When food fights back: Cebid primate strategies of larval paper wasp predation and the high-energy yield of high-risk foraging.

1   **When food fights back: Cebid primate strategies of larval paper wasp predation and**
2   **the high-energy yield of high-risk foraging.**

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1   **ABSTRACT:**

2   Optimal foraging theory predicts that well-defended potential foods should be

3   exploited only when energy pay-offs are great. Although stinging hymenopteran nests

4   are both well-defended and predated by primates, their larvae's energy yields rarely

5   have been calculated, and predation-linked foraging behaviors by primates infrequently

6   documented. Based on 58 opportunistic observations of primates raiding wasp nests

7   for larvae, we calculated energetic yields of low- and high-risk wasp nest predation for

8   *Cebus albifrons, Saimiri collinsi, S. sciureus* and *Sapajus apella,* and tested predictions

9   derived from optimal foraging theory. We recorded how nests were processed and by

10   which age-sex classes, eaten nest fragment sizes, number of occupied and empty cells,

11   and nest occupancy patterns (percent larvae/pupae, eggs, empty cells). Basal metabolic

12   rate (BMR) calculations showed energetic yields from 15 mins foraging on low-risk

13   nests (*Polybia quadricincta*) would meet energy needed to sustain adult female and

14   male *C. albifrons* BMR for 4.9 and 4.5 h, respectively; yields from high-risk

15   (*Chartergus artifex*) nests for 6.5 and 6.2 h; *Mischocyttarus* sp. nest yields (low risk,

16   but mimetically-resembling other wasps) would meet *Saimiri collinsi* BMR for 2.9 h

17   (female) and 2.3 h (male), and 2.6 h and 2.1 h, for the slightly larger *S. sciureus*,

18   respectively. The *Chartergus* energetic-yield value is nearly 20% of a 36g chocolate

19   bar (741 kJ). Our data provide quantitative support for the common assertion that wasp

20   larvae and pupae are high-yield foods for primates. As predicted by optimal foraging,

21   energetic yield is sufficient to offset the risk and pain of being stung. (249 words)

22

23   **Running header:** primate wasp nest predation energetics

2

2

26   "*Petruchio:* Come, come, you wasp; i' faith, you are too angry.

27   *Katherine*: If I be waspish, best beware my sting.

28   *Petruchio*: Who knows not where a wasp does wear his sting? In his tail."

29   William Shakespeare, *The Taming of the Shrew*

30

31   **INTRODUCTION**

32   Optimal foraging theory aims to explain how animals choose dietary items by balancing

33   energy gained versus time and energy expended in obtaining it (Sih & Christensen 2001;

34   Stephens *et al*. 2007). The optimal prey choice model predicts that more profitable foods

35   will have the greatest ratio of energy (or a nutritional variable to cost of obtaining the

36   item (Schoener 1971; Krebs *et al*. 1978; Stephens & Krebs 1986), with natural selection

37   favoring the highest rate of energy intake. Consequently, well-protected or strongly-

38   defended potential foods should be exploited only when energetic pay-offs are great

39   (Bateson 2002). While optimal foraging under such conditions has been studied in a

40   variety of taxa (Werner & Hall, 1974; Lemon 1991; Caro 1994; Sih & Christensen 2001),

41   it has been little studied in primates (but see Sayers *et al*. 2010), and mostly when diet

42   item exploitation poses little inherent risk (Altmann 1998; Nakagawa 1989). High-risk

43   foraging situations (e.g., exposure to predation, aggression from feeding competitors,

44   variance in food intake) adhere closely to classical optimal foraging scenarios (Kacelnik

45   & El Mounden 2013; Muckhernjee & Heithaus 2013). Additional risks may occur when

46   the food itself is dangerous and capable of self-defence (Muckhernjee & Heithaus 2013).

47   Although there are studies that have calculated the nutritional and energetic importance

48   of invertebrates to primates (Bryer *et al*. 2015; Bergstrom *et al*. 2019), aside from primate

49   hunting by chimpanzees (Gilby & Wrangham 2007), few have focused on what shapes

50   foraging decisions when food consists of animal prey capable of instant active defence.

51   While predation on vertebrates is relatively rare in non-human primates (Butynski

52 1982; Rose 1997; Heymann *et al.* 2000), eating arthropods is common (Janson & Boinski

53 1992; Nekaris & Bearder 2007; Bogart & Pruetz 2011; Rothman *et al.* 2014). Many

54 neotropical primates spend more time foraging for arthropods than for fruit (e.g.,

55 Terborgh 1983; Stone 2007a). Faunivores face the challenge of catching and processing

56 prey, and many potential food items are well-protected physically (e.g., urticaceous

57 caterpillars; Trebouet *et al.* 2018) and chemically (e.g., noxious beetles, millipedes;

58 Eisner & Meinward 1966; Eisner & Aneshansely 1999). Others have behavioral defences

59 and counter-attack predators, so posing a risk of pain or injury (Edmunds 1974;

60 Mukherjee & Heithaus 2013) or are cryptic and difficult to locate.

61   Arthropods are generally considered high-energy-yielding food items (McGrew

62 2001; Raubenheimer & Rothman 2013), rich in fat and protein (26-44% fat, 12-65%

63 protein by wet weight: Nakagawa 2003; McCabe & Fedigan 2007; Ghaly & Alkoaik

64 2009). While energetic values of insects are often calculated in foraging studies of birds

65 and bats (e.g., Catterall 1985; Encarnação & Dietz 2016), studies reporting primate

66 insectivory often mention the prey's high protein and/or fat content without providing its

67 overall energetic value (Milton & Nessimian 1984; Srivastava 1991; Deblauwe 2009).

68 When such data are provided, the prey are non-aggressive, non-stinging forms (such as

69 homoptera, orthoptera, lepidopteran larvae or gall-forming insects: Bryer et al. 2015;

70 O´Malley & Power 2014), or the studies do not identify the taxa involved and produce a

71 summed energetic value (´insects´: McCabe & Fedigan 2007). This information gap is

72 important to fill, since quantitative estimates of primate energetic needs and prey yield

73 are needed to fully understand how primates balance foraging risks related to injury or

74 pain. Currently, when species are potentially capable of aggressive defence, this aspect is

75 considered secondary to energetic gains (e.g., O´Malley & Power 2012, 2014 for

76 chimpanzees ingesting *Dorylus* army ants).

77   While many insect taxa eaten regularly by primates may be gathered safely (e.g.,

78 orthopterans: Barnett *et al*. 2013; Nickle & Heymann 1996; Stone 2007a: coccid scale

79 insects, Srivastava 1991; Struhsaker, 2010), others, such as Hymenoptera, possess

80 formidable aggressive defences: many social polistine paper wasps (Hymenoptera

81 Vespidae, Polistinae), for example, possess powerful stings (Gobbi & Zucchi 1985; Nagy

82 *et al.* 2007), and can be very aggressive (Judd 1998; Nonacs *et al.* 2004). Despite such

83 defences, a variety of neotropical vertebrates, including primates, feed on them and their

84 larvae (e.g., *Ateles chamek*: Felton *et al.* 2009; *A. marginatus*: dos Santos-Barnett *et al.*

85 2022; *Cacajao ouakary*: Barnett 2005; *Cebus capucinus*: Joyce 1993; *Cebus kaapori*: de

86 Oliveira *et al.* 2014; *Saimiri collinsi*: Stone 2006; *Saguinus geoffroyi*: Madden *et al.* 2010;

87 *Sapajus apella*: Izawa 1979), and wasp larvae may be either an important fallback food

88 (*sensu* Lambert 2010; e.g., Galetti & Pedroni 1994), or one component of a trophically-

89 diverse diet (e.g., Terborgh 1983; Stone 2007a). Furthermore, wasps and their larvae are

90 richer in fats and proteins than fruits (Redford *et al*. 1984; Rothman *et al.* 2014). They

91 also form high-energy spatially-clumped resources, which may add to their attractiveness:

92 wasp larvae energetic-yields appear similar to those of insects generally eaten by tropical

93 primates (e.g., Orthoptera, Coleoptera; O'Malley & Power 2014; Rothman *et al.* 2014),

94 but the clustered nature of in-nest wasp larvae provides rapid energetic gain, because there

95 is minimal search-time between prey items, which have few opportunities for escape or

96 concealment (Bryer *et al.* 2015),

97   Predation of a wasp nest is risky for primates. For example, Fragaszy *et al.* (2004:

98 49) describe how *C. capucinus* "grab a paper wasp nest and run with it, with the wasps

99 flying after the thief, stinging face and hands for tens of meters as the monkey flees".

100   However, how individuals process wasp nests to extract larvae has rarely been reported

101   in detail. In the current study, we collate observations of wasp nest predation by *Cebus*

102   *albifrons*, *Saimiri collinsi*, *S. sciureus* and *Sapajus apella* (Cebidae) at nests with

103   different risk-settings, i.e. low-risk nests, high-risk nests, and a case of mimicry, and

104   quantify the energetic yield of wasp nest predation by *C. albifrons*, *S. collinsi,* and *S.*

105   *sciureus*. The behaviours associated with the observed predation events are described in

106   Appendix A, energy calculations in Appendix Bi and ii. Based on an optimal prey

107   choice framework (Krebs & McCleery 1984; Hill *et al.* 1987), we predict that: (1)

108   energetic rewards of prey will be high to select for such high-risk foraging; (2)

109   individuals will employ handling strategies to minimize risk of prey attack (Perry &

110   Jiménez 2007); (3) as such activities are risky and require speed, dexterity, and practice

111   (Boinski & Fragaszy 1989; Fragaszy & Adam-Curtis 1997), they will be generally

112   conducted by adults, particularly since juveniles of many primate genera tend to be risk-

113   averse (Fairbanks 1993; Janson 1993; O´Malley & Fedigan 2005; Stone 2007b; Schmidt

114   2010; O´Mara 2015; Knott & DeLong 2017); and (4) following Clark (1994), risky

115   foraging will be less common in females, which have a larger reproductive asset than

116   males, especially as males generally exhibit risk-taking behaviors more frequently

117   (Reader & Laland 2001; Westergaard *et al.* 2003).

118

119   **METHODS**

120   **Study Species, Primates**

121   Members of the genera *Cebus, Sapajus,* and *Saimiri* are all highly faunivorous (Izawa

122   1979; Mallott *et al.* 2017; Paim *et al.* 2017), with *Saimiri collinsi* (Stone 2007a) and

123   *Saimiri sciureus* (Boinski *et al.* 2002) eating more insects than fruit. Members of these

124   genera are extremely dexterous and capable of fine digital manipulation of small and

125 fragile items (Janson & Boinski 1992; Fragaszy *et al*. 2004). Adult body size ranges from

126 0.6-1 kg (*Saimiri*) to 3-4 kg (*Cebus*) and 2-5 kg (*Sapajus*) (Smith & Jungers 1997).

127 We recorded data during general and species-focused primate studies, as well as from *ad*

128 *hoc* encounters (Appendix A). Observed group sizes ranged from 8-50 individuals (both

129 *Saimiri* spp.), of which approximately 50% were juveniles, and 6-19 (*Cebus*) and 4-9

130 (*Sapajus*), where approximately one-third were juveniles (defined as pre-reproductive

131 individuals, recognizable in a group by their smaller body mass and differently-shaped

132 heads: Stone 2006). For all species, juveniles were recently weaned; weaning occurs at 3

133 mo (*C. albifrons*), 8 mo (*Saimiri*), and 10-15 mo (*Sapajus*). After 10 and 8 mo,

134 respectively, individual *C. albifrons* and *S. collinsi* fully forage for themselves, although

135 still accompanying their mother (*C. albifrons*, Fragaszy & Adams-Curtis 1997; *S. apella*,

136 Gunst *et al*. 2008; Verderane & Izar 2019; *S. collinsi,* Stone 2006).

137

138 **Study Species, Wasps**

139 The biology of the four consumed wasp taxa is outlined below. Species were identified

140 by JWW, BR-T and Orlando Silveira (Museu Paraense Emilio Goeldi, Belém, Pará,

141 Brazil) from specimens and photographs of adults and nests.

142   *Polybia quadricincta*: This diurnal species is widespread in the Amazon-Guiana

143 Shield region. Adult total length is approximately 0.7 cm. Nests commonly have an outer

144 protective wall of carton (finely-masticated plant fibers) with 5-11 horizontally-stacked

145 combs within (Fig.1). Each comb comprises of carton cells in which larvae are raised and

146 pupate (Wenzel 1991, 2020). The sting of *P. quadricincta* is powerful (AA Barnett, pers.

147 exp). However, as a response to great stress or nest destruction (McCann *et al*. 2013),

148 *Polybia* species often adopt a nest-desertion strategy ("the absconding swarm": Hunt

149 2007), that allows the colony to return, rebuild, and continue (Sonnentag & Jeanne 2009;

150 Sazima 2014; Detoni *et al.* 2021). Accordingly, we categorized *P. quadricincta* nests as

151 low-risk.

152 *Apoica thoracica:* members of this genus are nocturnal; consequently, any diurnal

153 predators encounter the entire complement of defensive adults on the nest (van der Vecht

154 1973). Individuals are approximately 1.5 cm long and highly aggressive, attack *en masse*,

155 and have an agonizing sting. Nests may reach 8 cm in radius and have an open, umbrella-

156 like structure, a single larva-containing carton comb, with many hundreds of both cells

157 and defensive adults (see figs. 17A, 22B in Wenzel 1998). Accordingly, we categorized

158 *A. thoracica* as high-risk.

159 *Chartergus artifex*: Nests have multiple combs, stacked in a tube that may reach 50

160 cm in length (Wenzel 1998, 2020; Fig. 3). *Chartergus* adults are diurnal and reach 1.5 cm

161 in total length. Members of this genus are aggressive, *C. artifex* notably so (Richards

162 1978; Sarmiento & Saravia 1996). Defensive responses are generally extremely vigorous,

163 extensive, repeated, and prolonged (JW Wenzel, pers. obs). Accordingly, we categorized

164 *C. artifex* as high-risk.

165 *Mischocyttarus* sp.: A speciose diurnal wasp genus (some 250 species: Silveira *et*

166 *al.* 2015). Although some, like *M. drewseni* are larger, most species are 0.3-0.5 cm in

167 length. The nest is an inverted umbrella-shaped single-layered comb, rarely more than 2

168 cm in radius (Fig. 4). The colony numbers in tens, rather than hundreds. While

169 *Mischocyttarus* wasps readily sting in defence, they show desertion upon nest

170 disturbance. The sting is not strongly painful (JW Wenzel, pers. obs). Accordingly, we

171 categorized *Mischocyttarus* as low-risk.

172

173 **Study Sites**

174 We conducted observations at eight locations across Brazilian Amazonia (Table 1).

8

Table 1. *Summary of study site locations and characteristics*

Study site	Location	Seasonality
1: Ariaú Towers (*Cebus albifrons*)	Northern bank of the Rio Negro, 56 Km west of Manaus (03°12'S, 60°02'W), Amazonas State, Brazil.	Mix of *terra firme* and seasonally-flooded riverine forests (*igapó, sensu* Prance 1979). Heavy rainy season Oct–Jun, dry season Jul–Sept. River levels vary by 7-10 m, peaking in Jun-Aug.
2: Jaú National Park (*Cebus albifrons*)	Southern bank of the Rio Negro, 220 Km west of Manaus (03°12'S, 60°02'W), Amazonas State, Brazil.	As for #1
3: Rio Tapajós (*Cebus albifrons*)	Southern bank tributary of the Rio Amazonas, which it enters at Santarém city (2°25′S, 54°43′W), Pará State, Brazil.	*Igapó* forest. River levels vary by 5 m annually, highest levels Jan-May. Jun-Oct are the driest months (60-100mm rain)
4: Pousada Aldeia dos Lagos, Silves (*Cebus albifrons*)	Within Silves town (02°50'S, 58°12'W), 200 km east of Manaus, Amazonas State, Brazil.	*Terra firme* forest. Jun-Nov are the driest months (75-130 mm rain). Mar is the wettest (330 mm)
5: Vila Ananim (*Saimiri collinsi*)	Located 150 Km east of Belém city (01°11'S, 47°19'W), in the municipality of Peixe-Boi, Pará State, Brazil.	Rainfall highly seasonal. Wet season Jan-Jun, dry season Jul-Dec.
6: Campus I, National Institute for Amazonian Research (INPA) (*Saimiri sciureus*)	City of Manaus (03°12'S, 60°02'W), Amazonas State, Brazil.	20 ha fragment of secondary forest, some 100 years old, and isolated for around 50 years. Anthropized with academic buildings and educational centre (Bosque da Ciencia). Heavy rainy season Oct-Jun, dry season Jul-Sept. River levels vary by 7-10 m, peaking Jun-Aug.
7: Riparian forest, Igarape Mindu (*Saimiri sciureus*)	City of Manaus (03°12'S, 60°02'W), Amazonas State, Brazil.	Impacted riparian forest, part of extensive green corridor network in Manaus, surrounded by housing since the 1980s. Rainfall similar to #6.
8: Santa Rosa Farm (*Cebus albifrons, Saimiri sciureus, Sapajus apella*)	Rural community, 7 km east of Iranduba town (3°17'S, 60°11'W), Amazonas State, Brazil	Old secondary forest and rural orchards. Regional deforestation increasing, but large areas of old secondary and near-primary forest present. Some rural habitations and infrastructure present. Several areas where *Mauritia flexuosa* or *Attalea maripa* palms dominant. Rainfall similar to #6.

Observations

All observations were opportunistic (*ad libitum* sampling), occurring during fieldwork

for long-term behavioral studies (Jaú, Tapajós, Vila Anamim; sites 2, 3, and 5), long-term

residency (Campus 1, Mindu, Santa Rosa; sites 6, 7, and 8) or visits (Ariaú, Silves; sites

1 and 4). For each wasp nest predation event, we recorded the following variables: a) age-

sex class of individuals engaging in predation; b) all behaviors associated with wasp nest

predation, such as forms of nest manipulation, larval extraction behaviors, and actions

9

184   taken to minimize adult wasp attacks; c) total time taken to remove larvae (when

185   possible); d) ages of other individuals present and forms of participation, if any.

186   While the number of wasp nests that we could measure was small (N=14), the nests

187   of each genus are distinct and non-overlapping in size, form, and cell number (compare

188   images in Figs 1-4 with those in Richards 1978 and Wenzel 1998). Their sizes also lay

189   within the known ranges for the taxa (Richards 1978; Wenzel 1998). In addition, we

190   collected nest fragments whenever possible to supplement estimates of percentage

191   removal of larvae, counting the number of cells in a fragment and totaling the number

192   that had larvae large enough to fill a cell. We did not tally eggs and very small larvae.

193

194   **Measurement of Nest Energy-Yield**

195   *Data Analyses*: To test prediction 1 (energy yields of nest wasp predation will be high),

196   we calculated basal metabolic rates for *Cebus* and *Saimiri*, and yield of the wasp nest

197   sections from which larvae were eaten, using data on occupied cells percentage, cell

198   volumes, number of cells and wasp larvae energy content. Details of energy calculations

199   and value sources appear in Appendix Bi. To test prediction 2 individuals will employ

200   handling strategies to minimize risk of prey attack), we compared nest-processing

201   behaviors with wasp defensive forms, and with calculated energy yields. To examine

202   predictions 3 and 4 (nest predation will be more common in adults and males,

203   respectively), we used Chi-squared (χ^2) tests to compare numbers of observed wasp nest

204   predations per *Cebus* and *Saimiri* age and sex classes to expectations based on group

205   composition. All Chi-square tests had a Yates correction, 2-tailed probability and 1 df.

206

207   *Feeding bout gross calorific yield calculations*: We did not include adult wasps, as it

208   was not possible to estimate numbers ingested. We calculated energy yield based on the

209   number of larva-occupied cells in the area of nest exploited (Fig 1E), using standard

210   nutritional energy densities of 16.74kJ/g for protein and 37.65kJ/g for fat (FAO 2003),

211   mean dry weight percentages of 3.13% for lipids and 15.05% for proteins (obtained from

212   literature surveys: see below), and a consequent larval material energy value of 3.69kJ

213   per g (Appendix B-i). We then reduced calculated values by 15% to account for such

214   system losses as respiration and defecation (Goranzon *et al*. 1993). To assess the value of

215   such material to study primates, we calculated BMR for both genera (Appendix B-ii). We

216   used the energy content of a chocolate bar to provide an easily-appreciated and

217   internationally-accessible form of human-linked comparison.

218

219   ***Comparative energy yields of* Cebus *and* Saimiri *diet items:*** We compared the energy

220   values of wasp larval tissue and of non-larval diet items per 100 g of tissue. We then

221   compared mean energy yield per gram of larval wasp tissue with values gained from the

222   literature for items eaten at the times of the year that the nests were raided. We did this

223   analysis with data from *Cebus albifrons, Saimiri collinsii* and *S. sciureus*; we did not

224   include *S. apella* in energy calculations, as there were only two records, and they were

225   associated with but one class of nest (high-risk).

226   Inclusion of non-wasp larvae foodstuffs was based on presence in diet lists based

227   on unpublished data from AA Barnett and BM Bezerra for *C. albifrons* and *S. sciureus*,

228   collected in Jaú National Park, Amazonas, Brazil.

229

230   **Estimation of Wasp Sting Pain Generation Capacity**

231   As we cannot ethically subject monkeys to wasp stings and quantify their reactions, we

232   assumed that other primates feel levels of immediate pain and subsequent discomfort

233   similar to those experienced by humans. Hence, we used personal encounters of

234   experienced sphecologists to estimate relative sting pain between studied wasp genera.

235   Given the widely-recorded parallels in how human and non-human primates perceive

236   various forms of painful stimuli (Tillman *et al.* 1995; Ferdowsian & Merskin 2012;

237   Haggard *et al.* 2013), we believe human experience (Schmidt 2019) is a viable proxy.

238

239   **RESULTS**

240   **Field Observations**

241   We observed interactions between primates and wasp nests on 58 occasions (13 for *C.*

242   *albifrons*, 28 for *S. collinsi*, 15 for *S, sciureus* and 2 for *S. apella*: all events detailed in

243   Appendix A). Of these, 57 involved single animals and one which appeared to involve

244   collaborative predation. Active predation was observed on 45 occasions. Of the remaining

245   12, 8 involved juveniles investigating nests recently discarded by adults, 2 involved

246   unsuccessful nest attacks by juveniles, and 2 involved avoidance of high-risk nests

247   (*Apoica, Chertargus*) by adults. The active predation events involved four wasp genera:

248   *Polybia* (N=8 events; Fig. 1a-f)*, Apoica* (N=1; Fig. 2)*, Chartergus* (N=7; Fig. 3A, B), and

249   *Mischocyttarus* (N=29; Fig. 4A, B). In addition, at Jaú National Park and Rio Tapajós

250   (sites 2 and 3), we encountered a further 20 wasp nests damaged by *C. albifrons* but did

251   not see the actual event. While records of raided nests could not be used in the energy

252   calculations, or to determine behavioral strategies, we mention them to show that such

253   events are not necessarily rare, just infrequently met while in progress.

254   For *Polybia* nest predation, primate removal of larvae appeared close to 100%. While this

255   wasp has a powerful sting, we observed no extensive defensive activity by colony adults;

256   no signs of physical discomfort from nest-predating *C. albifrons*, and no records of wasps

257   stinging brood-consuming animals. This may relate to *Polybia* spp. use of the absconding

258   swarm nest-desertion strategy (Sazima 2014; Sonnentag & Jeane 2009). The only

259   collective predation event observed (three adult *C. albifrons*) involved an *Apoica* nest.

260   We observed both *Saimiri collinsi* and *S. sciureus* knocking down *Mischocyttarus* nests,

261   then eating in-cell larvae directly following adult nest-desertion. When juvenile primates

262   were present, they watched but were never seen to initiate nest-attacks (Fig. 1E).
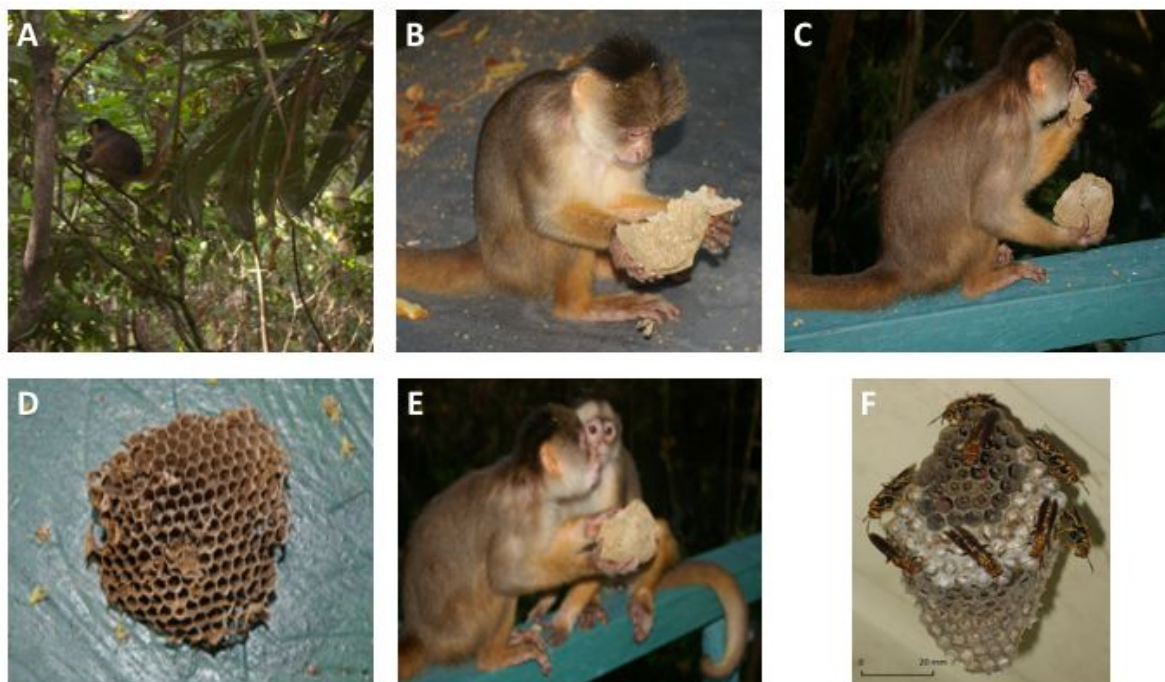

263

264   **Fig. 1** (A) An adult female *Cebus albifrons* removing the nest of a *Polybia quadricincta*
265   colony, which shows no defensive reaction. (B) The same individual using lips and teeth
266   to extract larval and adult *P. quadricineta* from their nest, as well as (C) extracting larvae
267   digitally. (D) The seventh layer of a seven-layer *P. quadricincta* nest, some 80% complete
268   and showing 188 cells. For each cell, the distance between two parallel walls is 3 mm.
269   Eggs and small larvae are present in 16 cells (E) Neither begging nor interfering, a
270   juvenile *C. albifrons* watches the adult female process a *Polybia* nest. (F) *Polistes*
271   *instabilis* nest included to show how cells may be free or occupied by eggs, larvae or
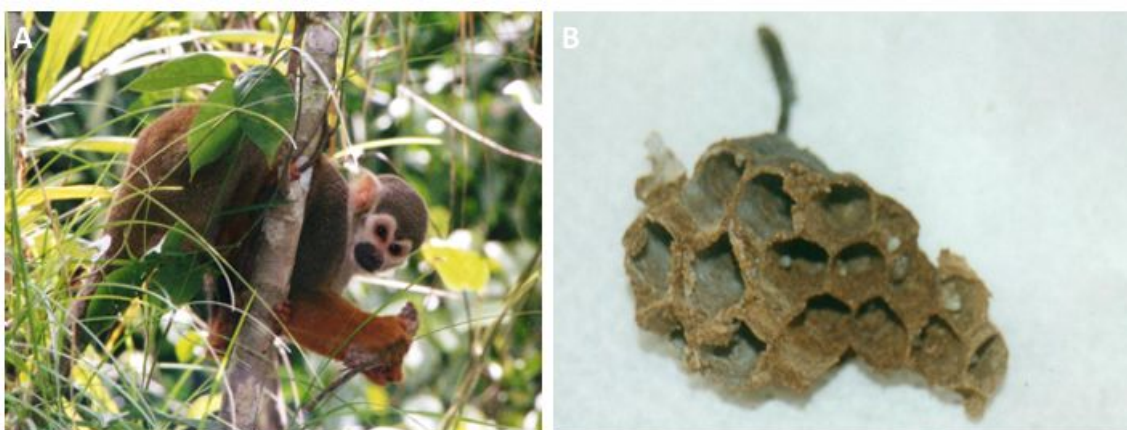272   pupae. Photos A-E by Adrian A Barnett; F by Sean O'Donnell.

13

273

Fig. 2. *Apoica* nest and adult wasps, eaten by *Cebus albifrons*. Photo by Adrian A Barnett.

276
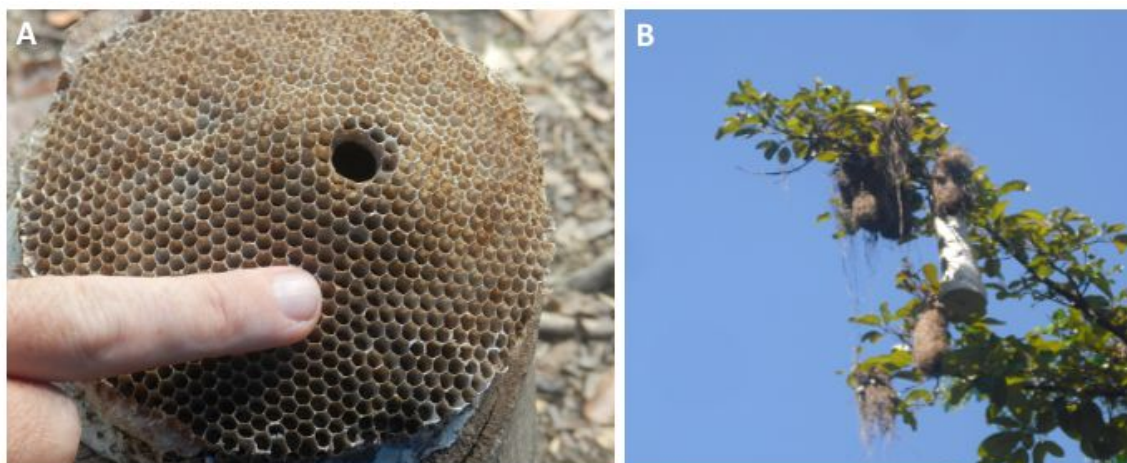
Fig. 3. (A) *Chartergus* spp. nest, one comb-layer. (B). *Chartergus* wasp nest (white) with

neighboring oropendula (*Psarocolius* sp.) nests (brown). Photos by Adrian A Barnett.

279

280

Fig. 4. (A) Adult male *Saimiri collinsi* consuming larvae from a *Mischocyttarus* colony

after knocking the nest to the ground. (B) Fragment (approximately 40%) of a

Mischocyttarus nest eaten by *S. collinsi.* Note the presence of eggs and small larvae. The

fragment is approximately 4 cm at greatest width. Photos by Anita I Stone.

285

Energy Yields (based on literature-derived protein-lipid data)

Literature surveys revealed *Polistes major* larvae are 63.5% protein and 34.5% fat;

Polybia occidentalis larvae yield 18.74kJ/g, and *Polybia* sp. larvae 20.21kJ/g (Ramos-

289 Elorduy *et al.* 1998)*.* This resembles values for whole adult European vespids (18.83–

290 25.1kJ/g: Török 1981).

291 Accordingly, the 25.7g of larval tissue in a *Polybia* nest could have provided 46 3kJ of

292 metabolisable energy (92% of male, 98% of female *C. albifrons* BMR; Table 2). For

293 comparison, this is some 60% of the energy in a 36 g chocolate bar (741 kJ). For

294 *Chartergus* the 26.7 g of larval tissue present could have provided about 466 kJ of

295 metabolisable energy (93% of male, 99% of female *C. albifrons* BMR). *Mischocyttarus*

296 nests held an estimated 5.7 g of larval tissue, yielding a gross energy value of 114 kJ (54%

297 of male and 67% of female *Saimiri collinsi* BMR, and 47% and 62.2%, respectively, for

298 male and female *S. sciureus*; 13% of the energy, 741 kJ, in a 36 g chocolate bar.

299 **TABLE 2**. *Energy yields of wasp nest attacks, in terms of Basic Metabolic Rate of* Cebus albifrons *and*
300 Saimiri collinsi *(using the methods of Ross [1992] and Stahl [1967] to calculate BMR)*

Primate species (BMR)	Wasp species[3]	Larval mass captured (g) per 100 cells consumed	Energy yield (meta-bolizable energy) (kJ)	Chocolate Bar Equivalent %[4]	% BMR (Ross; Stahl)	Hours of resting time supported by the energy gained	Feeding bout length (min)
Cebus albifrons (585 kj[1] [Ross] 752 [Stahls] kj/day[2])	*Polybia quadricincta*	25.8	95.3	12.9	16.3; or 12.7	3.9 – 3.1	10 (excluding processing)
	Chartergus (artifex)	34.9	129.2	17.4	22.1; 17.2	5.3 – 4.12	10-15 (excluding processing)
Saimiri collinsi (301.9 kj[1] - 392.7 kj/day[2])	*Mischo-cyttarus* sp.	5.7	21.1	2.8	7.08; 5.4	1.68 – 1.28	5 (including processing)

301 **Note:** [1] logBMR vs logMass regression; [2] using Stahl´s equation, which relates BMR (millilitres CL per
302 hour) to body weight (M in kg; [3] due to small sample size (N=1), and possible loss of material prior to
303 sampling, calculations were not possible for *Apoica thoracica*; [4] based on 36g Snickers® bar (Mars Inc).
304 (741 kJ: https://www.snickers.com)

305 Because *Polybia* and *Chartergus* nests differed in the number of cells in examined

306 layers (235 vs. 378: *Chartergus* 60.8% more), and in individual cell volumes (47.35 mm³

307 vs. 114.6 mm³: *Chartergus* 142% larger), energy yields also differed notably, with a

308   single *Chartergus* nest comb layer containing 135.6% of the metabolisable energy of the

309   entire *Polybia* nest (Appendix B-i). Meanwhile, tissue yields (21.1 kJ) from

310   *Mischocyttarus* sp. nests (5.71 g) would provide 4.2% and 4.7% of BMR for male and

311   female *C. albifrons* (around 62 and 68 min, respectively), of a 24-hour period. This may

312   explain why individuals of *C. albifrons*, a larger species, were not observed exploiting

313   such small nests.

314

315   **Comparative energy yields of *Cebus* and *Saimiri* diet items**

316   Mean energy yields (kJ per 100 g) of wasp larval tissue exceed the energy yields of a

317   similar mass of other foodstuffs by between 14.7 and 85.1% for *Cebus* (mean ± SD, 66.5

318   ± 22.6, N=9), and 4.9 and 80.1% for *Saimiri* (mean ± SD, 58.0 ± 32.5, N=5; Table 3). In

319   no cases were yields from plant-based foodstuffs greater than those for wasp larvae. This

320   analysis also emphasized the high percentage of protein in wasp larvae compared to other

321   foodstuffs, since, while the former are over 60% protein, protein levels in plant-based diet

322   items are notably lower (e.g., *Annona*, 1.4%: Villela *et al.* 2013; *Bactris*, 1.8-2.7%,

323   Yukuma *et al*. 2009; *Spondias,* 1.6%, Tiburski *et al*. 2011).

324

325   **TABLE 3.** *Energy yields per 100 g of* Cebus albifrons*, and* S. sciureus *foodstuffs*

Diet item	Energy value per 100g kJ (kcal) [1]	Energy yield of item as percentage of yield for 100 g wasp larva tissue [2,3]	Reference
Cebus albifrons		*Polybia*	
Spondias mombin (Anacardiaceae) fruit pulp	273.7 (65.42)	17.8	Tiburski et al. (2010)
Annona sp. (Anonaceae) fruit pulp	296.7 (70.91)	19.3	Vilella et al. (2013) [4]
Bactris gasipaes (Arecaceae) whole fruits	749.4-67.8 (179.1 -207.4)	48.7 – 56.4	Yuyama et al. (2003)
Mauritia flexuosa (Arecaceae) fruit pulp	794.1 (189.8)	51.6	Aguiar (1996)
Oenocarpus bataua (Arecaceae) fruit pulp	1327.2 (317.2)	86.3	Aguiar (1996)

Hevea spruceana (Euphorbiaceae) seeds	261.5 (62.5)	17.0	Roubach & Saint-Paul (1994)
Passiflora coccinea (Passifloraceae) pulp and seeds	228.4-275.7 (54.6-65.9)	14.8-17.9	Lima-Neto et al. (2017) [5]
Bellucia grossularioides (Melastomataceae) whole fruit	291.0 (69.55)	18. 9	Aguiar (1996)
Pouteria sp. (Sapotaceae) fruit pulp	298.6 (71.36)	19.0	Virgolin et al. (2017) [6]
Saimiri sciureus	*Mischocyttarus*		
Bactris sp. (Arecaceae) whole fruits	1450.25 (351.4)	95.1	Aguiar (1996)
Euterpe precatoria (Arecaceae) pulp	392.6 (93.83)	25.4	Fregonesi et al. (2010)
Mauritia flexuosa (Arecaceae) fruit pulp	794.1 (189.8)	51.3	Aguiar (1996)
Bellucia grossularioides (Melastomataceae) whole fruit	291.0 (69.55)	18.8	Aguiar (1996)
Pouteria sp. (Sapotaceae) fruit pulp	298.6 (71.36)	19.31	Virgolin et al. (2017) [6]

326 **NOTES:** [1] Given in literature as kcal, and converted here to kJ for consistency (kcal value in parentheses:
327 1 kcal = 4.184 kJ); [2] Using values for fully hydrated food items as this is how they would be ingested by
328 the primates; [3] Values (calculated from Table 2) = 369.7 for 100g of *Polybia quadricincta* larval tissue,
329 369.52 for *Mischocyttarus* sp.; [4] For *Annona crassifolia*; [5] For *Passiflora glandulosa*, *Passiflora alata* and
330 *Passiflora edulis;* [6] For *Pouteria caimito*

331

332 Thus, feeding from *Polybia* nests yields a mean of 33.2% more energy gram than an

333 equivalent mass of fruit (SD ± 23.37, range 16.4-86.3, N=9) for *C. albifrons*, while *S.*

334 *collinsi* will have gained a mean of 41.9% (SD ± 29.1, range 18.5-95.1, N=5) from feeding

335 from *Mischocyttarus* nests. This supports Prediction 1, that energy yields from nests

336 would be high compared to other food types available.

337 **Primate Nest Feeding Behaviour in Relation to Wasp Defence Intensity**

338 Variation exists between wasp species in both aggression levels and sting pain intensity,

339 with more aggressive species having more painful stings (Table 4). Wasp aggression

340 and sting intensity, as well as nest size, were related to primate feeding behaviours and

341 duration of foraging at wasp nests, with predation strategies adopted vary to reduce the

342 time a primate spends in proximity to a nest as aggression and sting-pain increase.

343 **TABLE 4.** *Cost/benefit summaries of attacks on four wasp species, considering;*
344 *aggression level, sting pain intensity and energy yield/unit time*

18

Wasp Species	Aggression Level[1]	Sting Pain Intensity[1]	Primate attack behaviour[2]	Energy Yield per Unit Time (kJ/min)[3]
Apoica	Extremely high	Extreme	Grab portion and run: several individuals	Data not available
Chartergus	Very high	High	Grab portion and run: single individuals	Data not available
Polybia	Moderate-Low	Moderate	Remove entire nest, near-immediate processing: single individuals	7.7
Mischocyttarus	Low	Moderate	Knock nest down, return later; or hit repeatedly, retreat, then return – repeat several times (tapping): single individuals	1.7

345   NOTES: [1] Based on field experience of JW and other experienced fieldworkers on Neotropical wasps (see acknowledgements); [2]
346   Table 1 contains details; [3] Based on duration of attacks (Table 1), and energy yields per nest type (Table 2)

347   This diversity of behaviours (see also Appendix A), supports Prediction 2, that individual

348   primates will deploy strategies that minimize risk of prey attack.

Differences in Raiding Primate Age and Sex

350   We observed 47 raids on wasp nests (all primate and wasp species combined), of which

351   44 were successful attacks by adults, involving 46 individual primates. The sex of 1 adult

352   was not determined while of the remaining 45, 19 were female and 26 were male ($\chi^2 =$

353   1.088, NS).

354   For age-classes, attacks did not occur in proportion to group age-classes composition.

355   When the adult/juvenile ratios of *C. albifrons, S. collinsi* and *S. sciureus* were averaged,

356   the expected number of attacks by younger individuals was 16 of the 49 observed events

357   (all adult and juvenile, successful and aborted, attacks combined: see Appendix A).

358   However, we recorded only three such events ($\chi^2 = 15.68$, p < 0.0001), only one of which

359   was successful (a juvenile *C. albifrons*; Appendix A, Event 13), while two (events 40 and

360   41) involved a juvenile *S. collinsi*, who withdrew after being badly stung, and without

361   reaching the nest. Therefore, we found support for Prediction 3 (raids on wasp nests will

362   be conducted by adults).

363   Of the 45 raids conducted by adults, we could not determine the sex of 1 adult, but of the

364   remaining 44, 19 were female and 25 were male ($\chi^2 = 1.088$, p>0.05). For relationships

19

365   between level of risk and sex of raiding adult, the number of males and females raiding

366   the low-risk *Mischocyttarus* nests did not differ significantly; *S. collinsi* (χ^2 =0.89,

367   p=0.96), or were at parity for *S. sciureus*. For *C. albifrons* raiding the medium-risk

368   *Polistes* nests, eight of nine records were from females ($\chi^2 = 5.44$, p = 0.019), while all

369   eight attacks (*C. albifrons* and *S. apella* combined) on high-risk nests (*Apoica* and

370   *Chartaegus* combined) involved adult males ($\chi^2 = 8.00$, p = 0.004). These findings

371   provide support for Prediction 4, that risky foraging behaviours will be less common in

372   adult females than in males.

373

374   **DISCUSSION**

375   Our predictions received full or partial support While wasp nests yield more energy per

376   gram than plant-based food, they must be accessed with specific strategies depending on

377   the nature of the wasp species defence.

378   *Prediction 1 (energy rewards will be large to compensate for high-risk foraging)*:

379   *Mischocyttarus* and *Polybia* wasp larvae energy values were high. An incomplete data set

380   meant it was not possible to calculate energy yield per-unit-time for *Apoica* and

381   *Chartergus*. However, given the larger number of larvae-containing cells in their nests, it

382   is likely that yields were proportionally higher for *Apoica* and *Chartergus* predation

383   events. Consequently, such risker events would yield higher pay-offs.

384   Vespid Hymenoptera are abundant in Amazonia, with 50-60 species in any one area

385   of *terra firme* forest (Silva & Silveira 2009; Somavila *et al.* 2015). Thus, widely ranging

386   and foraging primates, such as *Cebus* and *Saimiri* (Kinzey 1997), will encounter wasp

387   nests frequently. Larvae provide a higher nutrient to mass ratio than adult insects, are

388   more easily assimilated as thinner less-sclerotized exoskeletons are more quickly digested

389   and lack legs and wings which both fill the gut lumen and are indigestible (Janssen *et al.*

390   2017).

391   Other dangerous, but potentially high-yield foods, like scorpions and large

392   centipedes, though often abundant, may simply be avoided because of their lethality (such

393   venom can kill small mammals swiftly: Molinari *et al.* 2005). Their predation requires

394   investment in learning-based behaviour, only becoming energetically viable in scorpion-

395   specialists, (meerkats: Thornton & McAuliffe 2006). Despite their high energy content,

396   such potential prey become too dangerous for generalists such as *Cebus* and *Saimiri*

397   (Mukherjee & Heithaus 2013).

398   *Prediction 2 (primates would use specialized handling strategies to minimize risk*

399   *of being stung):* We found partial support for this prediction. We expected nests of each

400   wasp species to be treated differently, as they vary in defensive response vigor, and (as

401   perceived by humans) sting power and duration. Though *Polybia* (including *P.*

402   *quadricincta*) have a powerful sting (McCann *et al.* 2013), monkeys showed no signs of

403   being stung (Fig. 1A), and no wasps were observed to attack them while they consumed

404   nest contents (Fig. 1B,C). This may be due to the absconding swarm strategy

405   (O'Donnell & Jeanne 2002; Sonnentag & Jeane 2009; Sazima 2014) being an additional

406   anti-predator mechanism to sting-based next defence. The importance of the strategy

407   deployed by adult *Saimiri* when feeding on *Mischocyttarus* of knocking down nests and

408   waiting for adult wasps to leave (i.e., abscond) can be seen from the results of events 40

409   and 41 (Appendix A) where young animals were badly stung.

410   *Apoica* wasps are regarded with immense caution by rural Amazonians and

411   researchers, due to intense and long-lasting pain caused by their sting (Robert Jeanne,

412   Fernando Noll, and Sean O'Donnell, pers. comms.), and specologists consider them one

413   of the most dangerous wasps (Robert Jeanne, pers. comm.), which may explain why

414   *Saimiri* actively avoided such nests (Event 49, Appendix A). The attack on an *Apoica*

415   nest by three adult male *C. albifrons* was the only predation event where more than one

416   individual was involved and may have had a risk-spreading function (Mukherjee &

417   Heithaus 2013).

418   The *Chartergus* predation-events demonstrated the coordinated and vigorous nest

419   defence considered typical of polistine wasps (Chadab 1979). Monkeys raiding

420   *Chartergus* nests fled actively and appeared to receive stings, similar to events reported

421   by Fragaszy *et al.* (2004). The wasp genus is so aggressive that icteriid birds (*Cacicus,*

422   *Gymnostinops* and *Psarocolius* spp.) suspend their nests beside them for protection

423   (Robinson 1985; Quinn & Ueta 2008: Fig. 3B). Our data indicate that large nest-cell size,

424   and consequent high energy yields, justified the smash-grab-and-flee approach for the

425   primate, indicating the presence of alternative foraging strategies within the overall rubric

426   of insectivory and nest-based larval wasp predation. However, the active avoidance by a

427   group of *S. sciureus* of a *Chartergus* in their home range (Event 52, Appendix A) shows

428   not all primate species have this capacity.

429   Though painful (AI Stone, pers. exp.), a *Mischocyttarus* sting is less powerful than

430   *Polistes* (JW Wenzel, pers. exp.; Schmidt 2019). Additionally, *Mischocyttarus* wasps are

431   rarely aggressive, quickly deserting a threatened nest. However, many *Mischocyttarus*

432   spp. appear as Batesian mimics of other genera, more bellicose and/or with more powerful

433   stings*,* including: *Agelaia* (O'Donnell & Joyce 1999; Starr 1985 [as *Stenopolybia*]), and

434   *Polybia* (Garcete-Barrett 2014), with the deception being sufficient to promote avoidance

435   in visually-oriented predators (dragonflies: O'Donnell 1996; Rashed *et al.* 2005). *Saimiri*

436   monkeys used a different technique than *Cebus* and *Sapajus* capuchins to attack wasp

437   nests, knocking them to the ground and awaiting desertion by adult wasps (which takes

438   2-5 mins). Use of this technique indicates even though *Polistes* wasps are non-aggressive,

439   *Saimiri* exercise caution and risk-avoidance. It may also be a standard response by *Saimiri*

440   to wasp nests, since *S. oerstedi* display similar behaviour with *Polistes* wasps (Boinski &

441   Timm 1985).

442   Risk assessment occurs even when a species is fully or partially-immune to the

443   potential prey's venom (Rowe & Rowe 2006). For *Saimiri*, risk assessment may be a

444   mixture of actual and, due to *Apoica*-mimicry by *Mischocyttarus*, perceived risk *Apoica*

445   nest avoided: see Appendix A. *Saimiri* exploited only nests of wasp species either

446   physiologically (*Polistes*) or behaviorally (*Mischocyttarus*) low-risk. Both

447   *Mischocyttarus* and *Polistes* are abundant (providing, 20 and 24 respectively, of the 63

448   species inventoried by Silva & Silveira 2009). Thus, encounters with these less-dangerous

449   insects may be sufficiently frequent to provide energy and nutritional supplements for the

450   smaller *Saimiri*, leaving the higher-risk, but higher-yield, species for the larger *Cebus*.

451   *Prediction 3 (that adults would mostly predate nests)*: We found support, 93.8% of

452   predation events involved adults. Juveniles comprise almost 50% of social groups of *S.*

453   *collinsi* (Stone 2007a, b), however, juvenile squirrel monkeys were not engaged in wasp

454   nest predation, except of those that adults had discarded (Events 14-21, 47, 48, 53;

455   Appendix A). Both juvenile *Cebus* and *Saimiri* watched, rather than participated (*Cebus*

456   juveniles initiated 1: Event 13), indicating risky actions often require experience (two

457   young *S. collinsi* were badly stung when approaching nests: Events 40, 41,

458   Supplementary Material A). These observations might be expected when predation is

459   difficult and high-risk, requiring speed, coordination and dexterity (Westergaard *et al*.

460   1997; Stone 2006; Gunst *et al.* 2008, 2010a,b). Soley et al (2017) reported greater success

461   with a hard-to-process resource with painful defence capacity (hermit crabs) for *C.*

462   *capucinus*. In this context, it is interesting to note that the high-risk, high-speed attacks

463   on *Chartergus* require experience and coordination, yet in no case was another animal

464   seen observing the raider. It remains uncertain how experience is gained.

465   Foraging theory predicts individuals most likely to take risks and engage dangerous

466   prey will be younger, lower in social rank, hungry, and/or less-experienced (Mukherjee

467   & Heithaus 2013; Elbroch *et al*. 2017). However, wasp nest defences can only be

468   minimized or avoided with guile and speed, which come with practice. Wasp nest

469   predation appears to be the purview of adult *Cebus* and *Saimiri*, and like such items, can

470   only be processed by watching proficient individuals (Ottoni *et al*. 2005; Fig 1E), like the

471   successful use of stones and anvils in capuchins (De Resende *et al*. 2008). Gaining

472   capacity to attack wasp nests has parallels with how chimpanzees learn how to fish for

473   termites (Lonsdorf 2006), and process fruits (Corp & Byrne 2002; Bray *et al*. 2018), as

474   well as the ontogenetic enhancement of manual dexterity facilitating this (Boesch *et al*.

475   2019).

476   *Prediction 4 (risky foraging would be more common in males)*: We found support

477   for this prediction. While six of the seven observed *Polybia* predation events involved

478   adult female *C. albifrons*, all predation on *Chartergus* and *Apoica* involved males. For *S.*

479   *collinsi* feeding on *Mischocyttarus,* 40% of events involved adult females. These wasps

480   are non-aggressive, therefore little direct risk would be associated with predation.

481   Females with dependent young were not seen to attack nests (Events 14-41, 42-40,

482   Appendix A), which may explain reduced female participation.

483   Other studies have found a strong male-bias in capuchin monkey wasp-nest

484   predation (Fragaszy *et al*. 2004; WR Spironello, unpublished data: 13 events in 13

485   months), with similar bias recorded for other primates (Dufour 1987; Paoletti & Dreon

486   2005). This pattern is notable given lactating females have higher demands for protein

487   and fat (Herrera & Heymann 2004), and greater insect consumption (McCabe & Fedigan

488   2007). Lactating females may not exploit this resource due to the risk of infants being

489   stung, who do not leave their mother´s body surface until several months after birth

490   (*Cebus*: Young & Heard-Booth 2016; *Saimiri*: Tardif 1994; Byrne & Suomi 1995). The

491   low numbers of adolescents among those raiding nests (6.7% *Cebus*; 6.9% both *Saimiri*

492   combined: Appendix A) is also notable, since young *C. albifrons* have 2.5% higher

493   protein requirements than adults (Ausman & Hegsted 1980), emphasizing that

494   considerable restraint is exercised by adolescents. Observation of predation technique to

495   mitigate risk of sting by inexperienced individuals (Appendix A; Fig. 1E) parallels the

496   attention given by juveniles to other complex foraging tasks, such as nut-cracking

497   (Visalberghi 1987; De Resende *et al.* 2008).

498   Perhaps wasps are favoured primarily because of their taste, so that the primates

499   running risks to access them are not energy accountants, but gourmands. Taste preference

500   for pleasure alone is a rarely-explored aspect of primate foraging ecology, as when the

501   role of taste perception is assayed it is in the context of the capacity of this sense to inform

502   or forewarn about the composition of a potential foodstuff (Hellekant *et al.* 1993; Simmen

503   & Sabatier 1996; Dominy *et al.* 2001; Simmen *et al.* 2006). This possibility could be

504   investigated with in-field choice tests that presented wasp larvae and other insects of equal

505   energy yield using feeding platforms as used by Bicca-Marques & Garber (2003). The

506   importance of micro-nutrients, such as vitamins and minerals (Bryer *et al.* 2015), also

507   needs investigation.

508

509   **CONCLUSIONS**

510   Individual primate behavioral sequences were notably uniform during *Chartagus,*

511   *Mischocyttarus* and *Polybia* predation-events. Nevertheless, how primates processed

512   nests of each genus varied greatly. From this we conclude that, despite being a vigorously-

25

513   defended resource (in many cases by exceptionally powerful stings), when successful,

514   exploitation of nest-based wasp larvae has a high energy pay-off. Our results suggest that

515   the occasional energy bonanza derived from exploiting such challenging foods exceeds

516   that derived from more tractable items, such as fruit. Thus, such a form of exploitation is

517   a viable strategy if the predating primate has the dexterity and speed to achieve it

518   successfully, while simultaneously minimizing the risk of pain and injury.

519   As such, wasp-nest predation should be seen in the larger context of risky and

520   demanding items exploited by these primates. For example, *Saimiri* employ an "oven

521   mitt" technique when handling urticaceous caterpillars; cushioning their hand with the

522   tuft of fur at the end of their tail while grabbing the prey, then rubbing the caterpillar

523   vigorously against a branch or tail-fur to remove irritant hairs (Boinski & Fragaszy 1989;

524   Stone 2006).

525   Insectivory is generally considered the purview of smaller primates (Atsalis 2008;

526   McGrew 2001), and arthropods compose some 70% of the diet of *S. collinsi* (Stone

527   2007a), while Hymenoptera account for 40% of *S. collinsi* arthropod prey in some months

528   (Stone 2004). However, insects can comprise 46% of the *Cebus* monthly diet (Mallott *et*

529   *al.* 2017; McCabe & Fedigan 2007), and wasp larvae 15%-36% (Perry & Jimenéz, 2007;

530   Mallott *et al*. 2017). The high energy values revealed here (compare Table 2 and Table

531   3), allied with the possession of chitinases by *Cebus* (Janiak *et al*. 2017; Janiak 2018),

532   and the thin chitin coverings of wasp larvae, may explain the apparent contradiction of

533   how a comparatively large primate like *Cebus* can be so highly insectivorous for extended

534   periods of the year.

535

536   **Ethical Note**

537   All research complied with Brazilian law. We adhered to Association for the Study of

538   Animal Behaviour guidelines for research animal treatment (Buchanan *et al.* 2012), to the

539   Code of Best Practices for Field Primatology of the American Society of Primatologists

540   and   International   Primatological   Society

541   (www.asp.org/resources/docs/Code20of_Best_Practices20Oct202014.pdf). We did not

542   trap or handle study animals and maintained a minimum 2 m distance from individuals to

543   minimize stress.

544   **Data Availability**

545   The datasets analyzed during the current study are available from the corresponding

546   author on reasonable request.

547

577

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1000   **APPENDIX A**

1001 Behavioral observations of wasp nest predation by *Cebus albifrons*, *Saimiri collinsi*, *S. sciureus* and
1002 *Sapajus apella*

Event no.	Primate Species	Location (N; date)	Wasp Species	Observed behavior of individual engaging in predation	Behavior of associated individuals
1	*Cebus albifrons*	**Ariaú, AM** (one event; 23-VII-2009)	*Polybia quadricincta*	Adult female detached an entire nest (estimated height: 10 cm, diameter: 8 cm) from a tree, then carried the nest to a branch, spending 92 secs biting at the nest top. On breaching the wall, carton was removed with digits to expose layer one of larvae-filled cells; nest then raised, chalice-like, to face and larva nibbled out with lips. Once one layer was depleted of larvae, it was pulled away with digits, and the next accessed by trimming intervening carton with digits and teeth (Fig. 1A, B).	A juvenile observed the predation event from a distance of some 3m, and the processing from half-a-body length (Fig. 1E) but did not participate or share in the resulting food. Interactions with the adult female and the young accompanying male were limited, and no food sharing or begging were observed (Fig. 3), though the younger animal was observing the process closely.

				Accessing and eating each layer took approx. 60 sec; the entire process from initial observation to dropping final nest fragment took 12 mins 26 secs, with 10 mins 06 secs being actual feeding. Extraction appeared extremely effective – one retrieved layer had one larva remaining in 149 cells not containing eggs (Fig. 2: 39 cells have eggs).	
2-4		**Santa Rosa Farm, AM** (three events; 2 07.50, 10-IV-2020 3) 08.10, 22-VIII 2020 4) 06.45, 18-XII-2021)	*Polybia* sp(p).	Three cases of adult females foraging in *Mauritia flexuosa* (Arecaeae)-dominated vegetation on the margin of a small shallow lake and removing a spherical wasp nest from its site and moving to a broad open branch (Event 3), fallen log (Events 2 and 4) to process it. Processing took 9 mins 28 secs, and 12 mins 17secs, with Event 4 being interrupted when the monkey fled as a hawk landed nearby.	Associated individuals were in dispersed groups foraging on palm fruits, bromeliad bases and searching for animal prey in palm frond bases. Neither adults nor juveniles attempted steal the nest, interfere or beg food. However, the female in Event 2 was accompanied by a sub-adult who sat closely by and watched the processing and who investigated the empty nest remains once it´s presumed mother had finished.
5		**Jaú, AM** (one event; 08:34, 29-III-2007)	*Apoica thoracica*	Three adult *C. albifrons* were observed repeatedly rushing at a wasp nest positioned under a large horizontal tree branch, in flooded igapó forest, grabbing a portion and retreating a distance to pick through the prize. The water was littered with nest fragments, adult wasps and larvae (Fig. 5), which fish were avidly consuming.	All three animals were adult. No young animals observed in the vicinity.
6		**Silves, AM** (one event; 11:15,14-X-2011)	*Chartergus* (*artifex*)	An adult male *C. albifrons* was seen moving very quickly, on three limbs, through the forest canopy: one hand held a brown disk with a white rim; a broken portion of another disk was held in its mouth. An aggregation of numerous dark insects was flying	Adult animal acting alone

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				behind the primate who occasionally made high-pitched yips, as if responding to sudden discomfort. The animals disappeared further into the forest canopy. The primate did not pause to process food items while under observation. Backtracking revealed a white, pipe-like, nest suspended some 15 m in a tree. The bottom portion was missing. A carton layer of cells that had fallen to the ground was later retrieved and photographed (Fig 4), though all larvae had been removed.	
7,8		**Tapajós, PA.** (two events; 7) 11:47, 05-XII-2012 8) 07:30, 10-XII-2012)	*Chartergus* sp.	Both events occurred in uncut terra firme forest close to the community of Jutaí (03°23'17"S, 58°36'80"W). Event 7: After the remainder of the group had crossed, an adult male *C. albifrons* was seen leaping with unusual speed and vigor along a much-used arboreal trail that included a natural bridge of vines across a mud access road. In its mouth it held a roundel of comb from a wasp nest. The animal paused twice *en route* to bat at its face with its hands and was distracted enough by the wasps following it to mistime its traverse across the vine bridge and fall several meters. It headed to adjacent flooded forest where nest fragments with *Chartergus*'s characteristic central entrance hole were later found floating. Event 8: on a closed primary forest trail a loud buzzing was heard accompanied by sharp yips and falling wasp nest	Adult male acting alone (Event 7). Adult male, unknown if accompanied or not (Event 8).

				fragments. Dense vegetation obscured the event, but an adult male was seen bounding away with a large, white-and-dark object in its mouth. We then too had to leave. A return two days later found fragmentary remains of a *Chartergus* nest. Tracks indicated it had been visited by *Dasypus novemcinctus* and *Tamandua tetradactyla*. No larvae or eggs remained for retrieval.	
9,10		**Santa Rosa, AM** (two events; 9) 11.17, 7-VII-20 10) 07.22, 19-VII-21)	*Chartergus* sp.	In both events, the raided nests were on dead branches in the open canopy of large trees near an *Attalea* palm grove. In each case the adult male approached at speed, grabbed a portion of the nest a then headed towards the palm grove, pursued by wasps. Yip-like vocalizations were heard during one event.	In both events, the remainder of the group (6, 10 individuals, respectively) were foraging some 30-50m away in the *Attalea* grove. Processing of the nest remnant was not observed so it is not known if it was shared. or its processing observed.
11-13		**Tapajós, PA** (3 events; (11) 11:20, 23-IV-2013; (12) 09:55, 25-V-2013; (13) 09:48, 27-V-2013)	*Polybia* (*quadricincta*)	For events 11 and 13, nests (each approx. height 10 cm, diam. 8cm) were in flooded forest trees. Event 12 nest smaller (some 7 x 6cm) and on an isolated bush on a rock at the mouth of an unnamed stream at 4°56'35.596"S, 56°45'22.440"W). Event 11: An adult female separated from a group of 5 *C. albifrons* resting in a tree, some 5 m from the river margin, entered the lower canopy of a small leguminaceous tree, and removed a wasp nest, moved laterally some 5-6 m and began processing. Event 12: an adult female leapt into the water from riverside scrub and swam some 2.5 m to a small tree from which she swiftly plucked a wasp	Event 11: female accompanied by younger animal, who neither begged nor interfered, but appeared to be observing the process closely. Event 12: the three other, adult, members of the group watched, but did not attempt to share the prize, or beg. A youngster accompanied the adult female to the waterside and watched processing occur. Event 13: juvenile male acting alone (?)

				nest. She then climbed swiftly to the top of the 3.5m tree and jumped back to into the riverside vegetation and began processing the nest. Processing sequence, methods and timings were similar to those Ariaú (respectively, 75 and 87 secs to initially open the nest, 11 mins 13 secs and 14 mins 02 secs to process it – of which 9 mins 54 secs and 12 mins 30 secs, respectively, were direct feeding activities). Event 13: In the third event, to access the nest a juvenile male *C. albifrons* ran across some 5.5m of open rock, bare but for some low growth, grabbed the nest (which was in silhouette) and swiftly retreated with it to dense vegetation. The entire processing could not be observed but was finished within 8 mins.	
14-41	*Saimiri collinsi*	**Vila Ananim, PA** (28 events; 18 involving predation; March 2002-March 2003)	*Mischocyttarus* spp.	The technique used to obtain larvae always followed this sequence: the individual would first approach the nest cautiously, quickly use its hands to knock it to the forest floor, then quickly move away. Once the adult wasps had deserted the nest (1-3 minutes), the monkey then approached the nest on the ground and, using its fingers, extracted and consumed larvae from each crevice of the nest. An adult male holding a wasp nest and the fragment of a nest are shown in figure 6a.	Juveniles over 1 year old holding a discarded nest and searching for remaining larvae (N=8) (events 14-21), but entire behavioural sequence for nest predation only observed in adults (> 3 yrs old: N=18, events 22-39). On two occasions (events 40-41) young animals (a 5-month-old infant; a 9-month-old juvenile) approached a wasp nest and repeatedly got stung the face. They were not accompanied by their mother. While 7 of 18 adult feeding records came from females (38.9%), we never observed adult females with infants on their backs predate wasp nests.
42-49	*Saimiri sciureus*	**INPA Campus, AM**	*Mischocyttarus* spp.	The technique to obtain nests did not differ from that described for *S. collinsi.* Four of five	All individuals involved in predation of nests were adults (3 males, 2 females). No females had young on

		(8 events, 5 involving nest predation; Nov 2018-Aug 2019)		nests were recovered. These had 47, 52, 79, 90 cells (one was 60% complete; three appeared 80-90% occupied). Post-knockdown waiting times: 67, 97, -- and 182 seconds for retrieved nests (102 for unretrieved). Larval removal took 28, 32, 37, 47, 88 seconds.	their backs on following them. On two occasions (events 47, 48) juveniles watched and investigated nests once adults had finished eating from them. In one (Event 49) an adult male approached apparent *Apoica* nest, then withdrew quickly.
50-52	*Saimiri sciureus*	**Igarape Mindu, Manaus, AM** (3 events, 2 involving predation; Nov 2018-Aug 2019)	*Mischocyttarus* spp.	Processing as above. Post-knockdown waiting times: 64 and 127 seconds. Two nests recovered (50 and 57 cells, each some 90% occupied), processing time 37 and 41 seconds.	Both participants were adults (1 male, 1 female). Observation conditions (dense vegetation) meant it was not possible to discern if predation was observed by other individuals. When travelling within home range, a *Saimiri* group changed course, apparently to avoid *Chartergus* nests near oropendula (Icteridae) colony (Event 52).
53-56		**Santa Rose Farm, AM** (4 events; 53) 07.26, 25-VII-20 54) 09.10, 27-VIII-20 55) 07.58, 29-VII-21 56) 07.41, 02-VIII-21)	*Mischocyttarus* sp(p).	Records of two adult females (53, 55), one adult male (54), and an unsexed individual (56) feeding on small pendant wasp nests. In all cases they were knocked to the ground, left and then returned to and the larvae removed. Post-knockdown waiting times were: 84, 107, 74, and 91 seconds. Larval removal took 36, 28 and 39 seconds. Data for the unsexed individual was compromised by poor visibility.	During Event 53 a juvenile closely observed the actions of a female. In all other cases the animals appeared to be acting independently, although the rest of the group (counts of 10, 15, 8, and 22 animals, respectively) was actively foraging at various levels in the surrounding forest.
57, 58	*Sapajus apella*	**Santa Rose Farm, AM** (2 events; 57) 08.00, 19-IX-21 58) 15.17, 10-XII-21)	*Chartergus* sp.	In both cases, the adult males attacked nests suspended from the tips of branches of large trees overhanging telephone/power cables and accessed the nests by using these then enacting a smash-and-grab attack, before ascending very swiftly into neighboring trees and disappearing	In each case the animal appeared to be acting alone, with the rest of the group either over 50m away or not visible.

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1006   **APPENDIX B**
1007   **Calculations for: i) total number of larvae in nest, ii) basal metabolic rate of adult**
1008   **female *Cebus albifrons, Saimiri collinsi,* and *S. sciureus*.**
1009
1010   **i) Calculations of total numbers of larvae in nests of three wasp species**

1011   *Polybia* **nest:** Based on field observations at Ariaú Towers, the 10cm x 8cm nest was

1012   assumed to be a regular ellipse. Carton nest brood-cell layer 7 (Fig. 1D) retrieved had 188

1013   cells, and was estimated to be about 80% complete, hence originally held c. 225 cells.

1014   Layer 1 would have the same. Assuming layer 4 (the middle layer) was 18% wider than

1015   the ends, the number of cells in layers 2 & 6, 3 & 5, and 4 can be estimated as 253, 282,

1016   and 313 cells, respectively (1833 cells total for entire nest). Not all cells contain

1017   larvae/pupae. However, Richards (1978) recorded multiple *P. quadricincta* nests and

1018   found 33-45% of cells to hold larvae/pupae. Accordingly, we assumed a cell occupancy

1019   value of 33%, giving an estimate of 605 larvae for the predated *Polybia* nest.

1020   Based on measurements from 100 cells, mean cell volume was 47.4 mm³ (side base

1021   length = 1.5 mm, height = 8.1 mm: equation for the volume of a hexagonal prism is

1022 $V = A \times h = 6*1/2*1.5$ mm$\times 1.3$ mm$*8.1$ mm). Tests showed living wasp larvae did not

1023   sink, so, conservatively assuming larval wasp flesh density to be that of water gives 47.4

1024   mg (0.047 g) of larval tissue per cell, a minimum of 28.6 g of edible material for the entire

1025   nest. Allowing a further 10% reduction for error, gives an edible nest content of

1026   approximately 25.7 g.

1027   *Chartergus* **nest:** These nests are large (Fig. 3), and retrieved layer had 786 cells. The

1028   animal only took one nest layer. Retrieved *Chartergus* comb cells were 10mm heigh, and

1029   each hexa-side 2.4 mm long. Based on measurements of 100 cells, mean cell volume was

1030 $6*1/2*2.4$ mm$*2.4$ mm$* 10$ mm $= 149$ mm³, 214.3% bigger than *Polybia* nest cells.

1031   Making the same assumptions for larval tissue density as with *Polybia* gives a value of

1032 0.060 g per cell. If (as above) 33% possessed edible larvae/pupae, the nest contained

1033 approximately 34.9 g of larval tissue.

1034 ***Mischocyttarus* nests:** Nests from this genus are small (Fig. 4 A, B). We retrieved an 11

1035 cm x 4 cm nest portion that was assumed to be a regular ellipse. This nest had 40 cells

1036 and was about 90% complete. When whole, it probably had some 44 larvae/pupae-

1037 containing cells. Cell sides were 4.3 mm long and 10 mm high (volume = 480.4 mm^3).

1038 Using the same density and occupancy data as above, each cell contained 286 mg of

1039 larvae tissue, a minimum of 5.7 g of larval tissue for the complete layer.

1040 Six nests, retrieved after *S. sciureus* had fed on them, had 54, 72, 90, 103 cells

1041 (INPA), 55, and 63 cells (Mindu). Based on ten cells, mean cell volume was 223.48 mm^3

1042 (sides 3.2 mm; height 8.4 mm). Following the assumptions above, each full cell contained

1043 0.223 g of larval tissue. Assuming (as above) 33% larval/pupal occupancy, gives 4.01,

1044 5.35, 6.69, 7.58, 4.02, and 4.68 g of larval tissue for the six nests for which cell counts

1045 were possible.

1046

1047 **ii) Basal metabolic rate calculation**

1048 There appear to be no reports in the literature of *Cebus* or *Saimiri collinsi* BMR or

1049 movement energetics (including Snodgrass *et al.* (2007)´s primate bioenergetics review).

1050 BMR values were therefore estimated with allometric regression data in Ross (1992) via

1051 the equation: log(BMR=0.819 logBWt+.249; with BMR(ml O$_2$/hour); Bwt (g), assuming

1052 1ml/O$_2$=.0201KJ (where BWt = body weight).

1053 Ausman *et al*. (1985) give a BMR of 48.3 kcal/per day (=202 KJ/day) for *S.*

1054 *sciureus.* This is consistent with the figure of 245 KJ/day and 183 KJ/day calculated with

1055 the allometric equation for a 1000g male and 700g female, respectively. For consistency,

1056   We used the allometrically-derived value here, but very similar results would be obtained

1057   using Ausman *et al*. (1985).