the igapó after the main fruiting season ends, eating more insects and leaves and less fruit than during the season of highest fruit availability (see Figure 3). The size of the group also changes, with an average of 16.6 when fruits are abundant (N = 94, range 2-14, SD ± 9.3), and 6.5 during its nadir (N = 68, range 2-13, SD ± 3.0: Barnett 2010). In addition, the following is known:

Composition of the general diet:

In studies in Jaú between November 2006 and September 2008, golden-backed uacaris ate 189 items of botanical origin (including buds, flowers, leaves and fruits) derived from 136 identified plant species from 87 genera of 44 families (in addition, 12 others were not identified by family). Of the 189, 115 (60.8%) were fruits, of which 96 (83.5% of fruits 50.8% of all items) were eaten when immature (Figure 3a). Of the 115 fruits, 85 (73.9) had hard pericarps. All immature fruits were consumed for their seeds or arils. Of the 19 species consumed when ripe, were eaten whole or were consumed for their pulp or aril, with none specifically consumed only for their seed(s). Of the 44 plant families, Fabaceae, Sapotaceae and Lecythidaceae had the largest number of species consumed (19, 19, and 10 species, respectively). Weights of fruit consumed range from 160g (*Aldina latifolia*: Fabaceae) to less than 3g (various species, including *Mabea and Dryptes*, both Euphorbiaceae, and *Ternstroemia candolleana*, Theaceae). The largest fruit manipulated to extract a seed was 23 cm long x 11 cm wide (*Aldina latifolia*). The smallest were the spherical fruits (<1cm in diameter) of the genera *Calyptranthes*, *Eugenia*, and *Myrcia* (all Myrtaceae) and *Dryptes* (less than 5mm in diameter, but still processed with a bite in the sulcus to extract the seed: see below) . Overall, the three most consumed fruits were *Micropholis venulosa* (Sapotaceae: 19.7% of records), *Eschweilera tenuifolia* (Lecythidaceae: 11.6%) and *Buchenavia ochroprumna* (Combretaceae: 7.1%), all of which were consumed by their seeds.

A variety of non-fruit items have also been recorded, including: the pith of new shoots of *Hevea spruciana* (Euphorbiaceae); flowers of *E. tenuifolia* (Lecythidaceae) and *Codonanthe crassifolia* (Gesneriaceae); young leaves of *Buchenavia oxycarpa* and *B. ochroprumna* (Combretaceae), and the leaf bases of *Aechmea mertensii* (Bromeliaceae). In total, these types of items comprised 21.3% of the items in the diet recorded during the study period. Therefore, while each one had a lower significance overall, they were of important in those months when few fruits were available (Figure 3b).

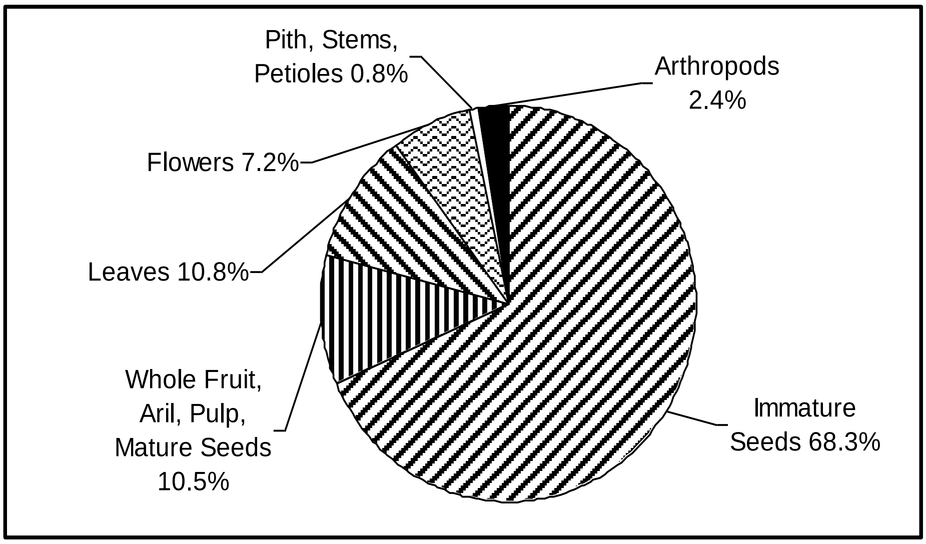


Figure 3(a). Annual diet of *Cacajao ouakary* in Jaú

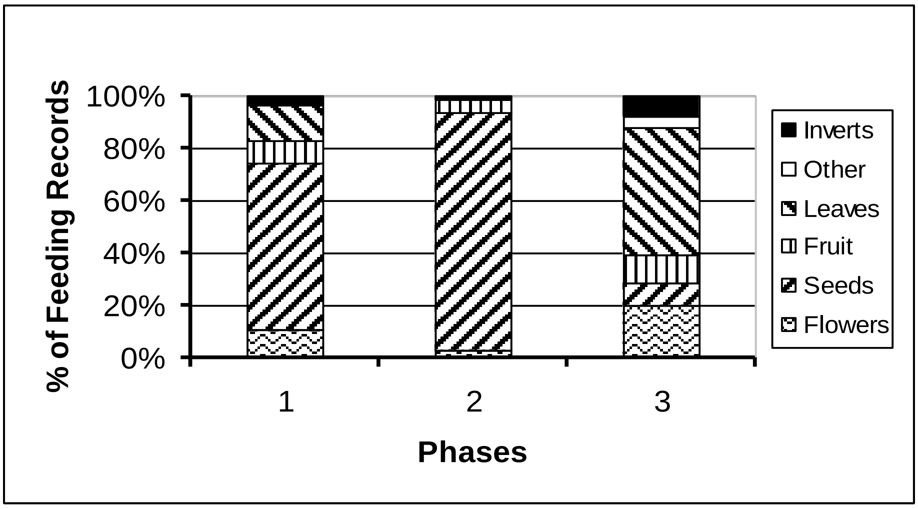


Figure 3(b). As proportions vary seasonally (Phase 1 = not flooded; 2 = flooded; 3 = water levels dropping)

Invertebrates were also consumed: an amblypigid (*Heterophrynus* cf. *batesii*: Phrynidae, Arachnida); wasp larvae (*Polybia*, Polistidae, Hymenoptera), shoot borers (Lepidoptera, possibly from the family Cossidae or Tortricidae; Coleoptera, possibly Curculionidae), which were extracted from both branches and leaf petioles of species of the families Clusiaceae, Fabaceae, Lauraceae, and Sapotaceae; microlepidoptera larvae extracted from the young leaves of *Swartzia polyphylla* (Fabaceae) that they fold and fasten in place with a type of silk; and Isoptera (probably *Nasutitermes*, Nasutitermitinae) harvested individually from their broken clay trails on tree branches. Insect consumption was more common when fruit abundance was low (Barnett et al. 2013).

Foraging

The uacaris were active in terra-firme when the igapó was dry. But at this time they also foraged on mats of germinated seeds on the dry floor of the igapó (Barnett, Almeida et al. 2011). These areas are the result of 'fruit rafts' floating on the surface of the water and getting stuck in some kind of obstruction, such as a branch or fallen trunk. They can be up to a several meters in length and contain hundreds of seeds, all of which germinate quickly to maximize growth and photosynthesis before the next flood (Parolin 2002, 2009). *Eschweilera tenuifolia* (Lecythidaceae) seeds were the most frequently consumed (88.9%) of the records. Uacaris were known to have visited and foraged at some seed mats, but totally ignored others (Barnett, Almeida et al. 2011). Research has shown not only a preference for the largest sized mats, but also for those close to arboreal refuges (such as vines and trees) and away from dense areas of vegetation, places where jaguars, and other potential predators, could hide. Considering this, Barnett, Almeida et al. (2011) interpreted the observed pattern as a form of risk-sensitive foraging.

The husk of a fruit is rarely equally hard over its entire surface. Those which are dehiscent have natural lines of weakness in the pericarp known as sulci. Non-dehiscent fruits will likely vary in husk (pericarp) thickness. For a seed predator, this variation offers a way to save energy with each bite and at the same time, minimize the risk of dental breaking. In line with this, Barnett, Bezerra et al. (2016) found that the bite marks on fruits were randomly distributed only on the surfaces of soft fruits. For other types of fruit, the bite sites were concentrated in the areas of the weakest and easiest skin to penetrate - both in the part where the husk is thinnest for species without sulci or, for those with sulci, in the sulcus itself. For species with hard shells, the areas where uacaris concentrated their bites were much easier to penetrate than the areas where uacaris do not bite (between 17 and 48%). Noting that 30% of the fruits in the golden-backed uacari diet are hard-husked, and have sulci, Barnett, Bezerra et al. (2016) considered this specificity as a mechanism to minimize the mechanical force applied during a bite, the overall energy expenditure and the risk of dental breakage.

Golden-backed uacaris also select fruit infested by insects (Barnett, Ronchi-Teles et al. 2017). Of the 101 types of fruits eaten by *C. ouakary*, 26 were infested by insects. Analyzes showed that uacaris were selecting fruits in 11 of the 26 species (42.3%). Selection of infested fruits was not based on any mechanical advantage derived from a pericarp weakened by excavations of insect larvae, because all hard species had sulci, within which the larvae did not burrow. The 11 species where the infested fruits were actively selected contributed over 25% of the diet, and the 26 species infested with larvae constituted 41.3% of the diet. Considering the various percentages of the species involved, Barnett, Ronchi-Teles et al. (2017) calculated that at least 10.7% of the items eaten by uacaris were fruits to be infested with insect larvae. Considering that the weight of the larvae varies between 0.4-5.5g each fruit, and that insect larvae are often 60-80% protein, and it was clear that this form of hidden insectivory can make a significant contribution to the nutritional balance of primates individual. Uacari and insects also interact in other ways. The presence of colonies of ants of the species *Pseudomyrmex viduus* in an individual from the *Macrolobium acaciifolium* tree (Fabaceae) can reduce the frequency of visitation of primates to 94% (34 visits to eat seeds in trees without ants vs. 2 visits to trees with ants). The frequency of visitation of macaws (Ara spp.), and parrots (*Amazona* spp.) were also less in *Macrolobium* trees with ants. Seed removal was also reduced (164 fruits eaten were found under trees without ants and only four below a number of trees equal in size and equal to those without ants).

Additional interactions between uacaris and their environment were also recorded in Jaú. Detailed study of four of the 17 species of insectivorous bird observed in association with the golden-backed uacaris showed that the frequency of hunting flights (sallies) increased significantly for *Galbula leucogastra* (Bronzy Jacamar, Galbulidae) and *Monasa nigrifrons* (Red-beaked Nunbird, Bucconidae), when uacaris were close (<14.9m), but not when they were more distant (15-30m). At the same time, the presence or absence of uacaris made no difference in the frequency of pecking frequecnies for two species of birds that follow uacaris who specialize in small insects on trunks and leaves (*Sakesphorus canadensis*, Black-crested Antshrike; *Hypocnemoides melanopogon*, Black-chinned Antbird - both Thamnophilidae) (Barnett & Shaw 2014).

The reaction of the jacamar and nunbird was explained by the insects (such as locusts) disturbed by the passage of the uacaris. However, for Thamnophilids, even if the presence of uacaris has not increased the prey capturability, following uacaris still has value because their presence, causes a significant reduction in the presence of medium- and small-sized birds of prey (the types that can eat small birds) (Barnett & Shaw 2014). The most probable reason for this reduction is the presence of large birds of prey such as the Harpy Eagle (*Harpyja harpia*) which follows uacari bands waiting for a predation opportunity (Barnett et al. 2012).

Seed dispersal

Combining date on seed behavior and germination from three separate field studies in the Brazilian Amazon states of Amazonas and Pará, Barnett, Boyle, Pinto et al. (2012) analyzed three species of Pitheciines, including *C. ouakary,* the patterns of seed survival in remnants of the fruits eaten and then discarded by the forest floor. They found that 30.7% of the 674 undamaged seeds that the uacaris dropped germinated. Among them were immature seeds that continued their ripening process away from the mother tree, after which they managed to germinate. Additionally, uacaris were observed to take fruits up to 20m away from the initial tree before consuming them.

Sleeping sites

A quantitative analysis of the trees used as dormitories by the golden-backed uacaris showed that they were very selective about the species of trees in which they sleep and where those trees are (Barnett, Shaw et al. 2012). Of all the 89 species of trees in igapó, uacaris used only 16 as nocturnal sleeping sites (18%). The two most frequently used species (*Hydrochorea marginata* and *Ormosia paraenses*: both Fabaceae) together comprise 41% of the records despite being infrequent in the forest

(Ivlev's Electivity Indices are 0.76 and 0.84, respectively). However, the third most preferred species (*Amanoa oblongifolia*, Euphorbiaceae: 11% of the records), was a common species and selectivity was almost nil. All three have large canopies, with large, horizontal main branches and unimpeded interiors. In comparison to the trees in general in the igapó, the trees used as sleeping sites had larger diameters and were taller. All of them also lacked vines and wasp nests, and were more often within 5m of open water than a random selection of 100 trees in the igapó. In general, uacaris sleep alone, one adult in each tree (mothers with dependant young being the obvious exception) or, when sleeping in the same canopy, separated widely. They always sleep on the last part of a large branch, behind the curtain of thin branches in the crown, but away from the central trunk. These behaviors were interpreted by Barnett, Shaw et al. (2012) as a middle ground to maximize the detection of night-active predators, both aerial (owls) and arboreal (cats).

Predation

An event of predation by a Harpy Eagle on a golden-backed uacari adult has been described by Barnett et al. (2011). The predator has been following a group of 15 animals for most of the day. Screams of alarm continued for almost 45 minutes after the attack, and the animals were grouped close together (something they rarely do when foraging or sleeping), and appeared to be mobbing the place where the attack had taken place. Associated with this, Mourthé & Barnett (2014) wrote that *C. ouakary* generalizes alarm reactions from aerial and ground predators using models based on their general appearances. Summarizing 229 interactions between uacaris and non-primate vertebrates, they reported that out of the 50 rates involved 10 were pseudo-predators (non-threatening species of which uacaris showed reactions of fear because they had a similarity to a predatory species in one way or another). Such encounters were common: daytime occurences between uacari and other species, and were recorded once every 0.7 hours of observation (n = 154). Of the 19, they were with species currently capable of predation (a meeting frequency of 1 every 5.7 hours of observation), and 135 were encounters with pseudo-predators (1 every 0.8 hours). The rest were non-threatening species that were always ignored by uacaris. Reactions to predators and pseudo-predators included stopping feeding, vigilance, retreatimg to more protected sites, and alarm calls. Such responses could disrupt the routine patterns of behavior for up to 10 minutes. Clearly important time that could be devoted to foraging has been wasted on every occasion, but it is clearly better and to be wrong and suffer a little bit of hunger than to be killed.

Additional studies on golden-backed uacaris

In addition to the studies of diet and habitat selection that are the focus of this chapter, a number of other studies on the golden-backed uacaris occurred in Jaú. They were made by Bruna Bezerra and focused on social behavior and vocalizations. Bezerra, Barnett et al. (2011) published an ethogram of *C. ouakary*, listing 35 categories of its behavior. Bezerra et al. (2010a) and Bezerra, Souto et al. (2011)

described the vocal repertoire of the species. Bezerra et al. (2012) considered the bioacoustic capabilities of *C. ouakary* vocalizations. The species also provided a model for experiments on the usefulness of vocalization playback as a survey methodology in primatology (Bezerra et al. 2010b). Against current use, these studies were published following Boubi et al. (2008) and using the name *C. melanocephalus* for the golden-backed uacari.

Variations in the ecology of the golden-spotted uacari between different study sites

The uacaris in Jaú have undoubtedly received more attention, but it is difficult to be sure if they are good representatives of the ecology of the species in general. Other species with wide distributions show differences in their diets, methods of reproduction and social organization, depending on the climate, phenology and soil fertility among other variables (e.g. Oates et al. 1990; Defler 1995; Tan 1999). In uacaris, variation between places was recorded for some key ecological aspects. For example, in the extent of movement between habitats it appears different between places; in Jaú studies using transects on the mainland have never recorded *C. ouakary* more than 500m away from the igapó (Barnett 2010), but at Caparú on the Rio Apaprois, Colombia, the species was recorded traveling for many kilometers inside the mainland (Delfer 1999). Diet is also variable, probably because of variations in composition of plant assemblies in the various parts of the distribution of *C. ouakary* (Barnett, Bezerra et al. 2013), especially since members of the *Eschweilera* genus, which generally dominate members' diets of the genus *Cacajao* (Ayres & Prance 2013), were recorded as important diet components in all three locations studied so far (Barnett, Bezerra et al. 2013).

DISCUSSION AND STUDIES IN THE FUTURE

Initial analysis of the ecology of the genus *Cacajao* came out of considerations of mandibular and dental anatomy, and the idea of uacaris and other pitheciids as sclerocarpic foragers was developed (Rosenberger & Kinzey 1976). The animals were considered specialists in immature seeds, packed in hard shells. In this scenario, the canines act as levers to open the fruit, and then the incisors were used as gouges to remove the seeds (Kinzey & Norconk 1990; Kinzey 1992). Subsequent fieldwork (Ayres 1986) showed that predictions were correct and hard fruits can be dominant in the *Cacajao* diet (but not always - see Bowler & Bodmer 2011). But studies in Jaú show that uacaris are far from simply being powerful nutcrackers. They selectively bite on the weakest parts of fruits, and within the available fruits they choose (in some species at least) those infested with insects. In addition, in addition to being highly specialized seed predators, these primates can function as important dispersers for some species of trees in the igapó. Also, such dispersion is not limited only to seeds derived from ripe fruits, because immature fruits taken from the tree could continue to ripen and the seeds germinate later, an aspect of dispersed ecology that is very neglected.

Invertebrate intake is usually recorded when the consumption of free and mobile animals is observed. Ingestion of invertebrates living within fruits can be an important way for primates to gain access to the proteins, fats and vitamins in which insects are rich, but which are not normally readily available in fruits. This aspect deserves more attention in both uacaris and other primates.

In some places, uacaris penetrate deep into the mainland. Elsewhere uacaris seem to delay movement for as long as possible, and then they are very close to the igapó. The variation can be linked to local conditions, with some using terra firma only slightly because they do not use terra firma for the rest of the year, however, they may be trying to avoid spending time in places where they may be less familiar - with all the collateral problems of diminished certainties in the location of food sources, and crop sizes (Norconk & Kinzey 1994), and the possibility and risks of increased predation (Ferrari 2009). Data on how uacaris use the various types of habitat in their place is the key to effective conservation and should be investigated with comparisons using various locations.

For reasons that are currently unclear, it appears that the golden-backed uacaris avoid contact with the várzea, even when there is no possibility of competition with *C. calvus* (a specialist in the floodplain in the region where the two species coexist). This avoidance seems to be completely complete: Rylands (1992) noticed that *C. ouakary* was absent from the forests along a river with white water in an area where all the other rivers had both uacari and black water. Also, in the southern part of the RDS Amanã, where white and black water systems are interconnected, golden-backed uacaris live in the igapó, red uacaris in Solimões (*C. c. rubicundus*) in the várzea (Vieira et al. 2009; Sergio Borges pers. comm.). Future studies on why this happens would be welcome and useful.

Also, the investigations by Bertuol (2015b) showed that the populations of the golden-backed uacaris in the most western part of its distribution (Cabeça do Cachorro, in Brazil and the areas close to Colombia) are genetically distinct from those in the east. This has already been suggested by Barnett (2005 and 2010) and Thomas Defler (pers. comm.) based on color patterns and sizes. Considering that one reason for the low current status (LC) of *C. ouakary* in the IUCN Red List and its wide distribution, a resolution of this situation could be considered a priority during further investigations on the uacari's ability to resist anthropization (following the investigations recently initiated by Rocha et al. 2015).

ACKNOWLEDGMENTS

For the editors of the book for the invitation, Eliana Andrade-Barnett for the tolerance and adjustments of Portuguese in the initial manuscript, to the other members of the INPA's Amazonian Mammals Research Group, and for the uacaris for their beauty and whimsy.

BIBLIOGRAPHY

Amaral JV, Muniz ICM, Avelar AA, Harada ML, Marques-Aguiar AS & JS Silva Jr. 2005. Primatas da Reserva do Desenvolvimento Sustentavial Amanã, Amazônas. *Programa e Livro de Resumos, XI Congresso Brasiliero de Primatologia* Bicca-Marques, J.C. (Ed.), Porto Alegre, Brazil. Summary no. 70.

Ayres JM. 1986. *The white uakaris and the Amazonian flooded forests*. Doctoral thesis, Cambridge University, Cambridge, England. 338 pp.

Ayres JM. 2006 *As matas de várzea do Mamirauá: médio Rio Solimões*. 3rd ed. Belém: Sociedade Civil Mamirauá. 123 pp.

Ayres JM & GT Prance. 2013. On the distribution of Pitheciin monkeys and Lecythidaceae trees in Amazonia. Em: Veiga L, Barnett A, Ferrari S & M Norconk (eds.) *Evolutionary Biology and Conservation of Titis, Sakis and Uacaris*. Cambridge University Press, Cambridge, United Kingdom. Pp. 127-144.

Barnett AA. 2005. *Cacajao melanocephalus*. *Mammalian Species* 776:1-6.

Barnett AA. 2010. *Diet, habitat, use and conservation ecology of the golden-backed uacari,* Cacajao melanocephalus ouakary*, in Jaú National Park, Amazonian Brazil.* Doctoral thesis, University of Roehampton, London, England. 469 pp. http://roehampton.openrepository.com/roehampton/handle/10142/231712

Barnett AA, Borges SH, de Castilho C, Neri FM & RL Shapley. 2002. Primates of the Jaú National Park, Amazonas, Brazil. *Neotropical Primates* 10: 65-70.

Barnett AA, de Castilho CV, Anicácio A & RL Shapley. 2005. Diet, habitat selection and natural history of *Cacajao melanocephalus ouakary* in Jaú National Park, Brazil. *International Journal of Primatology* 26:949-969.

Barnett A & AC da Cunha. 1991. The golden-backed uacari on the upper Rio Negro, Brazil. *Oryx* 25:80-88.

Barnett A.A, Schiel V, Deveny A, Valsko J, Spironello WR & C Ross. 2011. Predation on *Cacajao ouakary* and *Cebus albifrons* (Primates: Platyrrhini) by harpy eagles. *Mammalia* 75:169-172.

Barnett AA, Almeida T, Spironello WR, Sousa Silva W, MacLarnon A & C Ross. 2012. Terrestrial foraging by *Cacajao melanocephalus ouakary* (Primates) in Amazonian Brazil: is choice of seed patch size and position related to predation risk? *Folia Primatologica* 83:126-139.

Barnett AA, Boyle SA, Pinto LP, Lourenço WC, Almeida T, Sousa Silva W, Ronchi-Teles B, MacLarnon A, Shaw P, Ross C & WR Spironello. 2012. Primary seed dispersal by three Neotropical seed-predating primates (*Cacajao melanocephalus ouakary, Chiropotes chiropotes* and *Chiropotes albinasus*). *Journal of Tropical Ecology*28:543-555.

Barnett AA, Shaw P, Spironello WR, MacLarnon A & C Ross. 2012. Sleeping site selection by golden-backed uacaris, *Cacajao melanocephalus ouakary* (Pitheciidae), in Amazonian flooded forests. *Primates* 53:273-285.

Barnett AA, Ronchi-Teles B, Almeida T, Deveny A, Schiel-Baracuhy V, Souza-Silva W, Spironello W, Ross C & A MacLarnon. 2013. Arthropod predation by a specialist seed predator, the golden-backed uacari (*Cacajao melanocephalus ouakary*, Pitheciidae) in Brazilian Amazonia. *International Journal of Primatology* 34:470-485.

Barnett AA, Bezerra BM, Oliviera M, Queiroz H & TR Defler. 2013. *Cacajao ouakary* in Brazil and Colombia: patterns, puzzles and predictions. Em: Veiga L, Barnett A, Ferrari S & M Norconk (eds.) *Evolutionary Biology and Conservation of Titis, Sakis and Uacaris*. Cambridge University Press, Cambridge, United Kingdom. Pp. 179-195.

Barnett AA & P Shaw. 2014. More food or fewer predators? The benefits to birds of associating with a Neotropical primate varies with their foraging strategy. *Journal of Zoology* 294:224-233.

Barnett AA, Almeida T, Andrade R, Boyle S, Lima MG, MacLarnon A, Ross C, Souza Silva W, Spironello WR & B Ronchi-Teles. 2015. Ants in their plants: *Pseudomyrmex* ants reduce primate, parrot and squirrel predation on *Macrolobium acaciifolium* (Fabaceae) seeds in Amazonian Brazil. *Biological Journal of the Linnean Society* 114:260-273.

Barnett AA, Silva WS, Shaw PJA & RM Ramsay. 2015. Inundation duration and vertical vegetation stratification: a preliminary description of the vegetation and structuring factors in Borokotóh (hummock igapó), an overlooked, high-diversity, Amazonian habitat. *Nordic Journal of Botany* 33:601-614.

Barnett AA, Bezerra BM, Spironello WR, Shaw P, Ross C & A MacLarnon. 2016. Foraging with finesse: a hard-fruit-eating primate selects weakest areas as bite sites. *American Journal of Physical Anthropology* 160:113-125.

Barnett AA, Ronchi-Teles B, Sousa Silva W, Almeida T, Bezerra B, Gonçalves de Lima M, Spironello WR, MacLarnon A, Ross C & PJA Shaw. 2017. Covert carnivory ? A seed-predating primate, the golden-backed uacari, shows prefarences for insect-infested fruits. *Journal of Zoological Research* 1:16-31.

Bertuol F. 2015a. *Testando limites específicos dos uakaris pretos sensu Hershkovitz (1987) (Pitheciidae: Primates).* Masters Thesis, Instituto Nacional de Pesquisas da Amazônia (INPA), Brazil. 44 pp.

Bertuol F. 2015b. Testando limites específicos dos Uakaris Pretos (*Cacajao* spp.) *sensu* Hershkovitz (1987) (Pitheciidae: Primates). Sumario # 245, *XVI Congresso Brasiliero de Primatologia*, 13-17 November 2015, Manaus, Brazil.

Bezerra BM, Barnett AA, Souto A, & G Jones. 2010. Vocal repertoire of golden-backed uakaris (*Cacajao melanocephalus*): call structure and context. *International Journal of Primatology* 31:759-778.

Bezerra BM, Souto A, & G Jones. 2010. Responses of golden-backed uakaris, *Cacajao melanocephalus*, to call playback: implications for surveys in the flooded Igapó forest. *Primates* 51:327-336.

Bezerra BM, Barnett AA, Souto A, & G Jones. 2011. Ethogram and natural history of golden-backed uakaris (*Cacajao melanocephalus*). *International Journal of Primatology* 32:46-68.

Bezerra BM, Souto A, Radford AN & G Jones. 2011. Brevity is not always a virtue in primate communication. *Biology Letters* 7:23-25.

Bezerra BM, Souto A, & G Jones. 2012. Propagation of the loud "tchó" call of golden-backed uakaris, *Cacajao melanocephalus*, in the blackwater-swamp forests of the upper Amazon. *Primates* 53:317-325.

Boubli J-P, da Silva MNF, Amado MV, Hrbek T, Pontual FB & IP Farias. 2008. A taxonomic reassessment of *Cacajao melanocephalus* Humboldt (1811), with the description of two new species. *International Journal of Primatology* 29:723-741.

Bowler M & RE Bodmer. 2011. Diet and food choice in Peruvian red uakaris (*Cacajao calvus ucayalii*): selective or opportunistic seed predation? *International Journal of Primatology* 32:1109-1122.

Bobrowiec PED, Rosa LS, Gazarini J & Haugaasen T. 2014. Phyllostomid bat assemblage structure in Amazonian flooded and unflooded forests. *Biotropica* 46:312-321.

Correa SB, Winemiller KO, López-Fernández H & M Galetti. 2007. Evolutionary perspectives on seed consumption and dispersal by fishes. *Bioscience* 57:748-756.

da Cunha AC & AA Barnett. 1990. Sightings of the golden-backed uacari, *Cacajao melanocephalus ouakary*, on the Upper Rio Negro, Amazonas, Brazil. *Primate Conservation* 11:8-11.

de Figueiredo WMB. 2006. *A Filogeografia Molecular dos Primatas da Tribo Pitheciini* (*Gêneros* Pithecia, Chiropotes e Cacajao)*: implicações para o estudo da biogeografia histórica da Amazônia*. Doctoral Thesis, Universidade Federal do Pará, Belém. 247 pp.

Defler TR. 1995. The time budget of a group of wild woolly monkeys (*Lagothrix lagotricha*). *International Journal of Primatology* 16:107-120.

Defler TR. 1999. Fission-fusion behaviour in *Cacajao melanocephalus ouakary*. *Neotropical Primates* 7:5-8.

dos Reis NR AL Peracchi, Batista CB & GLM Rosa. 2015. *Primatas do Brasil – guia do campo.* Technical Books, São Paulo, Brazil. 148 pp.

Ferrari SF. 2009. Predation risk and antipredator strategies. Em: Garber PA, Estrada AC, Bicca-Marques J, Heymann EW & KB Strier (Eds.). *South American Primates: comparative perspectives in the study of behavior, ecology, and conservation*. Springer, New York, USA, Pp. 251-277.

Ferrari SF, Guedes PG, Figueiredo-Ready WM & AA Barnett. 2014. Reconsidering the taxonomy of the black-faced uacaris, *Cacajao melanocephalus* group (Mammalia: Pitheciidae), from the northern Amazon Basin. *Zootaxa* 3866:353-370.

Ferreira LV. 1997. Effects of the duration of flooding on species richness and floristic composition in three hectares in the Jaú National Park in floodplain forests in central Amazonia. *Biodiversity and Conservation* 6:1353-1363.

Groves C. 2001. *Primate Taxonomy*. Smithsonian Institute Press. Washington D.C., USA, 350 pp.

Haugaasen T & CA Peres. 2005. Primate assemblage structure in Amazonian flooded and unflooded forests. *Journal of Tropical Ecology* 21:133-145.

Haugaasen T & CA Peres. 2006. Floristic, edaphic and structural characteristics of flooded and unflooded forests in the lower Rio Purús region of central Amazonia, Brazil. *Acta Amazonica* 36:25-36.

Haugaasen T & CA Peres. 2007. Tree phenology in adjacent Amazonian flooded and unflooded forests. *Biotropica* 37:620-630.

Hershkoviyz P. 1987. Uacaries, new world monkeys of the genus *Cacajao* (Cebidae, Platyrrhini): A preliminary taxonomic review with the description of a new subspecies. *American Journal of Primatology* 12:1-53.

Kinzey W. 1992. Dietary and dental adaptations in the Pitheciinae. *American Journal of Physical Anthropology* 88:499-514.

Kinzey WG & MA Norconk. 1990. Hardness as a basis of fruit choice in two sympatric primates. *American Journal of Physical Anthropology* 81:5-15.

Mittermeier RA & AF Coimbra-Filho. 1977. Primate conservation in Brazilian Amazonia. In: Rainier III (Grimaldi) Prince of Monaco & GH Bourne (Eds.). *Primate Conservation*. Academic Press, New York, USA. Pp. 117-166.

Mourthé Í & AA Barnett. 2014. Crying Tapir: The functionality of errors and accuracy in predator recognition in two Neotropical high-canopy primates. *Folia Primatologica* 85:379-398.

Norconk MA & WG Kinzey. 1994. The challenge of Neotropical frugivory: travel patterns of spider monkeys and bearded sakis. *American Journal of Primatology* 34:171-183.

Oates JF, Whitesides GH, Davies AG, Waterman PG, Green SM, Dasilva GL & Mole S. 1990. Determinants of variation in tropical forest primate biomass: new evidence from West Africa. *Ecology* 71: 328-343

Parolin P. 2002. Submergence tolerance vs. escape from submergence: two strategies of seedling establishment in Amazonian floodplains. *Environmental and Experimental Botany* 48:177-186.

Parolin P. 2009. Submerged in darkness: adaptations to prolonged submergence by woody species of the Amazonian floodplains. *Annals of Botany* 103:359-376.

Parolin P, Armbruester N, Wittmann F, Ferreira L, Piedade MTF & WJ Junk. 2002. A review of tree phenology in central Amazonian floodplains. *Pesquisas Botanica* 52:195-222.

Prance GT. 1979. Notes on the vegetation types of Amazonia III – the terminology of Amazonian forest types subject to inundation. *Brittonia* 31:26-38.

Rocha A, Spironello WR & Barnett APA. 2015. *Assembléia de primatas no igapó do baixo Rio Negro*. Poster #109, XVI Congresso Brasiliero de Primatologia, 13-17 November 2015, Manaus, AM, Brasil.

Rosenberger AL & WG Kinzey. 1976. Functional patterns of molar occlusion in platyrrhine primates. *American Journal of Physical Anthropology* 45:281-297.

Rylands AB. 1992. *Relatorio*: *viagem ao Parque Nacional de Jaú.* Unpublished report to Fundação Vitória Amazônica, Manaus, 7 pp.

Rylands AB & RA Mittermeier. 2009. The diversity of the New World primates (Platyrrhini): an annotated taxonomy. Em: Garber PA, Estrada AC, Bicca-Marques J, Heymann EW & KB Strier (Eds.). *South American Primates: comparative perspectives in the study of behavior, ecology, and conservation*, *South American Primates*. Springer New York, USA. Pp. 23-54

Strier K. 1991. Diet in one group of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). *American Journal of Primatology* 23:113-126.

Tan CL. 1999. Group composition, home range size, and diet of three sympatric bamboo lemur species (Genus *Hapalemur*) in Ranomafana National Park, Madagascar. *International Journal of Primatology* 20:547–566.

Vieira T, Oliveira M, Queiroz H & J Valsecchi. 2009. Novas informações sobre a distribuição de *Cacajao calvus* na Reserva de Desenvolvimento Sustentável Mamirauá. *Uakari* 4:41-51.

Note: In this article, we analyzed whether there are differences in the responses of *Chiropotes albinasus* primates to threats from pseudo-predators and real predators.

3.2 HONEST ERROR, PRECAUTION OR ALERTNESS ADVERTISEMENT ? REACTIONS TO VERTEBRATE PSEUDOPREDATORS IN RED-NOSED CUXIÚS (*CHIROPOTES ALBINASUS*), A HIGH-CANOPY NEOTROPICAL PRIMATE

ADRIAN A. BARNETT[1,2,3], TADEU DE OLIVEIRA[4], RAFAELA FATIMA SOARES DA SILVA[5], SAMARA DE ALBUQUERQUE TEIXEIRA[3], **PAVEL TOMANEK[7]**, LUCY M. TODD[3], SARAH A. BOYLE[6]

[1] Núcleo de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, AM, Brazil

[2] Amazon Mammals Research Group, INPA, Manaus, AM, Brazil

[3] Centre for Research in Evolutionary Anthropology, Roehampton University, London, UK

[4] Departamento de Biologia, Universidade Estadual do Maranhão, São Luís, MA, Brazil

[5] Departamento de Zoologia, Museu Paraense Emílio Goeldi, Belém, PA, Brazil

[6] Department of Biology, Rhodes College, Memphis, TN, USA

[7] Department of Animal Behaviour, Czech University of Life Sciences, Prague, Czech Republic.

Correspondence

Adrian A. Barnett, Núcleo de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, AM, Brazil. Email: adrian.barnett1.biology@gmail.com

Published in:

Ethology - Volume 124 Issue 3 Ethology, pages: 177-187, - First published: 17 January 2018
https://doi.org/10.1111/eth.12721

ABSTRACT

Predation on primates is considered to have far-reaching effects on the foraging and social ecology of a species. Primate species display a variety of responses to predator proximity and attack, ranging from active physical defense and mobbing, to flight and concealment. Warning calls are often given, and potentially threatening animals may be tracked, either actively or with head movements. Such behaviors take time that could be used for other activities. Accordingly, there should be strong selection to respond only to those species that represent a genuine threat. However, primates give defense-based behaviors to non-predator species. We tested the hypotheses that responses to pseudopredators are (i) precautionary calls made by individuals following the Dinner/Life Principle, or (ii) represent the ontogeny of species recognition. Of the species that ellicted a response from the cuxiús, 80% resembled a primate predator; 95% of the encounters that elicited a response from the cuxiús occurred when the distance between the pseudopredator and cuxiús was ≤20 m. In regard to the fre- quency of responses to pseudopredators, we found no difference between adults and juveniles (47.6% and 52.4%, respectively) and no differences between adult males and adult females (60% and 40% of the responses, respectively). However, reactions to pseudopredators were of shorter duration (x̄ ± standard error (SE): 42.2 ± 15.9 s) than were reactions to actual predator species (x̄ ± SE: 1,024.3 ± 329.1 s). There were only three instances where alarm calls were made to species that did not resemble preda- tors, and 66.7% (N = 2) were made by adult cuxiús and only 33.3% (N = 1) were made by a juvenile cuxiú. Therefore, we found partial support for the Dinner/Life Principle hypothesis, but no support for the ontogeny hypothesis. Examination of such responses to pseudopredators in other primate and non-primate species may help understand the evolution of such behaviors.

Keywords: anti-predator defense, Life-Dinner Principle, monkey, predation, pseudopredator

INTRODUCTION

The impact of predation has farreaching consequences for the biology of the prey species (Bonsall & Hassell, 2007). In primates, the nature and intensity of predation may shape the social systems of primate species (Hill & Lee, 1998; Isbell, 1994; Treves, 1999), determine group size (Janson & Goldsmith, 1995), facilitate mixed-species associations (Heymann & Buchanan-Smith, 2000), and influence sleeping site choice (Ramakrishnan & Coss, 2001), group travel patterns (Boinski, Treves, & Chapman, 2000), and habitat use (Hill & Weingrill, 2007; Vidal & Cintra, 2006). The number of males in a group is often greater in species with greater predation risk (van Schaik & Hörstermann, 1994). Isbell (1994) emphasized need for detailed reporting of predation on primates, especially as, for most species, such events are generally episodic and rarely recorded. Several subsequent reviews (e.g., Aparecido Libório & Moura Martins, 2013; Ferrari, 2009; Hart, 2007; Stanford, 2002) have highlighted how much we still need to know.

A group under threat of predation may adopt a more protective travel order, have higher sleeping sites and smaller sleeping parties, and adjust their feeding sites (Wright, 1998).

Primates usually respond to aerial predators by choosing higher feeding sites and lower daytime rest sites, and as for mammal predators, primates prefer higher nighttime sites than daytime rest sites (Wright, 1998). It is interesting to point out the different behaviors primates pose when distinct predators approach the group (aerial predators, raptors, and tree-based predators, such as mammals).

However, detecting and responding to predator presence also takes up considerable time (Heymann, 1990): An individual scanning for predators cannot feed effectively (though primates do not, like birds and ungulates, need to drop their heads to feed, they nevertheless, need to focus on the items they are selecting and/or processing: Treves, 2000). Additionally, alarm calls can be dangerous as they potentially attract predator attention to the caller (Lima & Dill, 1990), and responding to such calls is highly disruptive to all other activities (Teichroeb & Sicotte, 2012), as are group defensive responses (Bartecki & Heymann, 1987; Crofoot, 2012; Tello, Huck, & Heymann, 2002). At the same time, risk-sensitive foraging means that primates under predation risk must finesse decisions in ways that are not always compatible with the maximization of food intake (Cowlishaw, 1997; Ferrari, 2009). Moreover, post-predation stress is also highly disruptive and results in loss of travel time and feeding opportunities, as well as temporarily sundering the general social equilibrium of the group (Engh et al., 2006; Gouzoules, Fedigan, & Fedigan, 1975).

Reactions to predators generally involve alarm calling, frequently followed by flight, concealment, or attack (Aparecido Libório & Moura Martins, 2013). Such responses may not be homogeneous across age and sex classes: Males may be more aggressive in their response to predator presence and females with young most likely to conceal themselves. In addition, individual traits may also influence alarm calling and defensive responses to predators, as well as vigilance levels (Baldellou & Henzi, 1992; Bolt, Sauther, Cuozzo, & Jacky, 2015; Cheney & Seyfarth, 1985; Gould, Fedigan, & Rose, 1997; Gould & Sauther, 2006; van Schaik & van Noordwijk, 1989; Wheeler, 2008). Vigilence, alarm calling, attack, concealment, and flight as responses by primate species have been recorded for a variety of known predators (constricting snakes: Heymann, 1987; Cisneros-Heredia, León-Reyes, & Seger, 2005; Perry, Manson, Dower, & Wikberg, 2003; Quintino & Bicca-Marques, 2013; vi- pers: Ferrari & Beltrao-Mendes, 2011; Foerster, 2008; large eagles: Barnett et al., 2011, 2015; Oversluijs Vasquez & Heymann, 2002; Shultz, 2001; de Souza Martins, de Lima, & de Sousa e Silva, 2005; small felids: Bianchi & Mendes, 2007; large felids: Matsuda & Izawa, 2008; Peetz, Norconk, & Kinzey, 1992), but primates will also react to other species that look like these predators, but do not belong to the predators’ taxonomic groups (e.g., coati, iguana, otters, storks, toucans, vultures: Mourthé & Barnett, 2014). Other prey taxa (e.g., California ground squirrels, Spermophilus beecheyi, Leger, Owings, & Gelfand, 1980; superb starlings, Spreo superbus, that associate with vervet monkeys, Seyfarth & Cheney, 1990) exhibit similar responses to non-predators.

For primates, such responses to non-predators are either re- ported but not commented on (Altmann & Altmann, 1970; Cordeiro, 1992; Defler, 1979; Digweed, Fedigan, & Rendall, 2005; Fischer & Hammerschmidt, 2002), considered to be errors of identification (Kemp & Kaplan 2011; Rylands, 1981; Wheeler, 2010) , or thought to show the hypersensitivity of the study group or species to predators (Boubli, 1999).

Responding with an alarm call or defensive behavior such as hiding or plummeting (all common defensive behavior: Ferrari, 2009) to a species that is not a predator could be a simple error of identification, a warning to actual predators that the group is alert, or an extension of the category of "predator" based on a precautionary principle (Mourthé & Barnett, 2014). The first is unlikely given the costs involved: Since wild mammals, including primates, are generally considered to be either energy or timelimited (Bernstein, Kacelnik, & Krebs, 1991), it is improbable that there would be much latitude for error, at least in adult animals. The second, while hard to prove, has been posited as a means of indicating capacity to perceive danger awareness and so disencourage predators from following a group (Cheney & Seyfarth, 1981; Fischer, 2016; Zuberbühler, Jenny, & Bshary, 1999). The third, discussed by Mourthé & Barnett (2014) and Suscke et al. (2017), considered such species to be "pseudopredators," taxa visually or be haviorally so similar to actual predators that, given the risks involved, fitness is enhanced by erring on the side of caution and making an alarm call. Effectively, this is a modification of the Life/Dinner Principle of Dawkins & Krebs (1979), where one animal loses its life if the predation attempt is successful and the other misses lunch if the predation attempt is not successful. Under such circumstances, the cautious interpretation of a pseudopredators' shape by a potential prey species simply cuts into the time available for foraging or other activities and so merely delays dinner, rather than risking becoming it. Lastly, there is also ontogeny to correct species identification, with the frequency of appropriately given alarm calls increasing as individuals get older (e.g., baboon and vervet monkeys: Fischer, 2016 dwarf mongoose, Helogale parvula: Rasa, 1987; and meerkat, Suricata suricatta: Hollén, Clutton- Brock, & Manser, 2008).

Consequently, we propose two alternative hypotheses to explain calls to pseudopredators, that such calls either (i) are precautionary calls made by individuals following the Dinner/Life Principle, or (ii) rep- resent the ontogeny of species recognition.

To test the Dinner/Life Principle, we predicted that:

1. Only species that closely resemble the visual appearance of actual predator species would be reacted to.
2. Responses to pseudopredators, like those to predators, are adjusted to likely risk of predation. Consequently, only animals coming within a certain minimum range would elicit alarm and/or defensive responses.
3. Adult group members would react to pseudopredators (either via alarm calls or other forms of anti-predator behavior) more frequently than juveniles. Of these adults, adult males would alarm call most often, while those that respond to such calls most intensely will be mothers with young. Such reactions would parallel the reactions made to actual predator species, where males are generally considered the most vigilent sex (van Schaik & van Noordwijk, 1989), and females with young are both encumbered and risk losing their entire current reproductive investment.
4. Reactions to pseudopredators would be shorter than to true predators.

To test the ontogeny hypothesis, we predicted that:

1. Juveniles, inexperienced in identifying predators, would alarm call more to non-predators than would adults.

METHODS

We studied the red-nosed cuxiú (*Chiropotes albinasus*), a 2.6–3.1-kg Neotropical primate. This species lives in multi-male groups and is a high-canopy species (Veiga & Ferrari, 2013). Sexing adults in the field is facilitated by the presence of a prominent and brightly colored scrotum in adult males. Alarm calls consist of loud and intense whistles, combined with a very high-pitched whinney-like *cacacacá–um–um*, while low-pitched whistles are often given for many minutes following attacks by predators such as harpy eagles (Barnett et al., 2017).

Data on the red-nosed cuxiú were collected during a 21-month study (April 2012–December 2013) on the Tapajós River, Pará State, Brazil (de Oliveira et al., 2016). Primate surveys were conducted in flooded river-margin forest along both banks from the town of Itaituba (04°16′33″S, 55°59′02″W) to the rapids at above the community of Machado, and along the Jamanxim River to the first set of impassable rapids ariver travel distance of some 400 km. Surveys were conducted during both the dry and wet seasons. In total, the data represent 710 hr of survey.

During ad libitum recording of contacted primate groups, the presence of all birds, large reptiles, and non-primate mammals that were visible within 100 m of the cuxiús under observation were recorded. The reaction (if any) by the cuxiús to these animals was recorded, along with the duration of the reaction and the age and sex of individuals involved.

We tested the prediction that only species that closely resemble the visual appearance of actual predator species would be reacted to. This was done by evaluating the number of species that resembled predators that received reactions and that did not receive reactions in comparison with species that resembled predators and whether or not they received reactions or did not receive reactions using a Chi-square test. We also tested this prediction using a Chi-square test to examine the overall frequency of reactions and no reactions based on the visual appearance of the species. We tested whether there was a difference in frequency of all responses by adults versus juveniles using a Chi-square test, and we tested whether there was a difference in frequency of all responses by adult males versus adult females using a Chi-square test. We then tested whether responses to pseudopredators were shorter than to true predators by comparing red-nosed cuxiús’duration of responses to pseudopredators to red-nosed cuxiús’duration of responses during seven raptor predation events (Barnett et al., 2017) using a Mann–Whitney U test.

RESULTS

Reactions to non-predator species

In 710 hr of direct observation of red-nosed cuxiús on the Rio Tapajós, 94 encounters with non-predators were recorded. Of the 22 taxa observed in proximity to the red-nosed cuxiús, defense-related responses were given to 10 taxa (45%; Table 1). Red-nosed cuxiús reacted to pseudopredator species that were large and dark, and resembled predatory species (Table 1). Of the species that received a response from cuxiús, 80% resembled predators while 20% did not. Of the species that did not receive a response, 33.3% resembled predators while 66.7% did not. These differences were significant ($\chi^2_1 = 4.79$, $p = .029$), supporting the first prediction of the Dinner/Life Principle, that only species that closely resemble the visual appearance of actual predator species would be reacted to. Furthermore, 85.7% of the reactions (Table 1) were to animals that resembled predators, while only 14.3% of the reactions were to animals that did not resemble predators. Of the 73 encounters where there was no reaction by the cuxiús, 15.1% of the encounters involved animals that resembled predators and 84.9% of the encounters involved animals that did not resemble predators. These were significant differences ($\chi^2_1 = 38.15$, $p < .001$) and also supported the first prediction of the Dinner/Life Principle.

Table 1. Operational definitions of behaviors associated with responses to predators by red-nosed cuxiús

Name of behavior	Operational definition	Examples of similar use of term
Head glance	A rapid (<5 s), deliberate, directed single movement only of the head that pauses when apparent direct line of sight is obtained to a particular object (an animal newly arrived in the vicinity, in the current study). The position to allow directed visual attention is brief (1–2 s) and the head then moves. Low intensity response, not accompanied by orientation of the rest of the body	Barros et al. (2008), Koenig (1988), Treves (2000)
Alarm call	A generally sharp high-pitched call that summons attention of the receivers, and acts to inform them of the presence or imminence of prejudicial entity or event	Treves (2000), Zuberbühler et al. (1999)
Move away	Directed motion away from a point source of potential discomfort or danger—of variable intensity, but not an intense response (viz. "fleeing")	Boinski et al. (2000), Goodman et al. (1993)
Sentinel	An individual occupying a generally exposed position and not engaged in feeding, resting or grooming, but with an alert appearance and appearing to be visually searching for potential danger	Baldellou and Henzi (1992), Overdorff (1988), Treves (1999)

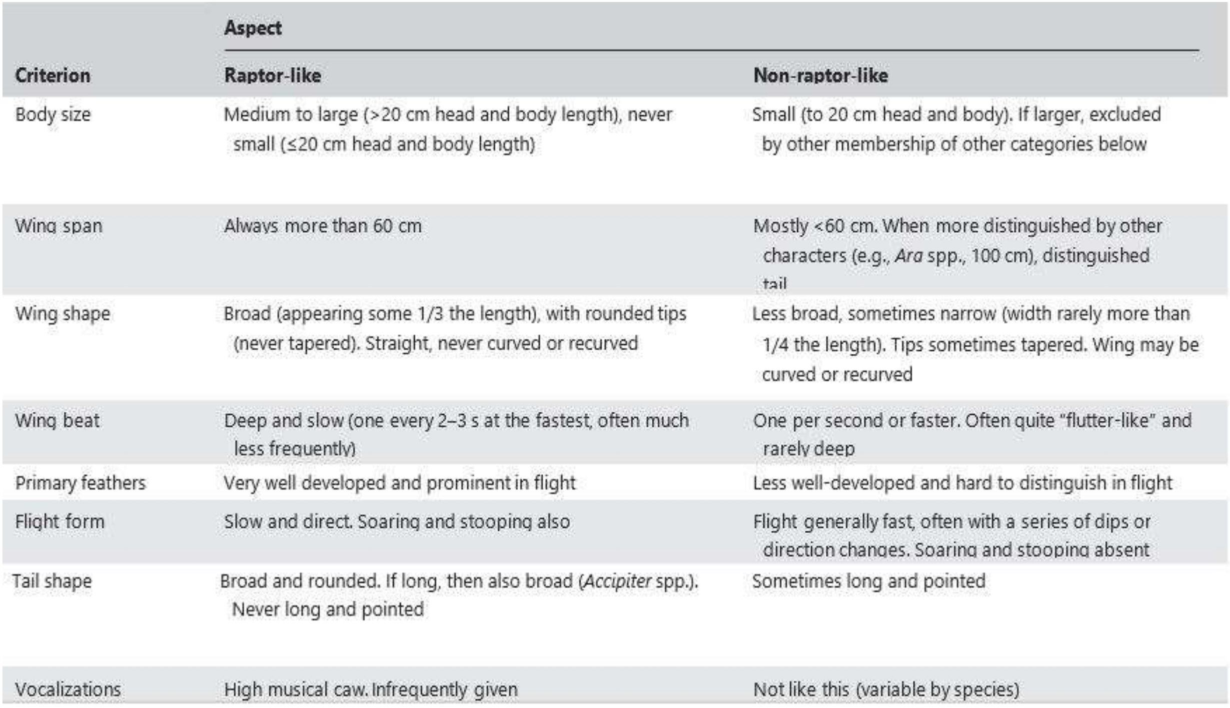
Of the 94 encounters, 21 (23.7%) resulted in one or more forms of defense related response. Within the 21 events, there were 30 reactions from the cuxiús (some events elicited multiple reactions), 50.0% (*N* = 15) involved alarm calls, 26.7% (*N* = 8) involved head glances, 20.0% (*N* = 6) involved moving away, and 3.3% (*N* = 1) involved sentinel observation (Table 1). Of the 21 events, several had simultaneous responses by several individuals, so that 42 individual responses were recorded (Table 2).

Table 2. Records of predation and predation attempts on *Cacajao* spp. (uacaris), *Chiropotes* spp. (cuxiús.), and *Pithecia* spp. (sakis)

Primate taxon	Predator species	Interaction type	Reference
Cacajao calvus ucayalii	*Eira barbara*	Mobbing, accompanied by calls	Bowler (2007)
Cacajao ouakary	*Harpia harpyja*	Successful predation of sub-adult	Barnett et al. (2011)
Chiropotes albinasus	*Harpia harpyja*	Remains in nest	Aguiar-Silva et al. (2014)
Chiropotes albinasus	*Harpia harpyja*, *Leucopternis* sp., *Spizaëtus tyrannus* Unidentified hawks	Eight attempted, and one successful, predation events reported (four by *H. harpyja;* two by *Leucopternis* sp., one by *S. tyrannus*, two by unidentified hawks). Seven attacks were against groups, one against a juvenile (successful) and one against an infant	Barnett et al. (2017)
Chiropotes chiropotes	*Harpia harpyja*	Successful predation of adult	Lenz and dos Reis (2011)
Chiropotes utahickae	*Harpia harpyja*	Successful predation of adult male	de Souza Martins et al. (2005)
Chiropotes utahickae	*Boa constrictor*	Successful predation	Ferrari et al. (2004)
Pithecia aequatorialis		Attempted predation (large unidentified raptors). Four events, two targeted at groups, two at juveniles/infants	De Luna et al. (2010)
Pithecia irrorata	*Harpia harpyja*	Remains in nest	Aguiar-Silva et al. (2014)
Pithecia pithecia	*Morphus guianensis*	Attempted (poss. successful) predation of immature female	Gilbert (2000)
Pithecia rylandsi	*Spizaëtus melanoleucus*	Successful predation	Adams and Williams (2017)

Of these 42 responses, most involved head glances (42.9%) and alarm calls (40.5%), followed by moving away (14.3%), and a sentinel observation (2.4%). Only 1 (4.8%) encounter that elicited a response occurred when the other species was more than 20 m from the cuxiús. For the remaining 20 (95.2%) of the encounters, the other species was ≤20 m from the cuxiús. Of these first alarm calls or physical responses (including head movements or whole body physical responses), these reactions by the cuxiús were first given six times by adult males, four times by adult females, and eight times by juveniles. There was no difference between adults and juveniles in the frequency that the reactions occurred ($\chi^2_1 = 0.22$, $p = .64$), and no difference in frequency of reactions by adult males compared to adult females ($\chi^2_1 = 0.40$, $p = .53$). On 19 occasions the sex of the adult caller could not be determined. On five occasions neither sex nor age of the first animals to call or act could be determined. When examining alarm call behavior separately, of the 17 alarm call responses (Table 2), 47.1% ($N = 8$) were made by juveniles, 23.5% ($N = 4$) by adult males, 5.9% ($N = 1$) by adult females, and 11.8% ($N = 2$) by adults that were not sexed. Because the number of adults was low and 28.6% of the adults were not sexed, we were unable to statistically test if there was a difference between male and females in their alarm calling behavior or in their responses to the alarm calls.

Table 3. Criteria used in operational definition of "raptor-like appearance"



Criterion	Aspect	
	Raptor-like	**Non-raptor-like**
Body size	Medium to large (>20 cm head and body length), never small (≤20 cm head and body length)	Small (to 20 cm head and body). If larger, excluded by other membership of other categories below
Wing span	Always more than 60 cm	Mostly <60 cm. When more distinguished by other characters (e.g., *Ara* spp., 100 cm), distinguished tail
Wing shape	Broad (appearing some 1/3 the length), with rounded tips (never tapered). Straight, never curved or recurved	Less broad, sometimes narrow (width rarely more than 1/4 the length). Tips sometimes tapered. Wing may be curved or recurved
Wing beat	Deep and slow (one every 2–3 s at the fastest, often much less frequently)	One per second or faster. Often quite "flutter-like" and rarely deep
Primary feathers	Very well developed and prominent in flight	Less well-developed and hard to distinguish in flight
Flight form	Slow and direct. Soaring and stooping also	Flight generally fast, often with a series of dips or direction changes. Soaring and stooping absent
Tail shape	Broad and rounded. If long, then also broad (*Accipiter* spp.). Never long and pointed	Sometimes long and pointed
Vocalizations	High musical caw. Infrequently given	Not like this (variable by species)

[a] *Neck length* and *beak length* not included as some non-predator species receiving defensive responses had (non-raptor-like) long necks and long beaks (*Mesembrinibis cayennensis*; *Ramphastos* and *Pteroglossu* spp., respectively).

On the six occasions when all or part of the group moved as a result of the presence of pseudopredators, the females were al- ways the first to leave, with males remaining behind for a period of approximately 10 s. Of the 42 responses, duration was recorded for 39 of them (Table 2). Overall mean response duration ± standard error was 42.2 ± 15.9 s. Mean duration was greatest for "sentinel" and "move away" behavior, and shorter for "head glance" and "alarm call" behavior. The mean bout duration ± standard error for seven responses to predation itself was 1,024.3 ± 329.1 s (Barnett et al., 2017). The difference was statistically significant (U = 0.00, N1 = 39; N2 = 7, p < .001).

Our prediction for the ontogeny hypothesis was that juvenile, inexperienced in identifying predators, would alarm call more to non-predators than would adults. However, of the 17 alarm calls made, there were only three instances where alarm calls were made to species that did not ressemble predators, and 66.7% (N = 2) were made by adult cuxiús and only 33.3% (N = 1) were made by a juvenile cuxiú.

DISCUSSION

Red-nosed cuxiús reacted to pseudopredator species that resembled predatory species (Table 1) and that came within 20 m of the cuxiús, and these reactions were shorter than the reactions to true predators. These findings support three of the four predictions of the Dinner/Life Principle. However, there was no support for age or sex differences in the responses to pseudopredators, which was a fourth prediction of the Dinner/Life Principle. For the ontogeny hypothesis, we did not find support for the prediction that juveniles, inexperienced in identifying predators, would alarm call more to non-predators than would adults (although the N is low, and a greater sample size might have found this).

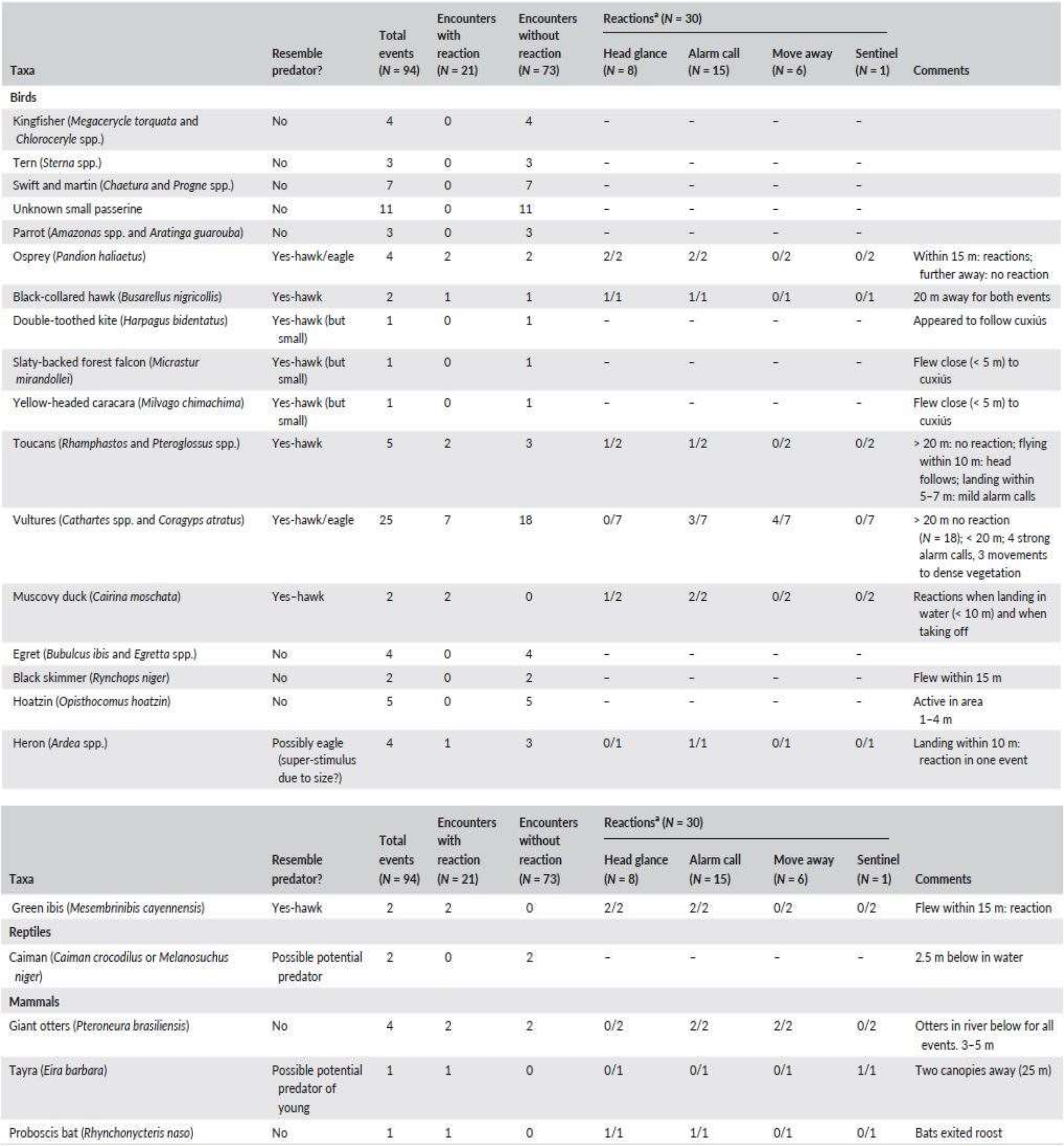
Red-nosed cuxiús primarily reacted to species that resembled predators and only infrequently reacted to species that do not visually resemble actual predators of cuxiús. The various reactions by red-nosed cuxiús to non-predatory bird and mammal species paralleled the reactions reported by Mourthé & Barnett (2014) for *Ateles paniscus* and *Cacajao ouakary*. As with *C. ouakary* (see Mourthé & Barnett, 2014), responses seem to be distance related: of the 21 reactions where inoffensive species were reacted to (Table 1), all but one were made when such animals were closer than 20 m to the primate group. The number of responses to pseudopredators was too small to an- alyze statistically whether it was more common for adult males to react first to the potential threats that pseudopredators posed. However, on the six occasions when all or part of the group moved as a result of the presence of pseudopredators, the females were always the first to leave, with males remaining behind for a period of some 10 s or so. There were no differences in juveniles and adults in their re- sponses, and both juveniles and adults responded to species that did not resemble predators. However, the responses by juveniles did not result in any form of defensive mobilization by the groups (such as quitting the area when males vocalized to vultures and otters), but did result in head glances by adults. Our results do not currently show support of ontogenetic processes being at work in predator recognition in this primate species, as reported for other primate species (Fischer, 2016).

Table 4. Duration (in s) of responses by red-nosed cuxiús to non-predator species

Response	**Number of individual responses (*N* = 42)**	**$\bar{x}$ (±standard error) duration (s)**	**Duration range (s)**
Head glance	18	6.8 (±0.6)	4–10
Alarm call	17	9.2 (±1.5)[a]	3–22
Move away	6	171.3 (±65.9)	52–480
Sentinel	1	367	367

[a] For three responses, no duration was recorded, so the mean (±standard error) was derived from 14 responses.

Table 5. Responses of red-nosed cuxiús to non-predator species



Taxa	Resemble predator?	Total events (N = 94)	Encounters with reaction (N = 21)	Encounters without reaction (N = 73)	Reactions[a] (N = 30) Head glance (N = 8)	Alarm call (N = 15)	Move away (N = 6)	Sentinel (N = 1)	Comments
Birds									
Kingfisher (*Megacerycle torquata* and *Chloroceryle* spp.)	No	4	0	4	–	–	–	–	
Tern (*Sterna* spp.)	No	3	0	3	–	–	–	–	
Swift and martin (*Chaetura* and *Progne* spp.)	No	7	0	7	–	–	–	–	
Unknown small passerine	No	11	0	11	–	–	–	–	
Parrot (*Amazonas* spp. and *Aratinga guarouba*)	No	3	0	3	–	–	–	–	
Osprey (*Pandion haliaetus*)	Yes-hawk/eagle	4	2	2	2/2	2/2	0/2	0/2	Within 15 m: reactions; further away: no reaction
Black-collared hawk (*Busarellus nigricollis*)	Yes-hawk	2	1	1	1/1	1/1	0/1	0/1	20 m away for both events
Double-toothed kite (*Harpagus bidentatus*)	Yes-hawk (but small)	1	0	1	–	–	–	–	Appeared to follow cuxiús
Slaty-backed forest falcon (*Micrastur mirandollei*)	Yes-hawk (but small)	1	0	1	–	–	–	–	Flew close (< 5 m) to cuxiús
Yellow-headed caracara (*Milvago chimachima*)	Yes-hawk (but small)	1	0	1	–	–	–	–	Flew close (< 5 m) to cuxiús
Toucans (*Rhamphastos* and *Pteroglossus* spp.)	Yes-hawk	5	2	3	1/2	1/2	0/2	0/2	> 20 m: no reaction; flying within 10 m: head follows; landing within 5–7 m: mild alarm calls
Vultures (*Cathartes* spp. and *Coragyps atratus*)	Yes-hawk/eagle	25	7	18	0/7	3/7	4/7	0/7	> 20 m no reaction (*N* = 18); < 20 m; 4 strong alarm calls, 3 movements to dense vegetation
Muscovy duck (*Cairina moschata*)	Yes-hawk	2	2	0	1/2	2/2	0/2	0/2	Reactions when landing in water (< 10 m) and when taking off
Egret (*Bubulcus ibis* and *Egretta* spp.)	No	4	0	4	–	–	–	–	
Black skimmer (*Rynchops niger*)	No	2	0	2	–	–	–	–	Flew within 15 m
Hoatzin (*Opisthocomus hoatzin*)	No	5	0	5	–	–	–	–	Active in area 1–4 m
Heron (*Ardea* spp.)	Possibly eagle (super-stimulus due to size?)	4	1	3	0/1	1/1	0/1	0/1	Landing within 10 m: reaction in one event
Green ibis (*Mesembrinibis cayennensis*)	Yes-hawk	2	2	0	2/2	2/2	0/2	0/2	Flew within 15 m: reaction
Reptiles									
Caiman (*Caiman crocodilus* or *Melanosuchus niger*)	Possible potential predator	2	0	2	–	–	–	–	2.5 m below in water
Mammals									
Giant otters (*Pteroneura brasiliensis*)	No	4	2	2	0/2	2/2	2/2	0/2	Otters in river below for all events. 3–5 m
Tayra (*Eira barbara*)	Possible potential predator of young	1	1	0	0/1	0/1	0/1	1/1	Two canopies away (25 m)
Proboscis bat (*Rhynchonycteris naso*)	No	1	1	0	1/1	1/1	0/1	0/1	Bats exited roost

[a] Reactions refer to the number of events when the reaction was noted. If there were multiple individuals reacting (e.g., two individuals alarm calling) during one event, then one reactionwas noted for a particular behavior. If two individuals alarm called and two different individuals exhibited head glances, then one response was noted for each of the two behavioral categories.

The response to pseudopredators has also been observed in birds (e.g., Morris, 1979; who reported pigeons being mistaken for raptors by passerine birds), and in other primates: e.g., Souza-Alves et al. (unpublished data) reported that ground active titi monkeys and marmosets reacted with alarm calls to sallying nunbirds (*Monasa* sp.). However, though pigeons, nunbirds, and ducks are unlikely to ever be a threat, it is true that some bird species may be predators, or attempt predation, on a very rare basis: McKinney (2009) observed two southern crested caracara (*Caracara plancus*) attempt to predate an infant mantled howler monkey (*Alouatta palliata*) in Costa Rica, and Lynch & Rimoli (2000) listed the species as a predator of yearling *Cebus nigritus*. Boinski (1987) recorded attacks by Swainson's toucans (*Rhamphastos swainsoni*) on infant Central American squirrel monkeys (*Saimiri oerstedi*), and Stafford & Murad Ferreira (1995) an attempt on a tufted marmoset (*Callithrix jacchus*) by a burrowing owl (*Athene cunicularia*). In addition, species that might not be able to successfuly subdue an adult of a species, may be able to do so with a juvenile (e.g., goshawk, *Accipiter gentilis* and *Rhinopithecus roxellana*: Zhang, Ren, & Li, 1999*).* For vultures, Lynch & Rimoli (2000) listed black and king vultures (*Coragyps atratus* and *Sarcoramphus papa*, re- spectively) as predators of yearling capuchins, while Dawson (1979) gave turkey vultures (*Cathartes aura*) as a potential predator of infant tamarins. The latter species is known to predate new-born capy- bara, *Hydrochaeris hydrochaeris* (Yáber & Herrera, 1994): At 1.5 kg (Moreira et al., 2013), these weigh as much as many infant and juvenile Neotropical primates and many adult callitrichids (Ford, 1994). Hence, a small gray area may exist between predators and pseudo- predators for some primate populations, and primate reactions to birds may reflect this. This may also be associated with the phenomenon of shape mimicry between birds, where inoffensive species do themselves gain protection by their resemblance to raptorial species (Sazima, 2010).

A group of red-nosed cuxiú at the Cristalino Biological Reserve (Soares da Silva, 2013) reacted with vocalizations and concealment when a pair of red-and-green macaws (*Ara chloropterus*) vocalized near the same cuxiú group. All individuals quickly jumped to the forest stratum below. Similarly, the passage of a large (50+) group of white- lipped peccaries (*Tayassu pecari*) caused a cuxiú above them to move to dense Riverside vegetation and remain quiet, or an extended period, even once the sounder had moved away. Similar reactions to large terrestrial herbivores have been reported for *Cacajao* and *Ateles* by Mourthé & Barnett (2014).

It should be noted that these responses contrast notably with those to true predators during actual or attempted predation. Under such circumstances, vocalizations are loud, intense and last for up to 15 min after the event (Barnett et al., 2017). The mean duration of a response to an actual predator was approximately 25 times longer than the average duration of a response to a pseudopredator. Thus, while such responses exist, they are not as intense as those to actual predation events. However, they occur more frequently (94 potential events, in the same period when nine predation events were observed: Barnett et al., 2017), and so still have the potential to be disruptive. As Rasa (1987) noted for the dwarf mongooses, predator avoidance behavior may take up a considerable portion of potential foraging time (18.2% in the dwarf mongoose), making full responses to all raptor-like birds or carnivore-like mammals time-consuming. A pseudopredator, precaution-mediated approach, appears to be the compromise (Tables 3–5).

Absence of response to presence of double-toothed kite, slaty-backed forest-falcon, and yellow-headed caracara may well have been because these small raptors traditionally follow primate groups to feed on insects disturbed by them (Barnett & Shaw, 2014), and not on the primates themselves. The observed absence of response to caiman may have occurred because they appear rarely to predate primates (we know of only two reports of such predation in the lit- erature, Rose et al., 2003 and Fichtel, Perry, & Gros-Louis, 2005; both referring to the same locality in Costa Rica), so these may be simply off the radar for *C. albinasus*. Tayra (*Eira barbara*) are known predators of small primates (Christen & Geissmann, 1994; Pook & Pook, 1981) and the young of large ones (e.g., Asensio & Gómez- Marín, 2002; Camargo & Ferrari, 2007; Stafford & Murad Ferreira, 1995). However, the response of the group to the apparently non- hunting individual appears too similar to context-dependant responses observed by Defler (1979) for *Cebus albifrons*, Haugaasen & Peres (2008) for *Saimiri* c.f. *ustus* and for *C. ouakary* by Mourthé & Barnett (2014).

Animals can tell between a hawk and a goose (Macedonia & Polak, 1989), and very young captive-born primates react to the hawk silhouette (Kemp & Kaplan, 2011). As Paulson (1973) pointed out, while there may be strong selection for predators to vary their appearance in order to side-step the search image of them held by their vigilent prey, such attempts are thwarted in silhouette by the essential physics of their flight patterns (Brown, 1963). Thus, because small hawks, large eagles, vultures, and storks all have aerodynamic aspects in common, they have a common appearance that, for an animal living in a dangerous world, it may simply be too risky to ignore and the delay required to distinguish between them could be fatal. Clearly, the importance of the reactions to pseudopredators and the effect on time budgets and the risk analysis trade-off it represents merits further attention. We found partial support for the Dinner/Life Principle hypothesis, but no support for the ontogeny hypothesis. This should spur examination of responses to pseudopredators in other primate and non-primate species, and so help advance the understanding the evolution of such behaviors.

ACKNOWLEDGEMENTS

AAB thanks Maracajá Ecological Consulting for the invitation to con- duct the survey work. TdeO wishes to thank CNEC/WorleyParsons and ELETROBRÁS for financial support of the mammal survey in the Tapajós river basin. RFSS thanks Ana C Mendes and Liza Maria Veiga (in memoriam), Cristalino Jungle Lodge, Museu Paraense Emílio Goeldi/Universidade Federal do Pará, fieldguide Leandro Pereira, and CNPq for financial support.

Adrian Barnett dedicates this paper to the memory of Donald Petrie (1958–2014), a fine and dedicated birder. This paper is contribution 31 from the Amazon Mammal Research Group and contribu- tion number 32 from the Igapó Study Project.

REFERENCES

Adams DB & Williams SM. 2017. Fatal attack on a Rylands' bald- faced saki monkey (*Pithecia rylandsi*) by a black-and-white hawk-eagle (*Spizaetus melanoleucus*). *Primates*, *58*, 361–365. https://doi.org/10.1007/s10329-017-0598-7

Altmann SA & Altmann J. 1970. *Baboon ecology: African field research*. Chicago, IL: University of Chicago Press.

Aguiar-Silva F H, Sanaiotti TM & Luz BB. 2014. Food habits of the Harpy Eagle, a top predator from the Amazonian rainforest can- opy. *Journal of Raptor Research*, *48*, 24–35. https://doi.org/10.3356/ JRR-13-00017.1

Aparecido Libório R & Moura Martins M. 2013. Body size in predator– prey interactions: An investigation of Neotropical primates and their predators. *Studies on Neotropical Fauna and Environment*, *48*, 81–87. https://doi.org/10.1080/01650521.2013.789724

Asensio N & Gómez-Marín F. 2002. Interspecific interaction and pred- ator avoidance behavior in response to tayra (*Eira barbara*) by mantled howler monkeys (*Alouatta palliata*). *Primates*, *43*, 339–341. https://doi.org/10.1007/BF02629607

Baldellou M & Henzi SP. 1992. Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. *Animal Behavior*, *43*, 451–461. https://doi.org/10.1016/ S0003-3472(05)80104-6

Barnett AA, Andrade ES, Ferreira MC, Soares JBG, da Silva VF & de Oliveira TG. 2015. Primate predation by black hawk-eagle (*Spizaetus tyrannus*) in Brazilian Amazonia. *Journal of Raptor Research*, *49*, 105–107. https://doi.org/10.3356/jrr-13-00090.1

Barnett AA, Schiel V, Deveny A, Valsko J, Spironello WR & Ross C. 2011. Predation on *Cacajao ouakary* and *Cebus albifrons* (Primates: Platyrrhini) by harpy eagles. *Mammalia*, *75*, 169–172.

Barnett AA & Shaw P. 2014. More food or fewer predators? The ben- efits to birds of associating with a Neotropical primate varies with their foraging strategy. *Journal of Zoology*, *294*, 224–233. https://doi.org/10.1111/jzo.12182

Barnett AA, Silla JM, de Oliveira T, Boyle SA, Bezerra BM, Spironello WR, Pinto LP. 2017. Run, hide or fight: Anti-predation strategies in endangered red-nosed cuxiú (*Chiropotes albinasus*, Pitheciidae) in southeastern Amazonia. *Primates*, *58*, 353–360. https:// doi.org/10.1007/s10329-017-0596-9

Barros M, Maior RS, Huston JP & Tomaz C. 2008. Predatory stress as an experimental strategy to measure fear and anxiety-related behav- iors in non-human primates. *Reviews in the Neurosciences*, *19*, 157–170. https://doi.org/10.1515/REVNEURO.2008.19.2-3.157

Bartecki U & Heymann EW. 1987. Field observation of snake-mobbing in a group of saddle-back tamarins, *Saguinus fuscicollis nigrifrons*. *Folia Primatologica*, *48*, 199–202. https://doi.org/10.1159/000156296

Bernstein C, Kacelnik A & Krebs JR. 1991. Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. *Journal of Animal Ecology*, *60*, 205–225. https://doi.org/10.2307/5455

Bianchi RDC & Mendes SL. 2007. Ocelot (*Leopardus pardalis*) predation on primates in Caratinga Biological Station, Southeast Brazil. *American Journal of Primatology*, *69*, 1173–1178. https://doi.org/10.1002/(ISSN)1098-2345

Boinski S. 1987. Birth synchrony in squirrel monkeys (*Saimiri oer- stedi*). *Behavioral Ecology and Sociobiology*, *21*, 393–400. https://doi. org/10.1007/BF00299934

Boinski S, Treves A & Chapman CA. 2000. A critical evaluation of the influence of predators on primates: Effects on group travel. In S. Boinski, & P. A. Gardner (Eds.), *On the move: How and why ani- mals travel in groups* (pp. 43–72). Chicago, IL: University of Chicago Press.

Bolt LM, Sauther ML, Cuozzo FP & Jacky IAY. 2015. Antipredator vocalization usage in the male ring-tailed lemur (*Lemur catta*). *Folia Primatologica*, *86*, 124–133. https://doi.org/10.1159/000369064

Bonsall MB & Hassell MP. 2007. Predator-prey interactions. In R. May, & A. McLean (Eds.), *Theoretical ecology: Principles and applications* (pp. 46–61). Oxford: Oxford University Press.

Boubli JP. 1999. Feeding ecology of black-headed uacaris (*Cacajao melanocephalus melanocephalus*) in Pico da Neblina National Park, Brazil. *International Journal of Primatology*, *20*, 719–749. https://doi.org/10.1023/A:1020704819367

Bowler M. 2007. *Conservation and ecology of red uakari monkey Cacajao calvus ucayalii in the Peruvian Amazon*. (Doctoral thesis submitted to DICE, University of Kent).

Brown RHJ. 1963. The flight of birds. *Biological Reviews*, *38*, 460–489. https://doi.org/10.1111/j.1469-185X.1963.tb00790.x

Camargo CC & Ferrari SF. 2007. Interactions between tayras (*Eira bar- bara*) and red-handed howlers (*Alouatta belzebul*) in eastern Amazonia. *Primates*, *48*, 147–150. https://doi.org/10.1007/s10329-006-0009-y

Cheney DL & Seyfarth RM. 1981. Selective forces affecting the pred- ator alarm calls of vervet monkeys. *Behaviour*, *76*, 25–60. https://doi. org/10.1163/156853981X00022

Cheney DL & Seyfarth RM. 1985. Vervet monkey alarm calls: Manipulation through shared information? *Behaviour*, *94*, 150–166. https://doi.org/10.1163/156853985X00316

Christen A & Geissmann T. 1994. A primate survey in northern Bolivia, with special reference to Goeldi's monkey, *Callimico goeldii*. *International Journal of Primatology*, *15*, 239–274. https://doi.org/10.1007/ BF02735276

Cisneros-Heredia DF, León-Reyes A & Seger S. 2005. Boa constrictor predation on a Titi monkey, *Callicebus discolor*. *Neotropical Primates*, *13*, 11–12. https://doi.org/10.1896/1413-4705.13.3.11

Cordeiro NJ. 1992. Behaviour of blue monkeys (*Cercopithecus mitis*) in the presence of crowned eagles (*Stephanoaetus coronatus*). *Folia Primatologica*, *59*, 203–206. https://doi.org/10.1159/000156660

Cowlishaw G. 1997. Trade-offs between foraging and predation risk de- termine habitat use in a desert baboon population. *Animal Behavior*, *53*, 667–686. https://doi.org/10.1006/anbe.1996.0298

Crofoot MC. 2012. Why mob? Reassessing the costs and benefits of primate predator harassment. *Folia Primatologica*, *83*, 252–273. https:// doi.org/10.1159/000343072

Dawkins R & Krebs JR. 1979. Arms races between and within species. *Proceedings of the Royal Society of London B: Biological Sciences*, *205*, 489–511. https://doi.org/10.1098/rspb.1979.0081

Dawson GA. 1979. The use of time and space by the Panamanian tam- arin, *Saguinus oedipus*. *Folia Primatologica*, *31*, 253–284. https://doi. org/10.1159/000155891

Defler TR. 1979. On the ecology and behavior of *Cebus albifrons* in eastern Colombia: I. Ecology. *Primates*, *20*, 475–490. https://doi. org/10.1007/BF02373430

De Luna AG, Sanmiguel R, Di Fiore A & Fernandez-Duque E. 2010. Predation and predation attempts on red titi monkeys (*Callicebus dis- color*) and equatorial sakis (*Pithecia aequatorialis*) in Amazonian Ecuador. *Folia Primatologica*, *81*(2), 86–95. https://doi.org/10.1159/0003 14948

Digweed SM, Fedigan LM & Rendall D. 2005. Variable specificity in the anti-predator vocalizations and behaviour of the white-faced capuchin, *Cebus capucinus*. *Behaviour*, *142*, 997–1021. https://doi. org/10.1163/156853905774405344

Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM & Cheney DL. 2006. Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proceedings of the Royal Society of London B: Biological Sciences*, *273*, 707–712. https://doi.org/10.1098/rspb.2005.3378

Ferrari SF. 2009. Predation risk and antipredator strategies. In P. A. Garber, A. Estrada, J. C. Bicca-Marques, E. Heymann, & K. Strier (Eds.), *South American primates: Comparative perspectives in the study of behav- ior, ecology, and conservation* (pp. 251–277). New York, NY: Springer. https://doi.org/10.1007/978-0-387-78705-3

Ferrari SF Beltrao-Mendes R. 2011. Do snakes represent the prin- cipal predatory threat to callitrichids? Fatal attack of a viper (*Bothrops leucurus*) on a common marmoset (*Callithrix jacchus*) in the Atlantic Forest of the Brazilian Northeast. *Primates, 52,* 207–209. https://doi. org/10.1007/s10329-011-0260-8

Ferrari SF, Pereira WL, Santos RR & Veiga LM. 2004. Fatal attack of a Boa constrictor on a bearded saki (*Chiropotes satanas utahicki*). *Folia Primatologica*, *75*, 111–113. https://doi.org/10.1159/000076272

Fichtel C, Perry S & Gros-Louis J. 2005. Alarm calls of white-faced ca- puchin monkeys: An acoustic analysis. *Animal Behavior, 70,* 165–176. https://doi.org/10.1016/j.anbehav.2004.09.020

Fischer J. 2016. *Monkeytalk: Inside the worlds and minds of primates*. Chicago, IL: Chicago University Press.

Fischer J & Hammerschmidt K. 2002. An overview of the Barbary ma- caque, *Macaca sylvanus,* vocal repertoire. *Folia Primatologica*, *73,* 32– 45. https://doi.org/10.1159/000060417

Foerster S. 2008. Two incidents of venomous snakebite on juvenile blue and Sykes monkeys (*Cercopithecus mitis stuhlmanni* and *C. m. albogularis*). *Primates*, *49*, 300–303. https://doi.org/10.1007/s10329-008-0098-x

Ford SM. 1994. Evolution of sexual dimorphism in body weight in platyrrhines. *American Journal of Primatology*, *34*, 221–244. https://doi. org/10.1002/(ISSN)1098-2345

Gould L, Fedigan LM & Rose LM. 1997. Why be vigilant? The case of the alpha animal. *International Journal of Primatology*, *18*, 401–414. https://doi.org/10.1023/A:1026338501110

Gilbert KA. 2000. Attempted predation on a white-faced saki in the Central Amazon. *Neotropical Primates*, *8*, 103–104. http://stat- ic1.1.sqspcdn.com/static/f/1200343/18197273/1337025445920/ NP8.3.pdf?token=6ZjwKQNX3rNrkOGUfbV3l%2FwfMJc%3D

Goodman SM, O'Connor S & Langrand O. 1993. A review of predation on lemurs: implications for the evolution of social behavior in small, nocturnal primates. In J. Ganzhorn (Ed.), *Lemur social systems and their ecological basis* (pp. 51–66). New York, NY: Springer US.

Gould L & Sauther ML(Eds.). 2006. *Lemurs: Ecology and adaptation* (p. 450). New York, NY: Springer.

Gouzoules H, Fedigan LM & Fedigan L. 1975. Responses of a trans- planted troop of Japanese macaques (*Macaca fuscata*) to bobcat (*Lynx rufus*) predation. *Primates, 16,* 335–349. https://doi.org/10.1007/ BF02381559

Hart D. 2007. Predation on primates: A biogeographical analysis. In S. Gursky-Doyen, & K. A. I. Nekaris (Eds.), *Primate anti-predator strategies* (pp. 27–59). New York, NY: Springer. https://doi. org/10.1007/978-0-387-34810-0

Haugaasen T & Peres CA. 2008. Associations between primates and other mammals in a central Amazonian forest landscape. *Primates*, *49*, 219–222. https://doi.org/10.1007/s10329-008-0081-6

Heymann EW. 1987. A field observation of predation on a moustached tamarin (*Saguinus mystax*) by an anaconda. *International Journal of Primatology*, *8*, 193–195. https://doi.org/10.1007/BF02735163

Heymann EW. 1990. Reactions of wild tamarins, *Saguinus mystax* and *Saguinus fuscicollis* to avian predators. *International Journal of Primatology*, *11*, 327–337. https://doi.org/10.1007/BF02193004

Heymann EW & Buchanan-Smith HM. 2000. The behavioural ecology of mixed-species troops of callitrichine primates. *Biological Reviews*, *75*, 169–190. https://doi.org/10.1017/S0006323199005460

Hill RA & Lee PC. 1998. Predation risk as an influence on group size in cercopithecoid primates: Implications for social structure. *Journal of Zoology*, *245*, 447–456. https://doi.org/10.1111/j.1469-7998.1998. tb00119.x

Hill RA & Weingrill T. 2007. Predation risk and habitat use in chacma baboons (*Papio hamadryas ursinus*). In S. Gursky-Doyen, & K. A. I. Nekaris (Eds.), *Primate anti-predator strategies* (pp. 339–354). New York, NY: Springer. https://doi.org/10.1007/978-0-387-34810-0

Hollén LI, Clutton-Brock T & Manser MB. 2008. Ontogenetic changes in alarm-call production and usage in meerkats (*Suricata suri- catta*): Adaptations or constraints? *Behavioral Ecology and Sociobiology*, *62*, 821–829. https://doi.org/10.1007/s00265-007-0508-x

Isbell LA. 1994. Predation on primates: Ecological patterns and evolu- tionary consequences. *Evolutionary Anthropology*, *3*, 61–71.

Janson CH & Goldsmith ML. 1995. Predicting group size in primates: Foraging costs and predation risks. *Behavioral Ecology*, *6*, 326–336. https://doi.org/10.1093/beheco/6.3.326

Kemp C & Kaplan G. 2011. Individual modulation of anti-predator re- sponses in common marmosets. *International Journal of Comparative Psychology*, *24*, 112–136.

Koenig A. 1998. Visual scanning by common marmosets (*Callithrix jac- chus*): Functional aspects and the specialr role of adult males. *Primates*, *39*, 85–90. https://doi.org/10.1007/BF02557746

Lenz BB & dos Reis AM. 2011. Harpy eagle-primate interactions in the central Amazon. *Wilson Journal of Ornithology*, *123*, 404–408. https://doi.org/10.1676/10-171.1

Leger DW. Owings DH.& Gelfand DL. 1980. Single-note vocalizations of California ground squirrels: Graded signals and situation-specificity of pred- ator and socially evoked calls. *Zeitschrift für Tierpsychologie*, *52*, 227–246.

Lima SL & Dill LM. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*, 619–640. https://doi.org/10.1139/z90-092

Lynch JW & Rimoli J. 2000. Demography of a group of tufted capuchin monkeys (*Cebus apella ngritus*) at the Estação Biológica de Caratinga, Minas Gerais, Brazil. *Neotropical Primates*, *8*, 44–49.

Macedonia JM & Polak JF. 1989. Assessment of avian threat in semi- captive ringtailed lemurs (*Lemur catta*). *Behaviour*, *111*, 291–304. https://doi.org/10.1163/156853989X00718

Matsuda I & Izawa K. 2008. Predation of wild spider monkeys at La Macarena, Colombia. *Primates*, *49*, 65–68. https://doi.org/10.1007/ s10329-007-0042-5

McKinney T. 2009. Anthropogenic change and primate predation risk: Crested caracaras (*Caracara plancus*) attempt predation on mantled howler monkeys (*Alouatta palliata*). *Neotropical Primates*, *16*, 24–27. https://doi.org/10.1896/044.016.0105

Moreira JR, Wiederhecker H, Ferraz MPMB, Aldana-Domínguez J, Verdade LM & MacDonald DW. 2013. Capybara demographic traits. In: J. R., Moreira, & K. M. P. M. B., Ferraz (Eds), Capybara: Biology, use and conservation of an exceptional neotropical species (pp. 147–167). New York, NY: Springer. https://doi.org/10.1007/978-1-4614-4000-0 Morris, F. T. (1979). Pigeons mistaken for predators by passerine species. Sunbird, 10, 75–76.

Mourthé Í & Barnett AA. 2014. Crying tapir: The functionality of errors and accuracy in predator recognition in two Neotropical high-canopy primates. *Folia Primatologica*, *85*, 379–398. https://doi.org/10.1159/000371634

de Oliveira TG, Mazim FD, Vieira OQ, Barnett APA, Silva GDN, Soares JB, Miranda CL. 2016. Nonvolant mammal megadiversity and conservation issues in a threatened central Amazonian hotspot in Brazil. *Tropical Conservation Science*, *9*, 1–16.

Overdorff D. 1988. Preliminary report on the activity cycle and diet of the red-bellied Lemur (Lemur rubriventer) in Madagascar. *American Journal of Primatology*, *16*, 143–153. https://doi.org/10.1002/ajp.1350160205

Oversluijs Vasquez, MR & Heymann EW. 2002. Crested eagle (*Morphnus guianensis*) predation on infant tamarins (*Saguinus my- stax* and *Saguinus fuscicollis*, Callitrichinae). *Folia Primatologica*, *72*, 301–303.

Paulson DR. 1973. Predator polymorphism and apostatic selection. *Evolution*, *27*, 269–277. https://doi.org/10.1111/j.1558-5646.1973. tb00672.x

Peetz A, Norconk MA & Kinzey WG. 1992. Predation by jaguar on howler monkeys (*Alouatta seniculus*) in Venezuela. American Journal of Primatology, 28, 223–228. https://doi.org/10.1002/(ISSN)1098-2345

Perry S, Manson JH, Dower G & Wikberg E. 2003. White-faced ca- puchins cooperate to rescue a groupmate from a boa constrictor. *Folia Primatologica*, 74, 109–111. https://doi.org/10.1159/000070008

Pook AG & Pook G. 1981. A field study of the socio-ecology of the Goeldi's monkey (*Callimico goeldii*) in northern Bolivia. *Folia Primatologica*, 35, 288–312. https://doi.org/10.1159/000155980

Quintino EP & Bicca-Marques JC. 2013. Predation of *Alouatta puruen- sis* by *Boa constrictor*. *Primates*, *54*, 325–330. https://doi.org/10.1007/ s10329-013-0377-z

Ramakrishnan U & Coss RG. 2001. Strategies used by bonnet macaques (*Macaca radiata*) to reduce predation risk while sleeping. *Primates*, *42*, 193–206. https://doi.org/10.1007/BF02629636

Rasa OAE. 1987. Vigilance behaviour in dwarf mongooses: Selfish or altruistic? *South African Journal of Science*, *83*, 587–590.

Rose LM, Perry S, Panger MA, Jack K, Manson JH, Gros- Louis J, Vogel,E. 2003. Interspecific interactions between *Cebus capucinus* and other species: Data from three Costa Rican sites. *International Journal of Primatology*, *24*, 759–796. https://doi. org/10.1023/A:1024624721363

Rylands AB. 1981. Preliminary field observations on the marmoset, *Callithrix humeralifer intermedius* (Hershkovitz, 1977) at Dardanelos, Rio Aripuana, Mato Grosso. *Primates*, *22*, 46–59. https://doi.org/10.1007/ BF02382556

Sazima I. 2010. Five instances of bird mimicry suggested for Neotropical birds: A brief reappraisal. *Revista Brasileira de Ornitologia*, *18*, 328–335.

van Schaik CP & Hörstermann M. 1994. Predation risk and the num- ber of adult males in a primate group: A comparative test. *Behavioral Ecology and Sociobiology*, *35*, 261–272. https://doi.org/10.1007/ BF00170707

van Schaik CP & van Noordwijk MA. 1989. The special role of male *Cebus* monkeys in predation avoidance and its effect on group com- position. *Behavioral Ecology and Sociobiology*, *24*, 265–276. https://doi. org/10.1007/BF00290902

Seyfarth R & Cheney D. 1990. The assessment by vervet monkeys of their own and another species' alarm calls. *Animal Behavior*, *40*, 754– 764. https://doi.org/10.1016/S0003-3472(05)80704-3

Shultz S. 2001. Notes on interactions between monkeys and African crowned eagles in Tai National Park, Ivory Coast. *Folia Primatologica*, *72*, 248–250. https://doi.org/10.1159/000049945

Soares da Silva RF. 2013. Comportamento e dieta de *Chiropotes albinasus* (I. Geoffroy & Deville, 1848), cuxiú-de-nariz-vermelho. Masters dissertation, Museu Paraense Emílio Goeldi and Universidade Federal do Pará, Belém, Brazil.

de Souza Martins S. de Lima EM & de Sousa e Silva JJr. 2005. Predation of a bearded saki (*Chiropotes utahicki*) by a harpy eagle (*Harpia harpyja*). *Neotropical Primates*, *13*, 7–10. https://doi.org/10.1896/ 1413-4705.13.1.7

Stafford BJ & Murad Ferreira F. 1995. Predation attempts on calli- trichids in the Atlantic coastal rain forest of Brazil. *Folia Primatologica*, *65*, 229–233. https://doi.org/10.1159/000156894

Stanford CB. 2002. Avoiding predators: Expectations and evidence in primate antipredator behavior. *International Journal of Primatology*, *23*, 741–757. https://doi.org/10.1023/A:1015572814388

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. https://doi.org/10.1007/s10329-016-0557-8

Teichroeb JA & Sicotte P. 2012. Cost-free vigilance during feeding in folivorous primates? Examining the effect of predation risk, scramble competition, and infanticide threat on vigilance in ursine colobus monkeys (*Colobus vellerosus*). *Behavioral Ecology and Sociobiology*, *66*, 453–466. https://doi.org/10.1007/s00265-011-1292-1

Tello NS, Huck M & Heymann EW. 2002. Boa constrictor at- tack and successful group defence in moustached tamarins, *Saguinus mystax*. *Folia Primatologica*, *73,* 146–148. https://doi.org/ 10.1159/000064795

Treves A. 1999. Has predation shaped the social systems of arboreal primates? *International Journal of Primatology*, *20*, 35–67. https://doi. org/10.1023/A:1020532216737

Treves A. 2000. Theory and method in studies of vigilance and aggregation. *Animal Behaviour*, *60*, 711–722. https://doi.org/10.1006/ anbe.2000.1528

Veiga LM & Ferrari SF. 2013. Ecology and behavior of bearded sakis. In L. M. Veiga, A. A. Barnett, M. Norconk, & S. F. Ferrari (Eds.), Evolutionary biology and conservation of Titis, Sakis and Uacaris (pp. 240–249).Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9781139034210

Vidal MD & Cintra R. 2006. Effects of forest structure components on the occurence, group size and density of groups of bare-face tamarin (*Saguinus bicolor*-primates: *Callitrichinae*) in Central Amazonia. Acta Amazonica, 36, 237–248. https://doi.org/10.1590/S0044-59672006000200014

Wheeler BC. 2008. Selfish or altruistic? An analysis of alarm call function in wild capuchin monkeys, *Cebus apella nigritus*. Animal Behavior, 76, 1465–1475. https://doi.org/10.1016/j.anbehav.2008.06.023

Wheeler BC. 2010. Production and perception of situationally variable alarm calls in wild tufted capuchin monkeys (*Cebus apella nigritus*). Behavioral Ecology and Sociobiology, 64, 989–1000. https://doi. org/10.1007/s00265-010-0914-3

Wright PC. 1998. Impact of predation risk on the behaviour of *Propithecus diadema edwardsi* in the rain forest of Madagascar. Behaviour, 135, 483–512. https://doi.org/10.1163/156853998793066186

Yáber MC & Herrera EA. 1994. Vigilance, group size and social status in capybaras. Animal Behavior, 48, 1301–1307. https://doi.org/10.1006/anbe.1994.1366

Zhang S, Ren B & Li B. 1999. A juvenile Sichuan golden monkey (*Rhinopithecus roxellana*) predated by a goshawk (Accipiter gentilis) in the Qinling Mountains. Folia Primatologica, 70, 175–176. https://doi.org/10.1159/000021693

Zuberbühler K, Jenny D & Bshary R. 1999. The predator deterrence function of primate alarm calls. Ethology, 105, 477–490. https://doi.org/10.1046/j.1439-0310.1999.00396.x

Note: The article evaluates the great influence of the size of the consumed fruits on the choice of food in *Cacajao ouakary* with regard to the complexity of their processing.

3.3 JUGGLING OPTIONS: MANIPULATION EASE DETERMINES PRIMATE OPTIMAL FRUIT-SIZE CHOICE

RENANN H. P. DIAS DA SILVA[1], MATHEUS J. CASTRO SA[2], FABRICIO B. BACCARO[3], **PAVEL TOMÁNEK**[4], ADRIAN A. BARNETT[3,4,5,6]

[1] Zoology Graduate Program, Amazonas Federal University, Manaus, Brazil

[2] Ecology Graduate Program, National Amazon Research Institute, Manaus, Brazil

[3] Biology Department, Amazonas Federal University, Manaus, Brazil

[4] School of Behavioral Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic

[5] School of Life Sciences, Roehampton University, London, UK

[6] Zoology Department, Pernambuco Federal University, Recife, Brazil

Correspondence

Renann H. P. Dias da Silva, Msc, Zoology Graduate Program, Amazonas Federal University, Av. Gal. Rodrigo Otávio Jordão Ramos, 3000, Sector South, Manaus, Amazonas, Brazil.

Email: renann.paiva@gmail.com

Published in:

Biotropica 2020; 52-6, p. 1275-1285, https://doi.org/10.1111/btp.12835

ABSTRACT

Optimal foraging theory predicts that animals will seek simultaneously to minimize food processing time and maximize energetic gain. To test this hypothesis, we evaluated whether a specialist seed-predator primate forages optimally when choosing among variable-sized thick-husked fruits. Our objects of study were the golden-backed uacari (*Cacajao ouakary*, Pitheciidae) and single-seeded pods of the macucu tree (*Aldina latifolia*, Fabaceae). We predict that golden-backed uacari will consume fruits of the size class that requires the least time to obtain, handle, and ingest. We used scan sampling, *ad libitum* to record feeding observations, and measured fruits, their penetrability, and the size of taxidermized *C. ouakary* hands. To test whether uacaris selected for optimal characteristics, we compared 8 metrics from 75 eaten and 105 uneaten seeds/fruits collected. Uacaris selected fruits of medium size and weight disproportionately to their abundance. Processing large fruits took six times longer than did medium-sized fruits, but seeds were only four times as large, that is, for energetic yield per unit time, thus choosing medium-sized pods was optimal. Disproportionate selection by *C. ouakary* of fruits of medium size and mass in relation to their abundance suggests active sub-sampling of the available weight–size continuum. This selectivity probably maximizes trade-offs between the energy derived from a seed, and time and energy expended in processing fruit to access this, so following optimal foraging theory predictions. The greater time spent processing large pods is attributed to difficulties manipulating objects five to seven times the size of the animal's palm and one-sixth its own body weight.

Keywords

Aldina latifolia, Amazon, *Cacajao ouakary*, flooded forest, foraging, hand size, igapó forest, seed predation

INTRODUCTION

Fruits and seeds vary in size (Michaels et al., 1988) both within and between species. The selection of fruits by primates and other frugivorous involves nutritional and sensory factors such as color (Melin et al., 2019), smell (Nevo et al., 2015), touch (Wrangham, 1975), level of toxins, hardness (Ayres, 1986; Barnett et al., 2016; Norconk & Veres, 2011), nutritional content (Felton et al., 2009; Rothman, Raubenheimer, & Chapman, 2011), and size (Corlett & Lucas, 1990; Flörchinger, Braun, Böhning-Gaese, & Schaefer, 2010; Stevenson, Pineda, & Samper, 2005). The size of the fruit, however, is considered as the primary selection criterion for many frugivorous species (Jordano, 1995a, 1995b, 2014; Martin, 1985; Mello, Leiner, Guimarães & Jordano, 2005). When foraging is not simply gape-limited (e.g., Nilsson & Bronmark, 2000), and with all else being equal, an individual should select food items that minimize handling time and maximize energetic yield (Tsujita, Sakai, & Kikuzawa, 2008). To achieve this, frugivores must make foraging decisions on at least three levels, choosing between fruits of different species, crops borne by individuals of the same species, and fruits simultaneously available on the same plant (Leighton, 1993; Sallabanks, 1993). Such hierarchical selection is most commonly based on fruit size, or otherwise linked to size-related constraints, including, the ratio of seed to overall fruit weight, and the weight and/or anatomical restrictions of the frugivores themselves (Hartstone-Rose & Perry, 2011; Jordano, 1995b; Mello et al., 2005).

As a result, foraging frugivorous primates must confront a series of challenges that often result in highly constrained time budgets (Norconk & Kinzey, 1994). For the majority of such species, pulp is the primary fruit part consumed. Such fruit generally have a relatively thin skin, making them easy and quick to process (Stevenson et al., 2005). However, this is not the case for species that eat unripe fruit seeds. Here, not only does the seed have to be accessed and extracted, but achieving this involves penetrating an often hard and relative unyielding pericarp, which may possess a variety of chemical and physical defenses to deter seed predators (Hanley, Lamont, Fairbanks, & Rafferty, 2007; Mack, 2000). This might be expected to extend handling times, putting additional pressure on time budgets and enhancing selection for efficient processing techniques and food item choice. Accordingly, seed predators should be very choosy about the size/weight combinations to which such processing techniques are applied, and the time invested in their application. This should especially be the case with very large fruits (>40 mm: Kuhlmann & Fagg, 2012) and seeds (> 20 mm: Cornejo & Janovec, 2010).

The golden-backed uacari (*Cacajao ouakary* (Spix, 1823): Pitheciinae, Pitheciidae) is a medium-sized Neotropical primate (mean weight: 3.5 kg, mean body length: 389 mm (♀) and 414 mm (♂): Hershkovitz, 1987), with a short, bushy, non-prehensile tail. Its principal habitat is the blackwater flooded forests (igapó) of the Rio Negro Basin, western Amazonia. In these areas, *C. ouakary* home range may exceed 2 km2 (Bezerra, Barnett, Souto, & Jones, 2011). *Cacajao ouakary* shows group fission–fusion behavior as a strategy to avoid scramble competition for resources. Therefore, they often travel and forage in small bands (2 to 26 individuals) the size of these varies seasonally (Barnett, 2010). These primates feed, mainly, on immature seeds (Barnett, Bowler, Bezerra, & Defler, 2013; Barnett, de Castilho, Shapley, & Anicácio, 2005). For such items, outer layers of the husk are removed with procumbent incisors and harder layers (if present) then punctured with hypertrophied canines, a process known as sclerocarpic foraging (sensu Kinzey, 1992).

The seeds which compose the diet of golden-backed uacari come from a variety of fruits whose sizes and weights range from the small (0.3 cm diameter, e.g., *Maprounea guyanensis* Aublet): Euphorbiaceae) to the substantial (over 10 cm in length and 250 g in weight, e.g., *Aldina latifolia* (Spruce ex Benth): Fabaceae) (Barnett, 2010). All known fruits over 50 g in mass in the uacari diet are eaten when unripe, except for *A. latifolia*. Processing individual fruits to gain access to seed(s) of such very large fruits may take several minutes (Barnett, unpublished data). Therefore, if uacaris were foraging optimally (MacArthur & Pianka, 1966), one might expect that, for plants such as *A. latifolia* where fruits are very large, they would: (i) Reject fruits where either the absolute weight or relative seed/ fruit weight ratio fell below that for other fruits available during a foraging bout; (ii) reject fruits too large to be easily manipulated, held or bitten into; and (iii) reject fruit that lie within an acceptable size range, but which have husk thicknesses that increase handling time and so make them non-optimal. Consequently, we predict that (1) when faced with an array of large heavy fruits, golden-backed uacaris will select a medial subset of the fruit sizes and seed/fruit weight ratios available, (2) larger fruits will be rejected due to time and/or difficulty in processing and (3) that the same will be true for those fruits with thicker husks. Although time spent manipulating food items has been widely considered as an optimal foraging variable (Hughes & Elner, 1979; Jubb, Hughes, & Rheinallt, 1983), the influence of physical size of the hand, in species that manually manipulate food items, has rarely been considered. Thus, the objective of this study was to evaluate whether fruit size, pericarp thickness, and relative seed/fruit weight ratio are selection criteria for *C. ouakary* species during large fruit foraging.

METHODS

Study area and subjects

We conducted our study in the blackwater seasonally flooded forest (*igapó,* sensu Prance, 1979) in Jaú National Park (1°53′15″S, 61°41′25″W), a 2.3 million ha protected area in central Brazilian Amazonia, situated some 220 km west of the city of Manaus on the south bank of the Rio Negro, Amazonas State (Figure S1). Igapó has an annual monomodal flood pulse, that is both of high amplitude (it may exceed 12 m) and long duration (up to 9 months) (Junk et al., 2011). Igapó has low plant species richness, and fruit production synchronized to the flood pulse (Ferreira & Parolin, 2007), with most species being hydro- or ichthyochorous (Correa, Winemiller, Lopez-Fernandez, & Galetti, 2007). Phenological synchrony is high, both within and between species. Accordingly, igapó fruit production peaks between March and June, that of leaves between July and October, at which time tree canopy fruit availability is low, and during November–February neither fruit nor young leaves are available in igapó (Barnett, 2010). The current work is part of a broader study of golden-backed uacari foraging ecology (Barnett, 2010; Barnett, Almeida, et al., 2012; Barnett et al., 2013, 2016; Barnett & Shaw, 2014; Bezerra et al., 2011) conducted between October 2006 and April 2008 in Jaú National Park.

To test foraging model predictions, we used fruits of *Aldina latifolia* Spruce ex Benth. (Papilionoideae. Fabaceae), a common riverside tree in Rio Negro igapó (Aguiar, 2015; Ferreira & Parolin, 2007; Montero, Piedade, & Wittmann, 2014; Parolin, Adis, Rodrigues, Amaral, & Piedade, 2004). The fruit is drupaceous, woody and tardily dehiscent (Ramos et al., 2016), with a fibrous endocarp. It is hydrochorous, with a stiff spongy mesoderm that acts as a floatation device (Figure S2a) (Parolin, De Simone, et al., 2004). The fruits have one (frequent) to two (rare, < 10%) ellipse-shaped seeds. After some 12 weeks afloat in the igapó, the fruit will dehisce and germinate (Figure S2b) (Barnett, unpublished data). With an average mass of 69–298.33 g, *A. latifolia* fruits are some of the largest and heaviest of any igapó tree (Barnett, 2010; Parolin, Wittmann, & Ferreira, 2013). They also show great variation in size and weight (Figure S2c) (see Table S4).

In the *C. ouakary* diet, 77% of all recorded fruits are ingested in the immature state and thus eaten after direct removal from the parent tree (Barnett, 2010). Almost all fruits eaten when ripe are small soft berries (e.g., *Eugenia* and *Calyptranthes*: Myrtaceae). The sole
large hard fruit eaten when mature are from *A. latifolia*. We never recorded these being eaten when immature, even though they mature contemporaneously with species whose immature seeds are common in the uacari diet, such as *Micropholis venulosa* (Mart. & Echler) Pierre (Sapotaceae) and *Eschweilera tenuifolia* (O. Berg) Miers (Lecythidaceae) (Barnett, 2010). Moreover, and unlike any other item in the uacari diet, eaten *Aldina* fruit are retrieved not from the canopy of their parent tree, but from the flooded igapó water surface, on which they are floating. During this period, *A. latifolia* trees no

longer have fruits in their canopies; instead, the entire annual crop is floating on the water surface within the igapó forest (Figure S2a).

At the time of *A. latifolia* c onsumption, only trees of the genera *Maprounea*., *Casearia* Jacq. (Salicaceae), and *Ternstroemia* Mutis ex L. f. (Pentaphylacaceae) were recorded as fruiting in igapó; all were small trees (< 3 m canopy width), with low crop volumes (e.g., *Casearia*, 155 g/canopy; *Ternstroemia*, 72 g/canopy: Barnett, 2010). Given individual *Aldina* fruit masses (even the smallest are larger than most other igapó fruits) and their abundance (when trapped by floating impedimenta and by branches of partially submerged trees), *Aldina* fruit densities can reach up to 30 per m2 (Barnett, unpublished data). These floating fruits likely represented the largest volume of fruit by species available in igapó at that time. Within the igapós of Jaú National Park, *A. latifolia* is abundant, ranking fourth for dominance and sixth in terms of importance index (Aguiar, 2015). In the area of study, individuals of *A. latifolia* exceeded 20 m in height and more than 100 cm dbh and had a very large canopies (mean volume: 169.6 m3), with abundant fruit crops (mean number per canopy: 256 □} 166.5) (Barnett, 2010).

Accordingly, *A. latifolia* occupies a singular place among the 144 plant species in the *C. ouakary* diet, in that it is a large and abundant species, that produces a large fruit crop which is available at a time when no other large fruits or, indeed, much fruit at all, is available for uacaris to consume. This extreme situation provides a strong test of optimal foraging theory, since it occurs in what is, for uacaris, a challenging period when striking a balance between maximizing energy gain and minimizing time spent is likely to be the key to surviving through to the next season of diet-item abundance.

Collection method

Feeding behavior, biometry, and fruit penetrability

During this study, we followed uacaris through their igapó habitat in wooden canoes. In a previous study (Barnett et al., 2005), uacaris were observed foraging together for floating *A. latifolia* fruits, suspending themselves by their feet to access the fruit from the water surface. They were already engaged in this activity when encountered, which they continued until the local supply of accessible *A. latifolia* appeared exhausted, except for very large fruits. The event was unexpected and novel and aspects such as of manipulation time were not recorded. The only data collected were the uneaten and feeding debris of eaten fruits (large fragments of freshly removed husk, see detail below), floating in the water under of trees where the group had been seen foraging. After collection, measurements were taken for length, width, total weight (whole fruits + constituent seed[s]), and pericarp thickness for all consumed and all non-consumed fruits encountered at the same maturation stage (i.e., floating under the fruiting trees).

Our data are a mixture of direct observation and indirect evidence. Data were collected in the same area studied by Barnett et al. (2005). Here, we made feeding observations of three adult uacaris (sex undetermined), recording the time of manipulation of each consuming fruit, once a foraging bout had ended, we used the same method to collect fallen fruits from the water as Barnett et al. (2005), to ensure data comparability.

To quantify feeding observations, we used scan sampling interspersed with *ad libitum* observations (Altmann, 1974). This was based on blocks of 90 s consisting of two 30 s scans, separated by 30 s of *ad libitum* observation. This mixed sampling strategy maximized collected data representativeness (Fragaszy, Boinski, & Whipple, 1992). Deployment of this strategy was helped by the fact that, at this time of year, fruit resources were scarce, and the uacaris foraged singly or in small groups (2– 4 animals). We recorded manipulation time (retrieval, de-husking, and seed processing) by direct observation, recording times them with an electronic stopwatch. We operationally defined these categories as follows: i) retrieval: the time from when the animal initially removed the floating fruit the water surface and, having carried the fruit to a specific location, sat to process it, ii) de-husk: the time from when the uacari held the fruit to its mouth and began to bite the husk until the husk covering was reduced sufficiently that the seed could be extracted, and iii) seed processing: the time required for the seed to be removed from the remains of the husk, and then processed dentally, timing terminating when the seed (or parts thereof) were swallowed. Note: *Aldina latifolia* fruits have a smooth surface and do not require any additional actions, such as removal of spines or hairs, to prepare them for dental processing.

Immediately following uacari foraging observations, any remaining *Aldina* fruits found under trees in which foraging had occurred were collected and measured. For the fruits that had their seeds consumed, the feeding debris, composed of large fallen fragments of freshly removed husk, were retrieved by a member of the field team from beneath feeding trees immediately after the uacaris had left, then pieced together to reconstitute the lumen in which the single seed had rested. Retrieval was aided by the very slow current in flooded igapó (less than 0.2 m/h-1: Barnett, Almeida, et al., 2015), besides few fruits are consumed by tree. Size measurements were made with SPI dial calipers (Swiss Precision Instruments, Garden Grove, CA, USA), and weights measured with Pesola balances (precision: 0.01g).

We could not collect eaten seed weights directly but because the primates often ate most of it (Balcomb & Chapman, 2003; Barnett, Boyle, et al., 2012), but we were able to derive eaten seed size from fruit lumen volumes. The size of the reassembled seed space was then measured, and the volume was calculated, and from this the weight, using mean densities of entire seeds. To test whether relative seed volume affected fruit-size choice, we measured seeds separately, and then treating the seed as a prolate triaxial ellipsoid, we calculated seed volume (V) using the formula: $V=4/3\pi\ ab^2$
where the value for the central diameter is the mean of two measurements from the center of the ellipse to the most distant point on the pod, being (a) is the half of length of the longest axis (seed length) and (b) the half of the shorter axis (seed width). This was used to calculate volumes for 65 seeds (44 uneaten and 21 eaten fruits: Table S1).

To ensure maximum comparability, we collected eaten and uneaten fruits from the same area and in the same time period. We aimed get a perfect balanced design, but given the nature of the data, we were not able to retrieve all information for every fruit (some eaten fruits were impossible to be pieced together to measure all variables). We measured fruit pericarp penetrability separately at points diametrically opposite on the medial circumference of the fruit surface in 8 eaten and 25 uneaten fruits (total 33 fruits). We also measured minimum and maximum husk thickness in 43 eaten and 53 uneaten fruits (total 96 fruits). To obtain the penetrability measures for these fruits, we used a prosthetic uacari canine (weight 4.5 g, height 4.2 mm, tip diameter 1 mm^2) mounted on a standard fruit penetrometer (Facchini FT 011 Fruit Firmness Tester, marketed by International Ripening Company, Norfolk, VA 23502–2095: see Barnett, Santos, Boyle, & Bezerra, 2015 for details) and measured penetrability at the fruit midpoint. To ensure repeatability, the penetrometer was mounted in a Fridley Fruit Tester - see Figure 3 (Barnett et al. 2015). A prosthetic uacari canine was used in place of the standard penetrometer head because previous studies (Barnett, Santos, et al., 2015) had shown that the standard penetrometer head substantially overestimates force required for husk penetration.

Hand allometry

We obtained measurements of uacaris hands from taxidermized specimens of adult C. ouakary (n = 13; ♀: 8 – ♂: 5), in three different museum collections (Table S2). We measured palm length (Figure S3a), palm base width (Figure S3b), and longest finger length (which, in Cacajao spp. is D2, the human ring finger) (Figure S3c). We obtained maximum hand lengths by summing the length of the palm, plus longest finger. All measurements were taken with calipers, or if the hand had contorted, with a string (Figure S3d) which was then subsequently measured with calipers. We excluded specimens where palm and/or finger lengths could not be measured reliably, due to specimen damage or inconsistency (e.g., hand with palm, but without fingers; hands with fingers, but with a torn palm; extremely contorted and dried-out hands).

Data analysis

To test whether the uacaris were selecting seeds of larger-sized fruit, we compared seven metrics recorded from eaten and uneaten seeds and fruits. To describe allometry patterns, we regressed seed length (mm) against fruit length (mm) (n = 57), fruit length (mm) against fruit weight (g) (n = 88), maximum husk thickness (mm) against fruit length (mm) (n = 79), and maximum husk thickness (mm) against fruit weight (g) (n = 58). The number of seeds/fruits measured varied as a result of the uacaris de-husking behavior, so that, for example, on occasion, only the length or the weight of a given fruit could be recovered reliably. For husk allometries, we also fitted an asymptotic model to account for possible disproportionalities in husk thickness during fruit ontogeny. We then compared model fit (linear and asymptotic) using the Akaike information criterion (AIC). The AIC is widely used to measure the goodness of fit of a particular model, relative to other models, when the data are the same (Akaike, 1974). We used the difference between models (Delta AIC > 2), to select the candidate model.

For the subset of observations for which fruit processing times were available (*n* = 21), we individually regressed fruit length (mm) against time spent: (i) retrieving fruit from the water, (ii) de-husking, and (iii) eating the seed. To test for possible fruit selection by uacaris, we performed an *F* t est to compare variances of total length, width, and maximum and minimum husk thickness between eaten and uneaten *A.latifolia* fruits. the null hypothesis for this test was that the ratio of the variances of the eaten and uneaten fruits would be equal to 1. To control for possible bias within an unbalanced sampling design (eaten = 56, uneaten fruits = 105), we used a bootstrap procedure (permutation with replacement). In each run, the eaten and uneaten fruit measures were randomized and *F* test variance computed. We then compared the statistics of the 999 permutations with the observed value to calculate the probability that the observed value was larger than random. Descriptive statistics and frequency of hand measurements were performed to obtain minimum, maximum, and average sizes. All analyses were made in R (R Core Team, 2016).

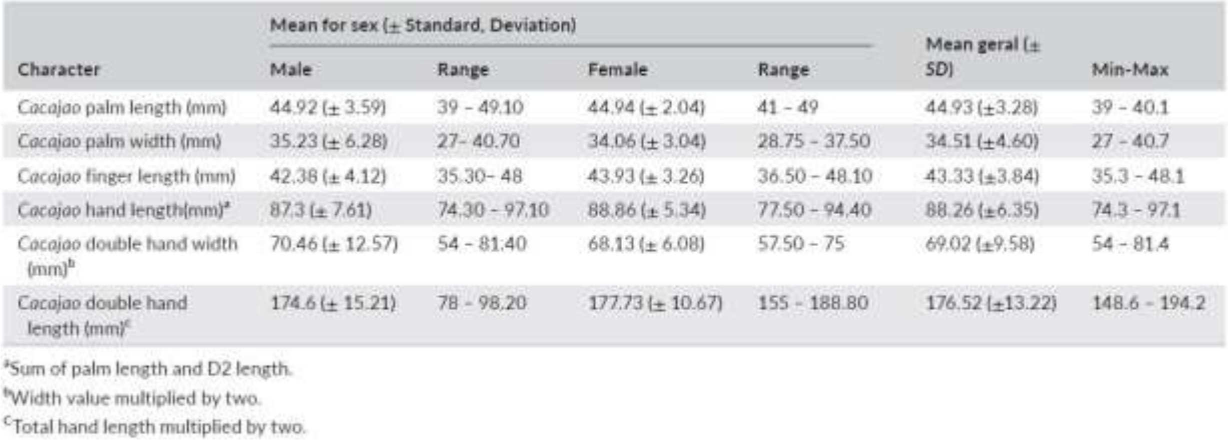
RESULTS

Fruit measurements

Three golden-backed uacaris were observed feeding on 21 *A. latifolia* fruits (details: Table S1), and a further 48 fruits were collected from feeding debris (Table S4). We also collected six *A. latifolia* fruits that uacaris had begun to process but then abandoned (measurement given in Table S3). Of these 75 fruits, greatest length, weight, and pericarp thickness could be unambiguously obtained for 56. These were compared statistically with measures from 105 uneaten *A. latifolia* fruits found floating in the uacari feeding area (Table S4). Mean ranges and standard deviations for hand measurement are given in Table 1 and for fruits in Table 2.

Observations

Table 1. Mean values of *Cacajao ouakary* (*n* = 13, ♂ 5 – ♀ 8) hand characteristics



	Mean for sex (± Standard, Deviation)					
Character	Male	Range	Female	Range	Mean geral (± SD)	Min-Max
Cacajao palm length (mm)	44.92 (± 3.59)	39 - 49.10	44.94 (± 2.04)	41 - 49	44.93 (±3.28)	39 - 40.1
Cacajao palm width (mm)	35.23 (± 6.28)	27- 40.70	34.06 (± 3.04)	28.75 - 37.50	34.51 (±4.60)	27 - 40.7
Cacajao finger length (mm)	42.38 (± 4.12)	35.30- 48	43.93 (± 3.26)	36.50 - 48.10	43.33 (±3.84)	35.3 - 48.1
Cacajao hand length(mm)[a]	87.3 (± 7.61)	74.30 - 97.10	88.86 (± 5.34)	77.50 - 94.40	88.26 (±6.35)	74.3 - 97.1
Cacajao double hand width (mm)[b]	70.46 (± 12.57)	54 - 81.40	68.13 (± 6.08)	57.50 - 75	69.02 (±9.58)	54 - 81.4
Cacajao double hand length (mm)[c]	174.6 (± 15.21)	78 - 98.20	177.73 (± 10.67)	155 - 188.80	176.52 (±13.22)	148.6 - 194.2

[a] Sum of palm length and D2 length.

[b] Width value multiplied by two.

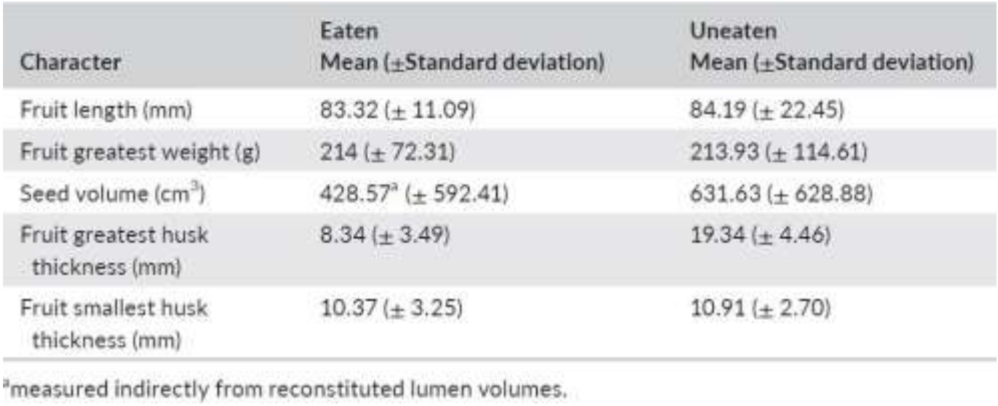
[c] Total hand length multiplied by two.

The three uacaris selected 21 fruits and abandoned six (Table S3). Once retrieved from the water surface, individual fruit were taken to a higher perch where the uacari used its incisors and canines to remove the pericarp, a process that took between 16 and 48 s per fruit (mean 31.10 *SD* ± 7.65, $n = 21$), with a further nine to 35 s to process the seed (mean 22.24 *SD* ± 6.43, $n = 21$). Handling times for the 21 eaten fruits, plus their estimated fruit weight and/or size and/or seed size, appear in Table S1. Of the eaten fruits, nine were retrieved with the original pericarp sufficiently intact that longest lengths could be measured (mean 96.5 mm, range 79.8 to 114.6 mm, *SD* ± 11.8). The only *A. latifolia* fruits that remained in the immediate vicinity after the foraging bout were very large, with a mean longest dimension of 173.6 mm (range 88 to 310.8 mm, *SD* ± 87.8, $n = 5$: the upper 10 percentile of measured *A. latifolia* fruits: Table 2).

There was no relationship between retrieval time and fruit size ($R2 < 0.01$, $F_{1,19} = 0.003$, $p = .951$; Figure 1a), but there was an increase in time taken to de-husk the fruit ($R^2 = 0.25$, $F_{1,19} = 7.681$, $p = .012$; Figure 1c), and time required to process seeds from larger fruits ($R^2 = 0.23$, $F_{1,19} = 7.202$, $p = .014$; Figure 1b). Once fruits are removed from the surrounding husk, the relationship between time taken to process a seed and its volume (in cm3) shows a very clear linear relationship ($R^2 = 0.96$, $p < .001$: Figure 1d). In addition, it was observed a proportional increase in seed size as much as in fruit size (Figure 2a) and weight (Figure 2b) increased ($R^2 = 0.71$, $F_{1,55} = 132.1$, $p < .001$; and $R^2 = 0.61$, $F_{1,47} = 78.06$, $p < .001$, respectively). Smaller and lighter fruits tended to have disproportionally thicker husks, compared to larger and heavier fruits ($R^2 = 0.61$, $F_{1,77} = 124.2$, $p < .001$; and $R^2 = 0.55$, $F_{1,56} = 72.53$, $p < .001$, respectively). In both cases, the asymptotic model had a better fit compared to a linear model (Delta AIC > 2).

There is a significant difference between the size ranges of the eaten and uneaten samples, with the uacaris selecting significantly more fruits in the 0.50–1.15 m range than if they had been selecting fruit sizes at parity (Figure 3a). This is also true for fruit width across the 0.40–1 m range ($p = .001$ in both cases) (Figure 3b). Neither maximum nor minimum fruit husk thickness had an influence on selection of individual *Aldina* fruit by uacaris ($p = .087$, 0.885, respectively) (Figure 3c-d).

Table 2. Mean fruit character values for *Aldina latifolia*, fruits eaten and uneaten by *Cacajao ouakary*



Character	Eaten Mean (±Standard deviation)	Uneaten Mean (±Standard deviation)
Fruit length (mm)	83.32 (± 11.09)	84.19 (± 22.45)
Fruit greatest weight (g)	214 (± 72.31)	213.93 (± 114.61)
Seed volume (cm^3)	428.57^a (± 592.41)	631.63 (± 628.88)
Fruit greatest husk thickness (mm)	8.34 (± 3.49)	19.34 (± 4.46)
Fruit smallest husk thickness (mm)	10.37 (± 3.25)	10.91 (± 2.70)

[a] measured indirectly from reconstituted lumen volumes.

Penetrometer values were obtained from 25 uneaten and 8 eaten *A. latifolia* fruits. The mean penetrability value for the exocarp (outer husk) was 3.94 kg/mm2 (range 3.5–4.3, *SD* ± 0.23), with a maximum thickness that varied from 1.50 to 3.32 mm (mean 2.43, *SD* ± 0.74). However, the very much thicker mesocarp (inner husk: up to 23 mm) was spongy and had a very low penetration resistance (mean 1.29 kg/mm2, range 1.14–1.46, *SD* ± 0.14, *n* = 11).

DISCUSSION

Fruit mass and size have long been considered key influences on patterns of frugivore foraging since, via handling-time costs, they may influence the speed by which energetic and nutritional rewards are gained (Foster, 1990; Martin, 1985). From the current data, it appears that golden-backed uacaris meet the predications for an optimally foraging organism and are eating fruits of mid-range weight and size, while those either smaller or larger than this median range are being dispensed. As can be seen, entire *Aldina* fruits similar in size to those eaten weighed 69.6 to 236 g, while uneaten fruits exceeded 325 g (max. 517 g: some 13% of adult male uacari body weight). The current data appear to support the size spectrum hypothesis of Scott & Murdoch (1983), where exploited prey size depends on the available prey size range relative to those sizes a predator can harvest most effectively.

Accordingly, it is surmised that bigger fruits were rejected for simply being too large for a uacari to manipulate effectively. Processing bout duration and fruit weight increased linearly, while husk thickness became proportionately thinner as fruit size increased. All else being equal, and if this were the only selection criterion in play, large fruits would be more attractive to uacaris. That they are not selected suggests that uacaris find larger and heavier fruits progressively more difficult to handle. As can be seen from the fruit processing data, large seeds would also make less efficient energy sources. Thus, while there is more seed mass available as fruit size increases, it takes disproportionately longer to obtain it. Since thinner husks are quicker to process, this result supports the notion that fruit selection is based on overall fruit size, rather than any other size-linked attribute.

Studies of how human hands grip a cylinder show that the greater the diameter, the smaller the contact area of the hand, leading to grip strength reduction due to reduced palm skin contact with the object (Edgren, Radwinx, & Irwin, 2004; Grant, Habes, & Steward, 1992).

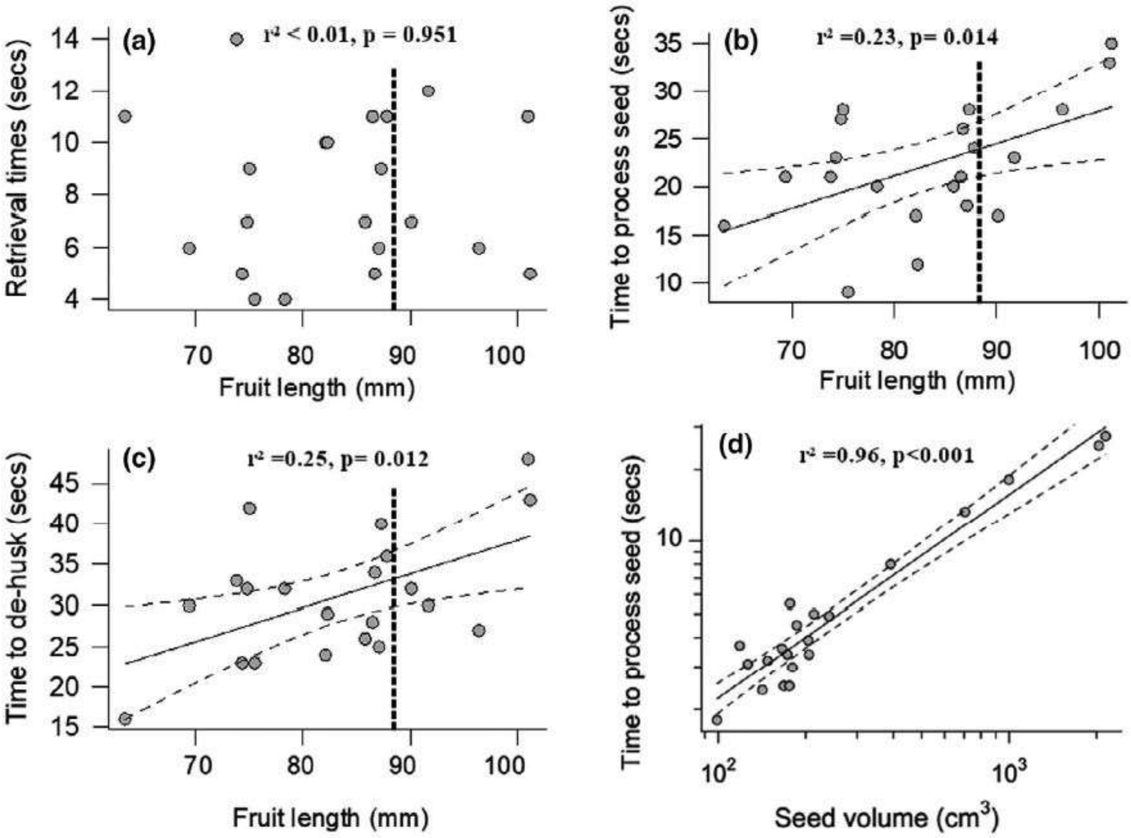


Figure 1. Time to retrieve (a), de-husk (b), and process seeds (c) in seconds, related to fruit length (mm) for 21 direct feeding observations. Relation between volume of individual *Aldina latifolia* seeds (cm3) and time (seconds) required to process the seed (d). Solid lines represent the model, while ticked lines show 95% confidence intervals. The dashed line represents the average *Cacajao ouakary* hand size (88.26 ± 6.35).

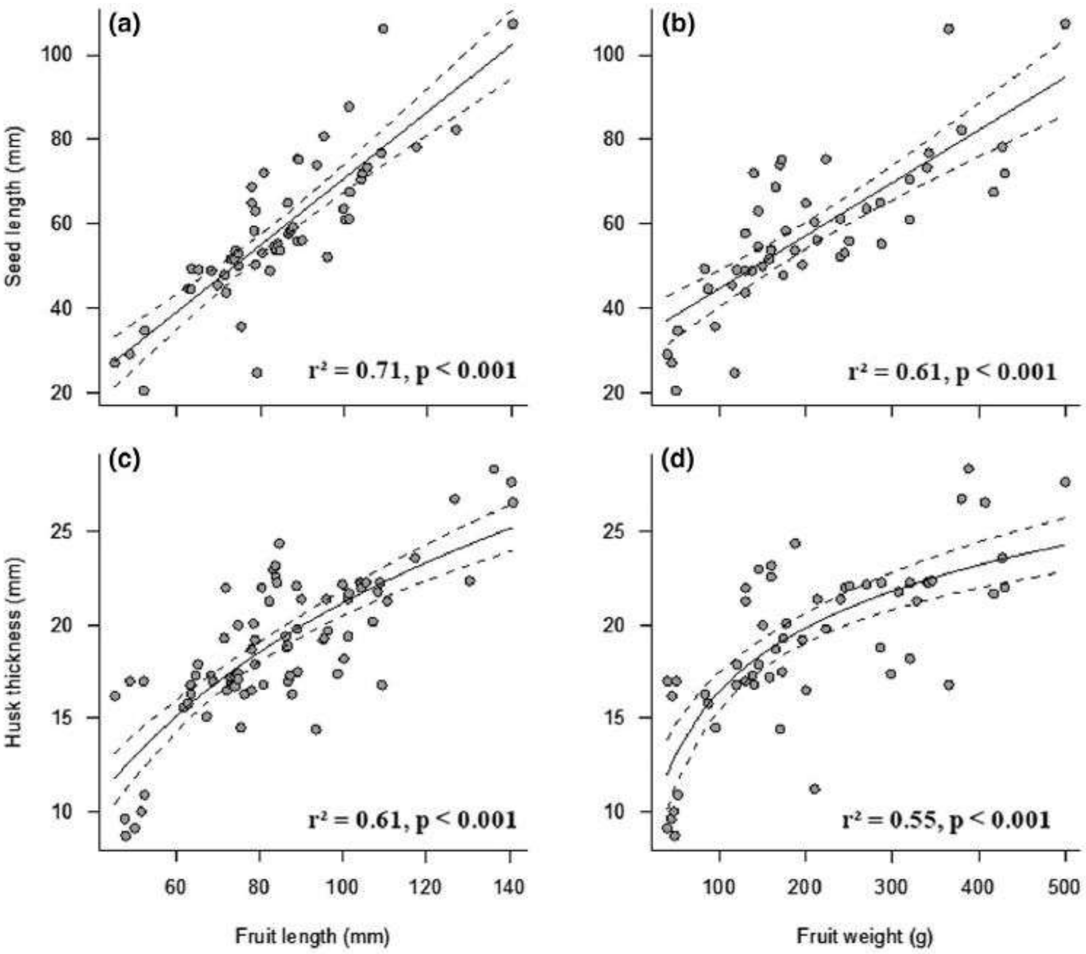


Figure 2. Relation between *Aldina latifolia* seed and fruit length (a), seed length and fruit weight, (b), maximum husk thickness and fruit length (c), and maximum husk thickness and fruit weight (d). The solid line represents the model; ticked lines show 95% confidence intervals

Additionally, young chimpanzees have better grabbing action when food items are small than when they are large (Seo & Armstrong, 2008), while adult male chimps have, on average, larger hands than females and show greater difficulty in manipulating small objects than do females (Hopkins et al. 2002). Therefore, fruits much smaller or larger than the hand would be difficult to handle. The size of fruits selected, therefore, may be linked to the physical limits of hand size. The overlap in size between the favored subset of fruit sizes and uacari full hand sizes supports this hypothesis. That uacaris apparently either test their limits, or sometimes make mistakes, is shown by the sizes of six abandoned fruits, where all but one was either notably larger or smaller than the eaten fruits. Selection of medium-sized *A. latifolia* fruits by *C. ouakary* represents an apparent example of a primate selecting a sub-sample from the available weight–size continuum, a selectivity that presumably maximizes the trade-off between the energy that may be derived from a seed, and the time and energy expended in processing the fruit to access this, either in terms of the nutritional value of the seed, or in terms of the time invested.

Studies investigating aspects of seed- or fruit-size preference in primates are infrequent, with many involving between-species rather than within-species comparisons (e.g., Catherine, 1996;

Chapman & Chapman, 1996; Gross-Camp, Mulindahabi, & Kaplin, 2009; Janson, Stiles, & White, 1986; Lambert, 2002; Sourd & Gautier-Hion, 1986) or considering other aspects, such as multi-species interactions (Gathua, 2000; Howe, 1980), the presence of irritant hairs (Lucas et al., 2001; Tutin, Parnell, & White, 1996), or defensive chemicals (Lucas et al., 2001; Wrangham & Waterman, 1981, 1983). The majority of size-based selection studies so far, consider the size of the fruit in relation to that of the body, the pulp ratio by seed size, crop volume (e.g., *Lagothrix lagothricha* (Humboldt, 1812): Stevenson et al., 2005; *Macaca fascicularis* (Raffles, 1821): Corlett & Lucas, 1990; *Ateles paniscus* (Linnaeus, 1758): Russo, 2003; *Saguinus* spp: Garber & Kitron, 1997), or all these factors together (*e.g., Pongo pygmaeus* (Linnaeus, 1,760): Leighton, 1993).

As is common in diet-item selection (Leighton, 1993), food choice by *C. ouakary* appears to have involved a hierarchical series of factors, including strong influences of crop size, and pulp/seed ratios (Barnett, 2010), as well as a possible relationship between *A. Latifolia* fruit size and handling time reported here. In the current study, the fruits are very large in relation to the selecting primate perhaps explains why individual fruit choice appears to be based more heavily on handling criteria than on considerations relating to energetic yield.

As with mollusk flesh/shell ratios (Behrens Yamada & Boulding, 1998; Hughes & Seed, 1981, 1995; Jubb, Hughes, & Rheinallt, 1983), it has been proposed that pulp/seed ratios may be more important than the actual fruit size. Prior to the current study, this has only been investigated for such pulp consumers as frugivorous birds (Howe & Vande Kerckhove, 1981; Traveset, Willson, & Gaither, 1995), bats (Mello et al., 2005), and orangutans (Leighton, 1993), where those fruits with higher proportional volumes of pulp were preferred. In the current study, the ratios are reversed, with individual fruits with larger seeds being selected; however, the handling-time preference based on cost–benefit optimality is clearly the same.

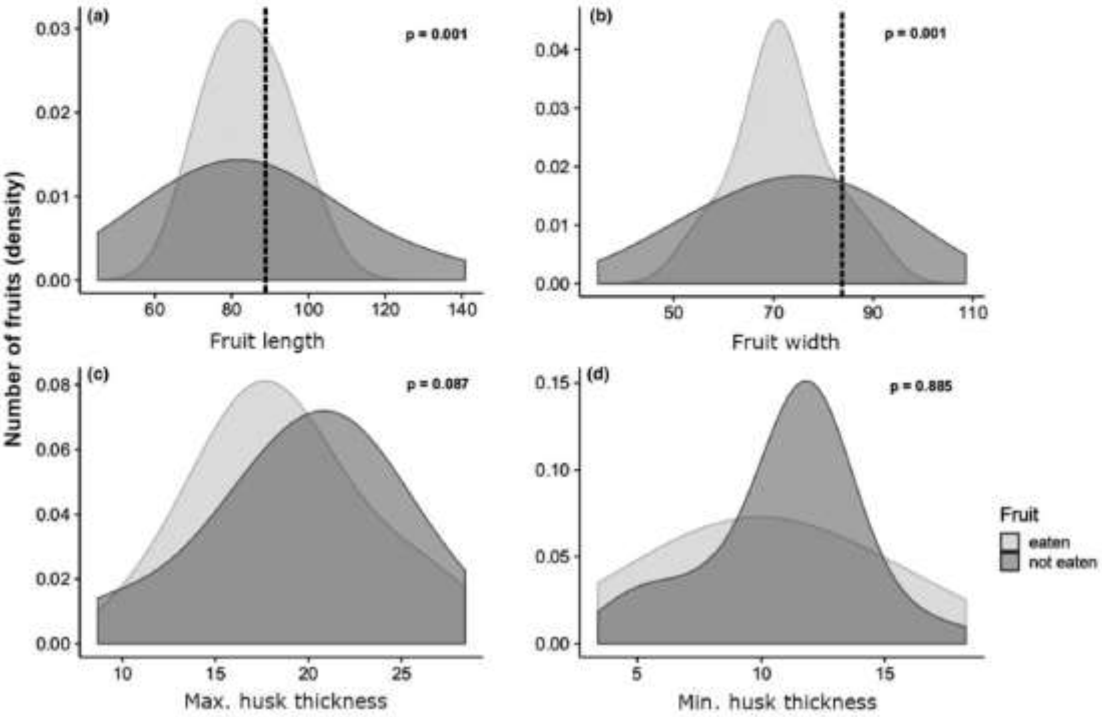


Figure 3. Length, width, and husk thickness as criteria for selection of *Aldina latifolia* fruits by *Cacajao ouakary*, for eaten (pale gray) and uneaten (dark gray) fruits. The graph (a) compares fruit length in the uneaten sample with those eaten by uacaris, while (b) does the same for fruit widths. The graphics (c-d), respectively, compare the distribution of maximum and minimum husk thicknesses in the eaten and uneaten samples. The dashed line represents the average *Cacajao ouakary* hand size (88.26 ± 6.35)

It is well established that prey size and resistance to being predated influence predator diet time choice, as well as capture, manipulation and ingestion times by (Boulding, 1984; Elner & Hughes, 1978; Hughes & Seed, 1981; Martin, 1985; Nilsson & Bronmark, 2000). Therefore, it is interesting to note that the timing of uacari consumption of *A. latifolia* fruits may have minimized energetic expenditure, since uacaris eaten the large hydrochorous fruits when they have been floating for several weeks and so substantially softer than when on the tree. The penetrability of the exocarp of an immature *A. latifolia* drupaceous fruit is one of the highest measured at the igapó forest study site (max.: 4.3 kg/mm^2: Barnett et al., 2016). However, in the current study, mature *A. latifolia* fruits collected from water at the same time as those consumed by uacaris, had substantially lower perforation resistance values (max.: 1.46 kg/mm^2), similarly to most other immature fruits in the uacari diet (for details of each specie, see Table 5: Barnett et al., 2016). It is likely that these characteristics facilitate access to the seed as well as reducing overall energy expenditure.

We cannot affirm that the optimal foraging behavior of the group observed in the present study is practiced by the other groups of *C. ouakary*, but there is a potential for this to occur. Specific behavior that occurs within a group can be of great importance to the population. The most efficient foraging strategies will be favored by natural selection and will spread to a population at the expense of those less efficient. Social facilitation occurs in many species of primates and other animals living in groups can learn from each other's behavior (Clayton, 1978; Galef Jr. & Giraldeau, 2001; Galef & Whiskin, 2000; Giraldeau & Caraco, 2000; Melin et al., 2014). But this has yet to be studied in *Cacajao* species. However, Barnett (2010) observed juveniles close to feeding adults, imitating the behaviors they used to extract seeds from large, hard fruits, even if the younger animals processed such fruits without success.

Studies of diet and food choice are common in primates, but those involving optimal foraging are rare. Here, we studied optimality in foraging behavior of the golden-backed uacari, a specialist Amazonian seed-eating primate. Results show biggest is not always best, because large fruit are hard to handle and take a long time to peel. Consequently, overall energy yield is less than that obtainable from medium-sized fruit, especially those the length of the uacaris hand. We concluded that the size of the fruit, thickness of the pericarp and relative weight/volume of seed/fruit are selection criteria for the species *Cacajao ouakary* during the foraging of large fruits of *Aldina latifolia*. In addition, our results suggest that the anatomy of the animal may be a limiting potential in the choice of fruits. Future studies using a larger number of animals and looking at both hand size and fruit size in relation to uacari maximum gape could also be highly informative, as could studies that consider the impact of such limitations on foraging by uacaris.

ACKNOWLEDGMENTS

RHPDS was funded by CNPq graduate grant number 133382/2015-0 and dedicates this paper to grandmother Doralcy Paiva Dias (in memoriam). We thank Maria Nazareth da Silva (INPA) and José de Souza e Silva Junior (Cazuza) (MPEG), Louise Thomsett, and colleagues (Natural History Museum London) for support and access to collections and specimens. Fieldwork was undertaken with CNPq-IBAMA Protected Area Study License 138/2006. IBAMA-Manaus issued monthly park research permits. We also thank Eliana dos Santos Andrade and Juliane G Menezes (logistics), Eduardo and Roberto (guides); Bruna Bezerra, Thaís Almeida, and Welma Silva (field coworkers); and Amazon Mammal Research Group (INPA). FBB is continuously supported by a productivity grant (CNPq #309600/2017-0).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.vmcvdncqj (Dias-Silva et al. 2020).

ORCID

Renann H. P. Dias da Silva - https://orcid. org/0000-0003-4819-7343

Matheus J. Castro Sa - https://orcid.org/0000-0003-1433-8929

Fabricio B. Baccaro - https://orcid.org/0000-0003-4747-1857

Pavel Tománek - https://orcid.org/0000-0003-4324-6150

Adrian A. Barnett - https://orcid.org/0000-0002-8829-2719

REFERENCES

Akaike H .1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control, 19(6), 716–723. https://doi. org/10.1109/tac.1974.1100705

Altmann J. 1974. Observational study of behavior: Sampling methods. Behaviour, 49(3), 227–266. https://doi.org/10.1163/15685 3974X00534

Ayres JMC. 1986. Uakaris and Amazonian flooded forest. (Doctoral thesis, University of Cambridge) . https://doi.org/10.17863/ CAM.7138 Balcomb, S. R., & Chapman, C. A. (2003). Bridging the gap: Influence of seed deposition on seedling recruitment in a primate–tree interaction. Ecological Monographs, 73(4), 625–642. https://doi. org/10.1890/02-4036

Barnett AA. 2010. Diet, habitat, use and conservation ecology of the golden-backed uacari, Cacajao melanocephalus ouakary, in Jaù National Park, Amazonian Brazil. (Doctoral thesis, University of Roehampton). https://pure.roeha mpton.ac.uk/porta l/en/stude ntThe ses/diet-habit at-use-and-conse rvati on-ecolo gy-of-the-golde n-backe d-ua

Barnett AA, Almeida T, Andrade R, Boyle S, de Lima MG, MacLarnon A, Ronchi-Teles B. 2015. Ants in their plants: *Pseudomyrmex* ants reduce primate, parrot and squirrel predation on *Macrolobium acaciifolium* (Fabaceae) seeds in Amazonian Brazil.Biological Journal of the Linnean Society, 114(2), 260–273. https://doi. org/10.1111/bij.12425

Barnett AA, Almeida T, Spironello WR, Sousa Silva W, MacLarnon A & Ross C. 2012. Terrestrial Foraging by *Cacajao melanocephalus ouakary* (Primates) in Amazonian Brazil: Is choice of seed patch size and position related to predation risk. Folia Primatologica, 83(2), 126–139. https://doi.org/10.1159/00034 3591

Barnett AA, Bezerra BM, Santos PJP, Spironello WR, Shaw PJA, MacLarnon A & Ross C. 2016. Foraging with finesse: A hard-fruit-eating primate selects the weakest areas as bite sites. American Journal of Physical Anthropology, 160(1), 113–125. https://doi.org/10.1002/ajpa.22935

Barnett AA, Bowler M, Bezerra BM & Defler TR. 2013. Ecology and behavior of uacaris (genus *Cacajao*). In L. M. Veiga, A. A. Barnett, S. F. Ferrari, & M. A. Norconk (Eds.), Evolutionary Biology and Conservation of Titis, Sakis and Uacaris (pp. 151–172). Cambridge: Cambridge University Press.

Barnett AA, Boyle SA, Pinto LP, Lourenço WC, Almeida T, Sousa Silva W, Spironello WR. 2012. Primary seed dispersal by three Neotropical seed-predating primates (*Cacajao melanocephalus ouakary*, *Chiropotes chiropotes* and *Chiropotes albinasus*). Journal of Tropical Ecology, 28(6), 543–555. https://doi.org/10.1017/S0266 46741 2000600

Barnett AA, de Castilho CV, Shapley RL & Anicácio A. 2005. Diet, habitat selection and natural history of *Cacajao melanocephalus ouakary* in Jaú National Park. Brazil. International Journal of Primatology, 26(4), 949–969. https://doi.org/10.1007/s1076 4-005-5331-5

Barnett AA, Santos PJP, Boyle SA & Bezerra BM. 2015. An improved technique using dental prostheses for field quantification of the force required by primates for the dental penetration of fruit. Folia Primatologica, 86(4), 398–410. https://doi.org/10.1159/00043 4677

Barnett AA & Shaw P. 2014. More food or fewer predators? The benefits to birds of associating with a Neotropical primate varies with their foraging strategy. Journal of Zoology, 294(4), 224–233. https://doi.org/10.1111/jzo.12182

Behrens YS & Boulding EG. 1998. Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. Journal of Experimental Marine Biology and Ecology, 220(2), 191–211. https://doi.org/10.1016/S0022 -0981(97)00122 -6

Bezerra BM, Barnett AA, Souto A & Jones G. 2011. Ethogram and natural history of golden-backed uakaris (*Cacajao melanocephalus*). International Journal of Primatology, 32(1), 46–68. https://doi.org/10.1007/s1076 4-010-9435-1

Boulding EG. 1984. Crab-resistant features of shells of burrowing bivalves: Decreasing vulnerability by increasing handling time. Journal of Experimental Marine Biology and Ecology, 76(3), 201–223. https://doi.org/10.1016/0022-0981(84)90189 -8

Catherine J. 1996. Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest. American Journal of Primatology, 40(3), 261–282. https://doi.org/10.1002/(SICI)1098-2345(1996)40:3<261:AID-AJP4>3.0.CO;2-W

Chapman CA , Chapman L J. 1996. Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. Journal of Tropical Ecology, 12(04), 491–504. https://doi.org/10.1017/S0266 46740 000972X

Clayton DA. 1978. Socially facilitated behavior. Quarterly Review of Biology, 53(4), 373–392. https://doi.org/10.1086/410789 Core Team, R. (2016). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Corlett RT, Lucas PW. 1990. Alternative seed-handling strategies in primates: Seed-spitting by long-tailed macaques (Macaca fascicularis). Oecologia, 82(2), 166–171. https://doi.org/10.1007/BF003 23531

Cornejo F, Janovec J. 2010. Seeds of Amazonian plants. Princeton University Press.

Correa SB, Winemiller KO, Lopez-Fernandez H & Galetti M. 2007. Evolutionary perspectives on seed consumption and dispersal by fishes. BioScience, 57(9), 748–756. https://doi.org/10.1641/b570907 de Aguiar, D. P. P.(2015). Influência dos fatores hidro-edáficos na diversidade, composição florística e estrutura da comunidade arbórea de igapó no Parque Nacional do Jaú, Amazônia Central. (Master dissertation, Instituto Nacional de Pesquisas da Amazônia).

Edgren CS, Radwinx RG Irwin CB. 2004. Grip force vectors for varying handle diameters and hand sizes. Human Factors, 46(2), 244–251. https://doi.org/10.1518/hfes.46.2.244.37337

Elner RW & Hughes RN. 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. Journal of Animal Ecology, 47(1), 103–116. https://doi.org/10.2307/3925

Felton AM, Felton A, Wood JT, Foley WJ, Raubenheimer D, Wallis IR & Lindenmayer DB. 2009. Nutritional ecology of *Ateles chamek* in lowland Bolivia: How macronutrient balancing influences food choices. International Journal of Primatology, 30(5), 675–696. https://doi.org/10.1007/s1076 4-009-9367-9

Ferreira LV & Parolin P. 2007. Tree phenology in Central Amazonian floodplain forests : Effects of water level fluctuation and precipitation at community and population level. Botânica Pesquisas, 58(1), 139–155. https://doi.org/10.2307/2261447

Flörchinger M, Braun J, Böhning-Gaese K & Schaefer HM. 2010. Fruit size, crop mass, and plant height explain differential fruit choice of primates and birds. Oecologia, 164(1), 151–161. https://doi.org/10.1007/s0044 2-010-1655-8

Foster MS. 1990. Factors influencing bird foraging preferences among conspecific fruit trees. Condor, 92(4), 844–854. https://doi. org/10.2307/1368720

Fragaszy DM, Boinski S & Whipple J. 1992. Behavioral sampling in the field: Comparison of individual and group sampling methods. American Journal of Primatology, 26(4), 259–275. https://doi.org/10.1002/ajp.13502 60404

Galef BG & Giraldeau LA. 2001. Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. Animal Behaviour, 61(1), 3–15. https://doi.org/10.1006/anbe.2000.1557

Galef BG Jr & Whiskin EE. 2000. Social influences on the amount of food eaten by Norway rats. Appetite, 34(3), 327–332. https://doi.org/10.1006/appe.2000.0319

Garber PA & Kitron U. 1997. Seed swallowing in tamarins: Evidence of a curative function or enhanced foraging efficiency? International Journal of Primatology, 18(4), 523–538. https://doi.org/10.1023/A:10263 59105653

Gathua M. 2000. The effects of primates and squirrels on seed survival of a canopy tree, *Afzelia quanzensis,* in Arabuko-Sokoke Forest. Kenya. Biotropica, 32(1), 127–132. https://doi.org/10.1111/j.1744-7429.2000.tb004 55.x

Giraldeau LA & Caraco T. 2000. Social Foraging Theory. Princeton University Press.

Grant KA, Habes DJ & Steward LL. 1992. An analysis of handle designs for reducing manual effort: The influence of grip diameter. International Journal of Industrial Ergonomics, 10(3), 199–206. https://doi.org/10.1016/0169-8141(92)90033 -V

Gross-Camp ND, Mulindahabi F & Kaplin BA. 2009. Comparing the dispersal of large-seeded tree species by frugivore assemblages in Tropical Montane Forest in Africa. Biotropica, 41(4), 442–451. https://doi.org/10.1111/j.1744-7429.2009.00511.x

Hanley ME, Lamont BB, Fairbanks MM & Rafferty CM. 2007. Plant structural traits and their role in anti-herbivore defence. Perspectives in Plant Ecology, Evolution and Systematics, 8(4), 157–178. https://doi.org/10.1016/j.ppees.2007.01.001

Hartstone-Rose A & Perry JM. 2011. Intraspecific variation in maximum ingested food size and body mass in *Varecia rubra* and *Propithecus coquereli*. Anatomy Research International, 2011, 1–8. https://doi.org/10.1155/2011/831943

Hershkovitz P. 1987. Uacaries, new world monkeys of the genus *Cacajao* (Cebidae, Platyrrhini): A preliminary taxonomic review with the description of a new subspecies. American Journal of Primatology, 12(1), 1–53. https://doi.org/10.1002/ajp.13501 20102

Hopkins WD, Cantalupo C, Wesley MJ, Hostetter AB & Pilcher DL. 2002. Grip morphology and hand use in chimpanzees (*Pan troglodytes*): Evidence of a left hemisphere specialization in motor skill. Journal of Experimental Psychology, 131, 412–423. https://doi. org/10.1037/0096-3445.131.3.412

Howe HF. 1980. Monkey dispersal and waste of a neotropical fruit. Ecology, 61(4), 944–959. https://doi.org/10.2307/1936763

Howe HF & Vande Kerckhove GA. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. Ecology, 62(4), 1093–1106. https://doi.org/10.2307/1937007

Hughes RN & Elner RW. 1979. Tactics of a predator, *Carcinus maenas*, and morphological responses of the prey, *Nucella lapillus*. Journal of Animal Ecology, 48(1), 65–78. https://doi.org/10.2307/4100

Hughes R & Seed R. 1981. Size selection of mussels by the blue crab *Callinectes sapidus*: Energy maximizer or time minimizer? Marine Ecology Progress Series, 6(1), 83–89. https://doi.org/10.3354/meps006083

Hughes RN & Seed R. 1995. Behavioural mechanisms of prey selection in crabs. Journal of Experimental Marine Biology and Ecology, 193(1–2), 225–238. https://doi.org/10.1016/0022-0981(95)00119 -0

Janson CH, Stiles EW & White DW. 1986. Selection on plant fruiting traits by brown capuchin monkeys: A multivariate approach. Frugivores and seed dispersal (pp. 83–92). Springer, Dordrecht. https://doi.org/10.1007/978-94-009-4812-9

Jordano P. 1995a. Angiosperm fleshy fruits and seed dispersers: A comparative analysis of adaptation and constraints in plant-animal interactions. American Naturalist, 145(2), 163–191. https://doi.org/10.1086/285735

Jordano P. 1995b. Frugivore-mediated selection on fruit and seed size: Birds and St. Lucie’s Cherry, *Prunus mahaleb*. Ecology, 76(8), 2627–2639. https://doi.org/10.2307/2265833

Jordano P. 2014. Fruits and frugivory. Seeds: the ecology of regeneration in plant communities, (Ed. 3), 18–61.

Jubb CA, Hughes RN & Rheinallt TAP. 1983. Behavioural mechanisms of size-selection by crabs, *Carcinus maenas* (L.) feeding on mussels, *Mytilus edulis* L. Journal of Experimental Marine Biology and Ecology, 66(1), 81–87. https://doi.org/10.1016/0022-0981(83)90029 -1

Junk WJ, Piedade MTF, Schöngart J, Cohn-Haft M, Adeney JM & Wittmann F. 2011. A classification of major naturally-occurring Amazonian lowland wetlands. Wetlands, 31(4), 623–40. https://doi.org/10.1007/s1315 7-011-0190-7

Kinzey WG. 1992. Dietary and dental adaptations in the Pitheciinae. American Journal of Physical Anthropology, 88(4), 499–514. https://doi.org/10.1002/ajpa.13308 80406

Kuhlmann M. 2012. Frutos e sementes do Cerrado atrativos para fauna: guia de campo, (1, pp. 8–360). Brasília: Editora Rede de Sementes do Cerrado.

Lambert JE. 2002. Exploring the link between animal frugivory and plant strategies: The case of primate fruit processing and post-dispersal seed fate. In C. A. B. International (Ed.), Seed dispersal and frugivory: Ecology, evolution and conservation (pp. 365–379). Wallingford.

Leighton M. 1993. Modeling dietary selectivity by Bornean orangutans: Evidence for integration of multiple criteria in fruit selection. International Journal of Primatology, 14(2), 257–313. https://doi.org/10.1007/BF021 92635

Lucas PW, Beta T, Darvell BW, Dominy NJ, Essackjee HC, Lee, PKD, Yuen TDB. 2001. Field kit to characterize physical, chemical and spatial aspects of potential primate foods. Folia Primatology, 72(1), 11–25. https://doi.org/10.1159/00004 9914

MacArthur RH & Pianka ER. 1966. On optimal use of a patchy environment. American Naturalist, 100(916), 603–609. https://doi.org/10.1086/282454

Mack AL. 2000. Did fleshy fruit pulp evolve as a defence against seed loss rather than as a dispersal mechanism? Journal of Biosciences, 25(1), 93–97. https://doi.org/10.1007/BF029 85186

Martin TE. 1985. Resource selection by tropical frugivorous birds: Integrating multiple interactions. Oecologia, 66(4), 563–573. https://doi.org/10.1007/BF003 79351

Melin AD, Nevo O, Shirasu M, Williamson RE, Garrett EC, Endo M, Kawamura S. 2019. Fruit scent and observer colour vision shape food-selection strategies in wild capuchin monkeys. Nature Communications, 10(1), 2407. https://doi.org/10.1038/s4146 7-019-10250 -9

Melin AD, Young HC, Mosdossy KN & Fedigan LM. 2014. Seasonality, extractive foraging and the evolution of primate sensorimotor intelligence. Journal of Human Evolution, 71, 77–86. https://doi.org/10.1016/j.jhevol.2014.02.009

Mello, MAR, Leiner NO, Guimarães PR & Jordano P. 2005. Size-based fruit selection of *Calophyllum brasiliense* (Clusiaceae) by bats of the genus *Artibeus* (Phyllostomidae) in a Restinga area, southeastern Brazil. Acta Chiropterologica, 7(1), 179–182. https://doi.org/10.3161/1733-5329(2005)7[179:SFSOCB]2.0.CO;2

Michaels HJ, Benner B, Hartgerink AP, Lee TD, Rice S, Willson MF & Bertin RI. 1988. Seed size variation: Magnitude, distribution, and ecological correlates. Evolutionary Ecology, 2(2), 157–166. https://doi.org/10.1007/BF020 67274

Montero JC, Piedade MTF & Wittmann F. 2014. Floristic variation across 600 km of inundation forests (igapó) along the Negro River, Central Amazonia. Hydrobiologia, 729(1), 229–246. https://doi.org/10.1007/s1075 0-012-1381-9

Nevo O, Garri RO, Salazar LTH, Schulz S, Heymann EW, Ayasse M & Laska M. 2015. Chemical recognition of fruit ripeness in spider monkeys (Ateles geoffroyi). Scientific Reports, 5, 14895. https://doi.org/10.1038/srep1 4895

Nilsson PA & Bronmark C. 2000. Prey vulnerability to a gapesize limited predator: Behavioural and morphological impacts on northern pike piscivory. Oikos, 88(3), 539–546. https://doi.org/10.1034/j.1600-0706.2000.880310.x

Norconk MA & Kinzey WG. 1994. Challenge of neotropical frugivory: Travel patterns of spider monkeys and bearded sakis. American Journal of Primatology, 34(2), 171–183. https://doi.org/10.1002/ajp.13503 40208

Norconk MA, & Veres M. 2011. Physical properties of fruit and seeds ingested by primate seed predators with emphasis on Sakis and Bearded Sakis. Anatomical Record, 294(12), 2092–2111. https://doi.org/10.1002/ar.21506

Parolin P, Adis J, Rodrigues WA, Amaral I & Piedade MTF. 2004. Floristic study in an igapó floodplain forest in Central Amazônia, Brazil (Tarumã-Mirim, Rio Negro). Amazoniana, 18 (1/2): 29–47. hdl.handle.net/11858/00-001M-0000-000F-DA53-3.

Parolin P, De Simone O, Haase K, Waldhoff D, Rottenberger S, Kuhn U, Junk WJ. 2004. Central Amazonian floodplain forests: Tree adaptations in a pulsing system. Botanical Review, 70(3), 357–380. https://doi.org/10.1663/0006-8101(2004)070 Parolin, P., Wittmann, F., & Ferreira, L. V. (2013). Fruit and seed dispersal in Amazonian floodplain trees: A review. Ecotropica, 19(1/2), 15–32.

Prance GT. 1979. Notes on the vegetation of amazonia iii. the terminology of Amazonian forest types subject to inundation. Brittonia, 31(1), 26. https://doi.org/10.2307/2806669

Ramos G, de Lima HC, Prenner G, de Queiroz LP, Zartman CE & Cardoso D. 2016. Molecular systematics of the Amazonian genus *Aldina*, a phylogenetically enigmatic ectomycorrhizal lineage of papilionoid legumes. Molecular Phylogenetics and Evolution, 97(1), 11–18. https://doi.org/10.1016/j.ympev.2015.12.017

Rothman JM, Raubenheimer D & Chapman CA. 2011. Nutritional geometry: Gorillas prioritize non-protein energy while consuming surplus protein. Biology Letters, 7(6), 847–849. https://doi.org/10.1098/rsbl.2011.0321

Russo SE. 2003. Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): Implications for selection. Oecologia, 136(1), 80–87. https://doi.org/10.1007/s0044 2-003-1239-y

Sallabanks R. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. Ecology, 74(5), 1326–1336. https://doi. org/10.2307/1940063

Scott MA & Murdoch WW. 1983. Selective predation by the backswimmer. Notonecta. Limnology and Oceanography, 28(2), 352–366. https://doi.org/10.4319/lo.1983.28.2.0352

Seo NJ, & Armstrong TJ. 2008. Investigation of grip force, normal force, contact area, hand size, and handle size for cylindrical handles. Human Factors, 50(5), 734–744. https://doi.org/10.1518/00187 2008X 354192

Sourd C & Gautier-Hion A. 1986. Fruit selection by a forest guenon. Journal of Animal Ecology, 55(1), 235–244. https://doi.org/10.2307/4704

Stevenson PR, Pineda M & Samper T. 2005. Influence of seed size on dispersal patterns of woolly monkeys (*Lagothrix lagothricha*) at Tinigua Park. Colombia. Oikos, 110(3), 435–440. https://doi.org/10.1111/j.0030-1299.2005.12898.x

Traveset A, Willson MF & Gaither JC. 1995. Avoidance by birds of insect-infested fruits of *Vaccinium ovalifolium*. Oikos, 73(3), 381–386. https://doi.org/10.2307/3545962

Tsujita K, Sakai S & Kikuzawa K. 2008. Does individual variation in fruit profitability override color differences in avian choice of red or white *Ilex serrata* fruits?. Ecological Research, 23(2), 445–450. https://doi.org/10.1007/s1128 4-007-0396-6

Tutin CEG, Parnell RJ & White F. 1996. Protecting seeds from primates: Examples from *Diospyros* spp. in the Lopé Reserve, Gabon. Journal of Tropical Ecology, 12(3), 371–384. https://doi.org/10.1017/ S0266 46740 0009573

Wrangham RW. 1975. Behavioural ecology of chimpanzees in Gombe National Park, Tanzania (Doctoral dissertation. University of Cambridge).

Wrangham RW & Waterman PG. 1981. Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea*: With special reference to reproductive strategies and tannin production. Journal of Animal Ecology, 50(3), 715–731. https://doi.org/10.2307/4132

Wrangham RW & Waterman PG. 1983. Condensed tannins in fruits eaten by chimpanzees. Biotropica, 15(3), 217–222. https://doi.org/10.2307/2387832

Note: In this article, we analyzed how the choice of nocturnal sleep and daytime rest of *Alouatta nigerrima* and *Alouatta discolor* was influenced by the most likely forms of predation (diurnal predators and nocturnal cats).

3.4 BEING HUNTED HIGH AND LOW: DO DIFFERENCES IN NOCTURNAL SLEEPING AND DIURNAL RESTING SITES OF HOWLER MONKEYS (*ALOUATTA NIGERRIMA* AND *ALOUATTA DISCOLOR*) REFLECT SAFETY FROM ATTACK BY DIFFERENT TYPES OF PREDATOR?

THAYS JUCÁ[1], SARAH BOYLE[2], GITANA CAVALCANTI[3], THIAGO CAVALCANTE[1], **PAVEL TOMANEK**[4], SALATIEL CLEMENTE[5], TADEU DE OLIVEIRA[6], AND ADRIAN A. BARNETT[1,7,8,9]*

[1] Amazonian Mammals Research Group, National Institute for Amazonian Research (INPA), Manaus, Amazonas 69067-001, Brazil

[2] Department of Biology, Rhodes College, Memphis, Tennessee 31270-901, USA

[3] Department of Ecology, Conservation and Wildlife Management, Institute of Biological Science, Federal University of Minas Gerais (UFMG), Belo Horizonte, Minas Gerais 31270-901, Brazil

[4] Department of Animal Science and Ethology, Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences Prague, Prague 165 00, Czech Republic

[5] Ecology and Natural Resource Management, Federal University of Acre (UFAC), Acre 69920-900, Brazil

[6] Department of Biology, Maranhão State University (UEMA), São Luís, Maranhão 65080-805, Brazil

[7] Zoology Department, Amazonas Federal University (UFAM), Manaus, Amazonas, 69077-000 Brazil

[8] Centre for Research in Evolutionary Anthropology, University of Roehampton, London SW15 5PJ, UK

[9] Department of Zoology, Federal University of Pernambuco (UFPE), Recife, Pernambuco 50670-420, Brazil

*__Corresponding author.__ Email: adrian.barnett1.biology@gmail.com

Published in:

Biological Journal of the Linnean Society 131 (1): 203–219. September 2020, https://doi.org/10.1093/biolinnean/blaa102

ABSTRACT

Predation risk is important in influencing animal behaviour. We investigated how the choice of nocturnal sleeping and diurnal resting sites by two species of primates was influenced by the most likely forms of attack (diurnal raptors and nocturnal felids). We recorded vertical and horizontal patterns of occupancy for 47 sleeping and 31 resting sites, as well as the presence of lianas or vines on trees. We compared the heights of trees used as resting or sleeping sites by the monkeys with those of 200 forest trees that the monkeys did not use. Trees used as nocturnal sleeping sites were taller than those used as diurnal resting sites, and taller than trees that the monkeys did not use. However, while trees used as diurnal resting sites were not significantly taller than non-used trees, diurnal resting sites were located on branches closer to the ground, closer to the main trunk of the tree and in trees with more lianas/vines than nocturnal sleeping sites. The differences in site location can be explained by the type of predator most likely to attack at a particular time: raptors in the day and felids at night.

Additional keywords: Amazonia – predation risk – primate – risk sensitivity.

INTRODUCTION

Predator-sensitive behaviour is widespread in animals and permeates many aspects of their biology including foraging, movement, group-dynamics and refuge occupation (Caro, 2005). Such responses have been documented in a wide variety of organisms [spiders (Reichert & Hedrick, 1990); insects (Kortet *et al.*, 2007); molluscs (Hamilton & Heithaus, 2001); fish (Magurran *et al.*, 1992); lizards (Díaz-Uriarte, 1999); birds (Larsen, 1991) and mammals (Bongi *et al.*, 2008)]. However, that differences in responses may exist depending on the predator, is an area still open for investigation, especially in terms of nocturnal and diurnal predator suites.

Primates show a variety of anti-predator behaviours, including avoidance of sites of potential ambush (Barnett *et al.*, 2012), predator-specific alarm call systems (Fichtel & Kappeler, 2002), and avoidance of particular lighting conditions (Nash, 2007), among others [see reviews by Stanford (2002), and chapters in Gursky & Nekaris (2007)]. However, another, the choice of sleeping sites is particularly suited to analysis of the influence of predator suites, since many variables of sleeping site choice can be directly quantified (Anderson, 1998), and suites of predators divided by their diel activity form into diurnal and nocturnal (Hill & Dunbar, 1998; Treves, 1999).

Sleeping site selection by non-human primates is considered to be an adaptative response to several ecological factors (Anderson, 2000). These factors include: proximity to early-morning feeding sites (Teichroeb *et al.*, 2012); parasite build-up avoidance (Hausfater & Meade, 1982; Brividoro *et al.*, 2019); thermoregulation (Smith *et al.*, 2007; Fan & Jiang, 2008); insect bite avoidance (Feilen & Marshall, 2017); and predation avoidance (Reichard, 1998; Phoonjampa *et al.*, 2010; Cheyne *et al.*, 2013a). Often, several of these factors can be involved simultaneously (Day & Elwood, 1999; Cheyne *et al.*, 2013b; Brotcorne *et al.*, 2014). For anti-predator strategies, different factors have been found to influence sleeping site selection, including: suitability for escape from predators (Albert *et al.*, 2011); minimizing detection by predators (Heymann, 1995; Ellison *et al.*, 2019); maximizing predator detectability (Barnett *et al.*, 2012); and complicating predator approach (Matsuda *et al.*, 2008a). However, in addition to sleeping during the night, diurnal primates often rest during the day, either to digest food, avoid heat stress, or conserve energy (Kurup & Kumar, 1993; Wallace, 2001; Zhou *et al.*, 2007).

The major predators of diurnal primates are mammalian carnivores (notably felids), raptorial birds (mostly eagles), and reptiles (mostly snakes, but occasionally large lizards) (Miller & Treves, 2007). In the Neotropics, with rare exceptions [e.g. Barnett *et al.* (2015) reported large eagles preying on tamarins], predator-prey pairings are largely size-related, with smaller felids and hawks preying on primates less than 2 kg in weight, and the larger species (e.g. jaguars and eagles) taking those of 2 kg and larger (Anderson, 1986; Ferrari, 2009). In addition, Amazonian felids tend to be nocturnally active (Emmons, 1987; Sunquist & Sunquist, 2002), while non-strigiform raptors take prey during the day (Robinson, 1994). The Neotropics has several large owls (e.g. Enríquez *et al.*, 2017; Motta-Junior *et al.*, 2017) that, based on the size of their known prey (e.g. Gómez de Silva *et al.*, 1997; Borges *et al.*, 2004; König *et al.*, 1999), should be capable of successfully attacking sleeping Neotropical primates. However, although predation by owls has been recorded for several lemur species (Goodman *et al.*, 1993; Goodman & Thorstrom, 1998; Stanford, 2002; Fichtel, 2007; Nash, 2007), it appears to occur rarely in the Neotropics, given that reviews by Isbell (1994), Boinski *et al.* (2000), Hart (2007), and Fichtel (2012) recorded no known published incidences of owl predation on non-strepsirhines. The only known interactions between owls and Neotropical primates have been with nocturnally active owl monkeys [*Aotus* spp. (Wright, 1994; Boinski *et al.*, 2000)]. Nevertheless, the record by Voirin *et al.* (2009) of a spectacled owl (*Pulsatrix perspicillata* Latham, 1790) preying on a sleeping three-toed sloth (*Bradypus variegatus* Schinz, 1825), and the record by Tomazzoni *et al.* (2004) of a great horned owl (*Bubo virginianus* Gmelin, 1788) preying on a young coypus (*Myocastor coypus* Molina, 1782), indicates that Neotropical owls are at least a potential threat to larger-bodied sleeping platyrrhines, as in both species the mass of predated individuals would have exceeded 2 kg (Guichón *et al.*, 2003; Hayssen, 2010). However, there are no records in the literature of Neotropical owl predation of primates and experienced owl biologists reported never having encountered or heard of any.

Many activities undertaken by primates appear to be risk-sensitive and structured by mechanisms and strategies that minimize the possibility of predation (Ferrari, 2009; Barnett *et al.*, 2012). In terms of sleeping sites, baboons, for example, are known to have a series of ranked sleeping site preferences, with steep cliffs inaccessible to leopards being greatly favoured (Hamilton, 1982), and to use specific safe sites to rest or groom during the day (Cowlishaw, 1997). Wright (1998) found that Milne- Edwards sifakas (*Propithecus edwardsi* Grandidier, 1871) chose nocturnal sleeping sites that were further from the ground than were diurnal resting sites since the main predator is the predominantly nocturnal fossa [*Cryptoprocta ferox* Bennett, 1833 (Lührs & Dammhahn, 2010)], as large diurnal eagles are now extinct in Madagascar (Goodman & Muldoon, 2016). Such behaviour appears to be related to how predators of primates attack; primates choose sites closer to the ground to avoid an aerial attack from outside the tree crown from above or the side, in the case of raptors (e.g. Fowler & Cope, 1964; Eason, 1989; Julliot, 1994; de Souza Martins *et al.*, 2005; Urbani *et al.*, 2012), and choose sites higher in the tree crown to avoid a pounce and/ or paw swipe (Emmons, 1987; Condit & Smith, 1994; Fay *et al.*, 1995) from inside the crown in the case of arboreal felines (e.g. Olmos, 1994; Miranda *et al.*, 2005; Bianchi & Mendes, 2007; Matsuda & Izawa, 2008; Matsuda *et al.*, 2008b), and other arboreal carnivores (Asensio & Gómez-Marín, 2002; Camargo & Ferrari, 2007).

The presence of lianas/vines in a tree has been shown to influence sleeping site selection in primate species, as lianas can be used by predators to get access to prey or, for snakes, as concealment sites (Tenaza & Tilson, 1985; Phoonjampa *et al.*, 2010; Cheyne *et al.*, 2012). For Neotropical monkeys, Barnett *et al.* (2012) reported that golden-backed uacari monkeys (*Cacajao ouakary* Spix, 1823) avoided trees that had lianas/vines in contact with the ground or in contact with other trees. Barnett *et al.* (2012) interpreted this behaviour as a method of reducing the possibility of non-avian attacks, by avoiding sites where such vegetation heightened accessibility.

Although it has been argued that the large body size of some primate clades [e.g. atelines > 6 kg (Ford & Davis, 1992)] may protect them from predators to some extent (Di Fiore, 2002), records of predation on howler monkeys (*Alouatta* spp.), for example, exist and include a wide array of predators such as carnivorous mammals (Peetz *et al.*, 1992; Asensio & Gómez-Martín, 2002; Bianchi *et al.*, 2007; Ludwig *et al.*, 2007), raptors (Sherman, 1991; Miranda *et al.*, 2006; Aguiar-Silva *et al.*, 2014), and snakes (Quintino & Bicca-Marques, 2013). Indeed, on some Amazonian river islands, red howler monkeys (*Alouatta juara* Elliot, 1910) form the main arboreal prey for jaguars (*Panthera onca* Linnaeus, 1758: Rabelo *et al.*, 2019).

Howler monkeys (genus *Alouatta*) are notable among Neotropical primates for the extent to which their patterns of diurnal activity are dominated by resting periods (Richard, 1970; Braza *et al.*, 1981; Estrada *et al.*, 1999; Cornick & Markowitz, 2002). These resting patterns are related to a predominantly folivorous diet and the energetic demands of leaf digestion (Nagy & Milton, 1979; Pavelka & Knopff, 2004). Howlers also tend to show regular use of a limited number of trees as nocturnal sleeping sites [Sekulic, 1982; Bravo & Sallenave, 2003; Kowalewski & Zunino, 2005: though see Chivers (1969) for contrary data]. In comparison with other similar-sized Neotropical arboreal mammals, howler monkeys tend to have smaller home ranges, larger bodies, and louder, longer-distance vocalizations that are discernible for up to 1 km (Sekulic & Sekulic, 1982; Whitehead, 1995; Cornick & Markowitz, 2002; Kitchen, 2004). Such behaviour could make nocturnal sleeping sites, as well as diurnal resting sites, potential foci of predation, since howler monkeys are more conspicuous and tend to revisit the same locations.

Sleeping site preferences are influenced by a number of different factors (Liu & Zhao, 2004), and, as explained above, the two principle suites of predators of Neotropical primates (carnivores and raptors) have different modes of attack. Therefore, our goals were to determine: (1) to what extent predation risk might influence choice of sleeping and resting sites for howler monkeys in Central Amazonia; and (2) the structural characteristics of such sites, based on the different attack modes of potential predators likely to attack at night and during the day. We hypothesized that the sleeping and resting sites of arboreal primate species are risk-sensitive to predation. We predicted that due to the greater risk of nocturnal mammalian predators hunting within the tree canopy at night, and higher risk of raptor attack during the day: (1) howler monkeys would choose taller and emergent trees for nocturnal sleeping than for diurnal resting; (2) howler monkeys would choose to rest closer to the main trunk of the tree during the day than during the night; and (3) howler monkeys would choose trees with more lianas/vines to rest during the day than to sleep in at night.

Thompson *et al.* (2014, 2016) showed that ambient temperatures and metabolic responses to cold and heat stress can influence choice of tree resting and sleeping sites by mantled howler monkeys (*Alouatta palliata* Gray, 1849). Although the current study's methodology did not include physical measurements of temperature (of the various environments or of the primates themselves), we predicted that: (4) if temperature is an important influence on diurnal resting and nocturnal sleeping site choice, horizontal position will differ depending on whether the day or the night was hot or cool.

MATERIAL AND METHODS

Study site

The study took place at two sites along the middle- Tapajós River, in riverine forests on either side of the community of Machado, and along the Jamanxim River to the first set of impassable rapids (Fig. 1: Sites 1 and 2, respectively), Pará State, Brazil (Fig. 1). We collected data on the margins of *igapó* seasonallyflooded forest (*sensu* Prance, 1979). Forests of this river basin are notably rich in vines and lianas (Gerwing & Farias, 2000). Although there are known differences in the fauna and flora of *terra firme* (non-flooded) forest on either side of the Tapajós River (de Oliveira *et al.*, 2016), due to the high incidence of water- and fishmediated seed dispersal (hydrochory and ichthyochory, respectively) in *igapó* trees (Anderson *et al.*, 2009; Correa *et al.*, 2015), the tree species composition of *igapó* forests do not differ on the two sides of the river (Barnett, unpubl. data).

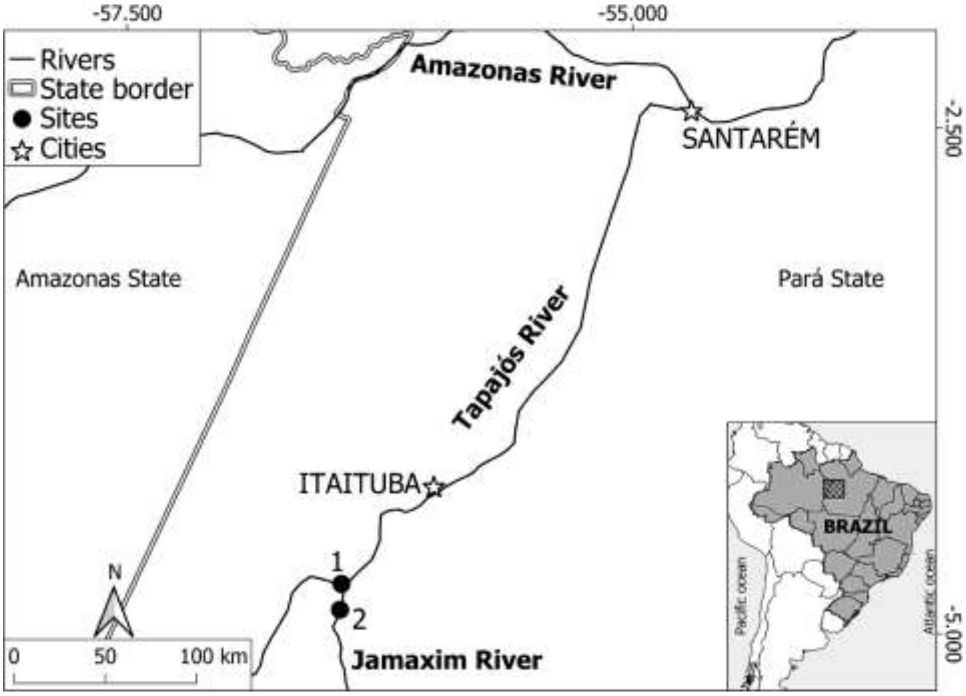


Figure 1. Study sites on the Tapajós River (main frame) and location of the river within Brazil (inset). Site 1 = Machado community; Site 2 = start of Jamaxim rapids.

Two howler monkey species occupy the Tapajós River basin in the areas we surveyed. Following the taxonomy of Gregorin (2006), these species are: Amazon black howler monkey (*Alouatta nigerrima* Lonnberg, 1941) on the western bank of the Tapajós River, and Spix's red-handed howler monkey (*Alouatta discolor* Spix, 1823) on the eastern bank of the Tapajós River. In addition, the study region has the highestknown mammalian diversity recorded in the Amazon Basin and has the full suite of potential mammalian carnivore predators (de Oliveira *et al.*, 2016). Large raptors are abundant in the locality, with primate predation at the study site being recorded by both harpy eagle (*Harpia harpyja* Linnaeus, 1798) and black hawk eagle [*Spizaetus tirannus* Wied, 1820 (Barnett *et al.*, 2015, 2017, 2018)].

Data collection

As part of a broader series of biological surveys linked with the environmental impact assessment of proposed dam construction in the region (e.g. de Oliveira *et al.*, 2014; Barnett *et al.*, 2017, 2018), we collected field data on howler monkeys between October 2013 and December 2014. We surveyed for these primates between 05:30 and 18:30 h from boats. Field observations at the study sites indicated that howler monkeys rarely leave the nocturnal sleeping site until one or more hours after dawn, and may begin entering nocturnal sleeping sites an hour or more before sunset (Barnett, Cavalcanti, de Oliveira, unpublished data). Therefore, we considered trees with resting howler monkeys as 'nocturnal sleeping sites' if animals were seen resting in them from 16:30 to 18:30 h or between 06:00

and 08:00 h. We classified trees in which animals were seen paused outside these times as 'diurnal resting sites'. In both cases we defined 'resting' as 'paused, often prone, not engaged in locomotion or feeding for periods exceeding 5 consecutive minutes'. To maximize the number of encounters, we stayed with each group for 10 min, and then continued the flooded forest surveys, moving along the river at a speed of approximately 4 km/h. Each encounter was treated as an independent observation, although the same groups could have been sampled on different days.

During the primate surveys, when we encountered resting howler monkeys, we recorded: tree maximum height (m), mean vertical and horizontal position of the group within the tree canopy (see below), and presence of lianas/vines and their three-dimensional within-canopy topography (see below).

Tree maximum height

We measured the heights of nocturnal sleeping trees, diurnal resting trees and 200 control trees (trees that howler monkeys were never seen to use for sleeping or resting during the study period). These non-used trees consisted of two control plots of 100 sequential trees, one set on each side of the main course of the Tapajós River. We first chose a visually distinct tree as the first non-used tree, and then collected data from 99 sequential riverside trees. To be included, individual trees had to have a canopy that could be visually distinguished and quantified. We estimated individual tree heights using Pythagorean trigonometry (Waring & Schlesinger, 1985) with a Tangent Height Gauge (Forestry Suppliers, Jackson, MS, USA) to provide the angle of elevation, and a Laser Rangefinder (Bushnell, Overland Park, Kansas, USA) for distance.

Position of howler monkey group within canopy

We recorded the position of all visible group members as a scan sample (Altmann, 1974), noting both the vertical and horizontal components of the group's position. For the vertical component, we visually estimated the centre point of the howler monkey group (Fig. 2), and then calculated mean group height using the same methods as for determining tree height. Perhaps because group sizes were small, there were no records of simultaneous occupancy of multiple trees by a resting or sleeping group. We recorded the horizontal position of the howler monkeys using the following designations: 1 = touching trunk or in vertical crotches of main trunk; 2 = first third (main body) of major branches; 3 = second third (and/or second division) of major branch; 4 = final third (or within tertiary or higher order division of branches, e.g. shoots and twigs of canopy) (Fig. 3). When more than one category was occupied by different individuals, we used the mode to provide a numerical value for group position.

Figure 2. The difference between (a) maximum canopy height and (b) mean group height (here simplified by the fact that group size = 1, circled). Horizontal position 4 (final third of major branch). Photo: A.A. Barnett.

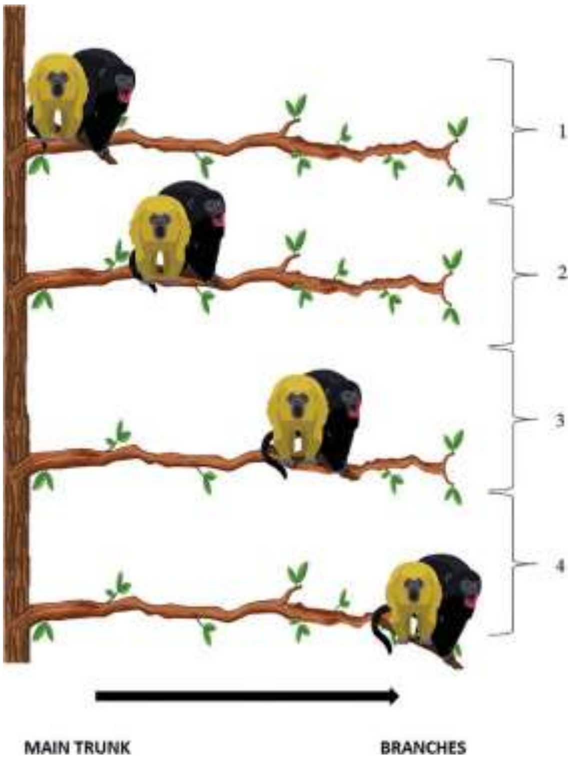


Figure 3. Schematic diagram to show the different horizontal sub-stations of branch use as defined for the current study. Note: branch tips are generally far leafier than shown here.

Liana/vine cover and topography

We recorded the presence or absence of lianas/vine on each tree. To quantify liana/vine presence, we categorized presence as: 0 = none visible; 1 = within tree crown light (five or fewer liana/vine loops or straight sections visible in the crown); 2 = within tree crown heavy (six or more liana/vine loops or straight sections visible in the crown); 3 = touching other crown and/or the ground (Fig. 4, left); and X = when lianas/vines were present but we could not visually separate the study crown from other tree crowns. In this case, we could not ascertain the extent of liana/vine contact or liana extension to the ground.

Figure 4. Emergent tree showing extensive type 3 vine coverage (vines touching the ground) (left) and emergent tree compared to surrounding canopy (right). The tree in the right has the form which the study typically recorded as being used by howler monkeys. Photo: A.A. Barnett.

Ambient thermal stress

Due to logistical considerations, we were unable to directly measure temperature or temperature fluctuations at sleeping or resting sites, nor within similar canopies. However, as a proxy, we obtained daily weather data from the website of the National Institute of Meteorology (INMET). We selected data from the meteorological station located in the city of Itaituba, PA, since this is the closest (~ 40 km) to the collection site. Single point data was available daily for maximum and mean temperature. Consequently, we investigated the relation between within-tree location of primate group and ambient temperature, with “hot” being defined as a maximum temperature equal to or greater than 30 °C and the average temperature equal to or greater than 28 °C, with “cool” being when the temperatures were below such values. We did not obtain data on behaviour during periods of rain, as we did not sample during such conditions.

Data analysis

First, we tested all the variables for normality with the Shapiro-Wilk test. Given mean canopy height for trees on both sides of the river did not differ, including (Mann Whitney U test: w = 4786, *P* = 0.602), or excluding (w = 2671, *P* = 0.624) emergent trees (Fig. 4, right), and given the great similarity in the ecology of howler monkeys (Kinzey, 1997; Gregorin, 2006; Kowalewski *et al.*, 2014), we combined sleeping and resting site data for the two howler species to increase sample size and statistical power.

We ran three Mann-Whitney U analyses to test for differences in: (1) heights of nocturnal sleeping trees vs. diurnal resting trees; and (2) heights of sleeping and resting trees vs. the non-used (control) trees. We used a *t*-test to test for differences in mean vertical heights of howler monkey groups at nocturnal sleeping sites vs. diurnal resting sites. We used Chi-square tests to determine if there were differences in: (1) mean troop horizontal position between nocturnal sleeping vs. diurnal resting trees; (2) liana/vine presence and coverage categories in nocturnal sleeping, diurnal resting trees and non-used trees; and (3) selection of emergent and non-emergent trees for nocturnal sleeping and diurnal resting from non-used trees. We also used a Chi-square test to compare relations of the average horizontal position of the group with the ambient temperature. This was done for night resting and day resting sites separately and with both sets combined. For the daytime rest data, we used only the categories of position 1, 2 and 3, since there were no records of howler monkeys resting during the day in position 4.

For all tests, we set significance values at 0.05. We conducted all statistical analyses with R v.3.6.1 (R Core Team, 2019), except for the Chi-square tests, which we performed in Microsoft Excel. All research protocols reported in this manuscript were reviewed and approved by the Brazilian Institute of the Environment and Renewable Natural Resources (IBAMA, which is part of the Brazilian Ministry of the Environment that regulates research with animals), and Chico Mendes Institute-Biology (ICMBio, which regulates field-based biological research in Brazil).

RESULTS

Tree maximum height

We did not observe any predation attacks on the howler monkeys during the study period. We located 47 nocturnal sleeping sites and 31 diurnal resting sites.

The median height of nocturnal sleeping trees was 18 m (N = 47, range = 13.8–23.8 m), and 16.3 m for diurnal resting trees (N = 31, range = 11.6–26.3) (Fig. 5). For the 200 *igapó* control trees, mean forest canopy height for the 143 non-emergent trees was 13.8 m (N = 143, range = 5.7–18.4 m). There were 57 (28.5 %) trees rising above the local mean canopy level sufficiently to be considered emergent trees (median height = 22.6 m, range = 17.7–37.9 m). Overall, for the control trees (emergent and non-emergent), median height was 15.5 m (Fig. 5).

Nocturnal sleeping trees were significantly taller than both non-used trees (emergent and non- emergent) ($N_1 = 47$, $N_2 = 200$, $U = 2759.0$, $P < 0.001$) and diurnal resting trees ($N_1 = 47$, $N_2 = 31$, $U = 539.0$, $P = 0.053$), but there was no significant difference in height between non-used trees and diurnal resting trees ($N_1 = 200$, $N_2 = 31$, $U = 2480.0$, $P = 0.073$). For nocturnal sleeping trees, 34% ($N = 16$) were non-emergent canopy trees (though all were at the upper level of the canopy), and 66% were emergent trees ($N = 31$). Whilst for day resting trees, 42% ($N = 13$) were non-emergent and 58% were emergent trees ($N = 18$). On the other hand, for non-used trees, most were non-emergent canopy trees (71.5%, $N = 143$), and only 28.5% ($N = 57$) were emergent trees. We found an association between the selection of emergent trees by howler monkeys and resting period ($\chi^2 = 23.557$, df = 2, $P < 0.001$), as the howler monkeys selected taller, emergent trees for nocturnal sleeping (Fig. 6).

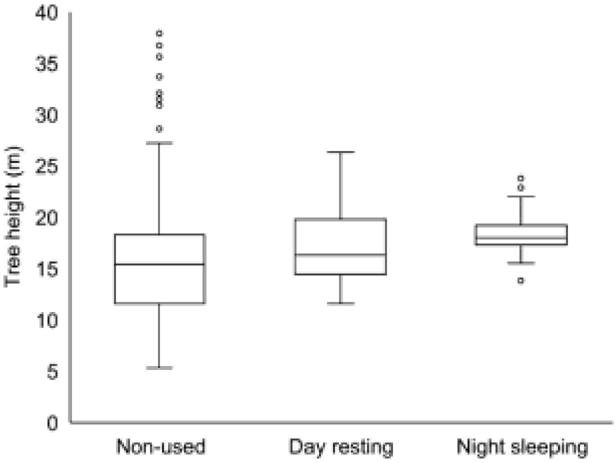


Figure 5. Height of non-used trees ($N = 200$), trees used as day resting ($N = 31$) and night sleeping sites ($N = 47$). The box indicates quartile range, the whiskers indicate maximum and minimum observations and the circles indicate the outliers.

Position of howler monkey group within canopy

Mean height for howler monkey groups in nocturnal sleeping trees and diurnal resting trees was 14.77 m (SD ± 2.09, $N = 47$, range = 10.0–19.4 m) and 11.95 m (SD ± 2.27, $N = 31$, range = 8.6–17.4), respectively (Fig. 7). These mean heights for the howler monkey groups differed (t = 5.5236, df = 60.42, $P < 0.001$); howler monkeys were located at a greater height above the water level in the tree while sleeping at night than while resting during the day.

There was an association between howler monkey group horizontal position and resting period (night sleeping vs. day resting) ($\chi^2 = 24.95$, df = 3, $P < 0.001$). Howlers most frequently slept on the middle vertical- part of branches (category 3) during the night and mostly rested in the first-horizontal-third of branches (category 2) during the day (Table 1). Small trees with open canopies (Fig. 8, right) were never observed being used for sleeping.

Liana/vine cover and topography

There was an association between liana/vine cover and resting period (χ^2 = 75.143, df = 6, *P* < 0.001): howler monkeys mostly slept at night in trees with no visible lianas/vines, and mostly rested during the day in trees with heavy lianas/vines, whereas most non-used trees had lianas/vines that touched other canopy and/or the ground (Table 2). Liana/vine data could only be unequivocally ascertained for 161 of the 200 trees that were not used by the howler monkeys (the other 39 trees had part of either the trunk or canopy obscured in a way that negated full categorization).

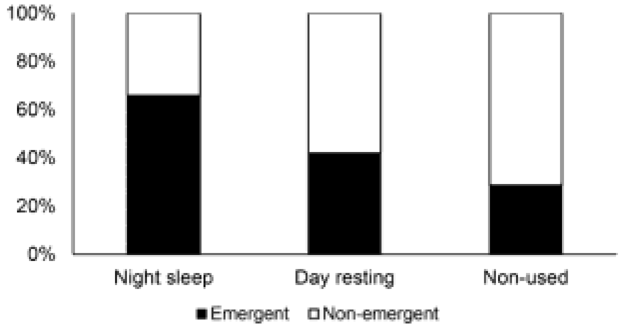


Figure 6. Proportion of emergent and non-emergent trees among the night sleeping, day resting and non-used trees

Ambient thermal stress

No association was found between ambient temperature and the average horizontal position of night-sleeping (χ^2 = 1.791, df = 3, P = 0.616), nor day- resting (χ^2 = 0.998, df = 3, P = 0.801) sites, nor when the data was combined (χ^2 = 1.141, df = 3, P = 0.767) (Table 3).

DISCUSSION

The choice of taller trees as both resting and sleeping sites has been widely recorded for primates, and is generally regarded as an adaptative response for either avoiding predators (Anderson, 1986; Stanford, 2002), or providing a longer time to respond to them, so enhancing the possibility of escape (Ydenberg & Dill, 1986; Martin-Klimoczko *et al.*, 2015). However, the additional differences recorded here in tree height and effective mean heights at which the howler groups occupied the diurnal resting and nocturnal sleeping trees indicates that additional responses exist. Here we interpret these differences as being based on the types of predators most likely to attack a group of primates in such a tree, with swooping aerial attacks by raptors being more common in the day and within-tree attacks by mammalian carnivores at night (Robinson, 1994; Sunquist & Sunquist, 2002; Miller & Treves, 2007; Ferrari, 2009).

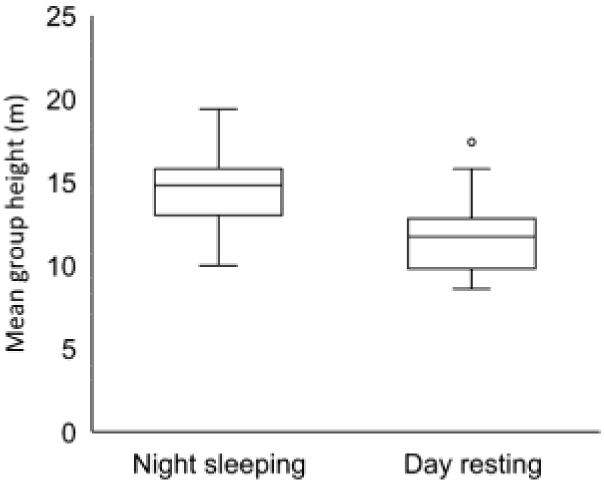


Figure 7. Mean group height at night sleeping (N = 47) and day resting (N = 31) sites.

Although no attacks on howlers were observed during the current study, in our Central Amazonia study area several attacks by raptors have been observed in the region on a similar-sized primate, the red-nosed bearded saki [*Chiropotes albinasus* Geoffrey & Deville, 1848 (Barnett *et al.*, 2017, 2018)], indicating that predation is an active element of primate life at this location. In addition, as noted by Ferrari (2009), in his review of the effects of predation in primate ecology and sociology, cultural transmission of anti-predator behaviours mean that such events can be infrequent yet still have an effect on observable behaviours.

We should note that although nocturnal sleeping trees were statistically taller than diurnal resting trees, height range was greater for diurnal resting trees (11.6–26.3 m) than nocturnal sleeping trees (13.8–23.8 m). Previous studies have found that howler monkeys use a limited number of tree species as sleeping sites, even when such tree species are not the most abundant at the study area (Kowalewski & Zunino, 2005; Brividoro *et al.*, 2019). Although the present study did not record the species or sizes of the trees used by the monkeys, the narrower range of tree height in nocturnal sleeping trees might indicate that nocturnal predators may have a stronger pressure in howler monkey's anti-predator behaviour.

Although we cannot say that the trees recorded as 'not-used' were, in fact, never-used by the howler monkeys, the observed differences are such that, for the time period studied, it is likely that the howler monkeys chose trees not only to reduce the chance of attack, but to increase the chance of warning of attack (especially at night when, as far as it known, no group members are vigilant), thereby enhancing the likelihood of escape. Consideration of such subtleties in predation avoidance strategies is a desirable development for future work in this field of study.

Table 1. Frequency of mean group horizontal position in night sleeping and day resting trees

Position category	Night sleeping trees		Day resting trees	
	N	%	*N*	%
1 - Touching trunk or in vertical crotches of main trunk	3	6.38	6	19.35
2 - First third (main body) of major branches	10	21.28	20	64.52
3 - Second third of major branch	21	44.68	5	16.13
4 - Final third	13	27.66	0	0
Total	47	100	31	100

Figure 8. Site selectivity – the two tall trees (arrowed) were both used as night sleeping sites (left). The intermediate vine covered trees were not; a small thin tree with very open canopy, used for feeding (note new leaves) (right). Photos: A.A. Barnett.

Table 2. Frequency of liana categories in night sleeping, day resting and non-used trees

Liana category trees	Night sleeping tree		Day resting trees		Non-used	
	N	%	*N*	%	*N*	%
0 - None visible	20	42.55	4	12.9	17	10.56
1 - Within canopy (light)	15	31.91	7	22.58	15	9.32
2 - Within canopy (heavy)	10	21.28	14	45.16	30	18.63
3 - Touching other canopy and/or the ground	2	4.26	6	19.35	99	61.49
Total	47	100	31	100	161	100

Chimpanzees create both ground-based and tree- based nests as sleeping sites and their sleeping behaviour is well-studied (Fruth & McGrew, 1998). It has been reported for both the Nigeria-Cameroon chimpanzee [*Pan troglodytes ellioti* Matschie, 1914 (Last & Muh, 2013)] and Central African chimpanzees [*Pan troglodytes troglodytes* Blumenbach, 1775 (Tagg *et al.* (2013)] that ground-based night-sleeping nests were only constructed where the threat of human-predation and disturbance was low. Although where human disturbance is low, humidity avoidance is more important than predator or mosquito avoidance in nest position selection (Koops *et al.*, 2012). In contrast, in Senegal, a comparison of nesting behaviour of *Pan troglodytes verus* (Schwarz, 1934) in high- and low-predator pressure areas with similar vegetation characteristics found nests were made lower in the latter (Pruetz *et al.*, 2008). Similar results were reported by for a Senegal (low predation risk)/Tanzania (high predation risk) comparison (Stewart & Pruetz, 2013). In bonobos (*Pan paniscus* Schwarz, 1929) females construct nests higher in trees to avoid the attentions of males (Fruth & Hohmann, 1993). Two other studies have examined and compared the resulting behavioural responses functionally-allied to the reduction of predation between nocturnal and diurnal resting sites: Wright (1998) studied Milne- Edward's sifaka (*Propithecus edwardsi* Grandidier, 1871) and Martin-Klimoczko *et al.* (2015) studied red- handed howler monkey (*Alouatta belzebul* Linnaeus, 1766) sleeping and resting sites. Both Wright (1998) and Martin-Klimoczko *et al.* (2015) examined the height at which primates rested in trees during these different periods and related the observed differences in potential predator's attack form. However, neither investigated the functional consequences of such predictions. Our current study appears to be the first to do so.

Table 3. Frequency of mean group horizontal position in hot and cool days/nights

Position category	Hot		Cool	
	N	%	*N*	%
1 - Touching trunk or in vertical crotches of main trunk	4	13.33	5	10.42
2 - First third (main body) of major branches	12	40	18	37.5
3 - Second third of major branch	8	26.67	18	37.5
4 - Final third	6	20	7	14.58
Total	47	100	31	100

In the current study, we found that howler monkeys rest closer to the main trunk during the day and sleep closer to terminal branches at night. Resting closer to the trunk of the tree might provide extra time to react to an aerial predator, especially since reactions to raptors often consist of dropping into lower vegetation and/or hiding in dense vegetation thickets (Miranda *et al.*, 2006;

Barnett *et al.*, 2017, 2018). In contrast, attacks in trees by mammalian carnivores generally involve the potential predator accessing the primates' locations either by climbing the tree trunk or lianas/ vines associated with the tree (Emmons, 1987; Bianchi & Mendes, 2007). By sleeping on thinner branches or closer to the terminal end of a branch, a primate can detect the approach of a heavier predator (Anderson, 2000), and thus gain extra warning time and time to escape from a predator that typically attacks via the tree trunk or main limbs of the tree. Consequently, sleeping on the thinner branches may, again, give extra warning time and time to escape from a predator consequently obliged to attack via the tree trunk or main limbs of the tree.

As predicted, howler monkeys chose trees with more lianas/vines to rest in during the day than to sleep in at night. This behaviour is in accordance with a strategy to prevent aerial attacks from raptors during the day that usually come from outside the canopy, because the raptors' access should be at least partially blocked by lianas/vines (see Barnett *et al.* 2017 for an example with red-nosed bearded saki monkeys, *Chiropotes albinasus* Geoffroy & Deville, 1848). In addition, Barnett *et al.* (2012) found that golden-backed uacari monkeys (*Cacajao ouakary* Spix, 1823) avoided sleeping at night in trees crowns connected to other tree crowns by lianas/vines that could be used by a mammalian predator to get access to prey. Comparing nocturnal sleep site characteristics of Kloss' gibbons (*Hylobates klossi* Miller, 1903) and Mentawai langurs (*Presbytis potenziani* Bonaparte, 1856), Tenaza & Tilson (1985) found that gibbons slept in lianas-free trees, whereas the langurs slept in trees with thick, woody lianas. However, there was high hunting pressure by humans in the study area; hunters used lianas to climb the trees, and thus the langurs were more susceptible to nocturnal human predation than the gibbons.

The current study did not include functional analysis of predation by snakes, even though snakes are known predators of primates (Isbell, 2006) of all sizes: small- bodied (Heymann, 1987; Corrêa & Coutinho, 1997; Tello *et al.*, 2002; Ferrari & Beltrão-Mendes, 2011), medium- bodied (Cisneros-Heredia *et al.*, 2005) and large-bodied (Perry *et al.*, 2003; Ferrari *et al.*, 2004), including the Purus red howler monkey, *Alouatta puruensis*, Lönnberg (1941), (Quintino & Bicca-Marques, 2013). Phoonjampa *et al.* (2010) found that pileated gibbons (*Hylobates pileatus* Gray, 1861) preferred to use trees without lianas as nocturnal sleeping sites, probably because liana tangles can be used as hiding sites for predaceous snakes. Also, lianas and vines enhance connectivity, and thus mobility, for arboreal snakes, and large-bodied animals have been recorded to use lianas to ascend into trees from the ground (Koenig *et al.*, 2007; Turner & Turner, 2016). The slower, quieter and more stealthy approach of snakes, and their ability to use both trunks and lianas/vines, means that the current study does not account for howler monkey strategies to reduce snake predation success or risk, especially as most tropical snake assemblages include species that are active diurnally, nocturnally or both (Hartmann *et al.*, 2009; Mukherjee & Heithaus, 2013). That said, we found that during the day the howler monkeys avoided trees with lianas/vines that touched the ground and/or another tree; such behaviour may be linked to avoidance of predation by snakes, but this subject is a topic for future study.

We should note that *igapó* as a river-margin forest may have influenced the relative importance of the factors analysed here. For example, the presence of a river on one side of the trees may have influenced non- raptor accessibility in ways that made lianas/vines more important than they might be in *terra firme* forest. Applying the methods used here in *igapó* forest to sleeping and resting sites in *terra firme* forests is therefore a desirable follow-up to the current study, as accessibility for terrestrial predators would likely be greater in *terra firme* forests. Such a follow-up would allow for additional testing of the hypotheses tested in the current study.

Comparison of site choices on hot and cool days and nights showed no difference in extent of position on the trunk of resting/sleeping sites, both when data was analysed separately and combined. If sites were being chosen in response to heat stress, then the animals might have been expected to choose areas closer to the trunk on hot days to gain shade protection and areas closer to the outer canopy on hot nights. This was not the case in the current study, the importance of minimizing predation seems to outweigh the thermal- comfort choices reported by Thompson *et al.* (2014, 2016); these thermal-comfort choices did not appear to be a strong influential factor in the current study. However, it is important to note that the temperature data available and used in the present study may not reflect microclimates experienced by the animals, and further study with on-site temperature data would be recommended.

In addition to studies of other species of large-bodied Neotropical primates (> 3 kg), it would be interesting if future studies were to include investigations of the influence of the presence of juveniles and infants on sleeping-site choice, since large, constricting snakes may take younger primates (Ferrari, 2009). This, to our knowledge, is a topic that has not received any investigative attention. It should also be noted that, while in the Neotropics all large arboreal lizards are iguaniids and almost entirely herbivorous (Troyer, 1984), terrestrial, Neotropical teiids of the genera *Salvator* and *Tupinambis* may reach 1.4 m and have been known to eat primate-sized mammals [e.g. *Rattus* (Sazima & D'Angelo, 2013)]. However, teiids are rarely arboreal (Kasperoviczus *et al.*, 2015), and there are no published records of them attacking primates. In contrast, however, the Paleotropics was inhabited by large carnivorous lizards (Varanidae) which are known predators of primates (Yeager, 1991;Řeháková-Petru *et al.*, 2012). Given that the abundance of such predators often far exceeds that of mammalian carnivores (de Miranda, 2017), the effect of their methods of approach on sleeping and resting site choice should also be considered, as should the possibility of predation by crocodiles for tree sites that overhang water (Galdikas, 1985).

The present study assumed a lack of aerial predation risk at night; however, use of arboreal camera traps at frequently-used sleeping sites could determine whether owls are a predation risk for howler monkeys and other arboreal animals. Whether owls predate Neotropical primates is currently unconfirmed, through evidence from the literature and personal experience of long-term workers indicates that it is, at the most, an exceedingly rare event (there are no known records). Likewise, such arboreal camera traps could help determine the sleeping patterns of primates and whether sleeping behaviours vary depending on predation risk. In addition, while the effects of predation threat on group size and spread have been studied in primates (Cowlishaw, 1997, 1999), the information gained has not yet been applied to sleeping behaviour [though there are models for birds: e.g. Tillmann (2009) for *Perdix*]. Thus, the data given here could help structure studies of the spacing and group group sizes of primates in day-resting and night-sleeping sites.

That potential prey may position themselves in different locations depending on predator type has received some attention in other taxa [e.g. redshanks being hunted by two diurnal raptors with differing attack strategies (Cresswell & Quinn, 2013); nocturnal and diurnal predators of grey partridge (Harmange C, Bretagnolle V, Chabaud N, Sarasa M, Pays O. Diel cycle in a farmland bird is shaped by contrasting predation and human pressures. Submited to Oikos.)]. Nevertheless, it seems to have been little applied to tree-roosting birds (Hinsley & Bellamy, 2000; Yuan *et al.*, 2012), and it is hoped that this paper may promote this. In addition, we call for a greater interchange, both methodologically and conceptually, between groups studying anti-predator strategies in various taxa. Thus, the impact of predation type and intensity on prey group size has been well studied in both fish (Magurran & Pitcher, 1987; Ashley *et al.*, 1993; Krause & Gosin, 1994), and primates (van Schaik & Hörstermann, 1994; Janson & Goldsmith, 1995; Hill & Lee, 1998), and clearly have common interests although the two rarely cite papers from the other field. However, we believe a cooperative and inter-disciplinary approach will be key to future advances.

ACKNOWLEDGEMENTS

T.J. thanks the staff of the MSc ecology program, the Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil, and the National Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnlógico—CNPq) for financial support during the period in which this paper was written (Grant 131785/2017-6). A.A.B. thanks Maracajá Ecological Consulting for the invitation to conduct the survey work. T.de.O. wishes to thank CNEC/ WorleyParsons and ELETROBRÁS for financial support of the mammal survey in the Tapajós River Basin. This paper is contribution 41 from the Amazonian Mammals Research Group, and contribution number 46 from the Igapó Study Project. None of the authors have a conflict of interest to declare. We thank two anonymous reviewers for their helpful comments.

REFERENCES

Aguiar-Silva FH, Sanaiott TM, Luz BB. 2014. Food habits of the harpy eagle, a top predator from the Amazonian rainforest canopy. *Journal of Raptor Research* 48: 24–35.

Albert A, Savini T, Huynen MC. 2011. Sleeping site selection and presleep behavior in wild pigtailed macaques. *American Journal of Primatology* 73: 1222–1230.

Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227–267.

Anderson CM. 1986. Predation and primate evolution. *Primates* 27: 15–39.

Anderson JR. 1998. Sleep, sleeping sites, and sleep-related activities: awakening to their significance. *American Journal of Primatology* 46: 63–75.

Anderson JR. 2000. Sleep-related behavioural adaptations in free-ranging anthropoid primates. *Sleep Medicine Reviews* 4: 355–373.

Anderson JT, Saldaña Rojas J, Flecker AS. 2009. High- quality seed dispersal by fruit-eating fishes in Amazonian floodplain habitats. *Oecologia* 161: 279–290.

Asensio N, Gómez-Marín F. 2002. Interspecific interaction and predator avoidance behavior in response to tayra (*Eira barbara*) by mantled howler monkeys (*Alouatta palliata*). *Primates* 43: 339–341.

Ashley EJ, Kats LB, Wolfe JW. 1993. Balancing trade-offs between risk and changing shoal size in northern red-belly dace (Phoxinus eos). *Copeia* 1993: 540–542.

Barnett AA, Almeida T, Spironello WR, Sousa Silva W, MacLarnon A, Ross C. 2012. Terrestrial foraging by *Cacajao melanocephalus ouakary* (primates) in Amazonian Brazil: is choice of seed patch size and position related to predation risk? *Folia Primatologica* 83: 126–139.

Barnett AA, Andrade ES, Ferreira MC, Soares JBG, da Silva VF, de Oliveira TG. 2015. Primate predation by black hawk-eagle (*Spizaetus tyrannus*) in Brazilian Amazonia. *Journal of Raptor Research* 49: 105–107.

Barnett AA , de Oliveira T , Soares da Silva RF, de Albuquerque Teixeira S, Tomanek P, Todd LM, Boyle SA. 2018. Honest error, precaution or alertness advertisement? Reactions to vertebrate pseudopredators in red-nosed cuxiús (*Chiropotes albinasus*), a high-canopy Neotropical primate. *Ethology* 124: 177–187.

Barnett AA, Shaw P, Spironello WR, MacLarnon A, Ross C. 2012. Sleeping site selection by golden-backed uacaris, *Cacajao melanocephalus ouakary* (Pitheciidae), in Amazonian flooded forests. *Primate* 53: 273–285.

Barnett AA , Silla JM , de Oliveira T , Boyle SA, Bezerra BM, Spironello WR, Setz EZ, da Silva RFS, de Albuquerque Teixeira S, Todd LM, Pinto LP. 2017. Run, hide, or fight: anti-predation strategies in endangered red-nosed cuxiú (*Chiropotes albinasus*, Pitheciidae) in southeastern Amazonia. *Primates* 58: 353–360.

Bianchi RDC, Mendes SL. 2007. Ocelot (*Leopardus pardalis*) predation on primates in Caratinga Biological Station, southeast Brazil. *American Journal of Primatology* 69: 1173–1178.

Boinski S, Treves A, Chapman CA. 2000. A critical evaluation of the influence of predators on primates: effects on group travel. In: Boinsky S, Garber PA, eds. *On the move: how and why animals travel in groups*. Chicago: University of Chicago Press, 43–72.

Bongi P, Ciuti S, Grignolio S, Del Frate M, Simi S, Gandelli D, Apollonio M. 2008. Anti-predator behaviour, space use and habitat selection in female roe deer during the fawning season in a wolf area. *Journal of Zoology* 276: 242–251.

Borges SH, Henriques LM, Carvalhaes A. 2004. Density and habitat use by owls in two Amazonian forest types. *Journal of Field Ornithology* 75: 176–182.

Bravo SP, Sallenave A. 2003. Foraging behavior and activity patterns of *Alouatta caraya* in the northeastern Argentinean flooded forest. *International Journal of Primatology* 24: 825–846.

Braza F, Alvarez F, Azcarate T. 1981. Behaviour of the red howler monkey (*Alouatta seniculus*) in the Llanos of Venezuela. *Primates* 22: 459–473.

Brividoro MV, Kowalewski MM, Scarry CJ, Oklander LI. 2019. Patterns of sleeping site and sleeping tree selection by black-and-gold howler monkeys (*Alouatta caraya*) in northern Argentina. *International Journal of Primatology* 40: 374–392.

Brotcorne F, Maslarov C, Wandia IN, Fuentes A, Beudels- Jamar RC, Huynen MC. 2014. The role of anthropic, ecological, and social factors in sleeping site choice by long- tailed macaques (*Macaca fascicularis*). *American Journal of Primatology* 76: 1140–1150.

Camargo CC, Ferrari SF. 2007. Interactions between tayras (*Eira barbara*) and red-handed howlers (*Alouatta belzebul*) in eastern Amazonia. *Primates* 48: 147–150.

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

Cheyne SM, Höing A, Rinear J, Sheeran LK. 2013a. Sleeping site selection by agile gibbons: the influence of tree stability, fruit availability and predation risk. *Folia Primatologica* 83: 299–311.

Cheyne SM, Höing M, Rinear AJ, Sheeran LK. 2012. Sleeping site selection by agile gibbons: the influence of tree stability, fruit availability and predation risk. *Folia Primatologica* 83: 299–311.

Cheyne SM, Rowland D, Höing A, Husson SJ. 2013b. How orangutans choose where to sleep: comparison of nest site variables. *Asian Primates Journal* 3: 13–17.

Chivers DJ. 1969. On the daily behaviour and spacing of howling monkey groups. *Folia Primatologica* 10: 48–102.

Cisneros-Heredia DF, León-Reyes A, Seger S. 2005. *Boa constrictor* predation on a titi monkey, *Callicebus discolor*. *Neotropical Primates* 13: 11–12.

Condit VK, Smith EO. 1994. Predation on a yellow baboon (*Papio cynocephalus cynocephalus*) by a lioness in the Tana River National Primate Reserve, Kenya. *American Journal of Primatology* 33: 57–64.

Cornick LA, Markowitz H. 2002. Diurnal vocal patterns of the black howler monkey (*Alouatta pigra*) at Lamanai, Belize. *Journal of Mammalogy* 83: 159–166.

Corrêa HKM, Coutinho PEG. 1997. Fatal attack of a pit viper, *Bothrops jararaca*, on an infant buffy-tufted ear marmoset (*Callithrix aurita*). *Primates* 38: 215–217.

Correa SB, Costa-Pereira R, Fleming T, Goulding M, Anderson JT. 2015. Neotropical fish-fruit interactions: eco- evolutionary dynamics and conservation. *Biological Reviews of the Cambridge Philosophical Society* 90: 1263–1278.

Cowlishaw G. 1997. Refuge use and predation risk in a desert baboon population. *Animal Behaviour* 54: 241–253.

Cowlishaw G. 1999. Ecological and social determinants of spacing behaviour in desert baboon groups. *Behavioral Ecology and Sociobiology* 45: 67–77.

Cresswell W, Quinn JL. 2013. Contrasting risks from different predators change the overall nonlethal effects of predation risk. *Behavioral Ecology* 24: 871–876.

Day RT, Elwood RW. 1999. Sleeping site selection by the golden-handed tamarin *Saguinus midas midas*: the role of predation risk, proximity to feeding sites, and territorial defence. *Ethology* 105: 1035–1051.

Di Fiore A. 2002. Predator sensitive foraging in ateline primates. In: Miller LE, ed. *Eat or be eaten: predator sensitive foraging among primates.* Cambridge: Cambridge University Press, 242–267.

Díaz-Uriarte R. 1999. Anti–predator behaviour changes following an aggressive encounter in the lizard *Tropidurus hispidus*. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266: 2457–2464.

Eason P. 1989. Harpy eagle attempts predation on adult howler monkey. *Condor* 91: 469–470.

Ellison G, Wolfenden A, Kahana L, Kisingo A, Jamieson J, Jones M, Bettridge C. 2019. Sleeping site selection in the nocturnal northern lesser galago (*Galago senegalensis*) supports antipredator and thermoregulatory hypotheses. *International Journal of Primatology* 40: 276–296.

Emmons LH. 1987. Comparative feeding ecology of felids in a Neotropical rainforest. *Behavioral Ecology and Sociobiology* 20: 271–283.

Enríquez PL, Eisermann K, Mikkola H, Motta-Junior JC. 2017. A review of the systematics of Neotropical owls (Strigiformes). In: Enriquez P, ed. *Neotropical owls*. Cham: Springer, 7–19.

Estrada A, Juan-Solano S, Martínez TO, Coates- Estrada R. 1999. Feeding and general activity patterns of a howler monkey (*Alouatta palliata*) troop living in a forest fragment at Los Tuxtlas, Mexico. *American Journal of Primatology* 48: 167–183.

Fan PF, Jiang XL. 2008. Sleeping sites, sleeping trees, and sleep-related behaviors of black crested gibbons (*Nomascus concolor jingdongensis*) at Mt. Wuliang, Central Yunnan, China. *American Journal of Primatology* 70: 153–160.

Fay JM, Carroll R, Kerbis JC, Harris D. 1995. Leopard attack on and consumption of gorillas in the Central African Republic. *Journal of Human Evolution* 29: 93–99.

Feilen KL, Marshall AJ. 2017. Multiple ecological factors influence the location of proboscis monkey (*Nasalis larvatus*) sleeping sites in West Kalimantan, Indonesia. *International Journal of Primatology* 38: 448–465.

Ferrari SF. 2009. Predation risk and antipredator strategies. In: Garber PA, Estrada A, Bicca-Marques JC, Strier K, eds. *South American primates; comparative perspectives in the study of behavior, ecology, and conservation*. New York: Springer, 251–277.

Ferrari SF, Beltrão-Mendes R. 2011. Do snakes represent the principal predatory threat to callitrichids? Fatal attack of a viper (*Bothrops leucurus*) on a common marmoset (*Callithrix jacchus*) in the Atlantic Forest of the Brazilian northeast. *Primates* 52: 207–209.

Ferrari SF, Pereira WLA, Santos RR, Veiga LM. 2004. Fatal attack of a *Boa constrictor* on a bearded saki (*Chiropotes satanas utahicki*). *Folia Primatologica* 75: 111–113.

Fichtel C. 2007. Avoiding predators at night: antipredator strategies in red-tailed sportive lemurs (*Lepilemur ruficaudatus*). *American Journalof Primatology* 69: 611–624.

Fichtel C. 2012. Predation. In: Mitani JC, Call J, Kappeler PM, eds. *The evolution of primate societies*. Chicago: University of Chicago Press, 169–194.

Fichtel C, Kappeler PM. 2002. Anti-predator behavior of group-living Malagasy primates: mixed evidence for a referential alarm call system. *Behavioral Ecology and Sociobiology* 51: 262–275.

Ford SM, Davis LC. 1992. Systematics and body size: implications for feeding adaptations in New World monkeys. *American Journal of Physical Anthropology* 88: 415–468.

Fowler JM, Cope JB. 1964. Notes on the harpy eagle in British Guiana. *The Auk* 81: 257–273.

Fruth B, Hohmann G. 1993. Ecological and behavioral aspects of nest building in wild bonobos (*Pan paniscus*). *Ethology* 94: 113–126.

Fruth B, McGrew WC. 1998. Resting and nesting in primates: behavioral ecology of inactivity. *American Journal of Primatology* 46: 3–5.

Galdikas BMF. 1985. Crocodile predation on a proboscis monkey in Borneo. *Primates* 26: 495–496.

Gerwing JJ, Farias DL. 2000. Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. *Journal of Tropical Ecology* 16: 327–335.

Gómez de Silva H, Pérez-Villafaña M, Santos-Moreno JA. 1997. Diet of the spectacled owl (*Pulsatrix perspicillata*) during the rainy season in northern Oaxaca, Mexico. *Journal of Raptor Research* 31: 385–387.

Goodman SM, Muldoon KM. 2016. A new subfossil locality for the extinct large Malagasy eagle *Stephanoaetus mahery* (Aves: Falconiformes): implications for time of extinction and ecological specificity. *The Holocene* 26: 985–989.

Goodman SM, O'Connor S, Langrand O. 1993. A review of predation on lemurs: implications for the evolution of social behavior in small, nocturnal primates. In: Kappeler PM, Ganzhorn JU, eds. *Lemur social systems and their ecological basis*. Boston: Springer, 51–66.

Goodman SM, Thorstrom R. 1998. The diet of the Madagascar red owl (*Tyto soumagnei*) on the Masoala Peninsula, Madagascar. *The Wilson Bulletin* 110: 417–421.

Gregorin R. 2006. Taxonomia e variação geográfica das espécies do gênero *Alouatta* Lacépède (Primates, Atelidae) no Brasil. *Revista Brasileira de Zoologia* 23: 64–144.

Guichón ML, Doncaster CP, Cassini MH. 2003. Population structure of coypus (*Myocastor coypus*) in their region of origin and comparison with introduced populations. *Journal of Zoology* 261: 265–272.

Gursky SL, Nekaris KAI. 2007. *Primate anti-predator strategies.* Boston: Springer.

Hamilton WJ. 1982. Baboon sleeping site preferences and relationships to primate grouping patterns. *American Journal of Primatology* 3: 41–53.

Hamilton IM, Heithaus MR. 2001. The effects of temporal variation in predation risk on anti-predator behaviour: an empirical test using marine snails. *Proceedings. Biological sciences* 268: 2585–2588.

Hart D. 2007. Predation on primates: a biogeographical analysis. In: Gursky-Doyen S, Nekaris K, eds. *Primate anti- predator strategies*. Boston: Springer, 27–59.

Hartmann PA, Hartmann MT, Martins M. 2009. Ecology of a snake assemblage in the Atlantic Forest of southeastern Brazil. *Papéis Avulsos de Zoologia* 49: 343–360.

Hausfater G, Meade BJ. 1982. Alternation of sleeping groves by yellow baboons (*Papio cynocephalus*) as a strategy for parasite avoidance. *Primates* 23: 287–297.

Hayssen V. 2010. *Bradypus variegatus* (Pilosa: Bradypodidae). *Mammalian Species* 42: 19–32.

Heymann EW. 1987. A field observation of predation on a moustached tamarin (*Saguinus mystax*) by an anaconda. *International Journal of Primatology* 8: 193–195.

Heymann EW. 1995. Sleeping habits of tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Mammalia; Primates; Callitrichidae), in northeastern Peru. *Journal of Zoology* 237: 211–226.

Hill RA, Dunbar RI. 1998. An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. *Behaviour* 135: 411–430.

Hill RA, Lee PC. 1998. Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. *Journal of Zoology* 245: 447–456.

Hinsley SA, Bellamy PE. 2000. The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. *Journal of Environmental Management* 60: 33–49.

Isbell LA. 1994. Predation on primates: ecological patterns and evolutionary consequences. *Evolutionary Anthropology* 3: 61–71.

Isbell LA. 2006. Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution* 51: 1–35.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. *Behavioral Ecology* 6: 326–336.

Julliot C. 1994. Predation of a young spider monkey (*Ateles paniscus*) by a crested eagle (*Morphnus guianensis*). *Folia Primatologica* 63: 75–77.

Kasperoviczus KN, Krüger AC, Marques OAV. 2015. An elongated meal: the tegu lizard *Salvator merianae* eats snakes and amphisbaenians. *Herpetology Notes* 8: 21–23.

Kinzey WG. 1997. New world primates: ecology, evolution, and behavior. In: Warren G, Kinzey WG, eds. *Foundations of human behavior*. New York: Aldine de Gruyter, 325–429.

Kitchen DM, Horwich RH, James RA. 2004. Subordinate male black howler monkey (*Alouatta pigra*) responses to loud calls: experimental evidence for the effects of intragroup male relationships and age. *Behaviour* 141: 703–723.

Koenig SE, Wunderle JM Jr, Enkerlin-Hoeflich EC. 2007. Vines and canopy contact: a route for snake predation on parrot nests. *Bird Conservation International* 17: 79–91.

König C, Weick F, Becking JH. 1999. *Owls: a guide to the owls of the world.* Sussex: Pica Press.

Koops K, McGrew WC, de Vries H, Matsuzawa T. 2012. Nest-building by chimpanzees (*Pan troglodytes verus*) at Seringbara, Nimba Mountains: antipredation, thermoregulation, and antivector hypotheses. *International Journal of Primatology* 33: 356–380.

Kortet R, Rantala MJ, Hedrick A. 2007. Boldness in anti- predator behaviour and immune defence in field crickets. *Evolutionary Ecology Research* 9: 185–197.

Kowalewski M, Garber PA, Cortéz-Ortiz L, Urbano B, Youlanos D. 2014. *Howler monkeys: behavior, ecology and conservation.* New York: Springer.

Kowalewski M, Zunino GE. 2005. The parasite behavior hypothesis and the use of sleeping sites by black howler monkeys (*Alouatta caraya*) in a discontinuous forest. *Neotropical Primates* 13: 22–26.

Krause J, Godin JGJ. 1994. Shoal choice in the banded killifish (Fundulus diaphanus, Teleostei, Cyprinodontidae): effects of predation risk, fish size, species composition and size of shoals. *Ethology* 98: 128–136.

Kurup GU, Kumar A. 1993. Time budget and activity patterns of the lion-tailed macaque (*Macaca silenus*). *International Journal of Primatology* 14: 27–39.

Larsen T. 1991. Anti-predator behaviour and mating systems in waders: aggressive nest defence selects for monogamy. *Animal Behaviour* 41: 1057–1062.

Last C, Muh B. 2013. Effects of human presence on chimpanzee nest location in the Lebialem-Mone forest landscape, southwest region, Cameroon. *Folia Primatologica* 84: 51–63.

Liu ZH, Zhao QK. 2004. Sleeping sites of *Rhinopithecus bieti* at Mt. Fuhe, Yunnan. *Primates* 45: 241–248.

Ludwig G, Aguiar LM, Miranda JM, Teixeira GM, Svoboda WK, Malanski LS, Shiozawa MM, Hilst CL, Navarro IT, Passos FC. 2007. Cougar predation on black-and-gold howlers on Mutum Island, southern Brazil. *International Journal of Primatology* 28: 39–46.

Lührs ML, Dammhahn M. 2010. An unusual case of cooperative hunting in a solitary carnivore. *Journal of Ethology* 28: 379–383.

Magurran AE, Pitcher TJ. 1987. Provenance, shoal size and the sociobiology of predator-evasion behaviour in minnow shoals. *Proceedings of the Royal Society of London. Series B. Biological Sciences* 229: 439–465.

Magurran AE, Seghers BH, Carvalho GR, Shaw PW. 1992. Behavioural consequences of an artificial introduction of guppies (*Poecilia reticulata*) in N. Trinidad: evidence for the evolution of anti-predator behaviour in the wild. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 248: 117–122.

Martin-Klimoczko L, Meunier H, Moura A. 2015. Sleeping sites choice by a wild group of howler monkeys (*Alouatta belzebul*) in the Atlantic Forest of Brazil. *Revue de Primatologie* 6: 4–7.

Matsuda I, Izawa K. 2008. Predation of wild spider monkeys at La Macarena, Colombia. *Primates* 49: 65–68.

Matsuda I, Tuuga A, Akiyama Y, Higashi S. 2008a. Selection of river crossing location and sleeping site by proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. *American Journal of Primatology* 70: 1097–1101.

Matsuda I, Tuuga A, Higashi S. 2008b. Clouded leopard (*Neofelis diardi*) predation on proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. *Primates* 49: 227–231.

Miller LE, Treves A. 2007. Predation on primates. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M, Bearder SK, eds. *Primates in perspective*. Oxford: Oxford University Press, 525–543.

Miranda EB. 2017. The plight of reptiles as ecological actors in the tropics. *Frontiers in Ecology and Evolution* 5: 159.

Miranda JMD, Bernardi IP, Abreu KC, Passos FC. 2005. Predation on *Alouatta guariba clamitans* Cabrera (Primates, Atelidae) by *Leopardus pardalis* (Linnaeus) (Carnivora, Felidae). *Revista Brasileira de Zoologia* 22: 793–795.

Miranda JMD, Bernardi IP, Moro-Rios RF, Passos FC. 2006. Antipredator behavior of brown howlers attacked by black hawk-eagle in southern Brazil. *International Journal of Primatology* 27: 1097–1101.

Motta-Junior JC, Braga ACR, Granzinolli MAM. 2017. The owls of Brazil. In: Enriquez P, ed. *Neotropical owls*. Cham: Springer, 97–158.

Mukherjee S, Heithaus MR. 2013. Dangerous prey and daring predators: a review. *Biological Reviews of the Cambridge Philosophical Society* 88: 550–563.

Nagy KA, Milton K. 1979. Energy metabolism and food consumption by wild howler monkeys (*Alouatta palliata*). *Ecology* 60: 475–480.

Nash LT. 2007. Moonlight and behavior in nocturnal and cathemeral primates, especially *Lepilemur leucopus*: illuminating possible anti-predator efforts. In: Gursky- Doyen S, Nekaris K, eds. *Primate anti-predator strategies*. Boston: Springer, 173–205.

de Oliveira TG, Mazim FD, Vieira OQ, Barnett AP, Silva GDN, Soares JB, Santos JP, da Silva VF, Araujo PA, Tchaika L, Miranda CL. 2016. Nonvolant mammal megadiversity and conservation issues in a threatened central Amazonian hotspot in Brazil. *Tropical Conservation Science* 9: 1–16.

de Oliveira TG, Vieira OQ, Kasper CB, Trevelin C, Barnett AA, Cavalcanti GN, Mazim FD, Santos JP, Santos CLC, Soares JBG, da Silva VF, Ferreira MCCS, Araújo PA, Silla JM, Miranda CL, Silva GN, Moura VEC, Silva RD, Everton LS. 2014. *EIS (Environmental Impact Study)/EIR (Environmental Impact Report) HD (Hydroelectric Development) São Luiz do Tapajós.* São Paulo, Brazil: CNEC Engenharia.

Olmos F. 1994. Jaguar predation on muriqui, Brachyteles arachnoides. *Neotropical Primates* 2: 16.

Pavelka MS, Knopff KH. 2004. Diet and activity in black howler monkeys (*Alouatta pigra*) in southern Belize: does degree of frugivory influence activity level? *Primates* 45: 105–111.

Peetz A, Norconk MA, Kinzey WG. 1992. Predation by jaguar on howler monkeys (*Alouatta seniculus*) in Venezuela. *American Journal of Primatology* 28: 223–228.

Perry S, Manson JH, Dower G, Wikberg E. 2003. White- faced capuchins cooperate to rescue a groupmate from a *Boa constrictor*. *Folia Primatologica* 74: 109–111.

Phoonjampa R, Koenig A, Borries C, Gale GA, Savini T. 2010. Selection of sleeping trees in pileated gibbons (*Hylobates pileatus*). *American Journal of Primatology* 72: 617–625.

Prance GT. 1979. Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. *Brittonia* 31: 26.

Pruetz JD, Fulton SJ, Marchant LF, McGrew WC, Schiel M, Waller M. 2008. Arboreal nesting as anti-predator adaptation by savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *American Journal of Primatology* 70: 393–401.

Quintino EP, Bicca-Marques JC. 2013. Predation of *Alouatta puruensis* by *Boa constrictor*. *Primates* 54: 325–330. R Core Team. 2019. *R: A language and environment for statistical computing.* Vienna: R Foundation for Statistical Computing.

Rabelo RM, Aragón S, Bicca-Marques JC. 2019. Prey abundance drives habitat occupancy by jaguars in Amazonian floodplain river islands. *Acta Oecologica* 97: 28–33.

Řeháková-Petru M, Peške L, Daněk T. 2012. Predation on a wild Philippine tarsier (*Tarsius syrichta*). *Acta Ethologica* 15: 217–220.

Reichard U. 1998. Sleeping sites, sleeping places, and presleep behavior of gibbons (*Hylobates lar*). *American Journal of Primatology* 46: 35–62.

Reichert SE, Hedrick AV. 1990. Levels of predation and genetically based anti-predator behaviour in the spider, *Agelenopsis aperta*. *Animal Behaviour* 40: 679–687.

Richard A. 1970. A comparative study of the activity patterns and behavior of *Alouatta villosa* and *Ateles geoffroyi*. *Folia Primatologica* 12: 241–263.

Robinson SK. 1994. Habitat selection and foraging ecology of raptors in Amazonian Peru. *Biotropica* 26: 443–458.

Sazima I, D'Angelo GB. 2013. Range of animal food types recorded for the tegu lizard (*Salvator merianae*) at an urban park in southeastern Brazil. *Herpetology Notes* 6: 427–430.

Sekulic R. 1982. Daily and seasonal patterns of roaring and spacing in four red howler *Alouatta seniculus* troops. *Folia Primatologica* 39: 22–48.

Sekulic R, Sekulic R. 1982. The function of howling in red howler monkeys (*Alouatta seniculus*). Behaviour 81: 38–54.

Sherman PT. 1991. Harpy eagle predation on a red howler monkey. *Folia Primatologica* 56: 53–56.

Smith AC, Knogge C, Huck M, Löttker P, Buchanan- Smith HM, Heymann EW. 2007. Long-term patterns of sleeping site use in wild saddleback (*Saguinus fuscicollis*) and mustached tamarins (*S. mystax*): effects of foraging, thermoregulation, predation, and resource defense constraints. *American Journal of Physical Anthropology* 134: 340–353.

de Souza Martins S, de Lima EM, de Sousa e Silva J Jr. 2005. Predation of a bearded saki *Chiropotes utahicki*) by a harpy eagle (*Harpia harpyja*). *Neotropical Primates* 13: 7–10.

Stanford CB. 2002. Avoiding predators: expectations and evidence in primate antipredator behavior. *International Journal of Primatology* 23: 741–757.

Stewart FA, Pruetz JD. 2013. Do chimpanzee nests serve an anti-predatory function? *American Journal of Primatology* 75: 593–604.

Sunquist F, Sunquist M. 2002. *Wild cats of the world.* Chicago and London: University of Chicago Press.

Tagg N, Willie J, Petre CA, Haggis O. 2013. Ground night nesting in chimpanzees: new insights from central chimpanzees (*Pan troglodytes troglodytes*) in south-east Cameroon. *Folia Primatologica* 84: 362–383.

Teichroeb JA, Holmes TD, Sicotte P. 2012. Use of sleeping trees by ursine colobus monkeys (*Colobus vellerosus*) demonstrates the importance of nearby food. *Primates* 53: 287–296.

Tello NS, Huck M, Heymann EW. 2002. *Boa constrictor* attack and successful group defence in moustached tamarins, *Saguinus mystax*. *Folia Primatologica* 73: 146–148.

Tenaza R, Tilson RL. 1985. Human predation and Kloss's gibbon (*Hylobates klossii*) sleeping trees in Siberut Island, Indonesia. *American Journal of Primatology* 8: 299–308.

Thompson CL, Williams SH, Glander KE, Teaford MF, Vinyard CJ. 2014. Body temperature and thermal environment in a generalized arboreal anthropoid, wild mantled howling monkeys (*Alouatta palliata*). *American Journal of Physical Anthropology* 154: 1–10.

Thompson CL, Williams SH, Glander KE, Vinyard CJ. 2016. Measuring microhabitat temperature in arboreal primates: a comparison of on-animal and stationary approaches. *International Journal of Primatology* 37: 495–517.

Tillmann J. 2009. Fear of the dark: night-time roosting and anti-predation behaviour in the grey partridge (*Perdix perdix* L.) *Behaviour* 146: 999–1023.

Tomazzoni AC, Pedó E, Hartz SM. 2004. Food habits of great horned owls (*Bubo virginianus*) in the breeding season in Lami Biological Reserve, southern Brazil. *Ornitologia Neotropical* 15: 279–282.

Treves A. 1999. Has predation shaped the social systems of arboreal primates? *International Journal of Primatology* 20: 35–67.

Troyer K. 1984. Diet selection and digestion in *Iguana iguana*: the importance of age and nutrient requirements. *Oecologia* 61: 201–207.

Turner G, Turner T. 2016. A field observation of concertina climbing in the scrub python (*Morelia amethistina*). *Queensland Naturalist* 54: 14.

Urbani B, Kvarnbäck J, González-Alentorn MR. 2012. Harpy eagle *Harpia harpyja* preying on an ursine howler monkey *Alouatta arctoidea* in northeastern Venezuela. *Revista Catala d'Ornitol* 28: 40–44.

van Schaik CP, Hörstermann M. 1994. Predation risk and the number of adult males in a primate group: a comparative test. *Behavioral Ecology and Sociobiology* 35: 261–272.

Voirin JB, Kays RW, Lowman MD, Wikelski M. 2009. Evidence for three-toed sloth (*Bradypus variegatus*) predation by spectacled owl (*Pulsatrix perspicillata*). *Edentata* 10: 15–20.

Wallace RB. 2001. Diurnal activity budgets of black spider monkeys, *Ateles chamek*, in a southern Amazonian tropical forest. *Neotropical Primates* 9: 101–107.

Waring RH, Schlesinger WH. 1985. *Forest ecosystems: concepts and management.* San Diego: Academic Press, Inc.

Whitehead JM. 1995. Vox Alouattinae: a preliminary survey of the acoustic characteristics of long-distance calls of howling monkeys. *International Journal of Primatology* 16: 121–144.

Wright PC. 1994. The behavior and ecology of the owl monkey. In: Baer JF, Weller RE, Kakoma I, eds. *Aotus: the owl monkey*. San Diego: Academic Press, 97–110.

Wright PC. 1998. Impact of predation risk on the behaviour of *Propithecus diadema edwards*i in the rain forest of Madagascar. *Behaviour* 135: 483–512.

Ydenberg RC, Dill LM. 1986. The economics of fleeing from predators. *Advances in the Study of Behavior* 16: 229–249.

Yeager CP. 1991. Possible antipredator behavior associated with river crossings by proboscis monkeys (*Nasalis larvatus*). *American Journal of Primatology* 24: 61–66.

Yuan BD, Jiang AW, Li XD, Lu CH. 2012. Roost habitat selection by birds: A review. *Chinese Journal of Ecology* 8: 39 pages.

Zhou Q, Wei F, Huang C, Li M, Ren B, Luo B. 2007. Seasonal variation in the activity patterns and time budgets of *Trachypithecus francoisi* in the Nonggang Nature Reserve, China. *International Journal of Primatology* 28: 657–671.

Note: In this article we have investigated the relationship between the potential threat levels by predators, pseudo-predators, and non-predators, and the subsequent energetic cost of behavioural reactions to these threats, in *Ateles belzebuth, Cacajao ouakary,* and *Chiropotes albinasus*.

3.5 CALLS FOR CONCERN: MATCHING ALARM RESPONSE LEVELS TO THREAT INTENSITIES IN THREE NEOTROPICAL PRIMATES

PAVEL TOMANEK[1]*, ITALO MOURTHE[2], SARAH A. BOYLE[3], ADRIAN A. BARNETT[4]

[1] Department of Ethology and Companion Animal Science, Czech University of Life Sciences Prague, Prague, Czech Republic

[2] Universidade Federal do Pará, Laboratório de Ecologia and Programa de Pós-graduação em Biodiversidade e Consevação, Altamira, PA, Brazil

[3] Department of Biology, Rhodes College, Memphis, TN, USA

[4] Department of Zoology, Pernambuco Federal University, Recife, PE *and* Amazon Mammal Research Group, National Institute of Amazon Research, Manaus, AM, Brazil

* Corresponding author

E-mail: tomanekpa@seznam.cz

Published in:

Acta Oecologica Volume 109, November 2020, *Article Number: 103646*

ISSN 1146-609X,

https://doi.org/10.1016/j.actao.2020.103646.

(https://www.sciencedirect.com/science/article/pii/S1146609X20301387)

ABSTRACT

Various species of animals maximise energy gained through foraging by minimising excessive energy spent on nonessential activities. Avoiding predation is key for maximising an individual's lifespan, as well as that of its kin; however, anti-predation behaviours can be energetically costly. We investigated the relationship between the potential threat levels by predators, pseudo-predators, and non-predators, and the subsequent energetic cost of behavioural reactions to these threats, in the white-bellied spider monkey (*Ateles belzebuth*), golden-backed uacari (*Cacajao ouakary*), and red-nosed cuxiú

(*Chiropotes albinasus*). We analysed a total of 270 interactions across three independent field studies of the three primate species. Our results revealed significant differences in the behavioural response to predators and non-predators for both *C. ouakary* and *C. albinasus*, but not for *A. belzebuth*. In terms of risk-categorized behaviours, response to predators differed from response to non-predators (being much more intense and energy intensive), while there was no difference in response to predators versus pseudo-predators. Thus, response to potential predators represents an integral part of the time-management and defence strategies of two of the three studied species, and should be integrated into future studies of primate responses to varying levels of predation threat.

Keywords

Predation . Energetic cost . Threat level . Predator . Non-predator . *Ateles* . *Cacajao* . *Chiropotes*

Research Highlights

We analysed the behavioural reactions by three primate species (*Ateles belzebuth*, *Cacajao ouakary*, and *Chiropotes albinasus*) to potential predation attempts, and examined the related energetic costs of these behavioural responses. Primates modified their reactions depending on whether the perceived potential attacker was, in fact, truly a predator. Behavioural reactions of medium intensities occurred when another species looked and/or behaved like a known predator (pseudo-predator). Field studies of behavioural reactions to predators are important for an understanding of the biological significance of predation.

INTRODUCTION

Primates often have to travel substantial daily distances to find appropriate food (Wrangham et al. 1993; Norconk & Kinzey 1994; Di Fiore 2003; Boyle et al. 2009; Schaffer 2013), often at great energetic cost (Grove 2012; Markham & Gesquiere 2017). It is widely thought that species with extensive daily ranges should minimize wasteful temporal or energetic expenditures, to optimize their time and energy budgets (Barton et al. 1992; Pontzer et al. 2014). While it is unlikely that a group of primates will be subject to frequent events of successful predation (Treves 1999a; Ferrari 2009; Barnett et al. 2017), predation attempts are quite common, as are encounters with pseudo-predators, which are species that look sufficiently similar to actual predators to elicit anti-predator reactions in potential prey (Mourthé & Barnett 2014). Indeed, frequency of pseudo-predator encounters may far exceed those with true predators (Barnett et al. 2018a). The responses of primates to predators vary, and can include reactive (e.g., alarm calling, chasing, mobbing, attacking or flight: Barnett et al. 2011; Ferrari 2009; de

Luna et al. 2010; di Fiore 2002; Miller & Treves 2007; Mourthé 2011; Mourthé & Barnett 2014) and crypsis-related behaviours (e.g., concealing, freezing: Guilford & Dawkins 1991; Miller & Treves 2007; Zuberbühler et al. 1997). Given that such predation-avoidance behaviours expend resources, both in terms of energy spent conducting them, and feeding opportunities lost while they are in process, it is expected that primates should optimize the time and energy they invest in responses based on the level of predation risk (Brown et al. 1999; Blanchard et al. 2011; Isbell 1994). Doing so avoids unnecessary energy expenditure.

Primates give alarm calls that distinguish between predator types, thereby eliciting behaviours appropriate for avoiding predation (e.g., ground-hunting felid, tree-based snake, aerial raptor: Zuberbühler 2000, 2001; Fichtel & Kappeler 2002; Crockford & Boesch 2003; Arnold & Zuberbühler 2006). In addition, individuals that optimally manage their energy budgets might be expected to respond appropriately to the level of threat that a potential predator represents, in terms of proximity and apparent hunting intent (Creel & Christianson 2008; Embar et al. 2011). Thus, the energetic costs of different antipredator reactions should match the level of threat. Alarm calls are expected to be used against low-level threats (to communicate to the predator that it has been seen: Zuberbühler et al. 1999), hiding against mid-level threats, and fleeing and mobbing against more intense threats (Ydenberg & Dill 1986). Such analyses should also include the possibility that brief-but-intense actions (e.g., branch thrashing), might be energetically equal to repeated low-cost actions (e.g., head turning when tracking a potential assailant).

However, matching energetic investment in reactions to threat intensities has been less frequently tested than predictions relating to threat types (Stankowich and Blumstein 2005; Embar et al. 2011). In addition, it is possible that specific sex-age classes might engage more frequently in predation reactions. For example, in a study of red-nosed cuxiús (*Chiropotes albinasus*), Barnett et al. (2018) found that adult males engage in defensive actions against predation threats more than adult females. One of the factors complicating thorough investigations of such phenomena is that both predation and predation attempts are rarely observed, even in long-term field studies of wild animals (Goodman et al. 1993; Isbell 1994; Hill & Dunbar 1998; Stanford 2002; Ferrari 2009; Gursky-Doyen & Nekaris 2007). Therefore, sample sizes are often small.

To overcome sample-size and rarity effects, we pooled data from independent field studies (Mourthé & Barnett 2014; Barnett 2010; Barnett et al. 2017, 2018) to investigate whether the intensity levels of antipredator responses of three neotropical primate species (white-bellied spider monkey, *Ateles belzebuth*; golden-backed uacari, *Cacajao ouakary*; and red-nosed cuxiú, *Chiropotes albinasus*) matched predator-threat levels. All three species are large- (*Ateles*: 8 kg on average; Smith and Jungers 1997) or medium-bodied (*Cacajao*: 2.9 kg; *Chiropotes*: 2.8 kg) species that exhibit fission-fusion social ecology (Aureli et al. 2008) and range widely in the upper canopy of Amazonian forests (Barnett 2010; Barnet et al. 2017, 2018; Mourthé 2014). Moreover, these three species share the same suite of arboreal and aerial predators (e.g., *Panthera onca*, *Harpia harpyja*, *Spizaetus tyrannus*, and *Boa constrictor*:

Martins et al. 2005; Barnett et al. 2011, 2017, 2018; Mourthé & Barnett 2014) and see tables 1A, 1B, 1C. Given that individuals of the primates have extensive daily ranges (and thus a high daily energetic output), we expected that these species would be extremely sensitive to means of optimizing overall energetic expenditure. As energy spent on predator avoidance forms part of the general energy budged (Grove 2012; Markham & Gesquiere 2017), we hypothesized that the energy investment spent by individuals is proportional to the intensity of the threat level imposed by potential predators. Using a combined data set that consisted of reactions of the primates to varying intensities of threat level, we tested the following predictions: (i) reactions of primates will vary with threat risks; and (ii) energetic expenditure will vary with threat risks. Because risk of predation is often lower in larger-bodied primates (Cheney & Wrangham 1987; Standford 2002; Zuberbühler & Jenny 2002), we expected a lower rate of reaction to potential predators by *Ateles* than by *Cacajao* and *Chiropotes* (Mourthé & Barnett 2014).

METHODS

We compiled data from field studies of *Ateles belzebuth* at Maracá Ecological Station, Roraima State, Brazil (Mourthé 2014; Mourthé & Barnett 2014); *Cacajao ouakary* at Jaú National Park, Amazonas State, Brazil (Barnett 2010); and *Chiropotes albinasus* in the region of Itaituba, on the mid-Tapajós river, Pará State, Brazil (Barnett et al. 2017, 2018; Fig. 1). All studies were conducted under license from the appropriate Brazilian environmental authorities (IBAMA and ICMBio), and obeyed the strictures therein. Field-methods were non-invasive, and no animals were harmed, handled, or manipulated during the course of the studies.

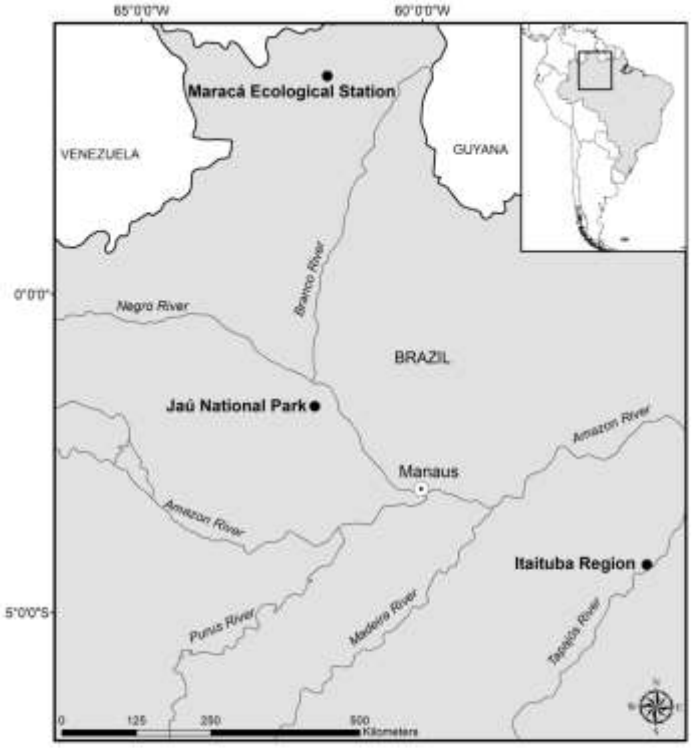


Figure. 1 Map of the Brazilian Amazon, showing the study area locations.

We used the primate’s point-of-view approach (Barnett 1995) when ranking levels of primate reactions to predators. We divided levels of reaction into four risk categories: low, medium, high, and extreme (Supplementary Material - Table 1), based on the likelihood that the actions would summon the attention of a predator to any individual primate, or the likelihood of that animal getting hurt or killed. We operationalized the limit for "close" as 15 m, the distance that previous studies estimated that predators induced alarm reactions in these three primate species (Mourthé & Barnett 2014; Barnett et al. 2018a).

We considered energetic expenditure from the point of the animal’s energy budget, so that activities resulting in an immediate expenditure of large amounts of energy, such as fleeing, were placed in the high-energy category. Concealment by individuals was also considered a high-energy response, since remaining still yet vigilant means an individual is unable to feed or rest (Supplementary Table 1). We divided threats into four levels, based on the following criteria: extreme (predator attack), high (predator or pseudo-predator close), medium (predator or pseudo-predator distant-but-approaching) and low (predator or pseudo-predator distant, non-predator in any position; Supplementary Table 1).

Table 1. Operational definitions of behaviours associated with responses to predators by three primate species (*Ateles belzebuth, Cacajao ouakary* and *Chiropotes albinasus*).

Name of behaviour	Assigned energetic level	Assigned threat level	Operational definition	Examples of similar use of term
Head glance	Low	Low	A rapid (<5 s), deliberate, directed single movement only of the head that pauses when apparent direct line of sight is obtained to a particular object (an animal newly arrived in the vicinity, in the current study). The position to allow directed visual attention is brief (1-2 seconds) and the head then moves. Low intensity response, not accompanied by orientation of the rest of the body.	Koenig (1988); Treves (2000); Barros et al. (2008)
Alarm call	Low (Medium if extended)	Low	A generally sharp high-pitched call that summons attention of the receivers, and acts to inform them of the presence or imminence of prejudicial entity or event.	Zuberbühler et al. (1999); Treves (2000)
Reposition	Medium	Medium (High if predator close)	Directed motion away from a point source of potential discomfort or danger – of variable intensity, but not an intense response (viz. ´fleeing´)	Goodman et al. (1993); Boinski et al. (2000)
Conceal	Medium (High if extended)	Medium (High if predator close)	Either move or drop into vegetation and remain hidden with little or no movement. Vocalizations rarely uttered. Often extended to 30 minutes or more.	Treves (2000); Ferrari (2009); Barnett et al. (2011)
Sentinel	Medium	Medium	An individual occupying a generally exposed position and not engaged in feeding, resting or grooming, but with an alert appearance and appearing to be visually searching for potential danger	Overdorff (1988); Baldellou and Henzi (1992); Treves (1999b)
Fleeing	High	High	Directed motion away from a point source of potential discomfort or danger. Rapid, and with extensive jumps.	Goodman et al. (1993); Boinski et al. (2000)
Mobbing	High	High	Action by individual or individuals of a group against a potential predator that is (or not) engaged in predation-related activity towards the group. Activity likely to involve physical approximation and loud vocalizations but rarely full physical contact. However, risk of opportunistic predation by predator exists	Bartecki and Heymann (1987); Ross (1993); Gursky (2005); Crofoot (2012); (Tórrez et al. 2012)
Attack	High	High	An individual or individuals engage in aggressive action against a non-conspecific that is attacking or preparing to attack the group. Action likely to involve physical contact with the potential to cause physical damage	Tello et al. (2002); Eberle and Kappeler (2008)
Death	Extreme	Extreme	Fatal attack – harpy eagle was seen to capture and fly away with an adult golden-backed uacari	Barnett et al. (2011)

Table 1-A: Known Predators of *Ateles*, *Cacajao* and *Chirpopotes*

Primate	**Predator**	**Interaction**	**Reference**
Ateles belzebuth	*Panthera onca*	Successful predation of adult male	Matsuda & Izawa (2008)
Ateles belzebuth	*Puma concolor*	Predation attempt on adult female	Matsuda & Izawa (2008)
Ateles geoffroyi	*Penthera onca* and *Puma concolor*	Evidence of predation from faecal analysis	Chincilla (1997)
Ateles geoffroyi	*Puma concolor*	Successful predation of subadult individual	Bursia et al. (2018)
Ateles geoffroyi	*Eira barbara*	Three attempts of predation on adults	Matsuda & Izawa (2008)
Ateles paniscus	*Morphnus guianensis*	Successful predation of young individual	Julliot (1994).
Cacajao calvus ucayalii	*Eira barbara*	Mobbing, accompanied by calls	Bowler (2007)
Cacajao ouakary	*Harpia harpyja*	Successful predation, sub-adult	Barnett et al. (2011)
Chiropotes albinasus	*Harpia harpyja*	Remains in nest	Aguiar-Silva et al. (2014)
Chiropotes albinasus	*Harpia harpyja, Leucopternis* sp., *Spizaëtus tyrannus* Unidentified hawk spp.	Nine predation events (eight attempts, one success): *H. harpyja*, 4; *Leucopternis* sp., 2; *S. tyrannus*, 1; unident. hawks, 2: Seven attacks against entire groups, one (successful) on juvenile, one on infant	Barnett et al. (2017)
Chiropotes sagulatus	*Harpia harpyja*	Successful predation of adult	Lenz & dos Reis (2011)
Chiropotes sagulatus	*Harpia harpyja*	Successful predation of sub-adult by a juvenile harpy	Calaça et al. (2016)
Chiropotes utahickae	*Harpia harpyja*	Successful predation of adult male	de Souza Martins et al. (2005)
Chiropotes utahickae	*Boa constrictor*	Successful predation of adult female	Ferrari et al. (2004)

Table 1-B: Known Pseudo-predators of *Ateles*, *Cacajao* and *Chiropotes* (anti-predator reactions observed)

Pseudopredator	**Primate**	**Reaction**	**Reference**
Reptiles			
Iguana iguana	*Cacajao ouakary*	Adolescents and females with young gave startle reactions and alarm calls	Mourté & Barnett (2014)
Birds			
Mesembrinibis cayennensis	*Cacajao ouakary*	Females with young animals nearby gave alarm calls	Mourté & Barnett (2014)
Mesembrinibis cayennensis	*Chiropotes albinasus*	Alarm calls when flew closer than 15m	Barnett et al. (2018)
Buteogallus urubitinga	*Cacajao ouakary*	Alarm calls given when animals flew within 15m (no calls if further away than this)	Mourté & Barnett (2014)
Busarellus nigricollis	*Chiropotes albinasus*	Alarm calls given when animals flew within 15m (no calls if further away than this)	Barnett et al. (2018)
Leucopternis melanops	*Cacajao ouakary*	Alarm calls given when animals flew within 15m (no calls if further away than this)	Mourté & Barnett (2014)
Leucopternis schistacea	*Cacajao ouakary*	Alarm calls given when animals flew within 15m (no calls if further away than this)	Mourté & Barnett (2014)
Pandion halieatus	*Chiropotes albinasus*	Alarm calls given when animals flew within 15m (no calls if further away than this)	Barnett et al. (2018)
Chondrohierax uncinatus	*Cacajao ouakary*	Alarm calls given when animals flew within 15m (no calls if further away than this)	Mourté & Barnett (2014)
Rostrhamus sociabilis	*Cacajao ouakary*	Alarm calls given when animals flew within 15m (no calls if further away than this)	Mourté & Barnett (2014)
Cathartes aura	*Cacajao ouakary*	Alarm calls given when animals flew within 15m (no calls if further away than this)	Mourté & Barnett (2014)
Cathartes spp.	*Chiropotes albinasus*	Alarm calls given when animals flew within 15m, also movements into deeper vegetation	
Coragyps atratus	*Cacajao ouakary*	Alarm calls given when animals flew within 15m (no calls if further away than this)	Mourté & Barnett (2014)
Coragyps atratus	*Chiropotes albinasus*	Alarm calls given when animals flew within 15m, also movements into deeper vegetation	Barnett et al. (2018)
Cairina moschata	*Cacajao ouakary*	Alarm calls given	Mourté & Barnett (2014)
Cairina moschata	*Chiropotes albinasus*	Alarm calls given	Barnett et al. (2018)
Amazonas spp.	*Cacajao ouakary*	Female with dependent young gave alarm call and dropped into denser vegetation	Mourté & Barnett (2014)
Rhamphastos spp.	*Chiropotes albinasus*	Reaction only if landed close (5-7m), alarm calls	Barnett et al. (2018
Pteroglossus spp.	*Chiropotes albinasus*	Reaction only if landed close (5-7m), alarm calls	Barnett et al. (2018)
Mammals			
Tapirus terrestris	*Ateles belzebuth*	Alarm calls given	Mourté & Barnett (2014)
Leopardalus wiedii	*Cacajao ouakary*	Female with young gave alarm call and visually followed the moving animal	Mourté & Barnett (2014)
Pteroneura brasiliensis	*Cacajao ouakary*	Group members uttered alarm calls	Mourté & Barnett (2014)
Pteroneura brasiliensis	*Chiropotes albinasus*	Group members uttered alarm calls, 50% of times	Barnett et al. (2018)
Rhynchonycteris naso	*Chiropotes albinasus*	Mild alarm calls when group quit roost	Barnett et al. (2018)

Table 1-C: Species known to be considered safe by *Ateles*, *Cacajao* and *Chiropotes* (no observable reaction or no alarm, even though were within distance at which predators or pseudo-predators are reacted to)

Subject taxon	**Primate Species**	**Reference**
Reptiles		
Melanosuchus niger	*Cacajao ouakary*	Mourté & Barnett (2014)
Caiman crocodilus or *Melanosuchus niger*	*Chiropotes albinasus*	Barnett et al (2018)
Birds		
Crax alector	*Ateles belzebuth*	Mourté & Barnett (2014)
Psophia leucoptera	*Ateles belzebuth*	Mourté & Barnett (2014)
Ardea spp.	*Cacajao ouakary*	Mourté & Barnett (2014)
Ardea spp.	*Chiropotes albinasus*	Barnett et al. (2018)
Bubulcus ibis	*Chiropotes albinasus*	Barnett et al. (2018)
Egretta spp.	*Cacajao ouakary*	Mourté & Barnett (2014)
Egretta spp.	*Chiropotes albinasus*	Barnett et al. (2018)
Rynchops niger	*Chiropotes albinasus*	Barnett et al. (2018)
Opisthacomus hoatzin	*Chiropotes albinasus*	Barnett et al. (2018)
Buteogallus urubitinga	*Ateles belzebuth*	Mourté & Barnett (2014)
Elanoides forficatus	*Cacajao ouakary*	Mourté & Barnett (2014)
Harpagus bidentatus	*Chiropotes albinasus*	
Micrastur sp. (prob. *mirandollei*)	*Cacajao ouakary*	Mourté & Barnett (2014)
Micrastur mirandollei	*Chiropotes albinasus*	Barnett et al. (2018)
Milvago chimichanga	*Chiropotes albinasus*	Barnett et al. (2018)
Ramphastos tucanus	*Ateles belzebuth*	Mourté & Barnett (2014)
Ramphastis tucanus	*Cacajao ouakary*	Mourté & Barnett (2014)
Amazonas farinosa/Amazonas festiva	*Cacajao ouakary*	Mourté & Barnett (2014)
Ara ararauna/Ara chloroptera/Ara macao	*Ateles belzebuth*	Mourté & Barnett (2014)
Ara ararauna/Ara chloroptera/Ara macao	*Ateles belzebuth*	Mourté & Barnett (2014)
Aratinga guarouba	*Chiropotes albinasus*	Barnett et al. (2018)
Neomorpha rufipennis	*Ateles belzebuth*	Mourté & Barnett (2014)
Galbulidae. Furnaridae, Thamnophilidae, Tyrannidae, Bucconidae, Cuculidae	*Cacajao ouakary*	Mourté & Barnett (2014)[1]
Picidae, Cerylidae, Colombidae, Pipridae, Trochilidae, Thraupidae	*Cacajao ouakary*	Mourté & Barnett (2014)[2]
Mammals		
Bradypus tridactylus	*Cacajao ouakary*	Mourté & Barnett (2014)[3]
Choloepus didactylus	*Cacajao ouakary*	Mourté & Barnett (2014)
Myrmecophaga tridactyla	*Ateles belzebuth*	Mourté & Barnett (2014)
Tamandua tetradactyla	*Cacajao ouakary*	Mourté & Barnett (2014)
Priodontes maximus	*Ateles belzebuth*	Mourté & Barnett (2014)
Mazama americana	*Ateles belzebuth*	Mourté & Barnett (2014)
Coendou prehensilis	*Ateles belzebuth*	Mourté & Barnett (2014)
Coendou prehensilis	*Cacajao ouakary*	Mourté & Barnett (2014)

Statistical analysis

We analyzed the probability of the primate responses towards different potential predators using a cumulative logistic model (Montopoli & Anderson 1991), with the class variable "species" (*Ateles, Cacajao, Chiropotes*) and its interaction with the variable "type of predator" (predator/non-predator/pseudo-predator). We added modeled probabilities over the lower ordered values (lower than the observational mean). We evaluated the models using Akaike information criterion (AIC). Then, we computed least-mean squares for the class variable "species", to compare behavioural reactions among the three species.

A Chi square test was used to evaluate significance of response. We then used an odds ratio score test to estimate the proportional odds assumption. This estimation quantifies how strongly the presence/absence of property A is associated with the presence/absence of property B in a given population (e.g., Morris and Gardner 1988). We used an analysis of maximum likelihood estimate (AMLE) with an association of predicted probabilities and observed responses (APPOR) to classify behavioural reactions according to three threat-intensity categories (low, medium, and high). The fourth category (extreme: fatal attack) was not included because the number of recorded events (n = 3) was too small for statistical analysis. We then used odds ratio estimates and profile-likelihood confidence intervals (Chen 1994) to estimate the effect of "predator/non-predator/pseudo-predator" species encounters. We used SAS, version 9.4 (SAS Inst. Inc. Cary, NC), with 95 % confidence limits, for all analyses.

RESULTS

We recorded 270 events (*Ateles*, n = 12; *Cacajao*, n = 155; *Chiropotes*, n = 103). All three species encountered non-predators more frequently than actual predators (Table 2).

Table 2. Primate encounters categorized by threat level to the encountering animal. Percentages are within parenthesis.

	Number of encounters by threat type (%)*				
Primate species	**Non-predators (low threat)**	**Pseudo-predators: distant (medium threat)**	**Pseudo-predators: close (medium threat)**	**Predators: distant (medium threat)**	**Predators: close or attempting predation (high threat)**
Ateles belzebuth (N=12)†	4 (33.3)	1 (8.3)	1 (8.3)	5 (41.8)	1 (8.3)
Cacajao ouakary (N=155)††	117 (75.6)	20 (12.9)	12 (7.7)	5 (3.2)	1 (0.6)
Chiropotes albinasus (N=103)†††	49 (47.6)	20 (19.4)	22 (21.4)	1 (1)	11 (10.6)
Total=270	170 (62.9)	41 (15.2)	35 (12.9)	11 (4.2)	13(4.8)

NOTES: *Pseudo-predators classified as predators due to primate reaction, not due to actual threat represented, following Mourthé and Barnett (2014); †All records reported in Mourthé and Barnett (2014); ††154 interactions reported in Mourthé and Barnett (2014), and one in Barnett et al. (2011); †††94 interactions reported in Barnett et al. (2018), of which two were potential attacks, and nine reported by Barnett et al. (2017) that were all predation attempts.

Behavioural reaction intensity was influenced by predator type (p < 0.001). *Cacajao* and *Chiropotes* showed significant reactions in their response to predators (*Cacajao*: p < 0.001, mean intensities = 0.50; *Chiropotes*: p < 0.001, mean intensities = 0.40) versus. non-predators (*Cacajao*: p < 0.001, mean intensities = 0.099; *Chiropotes*: p < 0.001, mean intensities = 0.20). In contrast, *Ateles* demonstrated no significant difference in response to predators versus non-predators (Fig. 2).

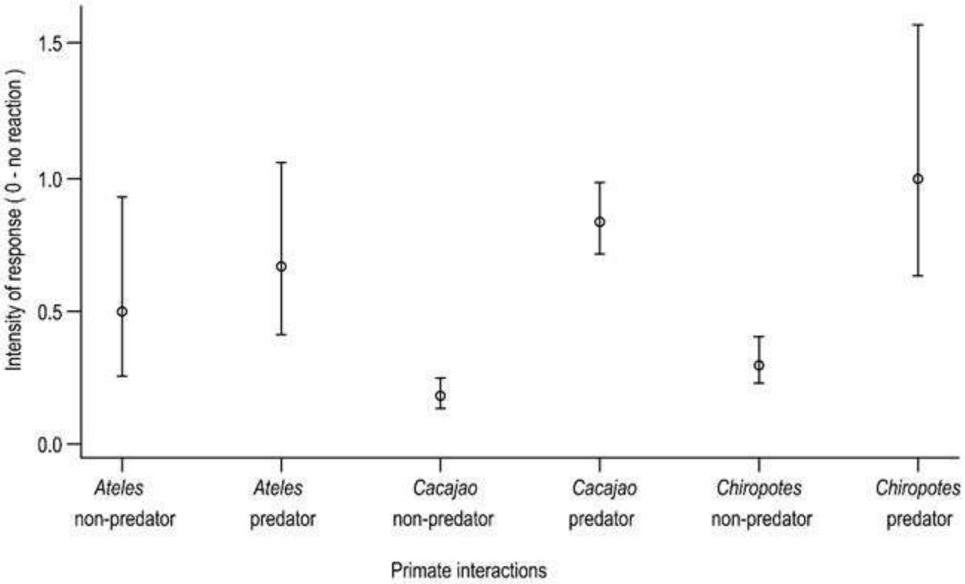


Figure 2. Least square means for intensity of response to predator and non-predator species, with 95% confidence limits represented by vertical bars.

In terms of risk-categorized behaviours, reactions were risker (i.e., high probability that the animal is hurt or killed) when directed towards predators than non-predators (p = 0.031), while the behavioural response to predators and pseudo-predators was not significant (p = 0.052). We found that there was a predator effect (the extent of the likely threat) on the energetic cost of a reactive response (p < 0.001). The energetic cost of such a response to a predator differed significantly from a response to a non-predator (p = 0.044). However, there was no significant difference in the energetic costs of responses to predators and pseudo-predators (p = 0.073).

The most frequent reaction to a non-predator species was a low-level threat response (Fig. 3), which is in accordance with the low-medium level of threat such species represent. Low-medium and high-level threat responses were most often aimed at predator species (Fig. 3). For pseudo-predators, the frequency of responses to medium-level threats was moderately elevated in comparison to non-predators, and high threat response frequencies were slightly elevated (Fig. 3).

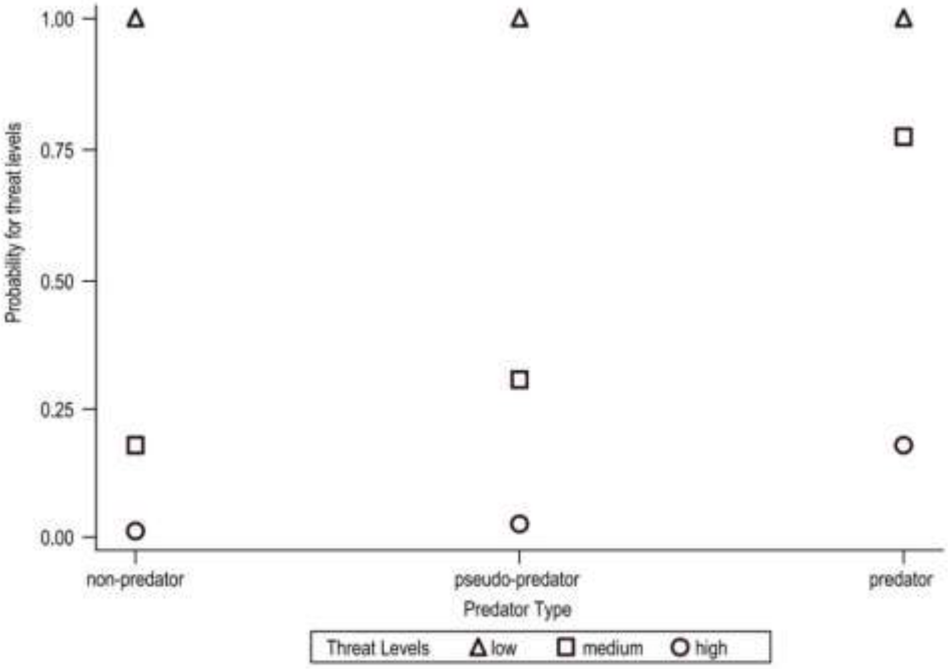


Figure 3. Predicted cumulative probabilities for behavioral reactions to various threat levels (no, low-medium and high) for different predator types (non-predator, predator, and pseudo-predator)

DISCUSSION

Primates adjust their behavioural reactions to predator threat levels in two ways. First, primates assess whether or not the species in proximity is a predator. Second, if the species is considered a predator, primates assess the apparent threat level the potential predator appears to pose, and then respond accordingly. Although we recorded examples of the most extreme threat level (fatal attack), as well as the reactions of the survivors of the attacks (Barnett et al. 2011), the number of such events observed (N = 3) was too small for statistical analysis. However, the behaviours recorded under such extreme circumstances did fit the predicted trends: following the fatal attack, the survivors grouped closer together and continued to give alarm calls, often for an extended period (e.g. Barnett et al. 2011). Overall, we found that the behavioural reactions to pseudo-predators were similar to those reactions to predators; however, after the concrete identification of the attacker, the final phase of the reaction was less intense.

No matter if distant or close, in our study pseudo-predators (e.g., vultures, large hawks, toucans and large ducks) were consistently considered by the primates as medium-level threats. Inherent in the concept of pseudo-predators is that these animals do not truly pose a danger, but the primates treat such pseudo-predators as threats because they are evolutionary adapted to respond to a series of stimuli which most often denote a predator. Providing that encounters with pseudo-predators do not consistently compromise individual energy budgets, such behavioural responses to non-predators presenting some of these stimuli can be adaptive responses (Dawkins and Krebs 1979) since there are times when the risks are real. For example, neither tapirs (*Tapirus* spp.) nor vultures (Cathartidae) are predators of the three primate species we studied, but primates have been recorded responding to these animals as if they were threats (Mourthé & Barnett 2014). From the perspective of the primates, responding to non-dangerous animals with energy-expending avoidance behaviours is more likely to enhance survival, compared with putting oneself at risk with an unanticipated encounter with a real predator. There is also an ontogenetic component: juvenile capuchin monkeys (*Cebus capucinus*) respond broadly to several potential predators, including harmless species, while they learn to make appropriate categorizations (Meno et al. 2013a).

The capacity to match the behavioural response to threat level may not depend solely on the individual assessment of the situation, but also be mediated by communication between group members, previous history of contact with predators (Lima & Dill 1990), and the size of predator and prey species (Mourthé & Barnett 2014; Libório & Martins 2013). Such matching may have a visual component (Tomasello et al. 1998), or occur because many species have graded calls that reflect threat intensity, often via an alteration of volume, pitch, or repetition rate (Fedurek and Slocombe 2011; Ducheminsky et al. 2014). Both *Ateles* and *Cacajao* produce louder calls when responding to high-level threats, compared to low-level threats (Matsuda & Izawa 2008; Mourthé 2011; Mourthé & Barnett 2014). In *C. ouakary*, threat escalation is communicated by the transition from "chock" to "cheng" alarm call. The former accompanies all events of low-level concern, while the latter is only heard in situations that are highly threatening (Barnett 2010; Bezerra et al. 2011). Similar results have been reported for baboons (Fischer et al. 2001), lemurs (Fichtel & Kappeler 2002), and chimpanzees (Crockford & Boesch 2003).

Other variables may also influence the match between behavioural reactions and threat levels, such as social learning (e.g., previous contact with predators, presence of conspecifics), and size of species involved (Griffin 2004; Mourthé & Barnett 2014; Libório & Martins 2013; Meno et al. 2013a, b). Although reactions to predators can be innate (Herzog and Hopf 1984), both social (e.g., witnessing predation) and individual (e.g., being the subject of an attack) experiences can influence individual learning processes relating to predation risk (Griffin 2004). Moreover, large species are attacked less often than smaller ones. To cope with a wider range of predators, smaller species show more sensitive, fine-tuned reactions to potential predators. Consequently, *Ateles* have fewer potential predators and respond less often to them than do smaller species (Di Fiore 2002), including the *Cacajao* and *Chiropotes* in the current study (Mourthé & Barnett 2014).

Field studies on behavioural reactions to predators are important in furthering the general understanding of the biological significance of species' behavioural responses to predation (Griffin 2004). We acknowledge that the categories for threat, risk, and energy expenditure used in the current study were subjective, as was our allocation of each of the behavioural events to these categories. However, studying predation in the wild is not an easy task because predation events, or even predation attempts, are rare and unpredictable, and their effects may be difficult to detect in social animals such as primates (Ferrari 2009).

In order to achieve sufficient sample sizes for analysis, we pooled our data from independent studies of three primate species, and then summed the reactions across time and space. Yet, levels of predation (and predation risk) may differ depending on the habitats used by the animals (Colishaw 1997), influencing the resultant behaviours in each, since animals can adjust threat-sensitive anti-predator behaviour to the background level of predation risk (Di Fiore 2002; Helfman1989; Brown et al. 2006). This difficulty can be overcome with studies that take into consideration predation-risk variables, such as differential vegetation density, and hence both prey and predator detectability (Embar et al. 2011).

Primates appear to be risk-sensitive animals, fine-tuning their reactions to potential predation events in a way that minimises unnecessary energy expenditure. Moreover, risk and threat assessment vary depending on size, so larger primates react in a generalized way, while smaller species react more selectively and spend more energy on behaviours with medium to high levels of risk. Low-risk threats, however, result in generalized low-energy reactions.

ACKNOWLEDGEMENTS

PT thanks Karel Novák and Helena Chaloupková. IM thanks ICMBio and Instituto Nacional de Pesquisas da Amazônia staff for providing permits and logistic support at MES, and is grateful to Ricardo Souza for his invaluable help during the fieldwork. The spider monkey study took place under licence SISBIO 23218-1,–and was funded by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Fundação Estadual do Meio Ambiente e Recursos Hídricos de Roraima, Mohamed bin Zayed Species Conservation Fund, and Idea Wild. IM also thanks the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) for his current PNPD scholarship granted through the Programa de Pós-graduação em Biodiversidade e Conservação (PPGBC-UFPA). AAB thanks Eduardo do Souza, Maria de Bom Jesus, Roberto Morreira, Thais Almeida, Bruna Bezerra, Eliana Santos Andrade, Welma Souza, for field-work help, and the IBAMA staff at Jaú. The authors thank the editor and two anonymous reviewers for their very helpful comments. This is contribution number 29 from the Amazonian Mammal Research Group, INPA, and number 53 from the Igapó Study Project.

ETHICAL STATEMENT

Funding

The spider monkey study was undertaken under licence SISBIO 23218-1, and funded by the Conselho Nacional de Desenvolvimento Científico e Tecnológico, Fundação Estadual do Meio Ambiente e Recursos Hídricos de Roraima, Mohamed bin Zayed Species Conservation Fund and Idea Wild. The uacari study was funded by the American Society of Primatologists, Columbus Zoo Conservation Fund, Sophie Danforth Conservation Fund, LSB Leakey Foundation (US), Leakey Fund (UK), Laurie Shapley, Margot Marsh Foundation, Oregon Zoo Conservation Fund, Percy Sladen Memorial Fund, Pittsburgh Zoo and Aquarium Conservation Fund, Primate Action Fund, Primate Conservation Inc., Roehampton University, and Wildlife Conservation Society. The cuxiú study received logistical support from Maracajá Ecological Consulting, and financial support from CNEC/WorleyParsons and ELETROBRÁS.

Conflict of Interest

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome. The data used were taken partly from previously published studies Barnett et al. (2017), Barnett et al. (2018), Mourthé (2011), Mourte and Barnett (2014) and partly from field work (Italo Mourthé) under license SISBIO 23218-1a.

Ethical approval

We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.

Data evaluated in this study are based only on observation of three primate species. We neither physically manipulated any of the animals, nor ever interrupted their behaviour during the course of the fieldwork observations.

Informed consent

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.

We understand that the Corresponding Author is the sole contact for the Editorial process (including Editorial Manager and direct communications with the office). He is responsible for communicating with the other authors about progress, submissions of revisions and final approval of proofs. We confirm that we have provided a current, correct email address which is accessible by the Corresponding Author and which has been configured to accept email from: tomanekpa@seznam.cz

Author contribution

Pavel Tománek wrote the text and conducted the statistical analysis; Italo Mourte collected field data on Ateles and commented on the text; Sarah Boyle edited the text and made statistic suggestions; Adrian Barnett collected field data on Cacajao, helped form the initial idea, and edited text.

REFERENCES

Arnold K, Zuberbühler K. 2006. The alarm-calling system of adult male putty-nosed monkeys, *Cercopithecus nictitans martini*. Animal Behaviour 72:643-653

Aguiar-Silva. FH, Sanaiotti TM, & Luz BB. 2014. Food habits of the Harpy Eagle, a top predator from the Amazonian rainforest canopy. Journal of Raptor Research, 48, 24–35.

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Fiore AD, Dunbar RI, Henzi SP, and Holekamp K. 2008. Fission-fusion dynamics: new research frameworks. Current Anthropology 49:627-654

Baldellou M, Henzi SP. 1992. Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. Animal Behaviour 43:451-461

Barnett AA. 1995. Primates: Expedition Field Techniques. London: Expedition Advisory Centre of Royal Geographical Society.

Barnett AA. 2010. Diet, habitat, use and conservation ecology of the golden-backed uacari, Cacajao melanocephalus ouakary, in Jaú National Park, Amazonian Brazil. [PhD thesis]. London (UK): Roehampton University. 456 p

Barnett AA, Schiel V, Deveny A, Valsko J, Spironello WR, Ross C. 2011. Predation on *Cacajao ouakary* and *Cebus albifrons* (Primates: Platyrrhini) by harpy eagles. Mammalia 75:169–172

Barnett AA, Bowler M, Bezerra BM, Defler TR. 2013.. Ecology and behavior of uacaris (genus *Cacajao*). In book: Evolutionary Biology and Conservation of Titis, Sakis and Uacaris. Chapter: Ecology and behavior of uacaris (genus Cacajao). Cambridge University Press (pp.151-172)

Barnett AA & Shaw P. 2014. More food or fewer predators? The benefits to birds of associating with a Neotropical primate varies with their foraging strategy. Journal of Zoology, 294: 224-233.

Barnett AA, Silla JM, de Oliveira T, Boyle SA, Bezerra BM, Spironello WR, Setz EZ, da Silva RFS, de Albuquerque Teixeira S, Todd LM, Pinto LP. 2017. Run, hide, or fight: anti-predation strategies in endangered red-nosed cuxiú (*Chiropotes albinasus*, Pitheciidae) in southeastern Amazonia. Primates 58:353-360

Barnett AA, de Oliveira T, da Silva RFS, de Albuquerque Teixeira S, Tomanek P, Todd LM, Boyle SA. 2018. Honest error, precaution or alertness advertisement? Reactions to vertebrate pseudopredators in red-nosed cuxiús (*Chiropotes albinasus*), a high-canopy neotropical primate. Ethology 124:177-187

Barros M, Alencar C, de Souza Silva MA, Tomaz C. 2008. Changes in experimental conditions alter anti-predator vigilance and sequence predictability in captive marmosets. Behavioural Processes 77:351-356

Bartecki U, Heymann EW. 1987. Field observation of snake-mobbing in a group of saddle-back tamarins, *Saguinus fuscicollis nigrifrons.* Folia Primatologica 48:199-202

Barton RA, Whiten A, Strum SC, Byrne RW, Simpson AJ. 1992. Habitat use and resource availability in baboons. Animal Behaviour 43:831-844

Bezerra BM, Barnett AA, Souto A, Jones G. 2011. Ethogram and natural history of golden-backed uakaris (Cacajao melanocephalus). International Journal of Primatology 32:46–68

Blanchard DC, Griebel G, Pobbe R, Blanchard RJ. 2011. Risk assessment as an evolved threat detection and analysis process. Neuroscience and Biobehavioral Reviews 35:991-998

Boinski S, Treves AD, Chapman CA. 2000. A critical evaluation of the influence of predators on primates: effects on group travel. In: On the move: how and why animals travel in groups. University of Chicago Press, Chicago Boinski S, Garber, P, eds, 43-72

Boyle SA, Lourenço WC, Da Silva LR, Smith AT. 2009. Travel and spatial patterns change when *Chiropotes satanas chiropotes* inhabit forest fragments. International Journal of Primatology 30: 515-531.

Bowler M. 2007.. Conservation and ecology of red uakari monkey Cacajao calvus ucayalii in the Peruvian Amazon. (Doctoral thesis, University of Kent).

Brown JS, Laundré JW, Gurung M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385-399

Brown GE, Rive AC, Ferrari MC, Chivers DP. 2006. The dynamic nature of antipredator behavior: prey fish integrate threat-sensitive antipredator responses within background levels of predation risk. Behavioral Ecology and Sociobiology 61:9-16

Busia L Smith-Aguilar SE, Aureli F, Schaffner CM & Ramos-Fernández G. 2018. Predation attacks on wild Spider Monkeys (Ateles geoffroyi). Folia Primatologica 89: 341-346.

Chen SX. 1994. Empirical likelihood confidence intervals for linear regression coefficients. Journal of Multivariate Analysis 49:24-40

Cheney DL, Wrangham RW. 1987. Predation. In: Smuts, B. B., Cheney. D. L., Seyfarth, R. M., Wrangham, R. W., Struhsaker, T. T. (eds) Primate Societies. The University of Chicago Press, Chicago, pp 227-239

Chinchilla FA. 1997. La dieta del jaguar (Panthera onca), el puma (Felis concolor), y el manigordo (Felis pardalis) (Carnivora: Felidae) en el Parque Nacional Corcovado, Costa Rica. Revista Biologia Tropical 45:1223–1229.

Calaça AM, Silva DA, & de Melo FR. (2016). Predação de cuxiú (Chiropotes sagulatus) por harpia (Harpia harpyja) na Floresta Nacional de Saracá-Taquera, Pará, Brasil. Biodiversidade Brasiliera 7: 89-94.

Cowlishaw G. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. Animal Behaviour 53:667-686

Creel S, Christianson D. 2008. Relationships between direct predation and risk effects. Trends in Ecology & Evolution 23:194-201

Crockford C, Boesch C. 2003. Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: analysis of barks. Animal Behaviour 66:115-125

Crofoot MC. 2012. Why mob? Reassessing the costs and benefits of primate predator harassment. Folia Primatologica 83:252-273

Dawkins R, Krebs JR. 1979. Arms races between and within species. Proceedings of the Royal Society of London, Series B: Biological Sciences 205:489–511.

De Luna AG, Sanmiguel R, Di Fiore A, Fernandez-Duque E. 2010. Predation and predation attempts on red titi monkeys (*Callicebus discolor*) and equatorial sakis (*Pithecia aequatorialis*) in Amazonian Ecuador. Folia Primatologica 81:86-95

de Souza Martins. S, de Lima EM & de Sousa e Silva JJr. 2005. Predation of a bearded saki (Chiropotes utahicki) by a harpy eagle (Harpia harpyja). Neotropical Primates, 13, 7–10.

Di Fiore A. 2002. Predator sensitive foraging in ateline primates. In: Miller LE (ed) Eat or be eaten: predator sensitive foraging among primates. Cambridge University Press, Cambridge, pp 242–267

Di Fiore A. 2003. Ranging behavior and foraging ecology of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Yasuni National Park, Ecuador. American Journal of Primatology 59: 47-66.

Ducheminsky N, Henzi SP, Barrett L. 2014. Responses of vervet monkeys in large troops to terrestrial and aerial predator alarm calls. Behavioral Ecology 25:1474-1484

Eberle. M., Kappeler PM. 2008. Mutualism, reciprocity, or kin selection? Cooperative rescue of a conspecific from a boa in a nocturnal solitary forager the gray mouse lemur. American Journal of Primatology 70:410-414

Embar K, Kotler BP, Mukherjee S. 2011. Risk management in optimal foragers: the effect of sight lines and predator type on patch use, time allocation, and vigilance in gerbils. Oikos 120:1657-1666

Fedurek P, Slocombe KE. 2011. Primate vocal communication: a useful tool for understanding human speech and language evolution? Human Biology 83:153-173

Ferrari SF, Pereira WL, Santos RR & Veiga LM. 2004. Fatal attack of a Boa constrictor on a bearded saki (Chiropotes satanas utahicki). Folia Primatologica, 75, 111–113.

Ferrari SF. 2009. Predation risk and antipredator strategies. In: Garber, P. A., Estrada, A., Bicca-Marques, J. C., Heymann, E. W., Strier, K. B. (eds) South American Primates — Comparative perspectives in the study of behavior, ecology, and conservation. Springer, New York, pp 251–277

Fischer J, Metz M, Cheney DL, Seyfarth RM. 2001. Baboon responses to graded bark variants. Animal Behaviour 61:925-931

Fichtel C, Kappeler PM. 2002. Anti-predator behavior of group-living Malagasy primates: mixed evidence for a referential alarm call system. Behavioral Ecology and Sociobiology 51:262-275

Goodman SM, O'Connor S, Langrand O. 1993. A review of predation on lemurs: implications for the evolution of social behavior in small, nocturnal primates. In: Lemur social systems and their ecological basis (pp. 51-66). Kappeler P, Ganzhorn JU Springer US, New York.

Griffin AS. 2004. Social learning about predators: a review and prospectus. Learning and Behavior 32:131-140

Grove M. 2012. Space, time, and group size: a model of constraints on primate social foraging. Animal Behaviour, 83: 411-419

Guilford T, Dawkins MS. 1991. Receiver psychology and the evolution of animal signals. Animal Behaviour 42:1-14

Gursky S. 2005. Predator mobbing in *Tarsius spectrum*. International Journal of Primatology 26:207-221

Gursky-Doyen S, Nekaris KAI. (Eds.). 2007. Primate anti-predator strategies. Springer Science & Business Media.

Heistermann M, Palme R, Ganswindt A. 2006. Comparison of different enzyme immunoassays for assessment of adrenocortical activity in primates based on fecal analysis. American Journal of Primatology 68:257-273

Helfman GS. 1989. Threat-sensitive predator avoidance in damselfish-trumpet fish interactions. Behavioral Ecology and Sociobiology 24:47-58

Herzog M, Hopf S. 1984. Behavioral responses to species-specific warning calls in infant squirrel monkeys reared in social isolation. American Journal of Primatology 7:99-106

Hill RA, Dunbar RIM. 1998. An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. Behaviour 135:411-430

Isbell LA. 1994. Predation on primates: ecological patterns and evolutionary consequences. Evolutionary Anthropology 3:61-71

Julliot C. 1994. Predation of a young spider monkey (Ateles paniscus) by a crested eagle (Morphnus guianensis). Folia Primatologica, 63, 75-77.

Koenig A. 1998. Visual scanning by common marmosets (*Callithrix jacchus*): functional aspects and the special role of adult males. Primates 39:85-90

Lenz BB & dos Reis AM. 2011. Harpy eagle-primate interactions in the central Amazon. Wilson Journal of Ornithology, 123, 404–408.

Libório RA, Martins MM. 2013. Body size in predator–prey interactions: an investigation of Neotropical primates and their predators. Studies on Neotropical Fauna and Environment 48:81-87

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640

Markham AC, Gesquiere LR. 2017. Costs and benefits of group living in primates: an energetic perspective. Philosophical Transactions of the Royal Society B: Biological Sciences, 372:20160239

Marquet F, Teichert T, Wu SY, Tung YS, Downs M, Wang S, Chen C, Ferrera V, Konofagou EE. 2014. Real-time, transcranial monitoring of safe blood-brain barrier opening in non-human primates. PloS One. 9(2):e84310

Martins SS, Lima EM, Silva Jr JS. 2005. Predation of a bearded saki (*Chiropotes utahicki*) by a harpy eagle (*Harpia harpyja*). Neotropical Primates 13:7-10

Matsuda I, Izawa K. 2008. Predation of wild spider monkeys at La Macarena, Colombia. Primates 49:65-68

Meno W, Coss RG, Perry S. 2013a. Development of snake-directed antipredator behavior by wild white-faced capuchin monkeys: I. Snake-species discrimination. American Journal of Primatology 75:281-291

Meno W, Coss RG, Perry S. 2013b. Development of snake-directed antipredator behavior by wild white-faced capuchin monkeys: II. Influence of the social environment. American Journal of Primatology 75:292–300

Miller LE, Treves A. 2007. Predation on primates – Past studies, current challenges, and directions for the future. In: Campbell, C. J., Fuentes, A., Mackinnon, K. C., Panger, M., Bearder, S. K. (eds) Primates in perspective. Oxford University Press, New York, pp 525–543

Montopoli GJ, Anderson DA. 1991. Logistic model for the cumulative effects of human intervention on bald eagle habitat. Journal of Wildlife Management 55:290-293

Morris JA, Gardner MJ. 1988. Calculating confidence intervals for relative risks (odds ratios) and standardised ratios and rates. British Medical Journal (Clinical Research Edition) 296:1313-1316

Mourthé I. 2011. Reactions of white-bellied spider monkeys to a predation attempt by a cougar. Neotropical Primates 18:28-29

Mourthé I. 2014. Response of frugivorous primates to changes in fruit supply in a northern Amazonian forest. Brazilian Journal of Biology 74:720-727

Mourthé I, Barnett AA. 2014. Crying tapir: the functionality of errors and accuracy in predator recognition in two Neotropical high-canopy primates. Folia Primatologica 85:379-398

Norconk MA, Kinzey WG. 1994. Challenge of neotropical frugivory: travel patterns of spider monkeys and bearded sakis. American Journal of Primatology, 171-183.

Overdorff D. 1988. Preliminary report on the activity cycle and diet of the red-bellied lemur (*Lemur rubriventer*) in Madagascar. American Journal of Primatology 16:143-153

Pontzer H, Raichlen DA, Gordon AD, Schroepfer-Walker KK, Hare B, O'Neill MC, Muldoon KM, Dunsworth HM, Wood BM, Isler K, Burkart J. 2014. Primate energy expenditure and life history. Proceedings of the National Academy of Sciences 111:1433-1437

Ross C. 1993. Predator mobbing by an all-male band of hanuman langurs (*Presbytis entellus*). Primates 34:105-107

Sánchez MM, Noble PM, Lyon CK, Plotsky PM, Davis M, Nemeroff CB, Winslow JT. 2005. Alterations in diurnal cortisol rhythm and acoustic startle response in nonhuman primates with adverse rearing. Biological Psychiatry 57: 373-381.

Shaffer CA. 2013. Ecological correlates of ranging behavior in bearded sakis (*Chiropotes sagulatus*) in a continuous forest in Guyana. International Journal of Primatology 34: 515-532.

Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. Journal of Human Evolution 32:523–559

Stanford CB. 2002. Avoiding predators: expectations and evidence in primate antipredator behavior. International Journal of Primatology 23:741-757

Stankowich T, Blumstein DT, 2005. Fear in animals: a meta-analysis and review of risk assessment. Proceedings of the Royal Society of London B: Biological Sciences 272:2627-2634

Tello NS, Huck M, Heymann EW. 2002. Boa constrictor attack and successful group defence in moustached tamarins, *Saguinus mystax*. Folia Primatologica 73:146-148

Tomasello M, Cal J, Hare B. 1998. Five primate species follow the visual gaze of conspecifics. Animal Behaviour 55:1063-1069

Tórrez L, Robles N, González A, Crofoot MC. 2012. Risky business? Lethal attack by a jaguar sheds light on the costs of predator mobbing for capuchins (*Cebus capucinus*). International Journal of Primatology 33:440-446

Treves A. 1999a. Has predation shaped the social systems of arboreal primates? International Journal of Primatology 20:35-67

Treves A. 1999b. Within-group vigilance in red colobus and red tail monkeys. American Journal of Primatology 48:113-126

Treves, A., 2000. Theory and method in studies of vigilance and aggregation. Animal Behaviour 60:711-722

Ydenberg. RC, Dill LM. 1986. The economics of fleeing from predators. Advances in the Study of Behavior 16:229-249

Wrangham RW, Gittleman JL, Chapman CA. 1993. Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. Behavioral Ecology and Sociobiology 32:199-209

Zuberbühler K. 2000. Referential labelling in Diana monkeys. Animal Behaviour 59:917-927

Zuberbühler K. 2001. Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli*. Behavioral Ecology and Sociobiology 50:414-422

Zuberbühler K., Jenny D. 2002. Leopard predation and primate evolution. J Hum Evol 43:873–886

Zuberbühler K, Jenny D, Bshary R. 1999. The predator deterrence function of primate alarm calls. Ethology 105:477-490

Zuberbühler K, Noë R, Seyfarth RM. 1997. Diana monkey long-distance calls: messages for conspecifics and predators. Animal Behaviour 53:589–604

4 DISCUSSION AND STUDIES IN THE FUTURE

The studies published in this work concerned selected neotropical primates in the family Pitheciidae, a family that also includes the uacari monkeys (*Cacajao*), the saki (*Pithecia*), the cuxiús (*Chiropotes*) and the titis (*Callicebus, Cheracebus, Plecturocebus*). The introductory article provides a description of the current state of knowledge of *C. ouakary*, in particular on the basis of studies carried out at the Parque Nacional do Jaú in the state of Amazonas in Brazil. Other published articles mentioned in the text focused on partial aspects of the life and behavior of this primate based on studies from Jaú National Park, Maracá Ecological Station and Amanã Sustainable Development Reserve.

The first topic mentioned in this work is a summary of current knowledge about the ecology and behavior of *Cacajao ouakary*. Other published articles dealt with the topics of predation, specifically the behavior of Ateliine primates (*Alouatta* and *Ateles* species) and *Chiropotes albinasus* (like *Cacajao* a Pitheciin primate) when under direct threat from potential and pseudo-predators, predators, the predation-risk sensitive choice of resting and sleeping sites, and food selection due to the energy intensity of its processing.

Predation in primates is generally thought to have wide-reaching effects on feeding behavior and the social ecology. Primate species display a variety of reactions to predators (Table 1), from active physical defense and mobbing, to escape and shelter (Caro 2005; Gursky-Doyen 2007).

Table 1. Operational definitions of behaviors associated with responses to predators by red-nosed cuxiús - table from published paper 3.2 "Honest errror, precaution or alertness advertisement..."

Name of behavior	Operational definition
Head glance	A rapid (<5 s), deliberate, directed single movement only of the head that pauses when apparent direct line of sight is obtained to a particular object (an animal newly arrived in the vicinity, in the current study). The position to allow directed visual attention is brief (1–2 s) and the head then moves. Low intensity response, not accompanied by orientation of the rest of the body
Alarm call	A generally sharp high-pitched call that summons attention of the receivers, and acts to inform them of the presence or imminence of prejudicial entity or event
Move away	Directed motion away from a point source of potential discomfort or danger—of variable intensity, but not an intense response (viz. "fleeing")
Sentinel	An individual occupying a generally exposed position and not engaged in feeding, resting or grooming, but with an alert appearance and appearing to be visually searching for potential danger

Warning calls are often issued and potentially threatening animals are either directly actively monitored or only by head movements (Gursky-Doyen & Nekaris 2007). Such behavior may take some time, when time could be devoted to other activities (Davies et al. 2012). Accordingly, there should be strong selection only in response to to those species which pose a real threat. We tested the hypotheses to which we respond pseudo-predators are the precautionary calls of the individuals who following the

Life-Dinner Principle (Dawkins & Krebs 1979), or represent the ontogenesis of species recognition (Barnett et al. 2018b).

Red-nosed cuxiús reacted to pseudopredator species that resembled predatory species and that came within 20 m of the red-nosed cuxiús (*Chiropotes albinasus*), and these reactions were shorter than the reactions to true predators. These findings support three of the four predictions of the Dinner/Life Principle. However, there was no support for age or sex differences in the responses to pseudopredators, which was a fourth prediction of the Dinner/Life Principle. For the ontogeny hypothesis, we did not find support for the prediction that juveniles, inexperienced in identifying predators, would alarm call more to non-predators than would adults. It is clear that many predators and pseudo-predators have a very similar appearance and that for an animal living in a dangerous world it can be very risky to ignore some species, and that delay needed to distinguish between them can be fatal. It is thus clear that it is important to respond appropriately to pseudo-predators, the question remains how much time loss this analysis poses in relation to how much risk this threat poses. We found partial support for the Dinner/Life Principle hypothesis, but no support for the ontogeny hypothesis. This should spur examination of responses to pseudopredators in other primate and non-primate species, and so help advance the understanding the evolution of such behaviors – Table 2.

Table 2. Records of predation and predation attempts on *Cacajao* spp. (uacaris), *Chiropotes* spp. (cuxiús.), and *Pithecia* spp. (sakis) - table from published paper 3.2 "Honest errror, precaution or alertness advertisement ?..."

Primate taxon	**Predator species**	**Interaction type**
Cacajao calvus ucayalii	*Eira barbara*	Mobbing, accompanied by calls
Cacajao ouakary	*Harpia harpyja*	Successful predation of sub-adult
Chiropotes albinasus	*Harpia harpyja*	Remains in nest
Chiropotes albinasus	*Harpia harpyja, Leucopternis* sp., *Spizaëtus tyrannus* Unidentified hawks	Eight attempted, and one successful, predation events reported (four by *H. harpyja;* two by *Leucopternis* sp., one by *S. tyrannus,* two by unidentified hawks). Seven attacks were against groups, one against a juvenile (successful) and one against an infant
Chiropotes chiropotes	*Harpia harpyja*	Successful predation of adult
Chiropotes utahickae	*Harpia harpyja*	Successful predation of adult male
Chiropotes utahickae	*Boa constrictor*	Successful predation
Pithecia aequatorialis		Attempted predation (large unidentified raptors). Four events, two targeted at groups, two at juveniles/infants
Pithecia irrorata	*Harpia harpyja*	Remains in nest
Pithecia pithecia	*Morphus guianensis*	Attempted (poss. successful) predation of immature female
Pithecia rylandsi	*Spizaëtus melanoleucus*	Successful predation

Dietary studies and food choices of primates are common, however those involving optimal foraging are rarer (Dias da Silva et al. 2020). We studied the optimality of within-species diet item choice by the golden-backed uacari, a specialist Amazon seed-eating primate. Optimal foraging theory predicts that animals will try to minimize food processing time while maximizing energy gain (Davies et al. 2012). To test this hypothesis, we evaluated whether a specialized primate seed actively chooses fruit when feeding on a particular tree species and if such choices can be explained by optimal foraging theory. The variables used were the size, mass and husk thickness of the fruits available. Study species were the golden-backed uacari (*Cacajao ouakary*, Pitheciidae) and the single-seeded pods of the makuku tree (*Aldina latifolia,* Fabaceae). We predicted that golden-backed uacari would consume fruits of the size class that required the least time to obtain, process, and ingest.

Results showed that biggest is not always the best, since large fruits are difficult to manipulate and take a long time to process (remove husk and access seeds). As a result, the energy yield per unit time is lower than that achievable from medium-sized fruit, which approximate to the length of the uacaris hand. We conclude that the size of the fruit, husk thickness and relative weight/volume of seeds/fruits are selection criteria for the species *Cacajao ouakary* when selecting which *Aldina latifolia* fruits to eat. In addition, our results suggest that animal anatomy (especially gape size) may limit potential fruit selection. Future studies using a larger larger sample, several species and analysing at both hands and the size and size of the fruit in relation to the maximum gape could also be highly informative, as well as studies that take into account the impact of such restrictions of the foraging of uacaris and other species that have large fruits in their diet.

The risk of predation is an important aspect of animal behavior, which affects not only daytime activities but also relaxation and night rest periods (Jucá et al. 2020). We therefore examined how site choice for night-time sleeping sites and those used day-time resting by two howler monkey species (*Alouatta* spp.) were affected by the most likely forms of attack (daily predators and nocturnal cats). We recorded vertical and horizontal occupancy patterns for 47 sleeping places and 31 resting places, as well as the presence of creepers or vines in the trees. We compared the heights of trees used as places of rest or sleep monkeys with 200 forest trees that the monkeys did not use. Trees used as night sleeping sites they were taller than those used as daily resting places, and taller than trees not used by monkeys. However, while the trees used as daily resting places were not significantly taller than the unused trees, the daily resting places were located on branches closer to the ground, closer to the main trunk of a tree and on trees with more creepers/vines than night sleeping sites. Differences in site location can be explained by the type of predator that is most likely to attack at certain times: aerial predators by day (eagles), and cats by night.

In the sleeping site study, we found that howler monkeys rested closer to the main trunk during the day and slept closer to terminal branches at night. Resting closer to the trunk of the tree might provide extra time to react to an aerial predator, especially since reactions to raptors often consist of dropping into lower vegetation and/or hiding in dense vegetation thickets (Miranda et al., 2006; Barnett et al., 2018). In contrast, attacks in trees by mammalian carnivores generally involve the potential predator accessing the primates' locations either by climbing the tree trunk or lianas/vines associated with the tree (Emmons, 1987; Bianchi & Mendes, 2007). By sleeping on thinner branches or closer to the terminal end of a branch, a primate can detect the approach of such a heavy predator (Anderson, 2000), and thus gain extra warning time and time to escape from a predator that typically attacks via the tree trunk or main limbs of the tree. Consequently, sleeping on the thinner branches may, again, give extra warning time and time to escape from a predator obliged to attack via the tree trunk or main limbs of the tree. This study did not include functional analysis of predation by snakes, even though snakes are known predators of primates (Isbell, 2006) of all sizes: that said, we found that during the day the howler monkeys avoided trees with lianas/vines that touched the ground and/or another tree; such behaviour may be linked to avoidance of predation by snakes, but this is a topic for future study.

Comparison of site choices on hot and cool days and nights showed no difference in extent of position on the trunk of resting/sleeping sites, both when data was analysed separately and combined. If sites were being chosen in response to heat stress, then the animals might have been expected to choose areas closer to the trunk on hot days to gain shade protection and areas closer to the outer canopy on hot nights. This was not the case for the study in question, so it appears that the importance of minimizing predation outweighs any thermal comfort-based choices reported by Thompson et al. (2014, 2016).

The sleeping site study assumed a lack of aerial predation risk at night; however, use of arboreal camera traps at frequently-used sleeping sites could determine whether owls are a predation risk for howler monkeys and other arboreal animals. Whether owls predate Neotropical primates is currently unconfirmed, through evidence from the literature and personal experience of long-term workers indicates that it is, at the most, an exceedingly rare event (Voirin et al. 2009). Likewise, such arboreal camera traps could help determine the sleeping patterns of primates and whether sleeping behaviours vary depending on predation risk. Thus, the data given here could help structure studies of the sparing and group group sizes of primates in day-resting and night-sleeping sites.

Various species of animals maximise energy gained through foraging by minimising excessive energy spent on nonessential activities. Avoiding predation is key for maximising an individual's lifespan, as well as that of its kin; however, anti-predation behaviours can be energetically costly (Caro 2005, Gursky-Doyen & Nekaris 2007). We investigated the relationship between the potential threat levels by predators, pseudo-predators, and non-predators, and the subsequent energetic cost of behavioural reactions to these threats, in the white-bellied spider monkey (*Ateles belzebuth*), golden-backed uacari (*Cacajao ouakary*), and red-nosed cuxiú (*Chiropotes albinasus*). We analysed a total of 270 interactions across three independent field studies of the three primate species. Primates adjust their behavioural reactions to predator threat levels in two ways. First, primates assess whether or not the species in proximity is a predator. Second, if the species is considered a predator, primates assess the apparent threat level the potential predator appears to pose, and then respond accordingly. Overall, we found that the behavioural reactions to pseudo-predators were similar to those reactions to predators; however, after the concrete identification of the attacker, the final phase of the reaction (avoidance) was less intense (if present at all).

The capacity to match the behavioural response to threat level may not depend solely on individual assessment of the situation, but also be mediated by communication between group members, previous history of contact with predators (Lima & Dill 1990), and the relative sizes of predator and prey species (Mourthé & Barnett 2014; Libório & Martins 2013). Such matching may have a visual component (Tomasello et al. 1998). Alternatively, for many species such matching is achieved by graded calls series that reflect threat intensity, often via an alteration of volume, pitch, or repetition rate (Fedurek and Slocombe 2011; Ducheminsky et al. 2014). Primates appear not only to be risk-sensitive animals, but to fine-tune their reactions to potential predation events in a way that minimises unnecessary energy expenditure (Gursky-Doyen & Nekaris 2007). Moreover, risk and threat assessment vary depending on size, so larger primates react in a generalized way, while smaller species react more selectively and spend more energy on behaviours with medium to high levels of risk (Tomanek et al. 2020). Our results revealed significant differences in the behavioural response to predators and non-predators for both *C. ouakary* and *C. albinasus*, but not for *A. belzebuth*. In terms of risk-categorized behaviours, response to predators differed from response to non-predators (being much more intense and energy intensive), while there was no difference in response to predators versus pseudo-predators. Thus, response to potential predators represents an integral part of the time-management and defence strategies of two of the three studied species, and should be integrated into future studies of primate responses to varying levels of predation threat.

5 FINAL PART – FUTURE CONSIDERATIONS

A) Information on the state of environmental protection of South American primates from the perspective of the activities of ARPA (Amazon Region Protected Areas).

The Amazon basin is a major geographical region contributing to the high biological diversity of South America. The basin encompasses an area about 7 million square kilometers in size. This vast equatorial ecosystem is home to one-fifth of the planet's plant and animal species. Rapid and extensive changes in the original distribution of primate habitats in the region as a result of human activity coupled with a general lack of knowledge of the basic biology, ecology and behavior makes conservation of South American primates a daunting task. Because of its high biological diversity the South American tropical vegetation is one of the world's greatest conservation challenges (Estrada 2009).

The Amazon Region Protected Areas Program (ARPA) originated in a 1998 promise by the Brazilian government to triple the area of the Amazon that was legally protected. The program was launched in 2003, supported by government agencies, NGOs and major donors. The program is based on a major two-year planning exercise with experts from different disciplines, representatives of the indigenous people and others. This defined a set of priority areas for new parks and reserves throughout the Amazon (ARPA 2016). The program is led by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA), which coordinates the process of identifying protected areas, creating them by law, preparing management plans and establishing staff and infrastructure. IBAMA works with local government authorities and community members. Implementation is overseen by a steering committee that includes representatives from government agencies and civil society (ARPA 2016). The first phase (2003), was the consolidation of 180 000 square kilometers of new protected areas. In February 2016 it was announced that the Federal Ministry of the Environment would include among the conservation areas supported under ARPA next areas. With these activities, the total area covered by ARPA in Brazil rose to 582 960.56 square kilometers (Três Unidades de Conservação ... 2014). Benefits include protecting habitats, ecosystems and biodiversity, reducing conflicts over land ownership, providing sustainable use options to local communities, creating barriers against deforestation and burning, maintaining forest coverage to lock up carbon, and avoid changes to rainfall patterns (ARPA 2016) – Fig. 11.

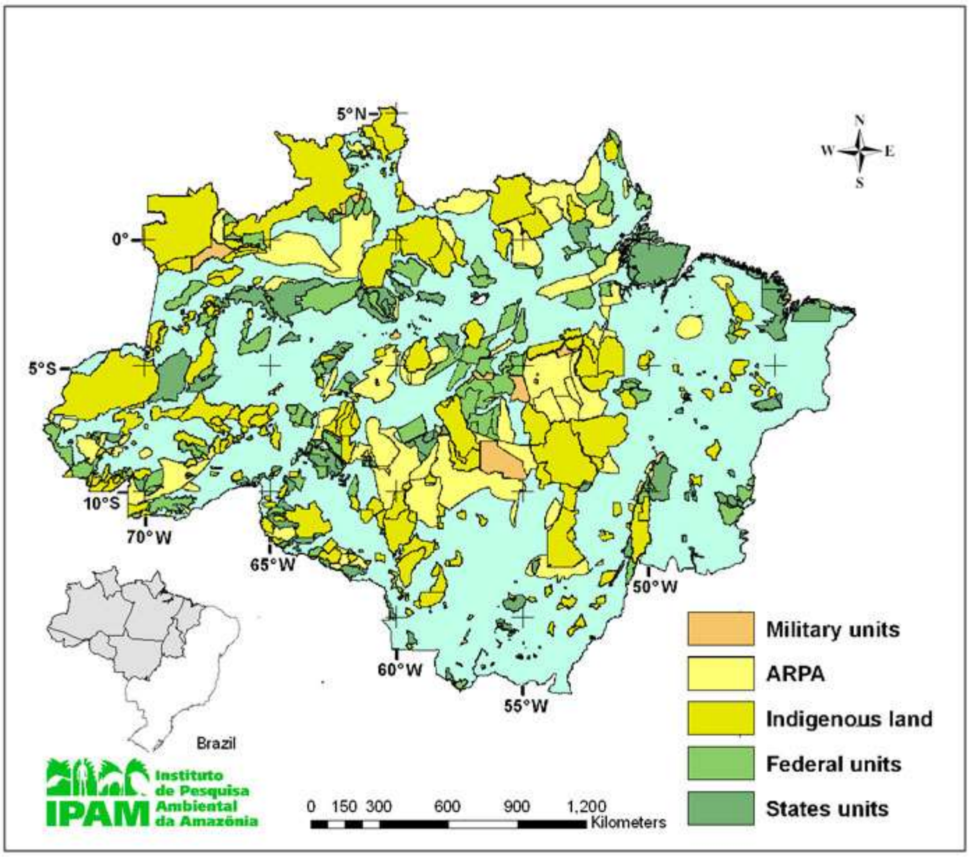


Figure 11. Current and future planned protected areas (ARPA) in the Brazilian Amazon.

B) Set of nearest publications ready for publication

Barnett AA, dos Santos-Barnett TC, Muir J, **Tomanek P**, Gregory T, Matte AL, Bezerra BM, de Oliveira T & Boyle SA. Beans with bugs: covert carnivory, infested seed selection by the Red-nosed Cuxiu *Chiropotes albinasus*, Pitheciidae), a seed-predator that benefits its prey plants. For *Biotropica* IF 2.89

Barnett AA, dos Santos-Barnett TC, Baccaro F, Bezerra BM, Muir J, Dias-da-Silva RHP, **Tomanek P** & Boyle SA. Deciding to decide: choice patterns for optimizing fruit selection in three Neotropical primates (*Ateles chamek*, *A. marginatus*, and *Chiropotes albinasus*). For *Oecologia* IF 3.091

Barnett AA, Soares C, **Tomanek P**, Da Silva RHP, Bezerra BM, Boyle S & Baccaro F. Pod juggling parrots: parsing pod size, toxic larval infestations and handling time in *Enterolobium schomburgkii* by psittacids of different sizes. For *Current Zoology* IF 2.351

Barnett AA, **Tomanek P**, Da Silva RHP, Muir J, Bezerra BM, Boyle S & Baccaro F. Inter-generic competition and niche shifts in diet-specialist primates: forest strata use, diet and physical size in Amazonian *Pithecia, Chiropotes* and *Cacajao* (Pitheciidae). For *Journal of Animal Ecology* IF 4.36

C) Articles in preparation

Tomanek P, Barnett AA. The ontogeny of anti-predator defence behavior in neotropical primates. Potentially for *Behavioral Biology & Sociobiology* IF 2.207

Tomanek P, Barnett AA. Young or inferm preferred: is predator selection of primate individuals selective or opportunistic ? – a test with neotropical primates. Potentially for *Biotropica* IF 2.89

D) Future research

Uacaris generally tend to occur at low densities. A population reduction of at least 30% is suspected over the course of three generations (30 years), including the current (2018-2028) and two subsequent generations (2028-2048), due to habitat degradation and other threats (Veiga et al. 2020). The true on-the-ground situation of wild *Cacajao* populations is unknown in any part of its range except some small protected sectors. The species' status and the existence of threats, and how these might be trending, have not been surveyed in any of the other protected areas in its range, nor have the distributional limits, population densities, threats, or their trends been assessed in relation to this species. Thus, though the areas that are protected in some form is substantial, the value of such protection and the size and disposition of the *Cacajao* populations within these areas, and the threats facing them there, have yet to be assessed in anything beyond the most cursory form (Barnett 2010).

This dissertation mainly concerned two genera in the subfamily Piteciindae, neotropical primates of the family Pitheciidae, *Cacajao,* and *Chiropotes*. The subsequent planned research will include the field behavioral ecology of *Cacajao calvus rubicundus*, which is one of the least studied South American primates. The main issue of this further work will be how seasonal fluctuations affect the ecology of feeding, the structure of activity and the home area of *C. c. rubicundus* in the Mamirauá Reserve, Amazon, Brazil. No detailed ecological studies have been performed on this subspecies. Table 3 lists the fieldwork published so far on this animal.

Table 3. An overview of previously published fieldwork on *C. c. rubicundus*.

Author	Year	Name	Journal
Vieira T ; Oliveira M ; Queiroz H ; Valsecchi J	2008.	New information on the distribution of *Cacajao calvus* in the Mamirauá Sustainable Development Reserve	*Uakari* 4: 41-51
Rylands AB	1984.	Primates and conservation areas in Brazilian Amazonia.	*Primate Eye* 24: 22-25
Ranft R; John JL	1983	Primates of the lower Rio Jurua in Brazil.	*Primate Conservation* 3: 18-19
Rylands A ; Mittermeier R	1983.	Parks, reserves and primate conservation in Brazilian Amazonia	*Oryx* 17: 78-87
Mittermeier RA ; Coimbra-Filho AF	1977	Primate conservation in Brazilian Amazonia.	In: *Primate Conservation*. Prince Rainier III G. H. Bourne, (eds.) New York: Academic Press. Pp. 117-166

None of the above involved detailed fieldwork, being reports of sightings made during primate surveys, with some notes on habitat use, group size, and occasional feeding observations. Thus, given the sparse state of current knowledge, future results will be important for understanding the behavioral ecology of this genus that remains one of the least studied among the Neotropical primates (Robinson et al. 2008). In the long term, there will be a contribution to a comparative perspective of the diversity of the behavioral responses of *C. c. rubicundus* to ecological fluctuations in the flooded forest.

The study area selected is located near the Community Porto Alves, on the Rio Ati Paraná do Aiupiá – Fig. 12. This area is located in the Mamirauá Sustainable Development Reserve and prior approval for IDSM research coordinator Mamirauá has already been obtained for this research.

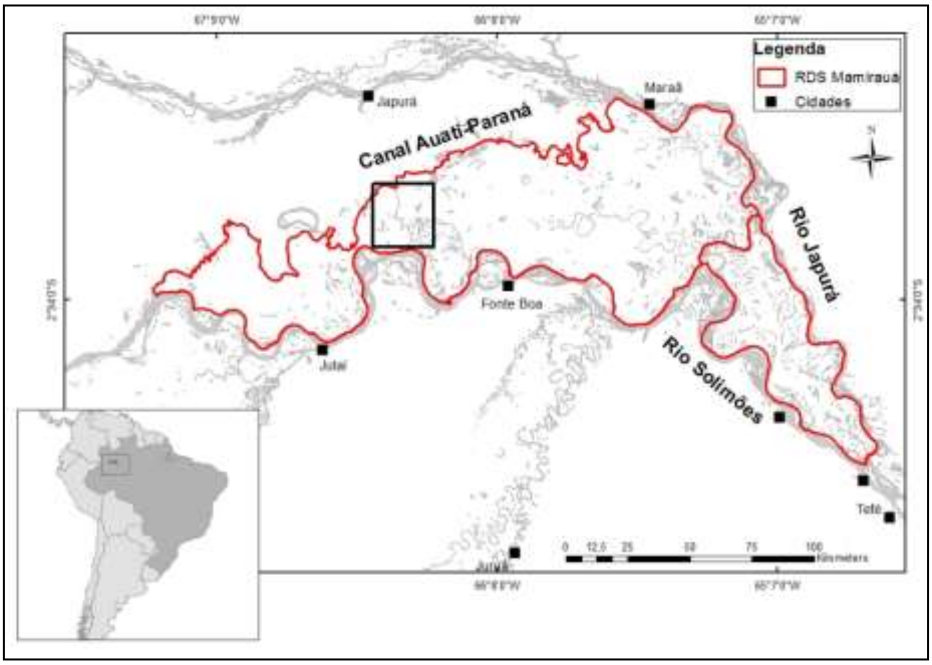


Figure 12. Field Site for future studies - Porto Alves Community, near Rio Ati Paraná do Aiupiá in SDR Mamiraua (Square).

List of the topics I plan to study concerning the ecology and behaviour of the Rio Solimões Red Uacari, *Cacajao calvus rubicundus.*

1. To conduct a floristic survey in the study area to understand the habitat structure and verify, through phenological data, the seasonal variation in availability of food resources.
2. To assess the influence of seasonal variation on the diet, activity pattern, the home range and daily travel of *C. c. rubicundus.*
3. Investigate whether the hardness of the fruit can be considered a criterion of choice of food.
4. To study the seasonal influence on the social organisation of *C. c. rubicundus*.

6 REFERENCES FOR THE INTRODUCTION, LITERATURE REVIEW, DISCUSSION AND FINAL PART

ARPA (Amazon Region Protected Areas Programme) – WWF. 2016. World Bank, retrieved 2016-08-07.

Anderson JR. 2000. Sleep-related behavioural adaptations in free-ranging anthropoid primates. *Sleep Medicine Reviews* 4: 355–373.

Adis J, Erwin TL, Battirola LD & Ketelhut SM. 2010. The importance of Amazonian floodplain forests for animal biodiversity: beetles in canopies of floodplain and upland forests. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (Eds) Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer Dordrecht Heidelberg. London. 615p.

Albert A, Savini T, Huynen MC. 2011. Sleeping site selection and presleep behavior in wild pigtailed macaques. *American Journal of Primatology* 73: 1222–1230.

Alvarenga GC, Ramalho EE, Baccaro FB, da Rocha DG, Ferreira-Ferreira J, Bobrowiec PED. 2018. Spatial patterns of medium and large size mammalassemblages in varzea and terra firme forests, Central Amazonia, Brazil. *PLoS ONE* 13(5): 1-19.

Arnold, K., Zuberbühler, K. 2006. The alarm-calling system of adult male putty-nosed monkeys, *Cercopithecus nictitans martini*. *Animal Behaviour* 72: 643-653

Aureli F, Schaffner CM, Boesch Ch, Bearder SK, Call J, Chapman CA, Connor R, Fiore AD, Dunbar RIM, Henzi SP, Holekamp K, Korstjens AH, Layton R, Lee P, Lehmann J, Manson JH, Ramos-Fernandez G, Strier KB, van Schaik CP. 2008. Fission-fusion dynamics: new research frameworks. *Current Anthropology* 49: 627-654.

Ayres JM. 1986. Uakaris and Amazonian flooded forest. PhD Thesis. University of Cambridge, UK. 338p.

Barnett AA. 2005. *Cacajao melanocephalus*. *Mammalian Species* 776: 1-6.

Barnett AA. 2010. Diet, habitat use and conservation ecology of the golden-backed uacari, *Cacajao melanocephalus ouakary*, in Jaú National Park, Amazonian Brazil [dissertation]. London (UK): Roehampton University. 456 p.

Barnett AA, Boyle SA, Norconk MM, Plminteri S, Santos RR, Veiga LM, Alvim HG, Bowler M, Chism J, Di Fiore A, Fernandez-Doque E, Guimara ACP, Harrison-Levine A, Haugaasen T, Lehman S, Mackinnon KC, De Melo FR, Moreira LS, Moura VS, Phillips CR, Pinto LP, Port-Carvalho M, Setz EZF, Shaffer Ch, Da Silva LR, Da Silva S, Soares RF, Thompson CL, Vieira TM, Vreedzaam A, Walker-Pacheco SE, Spironello WR, Maclarnon A, Ferrari S. 2012a. Terrestrial Activity in Pitheciins (*Cacajao, Chiropotes,* and *Pithecia*). *American Journal of Primatology* 74: 1106–1127.

Barnett AA, Almeida T, Spironello WR, Sousa Silva W, MacLarnon A & Ross C. 2012b. Terrestrial foraging by *Cacajao melanocephalus ouakary* (Primates) in Amazonian Brazil: is choice of seed patch size and position related to predation-risk? *Folia Primatololgica* 83: 126-139.

Barnett AA, Boyle SA, Pinto LP, Lourenço WC, Almeida T, Silva WS, Ronchi-Teles B, Bezerra BM, Ross C, MacLarnon A & Spironello WR. 2012c. Primary seed dispersal by three Neotropical seed-predating primates (*Cacajao melanocephalus ouakary, Chiropotes chiropotes* and *Chiropotes albinasus*). *Journal of Tropical Ecology* 28: 543-555.

Barnett AA, Pinto LP, Bicca-Marques JC, Ferrari SF, Gordo M, Guedes PG, Lopes MA, Opazo JC, Port-Carvalho M, Dos Santos RR, Soares RF, Spironello WR, Veiga LM, Vieira TM & Boyle SA. 2012. A Proposal for the common names of *Chiropotes* (Pitheciinae: Primates). *Zootaxa* 3507: 79–83.

Barnett AA, Ronchi-Teles B, Almeida T, Deveny A, Schiel-Baracuhy V, Souza-Silva W, Spironello W, Ross & A. MacLarnon C. 2013. Arthropod Predation by a Specialist Seed Predator, the Golden-backed Uacari (*Cacajao melanocephalus ouakary*, Pitheciidae) in Brazilian Amazonia. *International Journal of Primatology* 34: 470-485.

Barnett AA & Jucá T. 2018. Primates of igapó forests. Ch.8: IN: Randall W Myster (editor), Igapó: blackwater flooded forests of the Amazon. Springer-Switzerland. pp. 121-133. ISBN 978-3-319-90121-3

Barnett AA, Tománek P, Todd LM. 2018a. A ecologia do uacari-de-costas-douradas (Cacajao ouakary) (Pitheciidae) na bacia Amazônica. IN Bernardo Urbani, Martín Kowalewski, Rogério Grasseto Teixeira da Cunha, Stella de la Torre & Liliana Cortés-Ortiz (editors), *La primatología en Latinoamérica 2 – A primatologia na America Latina 2*. Instituto Venezolano de Investigacoes Cientificas, Caracas, pp 219-228. ISBN 9789-8026-1185-0

Barnett AA, Tománek P, Todd LM. 2018b. A ecologia do uacari-de-costas-douradas (Cacajao ouakary) (Pitheciidae) na bacia Amazônica. IN Bernardo Urbani, Martín Kowalewski, Rogério Grasseto Teixeira da Cunha, Stella de la Torre & Liliana Cortés-Ortiz (editors), *La primatología en Latinoamérica 2 – A primatologia na America Latina 2*. Instituto Venezolano de Investigacoes Cientificas, Caracas, pp 219-228. ISBN 9789-8026-1185-0

Barnett AA, de Oliveira T, Soares da Silva RF, de Albuquerque Teixeira S, Tomanek P, Todd LM, Boyle SA. 2018b. Honest error, precaution or alertness advertisement? Reactions to vertebrate pseudopredators in red-nosed cuxiús (*Chiropotes albinasus*), a high-canopy neotropical primate. *Ethology* 124(3): 177-187. https://doi.org/10.1111/eth.12721

Barnett AA. 2019. Primates in Amazonian flooded forests: a review. Ch. 27 IN Katarzyna Nowak, Adrian A Barnett & Ikki Matsuda (editors), Primates in Flooded Habitats: Ecology and Conservation. Cambridge University Press, ISBN 978-1-107-13431-7 (print);pp. 217-225. https://doi.org/10.1017/9781316466780.028

Bateson M. 2002. Recent advances in our understanding of risk-sensitive foraging preferences. *Proceedings of the Nutrition Society* 61: 509-516.

Bertuol F. 2015a. *Testando limites específicos dos uakaris pretos sensu Hershkovitz (1987) (Pitheciidae: Primates).* Masters Thesis, Instituto Nacional de Pesquisas da Amazônia (INPA), Brazil. 44 pp.

Bianchi RDC & Mendes SL. 2007. Ocelot (*Leopardus pardalis*) predation on primates in Caratinga Biological Station, Southeast Brazil. *American Journal of Primatology 69:* 1173–1178. https://doi.org/10.1002/(ISSN)1098-2345

Boubli J. 1999. Feeding ecology of black-headed uacaris (*Cacajao melanocephalus melanocephalus*) in Pico da Neblina National Park, Brazil. *International Journal of Primatology* 20:719–749.

Boubli J. 2020. *Cacajao melanocephalus*. *The IUCN Red List of Threatened Species* 2020: e.T160875418A160876028. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T160875418A160876028.en

Boubli JP, Silva MNF, Amado MV, Herbk T, Pontual FB & Farias I. 2008. A taxonomic reassessment of black uakari monkey, *Cacajao melanocephalus*, Humboldt (1811), with the description of two new species. *International Journal of Primatology* 29: 723–741.

Boubli JP & Tokuda M. 2008. Socioecology of black uakari monkeys, *Cacajao hosomi*, in Pico da Neblina National Park, Brazil: the role of the peculiar spatial-temporal distribution of resources in the Neblina Forests. *Primate Report* 75: 3–10.

Boubli JP & Ditchfield AD. 2000. The Time of Divergence between the Two Species of Uacari Monkeys: *Cacajao calvus* and *Cacajao melanocephalus*. *Folia Primatologica* 71: 387-91.

Bowler M & Bodmer R. 2009. Social behavior in fission–fusion groups of red uakari monkeys (*Cacajao calvus ucayalii*). *American Journal of Primatology* 71: 976–987.

Bowler M & Bodmer R. 2011. Diet and food choice in Peruvian red uakaris (*Cacajao calvus ucayalii*): selective or opportunistic seed predation? *International Journal of Primatology* 32: 1109–1122.

Bowler M, Knogge C, Heymann EW & Zinner D. 2012. Multilevel societies in New World Primates? Flexibility may characterize the organization of Peruvian red uakaris (*Cacajao calvus ucayali*i). *International Journal of Primatology 33*: 1110–1124.

Cardoso NA; Valsecchi J; Vieira T & Queiroz HL. 2014. New records and range expansion of the white bald uakari (*Cacajao calvus calvus*, I. Geoffroy, 1847) in Central Brazilian Amazonia. *Primates* 55: 199–206.

Caro T. 2005. Antipredator defenses in birds and mammals. University of Chicago Press.

Clark CW & Dukas R. 1994. Balancing foraging and antipredator demands: an advantage of sociality. *American Naturalist* 144: 542-548.

Correa SB, Winemiller KO, Lopez-Fernandez H & Galetti M. 2007. Evolutionary perspectives on seed consumption and dispersal by fishes. *Bioscience* 57: 748-756.

Correa SB & Winemiller KO. 2014. Niche partitioning among frugivorous fishes in response to fluctuating resources in the Amazonian floodplain forest. *Ecology* 95: 210-224.

Cunningham EP & Janson CH. 2006. *Pithecia pithecia*'s behavioral response to decreasing fruit abundance. *American Journal of Primatology* 68: 491–497.

Davies NB, Krebs JR & West SA. 2012. An introduction to behavioural ecology. John Wiley & Sons.

Dawkins R & Krebs JR. 1979. Arms races between and within species. *Proceedings of the Royal Society of London. Series B. Biological Sciences* 205: 489-511.

Defler TR. 2001. *Cacajao melanocephalus ouakary* densities on the lower Apaporis river, Colombian Amazon *Primate Report* 61: 31-36.

Di Fiore A, Link A & Dew JL. 2008. Diets of wild spider monkeys. In: Campbell CJ (Ed) Spider monkeys: behavior, ecology and evolution of the genus *Ateles*. Cambridge University Press, Cambridge. 410p.

Dias da Silva RHP, Castro Sa MJ, Baccaro FB, Tománek P, Barnett AA. 2020. Juggling options: Manipulation ease determines primate optimal fruit-size choice. *Biotropica* 52(6): 1275-1285. https://doi.org/10.1111/btp.12835.

Ducheminsky N, Henzi SP, Barrett L. 2014. Responses of vervet monkeys in large troops to terrestrial and aerial predator alarm calls. *Behavioral Ecology* 25: 1474-1484.

Eeley HAC, Lawes MJ. 1999. Large-scale patterns of species richness and species range size in anthropoid primates. In: Fleagle JG, Janson CH, Reed KE, editors. Primate communities. Cambridge: Cambridge University Press. p. 191–219.

Ellison PT. 2003. Energetics and reproductive effort. *American Journal of Human Biology* 15: 342-351.

Ellison G, Wolfenden A, Kahana L, Kisingo A, Jamieson J, Jones M, Bettridge C. 2019. Sleeping site selection in the nocturnal northern lesser galago (*Galago senegalensis*) supports antipredator and thermoregulatory hypotheses. *International Journal of Primatology* 40: 276–296.

Estrada A. 2009. Primate Conservation in South America: The~Human and Ecological Dimensions of the Problem. In book South American Primates, Springer Science+Business Media. p. 463-505. DOI: 10.1007/978-0-387-78705-3_18.

Estrada A, Garber AP, Rylands AB, Roos C, Fernandez-Duque E, Di Fiore A, Nekaris KA-I, Nijman V, Heymann EW, Lambert JE, Rovero F, Barelli C, Setchell JM, Gillespie TR, Mittermeier RA, Arregoitia LV, de Guinea M, Gouveia S, Dobrovolski R, Shanee S, Shanee N, Boyle SA, Fuentes A, MacKinnon KC, Amato KR, Meyer

ALS, Wich S, Sussman RW, Pan R, Kone I, Li B. 2017. Impending extinction crisis of the world's primates: Why primates matter. *Science Advances* 3, e1600946.

Fedurek P, Slocombe KE. 2011. Primate vocal communication: a useful tool for understanding human speech and language evolution? *Human Biology* 83: 153-173.

Fernandez-Duque E, Di Fiore A, Huck M. 2012. The behavior, ecology, and social evolution of New World monkeys. In: The Evolution of Primate Societies (Mitani J, Call J, Kappeler P, Palombit R, & Silk J, eds).pp. 43-64. Chicago: University of Chicago Press.

Ferrari SF, Guedes PG, Figueiredo-Ready WM & AA Barnett. 2014. Reconsidering the taxonomy of the black-faced uacaris, *Cacajao melanocephalus* group (Mammalia: Pitheciidae), from the northern Amazon Basin. *Zootaxa* 3866: 353-370.

Ferreira-Ferreira, J., Silva, T.S.F., Streher, A.S., Affonso, A.G., Furtado, L.F.A., Forsberg, B.R., Valsecchi, J., Queiroz, H.L., Novo, E.M.L.M. 2015. Combining ALOS/PALSAR derived vegetation structure and inundation patterns to characterize major vegetation types in the Mamirauá Sustainable Development Reserve, Central Amazon floodplain, Brazil. *Wetlands Ecology and Management* 23: 41–59.

Ferreira LV, Parolin P. 2007. Tree phenology in central Amazonian floodplain forests: effects of water level fluctuation and precipitation at community and population level. *Pesquisas Botánica* 58: 139-156.

Figueiredo-Ready WB, Schneider H, Ferrari SF, Harada ML, DaSilva JMC, Silva-Jr JS & Bates JM. 2013. A molecular phylogeography of the uacaris (*Cacajao*). Pp. 23–30 in: Veiga LM, Barnett AA, Ferrari S & Norconk MA (eds) evolutionary Biology and Conservation of Titis, Sakis and Uacaris. Cambridge University Press, Cambridge.

Fortes VB & Bicca-Marques JC. 2005. Ecologia e comportamento de primatas: métodos de estudo de campo. Caderno La Salle XI 2 (1): 207–218.

Garber PA. 1987. Foraging strategies living primates. *Annual Review of Anthropology* 16: 339–364.

Grove, M., 2012. Space, time, and group size: a model of constraints on primate social foraging. *Animal Behaviour* 83: 411-419

Gursky-Doyen S. & Nekaris KAI (editor). 2007. Primate Anti-predator Strategies. Springer. Developments in Primatology: Progress and Prospects series. 393 p. ISBN-13: 978-0387348070

Haugaasen T & Peres CA. 2005. Primate assemblage structure in Amazonian flooded and unflooded forests. *International Journal of Primatology* 67: 243–258.

Hershkovitz P. 1987. Uakaries. New world monkeys of the genus *Cacajao* (Cebidae, Platyrrhini): a preliminary taxonomic review with a description of a new subspecies. *American Journal of Primatology* 12: 1–53.

Hess LL, Melack JM, Novo EMLM, Barbosa CCF & Gastil M. 2003. Dual-season mapping of wetland inundation and vegetation for the central Amazon basin, *Remote Sensing & Environment* 87: 404–428.

Heymann EW. 1992. The red uakari (*Cacajao calvus ucayalii*): some field observations and speculations on a little-known species. *Primate Eye* 47: 6–7.

IUCN 2021. The IUCN Red List of Threatened Species. Version 2020-3. https://www.iucnredlist.org

Isbell LA. 1994. Predation on primates: Ecological patterns and evolu- tionary consequences. *Evolutionary Anthropology, 3,* 61–71.

James S, Donato D, Pouliquen JF, Ruiz-García M, Lavergne A, Lacoste V. 2018. DNA polymerase sequences of New World monkey cytomegaloviruses: another molecular marker with which to infer Platyrrhini systematics. *Journal of Virology* 92:e00980-18.

Jordan CF, Cuevas E, Medina E. 2013. NPP Tropical Forest: San Carlos de Rio Negro, Venezuela, 1975-1984, R1. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A. doi:10.3334/ORNLDAAC/479.

Jucá T, Boyle S, Cavalcanti G, Cavalcante T, Tomanek P, Clemente S, de Oliveira T, Barnett AA. 2020. Being hunted high and low: do differences in nocturnal sleeping and diurnal resting sites of howler monkeys (*Alouatta nigerrima* and *Alouatta discolor*) reflect safety from attack by different types of predator ? *Biological Journal of the Linnean Society* 131, 203–219.

Junk WJ. 2013. The Central Amazon Floodplain: Ecology of a Pulsing System. Springer Science & Business Media. 528p.

Junk WJ, Piedade MTF, Wittmann F, Schongart J, Parolin P. 2010. Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Springer Science & Business Media. 618p.

Junk WJ, Piedade MTFP, Schöngart J & Wittmann F. 2012. A classification of major natural habitats of Amazonian white-water river floodplains (várzeas). *Wetlands Ecology and Management* 1:1–14.

Kinzey WG & Norconk MA. 1990. Hardness as a basis of fruit choice in two sympatric primates. *American Journal of Physical Anthropology* 81: 5–15.

Kinzey WG. 1992. Dietary and dental adaptations in the Pitheciinae. *American Journal of Physical Anthropology* 88: 499-514.

Kinzey WG & Norconk MA. 1993. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *International Journal of Primatology* 14: 207–227.

Kramer KL & Ellison PT. 2010. Pooled energy budgets: Resituating human energy-allocation trade-offs. *Evolutionary Anthropology* 19: 136-147.

Ledogar JA, Winchester JM, Clair EMSt, Boyer DM. 2013. Diet and Dental Topography in Pitheciine Seed Predators. *American Journal of Physical Anthropology* 150:107–121

Ledogar JA, Luk THY, Perry JMG, Neaux D, Wroe S. 2018. Biting mechanics and niche separation in a specialized clade of primate seed predators. *PLoS ONE* 13(1): e0190689.

Libório RA, Martins MM. 2013. Body size in predator–prey interactions: an investigation of Neotropical primates and their predators. *Studies on Neotropical Fauna and Environment* 48:81-87.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619-640.

MacArthur RH & Levins R. 1967. The limiting similarity, convergence and divergence of coexisting species. *American Naturalist* 101: 377–385.

Matsuda I, Tuuga A, Akiyama Y, Higashi S. 2008a. Selection of river crossing location and sleeping site by proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. *American Journal of Primatology* 70: 1097–1101.

Markham, A.C., Gesquiere, L.R.. 2017. Costs and benefits of group living in primates: an energetic perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372: 20160239

Marsh LK. 2014. A taxonomic revision of the saki monkeys, *Pithecia* Desmarest, 1804. *Neotropical Primates* 21: 1–163.

Melack JM, Hess LL. 2010. Remote Sensing of the Distribution and Extent of Wetlands in the Amazon Basin. In: Junk W., Piedade M., Wittmann F., Schöngart J., Parolin P. (eds) Amazonian Floodplain Forests. Ecological Studies (Analysis and Synthesis), vol 210. Springer, Dordrecht. https://doi.org/10.1007/978-90-481-8725-6_3.

Miranda JMD, Bernardi IP, Moro-Rios RF, Passos FC. 2006. Antipredator behavior of brown howlers attacked by black hawk-eagle in southern Brazil. *International Journal of Primatology* 27: 1097–1101.

Monteza-Moreno CM, Crofoot MC, Grote MN, Jansen PA. 2020. Increased terrestriality in a Neotropical primate living on islands with reduced predation risk. *Journal of Human Evolution* 143. 102768

Mourthé I, Barnett AA. 2014. Crying tapir: the functionality of errors and accuracy in predator recognition in two Neotropical high-canopy primates. *Folia Primatologica* 85: 379-398.

Norconk MA. 2007. Sakis, uakaris, and titi monkeys—behavioral diversity in a radiation of primate seed predators. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M, Bearder SK (eds) Primates in perspective. Oxford University Press, New York, pp 123–138.

Norconk MA & Setz EZ. 2013. Ecology and behavior of saki monkeys (genus *Pithecia*). In Veiga LM, Barnett AA, Ferrari SF, Norconk MA (Eds.), Evolutionary Biology and Conservation of Titis, Sakis and Uacaris. Cambridge: Cambridge University Press, pp. 262-271.

Palminteri S, Powell GV, Peres CA. 2012. Advantages of granivory in seasonal environments: feeding ecology of an arboreal seed predator in Amazonian forests. Oikos 121(11): 1896-1904.

Parolin P. 2001. Seed germination and early establishment of 12 tree species from nutrient-rich and nutrient-poor Central Amazonian floodplains. *Aquatic Botany* 1477: 1 –15.

Parolin P, Armbruester N, Wittmann F. 2002. A review of tree phenology in Central Amazonian floodplains. *Pesquisas Bôtanica* 52: 195–222.

Peel MC, Finlayson BL & McMahon TA. 2007. Updated world map of the Koppen-Geiger climate classification. *Hydrology and Earth Systems Science* 11: 1633–1644.

Peres CA. 1997. Primate community structure at twenty western Amazonian flooded and unflooded forests. *Journal of Tropical Ecology* 13: 381–405.

Peres CA, Janson CH. 1999. Species coexistence, distribution and environmental determinants of neotropical primate richness: a community-level zoogeographic analysis. In: Fleagle JG, Janson CH, Reed KE, editors. Primate communities. Cambridge: Cambridge University Press. p 55–74.

Pinto LP, Barnett AA, Bezerra BM, Boubli JP, Bowler M, Cardoso NA, Caselli CB, Rodríguez MJO, Santos RR, Setz EZF & Veiga LM. 2013. Why we know so little: the challenges of fieldwork on the Pitheciids. In: Veiga, LM, Barnett AA, Ferrari SF & Norconk MA (eds.). Evolutionary Biology and Conservation of Titis, Sakis and Uacaris Cambridge University Press: Cambridge, UK, pp. 145-150.

Prance GT. 1979. Notes on the vegetation types of Amazonia III – the terminology of Amazonian forest types subject to inundation. *Brittonia* 31: 26-38.

Pinto LP, Soares da Silva RF, de Oliveira ACM, Barnett AA, †Veiga LM & Setz EZF. 2018. Diet and foraging behavior of *Chiropotes albinasus* (I. Geoffoy & Deville 1848) at two sites in south-eastern Brazilian Amazonia. IN In Bernardo Urbani, Martín Kowalewski, Rogério Grasseto Teixeira da Cunha. Stella de la Torre & Liliana Cortés-Ortiz (editors), La primatología en Latinoamérica 2 – A primatologia na America Latina 2. Instituto Venezolano de Investigacoes Cientificas, Caracas, pp. 199-218.

Plante S, Colcher F, Calme S. 2014. Foraging strategy of a neotropical primate: how intrinsic and extrinsic actors influence destination and residence time. *Journal of Animal Ecology* 83: 116–125.

Pontzer, H., Raichlen, D. A., Gordon, A. D., Schroepfer-Walker, K. K., Hare, B., O'Neill, M. C., Muldoon, K. M., Dunsworth, H. M., Wood, B. M., Isler, K., Burkart, J. 2014. Primate energy expenditure and life history. *Proceedings of the National Academy of Sciences* 111:1433-1437

Rylands AB, Mittermeier RA. 2009. The Diversity of the New World Primates (Platyrrhini): An Annotated Taxonomy. In: Garber P.A., Estrada A., Bicca-Marques J.C., Heymann E.W., Strier K.B. (eds) South American Primates. Developments in Primatology: Progress and Prospects. Springer, New York, NY. https://doi.org/10.1007/978-0-387-78705-3_2

Robinson JG, Wright PC & Kinzey WG. 2008. Monogamous Cebids and Their Relatives: Intergroup Calls and Spacing. In Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW. Primate Societies. University of Chicago Press, pp. 44.

Rosenberger AL. 2020. New world monkeys, The Evolutionary Odyssey. Princeton University Press, ISBN: 978-0-691-14364-4

Shaffer C. 2012. Ranging behavior, group cohesiveness, and patch use in northern bearded sakis (*Chiropotes sagulatus*) in Guyana [dissertation]. Washington University in St. Louis. 332 p.

Shaffer, C. A. 2013. Ecological correlates of ranging behavior in bearded sakis (*Chiropotes sagulatus*) in a continuous forest in Guyana. *International Journal of Primatology* 34: 515-532.

Sioli H. 1956. As águas da Região do Alto Rio Negro. *Bol. Tec. do Ins. Agron. do Norte* 32:117-155.

Studd EK, Boutin S, McAdam AG, Krebs CJ & Humphries MM. 2015. Predators, energetics and fitness drive neonatal reproductive failure in red squirrels. *Journal of Animal Ecology* 84: 249-259.

Terborgh J & Janson CH. 1986. The socioecology of primate groups. *Annual Review on Ecology and Systematics* 17: 111-135.

Thompson CL, Williams SH, Glander KE, Teaford MF, Vinyard CJ. 2014. Body temperature and thermal environment in a generalized arboreal anthropoid, wild mantled howling monkeys (*Alouatta palliata*). *American Journal of Physical Anthropology* 154: 1–10.

Thompson CL, Williams SH, Glander KE, Vinyard CJ. 2016. Measuring microhabitat temperature in arboreal primates: a comparison of on-animal and stationary approaches. *International Journal of Primatology* 37: 495–517.

Tomanek P, Mourthe I, Boyle S, Barnett AA. 2020. Calls for concern: Matching alarm response levels to threat intensities in three Neotropical Primates. *Acta Oecologica* 109: 1-7.

Tomasello M, Cal J, Hare B. 1998. Five primate species follow the visual gaze of conspecifics. *Animal Behaviour* 55:1063-1069.

Três Unidades de Conservação de Rondônia são inseridas no programa Áreas Protegidas. 2016. *Jornal O Nortão*, retrieved 2016-08-07.

Veiga LM, Bowler M, Silva Jr J, Queiroz H, Boubli J & Rylands AB. 2020. *Cacajao calvus*. *The IUCN Red List of Threatened Species* 2020: e.T3416A17975917. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T3416A17975917.en.

Vieira T, Oliveira M, Queiroz H & Valsecchi J. 2008. Novas informações sobre a distribuição de *Cacajao calvus* na Reserva de Desenvolvimento Sustentável Mamirauá. *Uakari* 4:41–51.

Vogel E, Kivai S & Alavi S. 2017. Foraging Strategies. In book: The International Encyclopedia of Primatology. ISBN: 9780470673379. DOI: 10.1002/9781119179313.wbprim0336.

Voirin JB, Kays R, Lowman MD & Wikelski M. 2009. Evidence for three-toed sloth (*Bradypus variegatus*) predation by spectacled owl (*Pulsatrix perspicillata*). *Edentata* 10, 15-20.