RESEARCH ARTICLE

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

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Funding information
American Society of Primatologists; LSB Leakey Foundation; Wildlife Conservation Society

Abstract

Optimal foraging theory predicts that well-defended potential foods should be exploited only when energy pay-offs are great. Although stinging hymenopteran nests are both well-defended and predated by primates, their larvae's energy yields rarely have been calculated, and predation-linked foraging behaviours by primates infrequently documented. Based on 58 opportunistic observations of primates raiding wasp nests for larvae, we calculated energetic yields of low- and high-risk wasp nest predation for *Cebus albifrons*, *Saimiri collinsi*, *S. sciureus* and *Sapajus apella*, and tested predictions derived from optimal foraging theory. We recorded how nests were processed and by which age-sex classes, eaten nest fragment sizes, number of occupied and empty cells, and nest occupancy patterns (percent larvae/pupae, eggs, empty cells). Basal metabolic rate (BMR) calculations showed energetic yields from 15 min foraging on low-risk nests (*Polybia quadricincta*) would meet energy needed to sustain adult female and male *C. albifrons* BMR for 4.9 and 4.5 h, respectively; yields from high-risk (*Chartergus artifex*) nests for 6.5 and 6.2 h; *Mischocyttarus* sp. nest yields (low risk, but mimetically resembling other wasps) would meet *S. collinsi* BMR for 2.9 h (female) and 2.3 h (male), and 2.6 and 2.1 h, for the slightly larger *S. sciureus*, respectively. The *Chartergus* energetic-yield value is nearly 20% of a 36 g chocolate bar (741 kJ). Our data provide quantitative support for the common assertion that wasp larvae and pupae are high-yield foods for primates. As

predicted by optimal foraging, energetic yield is sufficient to offset the risk and pain of being stung.

Petruchio: Come, come, you wasp; i' faith, you are too angry.
Katherine: If I be waspish, best beware my sting.
Petruchio: Who knows not where a wasp does wear his sting? In his tail.

William Shakespeare, *The Taming of the Shrew*

INTRODUCTION

Optimal foraging theory aims to explain how animals choose dietary items by balancing energy gained versus time and energy expended in obtaining it (Sih & Christensen, 2001; Stephens et al., 2007). The optimal prey choice model predicts that more profitable foods will have the greatest ratio of energy (or a nutritional variable to cost of obtaining the item; Krebs et al., 1978; Schoener, 1971; Stephens & Krebs, 1986), with natural selection favouring the highest rate of energy intake. Consequently, well-protected or strongly-defended potential foods should be exploited only when energetic pay-offs are great (Bateson, 2002). While optimal foraging under such conditions has been studied in a variety of taxa (Caro, 1994; Lemon, 1991; Sih & Christensen, 2001; Werner & Hall, 1974), it has been little studied in primates (but see Sayers et al., 2010), and mostly when diet item exploitation poses little inherent risk (Altmann, 1998; Nakagawa, 1989). High-risk foraging situations (e.g., exposure to predation, aggression from feeding competitors, variance in food intake) adhere closely to classical optimal foraging scenarios (Kacelnik & El Mouden, 2013; Mukherjee & Heithaus, 2013). Additional risks may occur when the food itself is dangerous and capable of self-defence (Mukherjee & Heithaus, 2013). Although there are studies that have calculated the nutritional and energetic importance of invertebrates to primates (Bergstrom et al., 2019; Bryer et al., 2015), aside from primate hunting by chimpanzees (Gilby & Wrangham, 2007), few have focused on what shapes foraging decisions when food consists of animal prey capable of instant active defence.

While predation on vertebrates is relatively rare in non-human primates (Butynski, 1982; Heymann et al., 2000; Rose, 1997), eating arthropods is common (Bogart & Pruetz, 2011; Janson & Boinski, 1992; Nekaris & Beader, 2007; Rothman et al., 2014). Many neotropical primates spend more time foraging for arthropods than for fruit (Stone, 2007a; Terborgh, 1983). Faunivores face the challenge of catching and processing prey, and many potential food items are well-protected physically (e.g., urticaceous caterpillars; Trebouet et al., 2018) and chemically (e.g., noxious beetles, millipedes; Eisner & Aneshasley, 1999; Eisner & Meinward, 1966). Others have behavioural defences and counter-attack predators, so posing a risk of pain or injury (Edmunds, 1974; Mukherjee & Heithaus, 2013) or are cryptic and difficult to locate.

Arthropods are generally considered high-energy-yielding food items (McGrew, 2001; Raubenheimer & Rothman, 2013), rich in fat and protein (26%–44% fat, 12%–65% protein by wet weight: Ghaly & Alkoaik, 2009; McCabe & Fedigan, 2007; Nakagawa, 2003). While

energetic values of insects are often calculated in foraging studies of birds and bats (Catterall, 1985; Encarnação & Dietz, 2006), studies reporting primate insectivory often mention the prey's high protein and/or fat content without providing its overall energetic value (Deblauwe, 2009; Milton & Nessimian, 1984; Srivastava, 1991). When such data are provided, the prey are non-aggressive, non-stinging forms (such as homoptera, orthoptera, lepidopteran larvae or gall-forming insects: Bryer et al., 2015; O'Malley & Power, 2014), or the studies do not identify the taxa involved and produce a summed energetic value ('insects': McCabe & Fedigan, 2007). This information gap is important to fill, since quantitative estimates of primate energetic needs and prey yield are needed to fully understand how primates balance foraging risks related to injury or pain. Currently, when species are potentially capable of aggressive defence, this aspect is considered secondary to energetic gains (e.g., O'Malley & Power, 2012, 2014 for chimpanzees ingesting *Dorylus* army ants).

While many insect taxa eaten regularly by primates may be gathered safely (e.g., orthopterans: Barnett et al., 2013; Nickle & Heymann, 1996; Stone, 2007a: coccid scale insects, Srivastava, 1991; Struhsaker, 2010), others, such as Hymenoptera, possess formidable aggressive defences: many social polistine paper wasps (Hymenoptera Vespidae, Polistinae), for example, possess powerful stings (Gobbi & Zucchi, 1985; Nagy et al., 2007), and can be very aggressive (Judd, 1998; Nonacs et al., 2004). Despite such defences, a variety of neotropical vertebrates, including primates, feed on them and their larvae (e.g., *Ateles chamek*: Felton et al., 2009; *A. marginatus*: dos Santos-Barnett et al., 2022; *Cacajao ouakary*: Barnett, 2005; *Cebus capucinus*: Joyce, 1993; *Cebus kaapori*: De Oliveira et al., 2014; *Saimiri collinsi*: Stone, 2006; *Saguinus geoffroyi*: Madden et al., 2010; *Sapajus apella*: Izawa, 1979), and wasp larvae may be either an important fallback food (sensu Lambert, 2010; e.g., Galetti & Pedroni, 1994), or one component of a trophically diverse diet (Stone, 2007a; Terborgh, 1983). Furthermore, wasps and their larvae are richer in fats and proteins than fruits (Redford et al., 1984; Rothman et al., 2014). They also form high-energy spatially clumped resources, which may add to their attractiveness: wasp larvae energetic-yields appear similar to those of insects generally eaten by tropical primates (e.g., Orthoptera, Coleoptera; O'Malley & Power, 2014; Rothman et al., 2014), but the clustered nature of in-nest wasp larvae provides rapid energetic gain, because there is minimal search-time between prey items, which have few opportunities for escape or concealment (Bryer et al., 2015).

Predation of a wasp nest is risky for primates. For example, Fragaszy et al. (2004: 49) describe how *C. capucinus* "grab a paper wasp nest and run with it, with the wasps flying after the thief, stinging face and hands for tens of meters as the monkey flees". However, how individuals process wasp nests to extract larvae has rarely been reported in detail. In the current study, we collate observations of wasp nest predation by *Cebus albifrons*, *S. collinsi*, *S. sciureus* and *S. apella* (Cebidae) at nests with different risk-settings, that is, low-risk nests, high-risk nests, and a case of mimicry, and quantify the energetic yield of wasp nest predation by *C. albifrons*, *S. collinsi*, and *S. sciureus*. The behaviours associated with the observed predation events are described in Appendix S1, energy calculations in Appendix S2. Based on an optimal prey choice framework (Hill et al., 1987; Krebs & McCleery, 1984), we predict that: (1) energetic rewards of prey will be high to select for such high-risk foraging; (2) individuals will employ handling strategies to minimize risk of prey attack (Perry & Jiménez, 2007); (3) as such activities are risky and require speed, dexterity, and practice (Boinski & Fragaszy, 1989; Fragaszy & Adam-Curtis 1997), they will be generally conducted by adults, particularly since juveniles of many primate

genera tend to be risk-averse (Fairbanks, 1993; Janson, 1993; Knott & DeLong, 2017; O'Malley & Fedigan, 2005; O'Mara, 2015; Schmidt 2010; Stone, 2007b); and (4) following Clark (1994), risky foraging will be less common in females, which have a larger reproductive asset than males, especially as males generally exhibit risk-taking behaviours more frequently (Reader & Laland, 2001; Westergaard et al., 2003).

METHODS

Study species, primates

Members of the genera *Cebus*, *Sapajus*, and *Saimiri* are all highly faunivorous (Izawa, 1979; Mallott et al., 2017; Paim et al., 2017), with *S. collinsi* (Stone, 2007a) and *Saimiri sciureus* (Boinski et al., 2002) eating more insects than fruit. Members of these genera are extremely dexterous and capable of fine digital manipulation of small and fragile items (Fragaszy et al., 2004; Janson & Boinski, 1992). Adult body size ranges from 0.6 to 1 kg (*Saimiri*) to 3–4 kg (*Cebus*) and 2–5 kg (*Sapajus*) (Smith & Jungers, 1997).

We recorded data during general and species-focused primate studies, as well as from ad hoc encounters (Appendix S1). Observed group sizes ranged from 8 to 50 individuals (both *Saimiri* spp.), of which approximately 50% were juveniles, and 6–19 (*Cebus*) and 4–9 (*Sapajus*), where approximately one-third were juveniles (defined as pre-reproductive individuals, recognizable in a group by their smaller body mass and differently shaped heads: Stone, 2006). For all species, juveniles were recently weaned; weaning occurs at 3 months (*C. albifrons*), 8 months (*Saimiri*), and 10–15 months (*Sapajus*). After 10 and 8 months, respectively, individual *C. albifrons* and *S. collinsi* fully forage for themselves, although still accompanying their mother (*C. albifrons*, Fragaszy & Adams-Curtis, 1997; *S. apella*, Gunst et al., 2008; Verderane & Izar, 2019; *S. collinsi*, Stone, 2006).

Study species, wasps

The biology of the four consumed wasp taxa is outlined below. Species were identified by JWW, BR-T and Orlando Silveira (Museu Paraense Emilio Goeldi, Belém, Pará, Brazil) from specimens and photographs of adults and nests.

Polybia quadricincta: This diurnal species is widespread in the Amazon-Guiana Shield region. Adult total length is approximately 0.7 cm. Nests commonly have an outer protective wall of carton (finely-masticated plant fibres) with 5–11 horizontally-stacked combs within (Figure 1). Each comb comprises of carton cells in which larvae are raised and pupate (Wenzel, 1991, 2020). The sting of *P. quadricincta* is powerful (A. A. Barnett, pers. exp). However, as a response to great stress or nest destruction (McCann et al., 2013), *Polybia* species often adopt a nest-desertion strategy ("the absconding swarm": Hunt, 2007), that allows the colony to return, rebuild, and continue (Detoni et al., 2021; Sazima, 2014; Sonnentag & Jeanne, 2009). Accordingly, we categorized *P. quadricincta* nests as low-risk.

Apoica thoracica: members of this genus are nocturnal; consequently, any diurnal predators encounter the entire complement of defensive adults on the nest (Van Der Vecht, 1973). Individuals are approximately 1.5 cm long and highly aggressive, attack *en masse*, and have an agonizing sting. Nests may reach 8 cm in radius and have an open, umbrella-like structure, a single larva-containing carton comb, with many hundreds of both cells and defensive adults (see figures 17A, 22B in Wenzel, 1998). Accordingly, we categorized *A. thoracica* as high-risk.
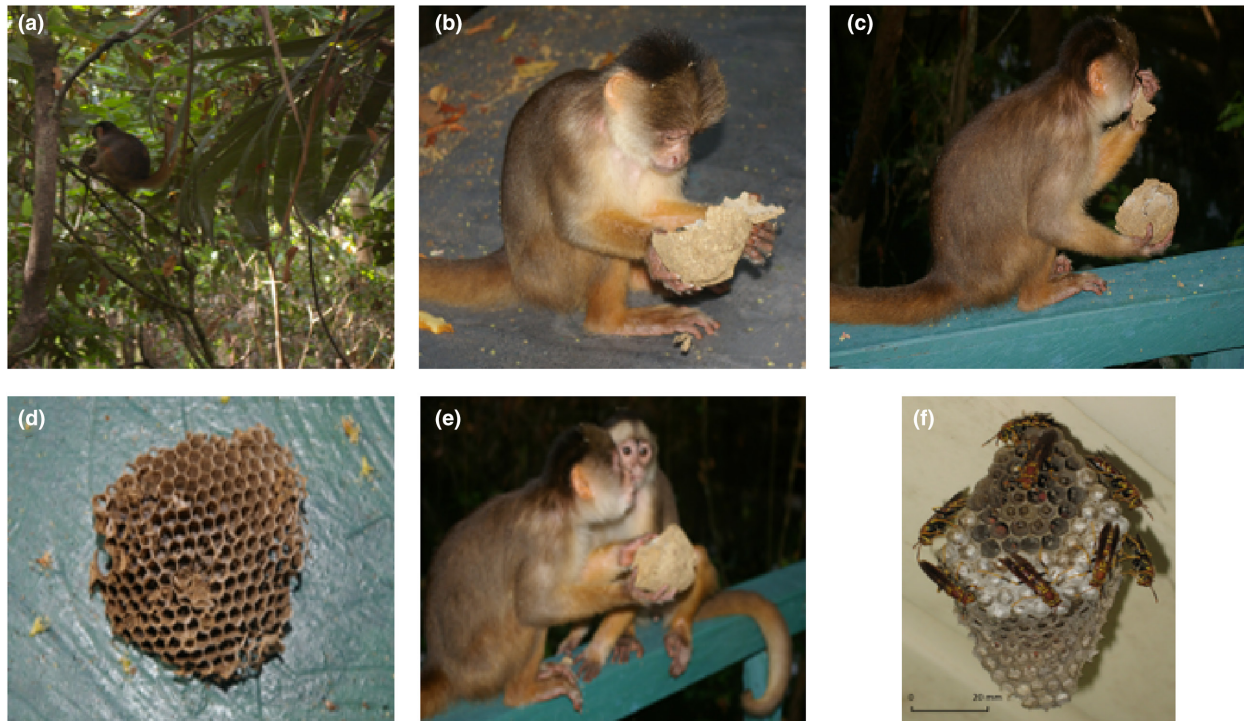
FIGURE 1 (a) An adult female *Cebus albifrons* removing the nest of a *Polybia quadricincta* colony, which shows no defensive reaction. (b) The same individual using lips and teeth to extract larval and adult *P. quadricineta* from their nest, as well as (c) extracting larvae digitally. (d) The seventh layer of a seven-layer *P. quadricincta* nest, some 80% complete and showing 188 cells. For each cell, the distance between two parallel walls is 3 mm. Eggs and small larvae are present in 16 cells. (e) Neither begging nor interfering, a juvenile *C. albifrons* watches the adult female process a *Polybia* nest. (f) *Polistes instabilis* nest included to show how cells may be free or occupied by eggs, larvae or pupae. Photos (a–e) Adrian A. Barnett; (f) Sean O'Donnell.

Chartergus artifex: Nests have multiple combs, stacked in a tube that may reach 50 cm in length (Wenzel, 1998, 2020; Figure 3). *Chartergus* adults are diurnal and reach 1.5 cm in total length. Members of this genus are aggressive, *C. artifex* notably so (Richards, 1978; Sarmiento & Saravia, 1996). Defensive responses are generally extremely vigorous, extensive, repeated, and prolonged (J. W. Wenzel, pers. obs.). Accordingly, we categorized *C. artifex* as high-risk.

Mischocyttarus sp.: A speciose diurnal wasp genus (some 250 species: Silveira et al., 2015). Although some, like *M. drewseni* are larger, most species are 0.3–0.5 cm in length. The nest is an inverted umbrella-shaped single-layered comb, rarely more than 2 cm in radius (Figure 4). The colony numbers in 10, rather than 100. While *Mischocyttarus* wasps readily sting in defence, they show desertion upon nest disturbance. The sting is not strongly painful (J. W. Wenzel, pers. obs.). Accordingly, we categorized *Mischocyttarus* as low-risk.

Study sites

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

Observations

All observations were opportunistic (ad libitum sampling), occurring during fieldwork for long-term behavioural studies (Jaú, Tapajós, Vila Anamim;

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 (*C. 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 (*C. 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 (60–100 mm rain)
4: Pousada Aldeia dos Lagos, Silves (*C. 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 (*S. 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 (*C. albifrons*, *S. 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

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 behaviours associated with wasp nest predation, such as forms of nest manipulation, larval extraction behaviours, and actions taken to minimize adult wasp attacks; (c) total time taken to remove larvae (when possible); (d) ages of other individuals present and forms of participation, if any.

While the number of wasp nests that we could measure was small ($N = 14$), the nests of each genus are distinct and non-overlapping in size, form, and cell number (compare images in Figures 1–4 with those in Richards, 1978; Wenzel, 1998). Their sizes also lay within the known ranges for the taxa (Richards, 1978; Wenzel, 1998). In addition, we collected nest fragments whenever possible to supplement estimates of percentage removal of larvae, counting the number of cells in a fragment and totaling the number that had larvae large enough to fill a cell. We did not tally eggs and very small larvae.

Measurement of nest energy-yield

Data analyses

To test prediction 1 (energy yields of nest wasp predation will be high), we calculated basal metabolic rates for *Cebus* and *Saimiri*, and yield of the

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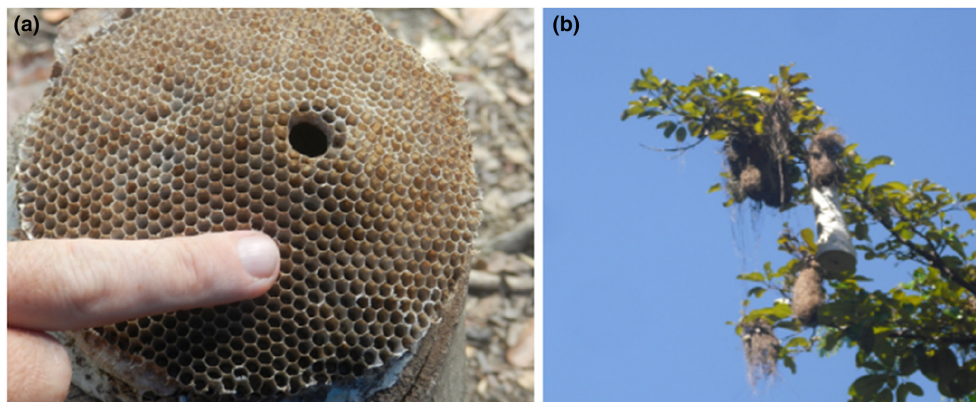

FIGURE 3 (a) *Chartergus* spp. nest, one comb-layer. (b) *Chartergus* wasp nest (white) with neighbouring oropendula (*Psarocolius* sp.) nests (brown). Photos by Adrian A. Barnett.

wasp nest sections from which larvae were eaten, using data on occupied cells percentage, cell volumes, number of cells and wasp larvae energy content. Details of energy calculations and value sources appear in Section 1 in Appendix S2. To test prediction 2 individuals will employ handling strategies to minimize risk of prey attack, we compared nest-processing behaviours with wasp defensive forms, and with calculated energy yields. To examine predictions 3 and 4 (nest predation will be more common in adults and males, respectively), we used Chi-squared (χ^2) tests to compare numbers of observed wasp nest predations per *Cebus* and *Saimiri* age and sex classes to expectations based on group composition. All Chi-square tests had a Yates correction, 2-tailed probability and 1 df.
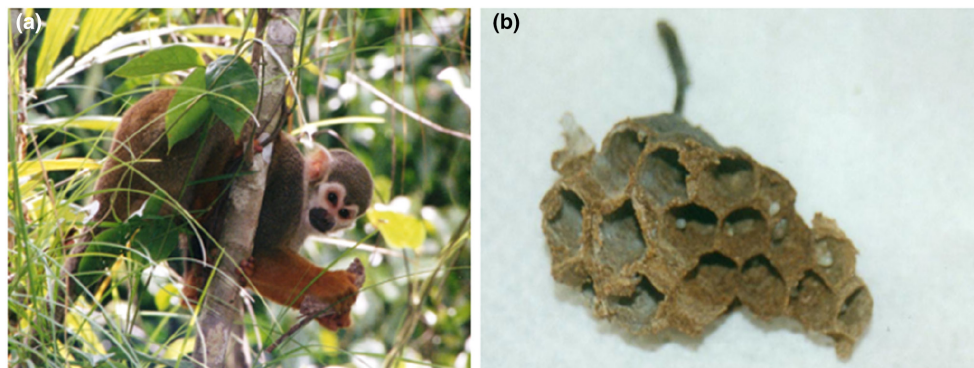
FIGURE 4 (a) Adult male *Saimiri collinsi* consuming larvae from a *Mischocyttarus* colony after knocking the nest to the ground. (b) Fragment (approximately 40%) of a *Mischocyttarus* nest eaten by *S. collinsi*. Note the presence of eggs and small larvae. The fragment is approximately 4 cm at greatest width. Photos by Anita I. Stone.

Feeding bout gross calorific yield calculations

We did not include adult wasps, as it was not possible to estimate numbers ingested. We calculated energy yield based on the number of larva-occupied cells in the area of nest exploited (Figure 1e), using standard nutritional energy densities of 16.74 kJ/g for protein and 37.65 kJ/g for fat (FAO, 2003), mean dry weight percentages of 3.13% for lipids and 15.05% for proteins (obtained from literature surveys: see below), and a consequent larval material energy value of 3.69 kJ/g (Section 1 in Appendix S2). We then reduced calculated values by 15% to account for such system losses as respiration and defecation (Goranzon et al., 1983). To assess the value of such material to study primates, we calculated BMR for both genera (Section 2 in Appendix S2). We used the energy content of a chocolate bar to provide an easily appreciated and internationally accessible form of human-linked comparison.

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

We compared the energy values of wasp larval tissue and of non-larval diet items per 100 g of tissue. We then compared mean energy yield per gram of larval wasp tissue with values gained from the literature for items eaten at the times of the year that the nests were raided. We did this analysis with data from *C. albifrons*, *Saimiri collinsii* and *S. sciureus*; we did not include *S. apella* in energy calculations, as there were only two records, and they were associated with but one class of nest (high-risk).

Inclusion of non-wasp larvae foodstuffs was based on presence in diet lists based on unpublished data from AA Barnett and BM Bezerra for *C. albifrons* and *S. sciureus*, collected in Jaú National Park, Amazonas, Brazil.

Estimation of wasp sting pain generation capacity

As we cannot ethically subject monkeys to wasp stings and quantify their reactions, we assumed that other primates feel levels of immediate pain and subsequent discomfort similar to those experienced by humans. Hence, we used personal encounters of experienced sphecologists to estimate relative sting pain between studied wasp genera. Given the widely recorded parallels in how human and non-human primates perceive various

forms of painful stimuli (Ferdowsian & Merskin, 2012; Haggard et al., 2013; Tillman et al., 1995), we believe human experience (Schmidt, 2019) is a viable proxy.

RESULTS

Field observations

We observed interactions between primates and wasp nests on 58 occasions (13 for *C. albifrons*, 28 for *S. collinsi*, 15 for *S. sciureus* and 2 for *S. apella*: all events detailed in Appendix S1). Of these, 57 involved single animals and one which appeared to involve collaborative predation. Active predation was observed on 45 occasions. Of the remaining 12, eight involved juveniles investigating nests recently discarded by adults, two involved unsuccessful nest attacks by juveniles, and two involved avoidance of high-risk nests (*Apoica*, *Chertargus*) by adults. The active predation events involved four wasp genera: *Polybia* (*N* = 8 events; Figure 1a–f), *Apoica* (*N* = 1; Figure 2), *Chartergus* (*N* = 7; Figure 3a,b), and *Mischocyttarus* (*N* = 29; Figure 4a,b). In addition, at Jaú National Park and Rio Tapajós (sites 2 and 3), we encountered a further 20 wasp nests damaged by *C. albifrons* but did not see the actual event. While records of raided nests could not be used in the energy calculations, or to determine behavioural strategies, we mention them to show that such events are not necessarily rare, just infrequently met while in progress.

For *Polybia* nest predation, primate removal of larvae appeared close to 100%. While this wasp has a powerful sting, we observed no extensive defensive activity by colony adults; no signs of physical discomfort from nest-predating *C. albifrons*, and no records of wasps stinging brood-consuming animals. This may relate to *Polybia* spp. use of the absconding swarm nest-desertion strategy (Sazima, 2014; Sonnentag & Jeanne, 2009). The only collective predation event observed (three adult *C. albifrons*) involved an *Apoica* nest. We observed both *S. collinsi* and *S. sciureus* knocking down *Mischocyttarus* nests, then eating in-cell larvae directly following adult nest-desertion. When juvenile primates were present, they watched but were never seen to initiate nest-attacks (Figure 1e).

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 18.74 kJ/g, and *Polybia* sp. larvae 20.21 kJ/g (Ramos-Elorduy et al., 1998). This resembles values for whole adult European vespids (18.83–25.1 kJ/g: Török, 1981).

Accordingly, the 25.7 g of larval tissue in a *Polybia* nest could have provided 46 3 kJ of metabolizable energy (92% of male, 98% of female *C. albifrons* BMR; Table 2). For comparison, this is some 60% of the energy in a 36 g chocolate bar (741 kJ). For *Chartergus* the 26.7 g of larval tissue present could have provided about 466 kJ of metabolizable energy (93% of male, 99% of female *C. albifrons* BMR). *Mischocyttarus* nests held an estimated 5.7 g of larval tissue, yielding a gross energy value of 114 kJ 54% of male and 67% of female *S. collinsi* BMR, and 47% and 62.2%, respectively, for male and female *S. sciureus*; 13% of the energy, 741 kJ, in a 36 g chocolate bar.

Because *Polybia* and *Chartergus* nests differed in the number of cells in examined layers (235 vs. 378: *Chartergus* 60.8% more), and in

individual cell volumes (47.35 mm^3 vs. 114.6 mm^3: *Chartergus* 142% larger), energy yields also differed notably, with a single *Chartergus* nest comb layer containing 135.6% of the metabolizable energy of the entire *Polybia* nest (Section 1 in Appendix S2). Meanwhile, tissue yields (21.1 kJ) from *Mischocyttarus* sp. nests (5.71 g) would provide 4.2% and 4.7% of BMR for male and female *C. albifrons* (around 62 and 68 min, respectively), of a 24-h period. This may explain why individuals of *C. albifrons*, a larger species, were not observed exploiting such small nests.

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

Mean energy yields (kJ per 100 g) of wasp larval tissue exceed the energy yields of a similar mass of other foodstuffs by between 14.7% and 85.1% for *Cebus* (mean ± SD, 66.5 ± 22.6, $N = 9$), and 4.9% and 80.1% for *Saimiri* (mean ± SD, 58.0 ± 32.5, $N = 5$; Table 3). In no cases were yields from plant-based foodstuffs greater than those for wasp larvae. This analysis also emphasized the high percentage of protein in wasp larvae compared to other foodstuffs, since, while the former are over 60% protein, protein levels in plant-based diet items are notably lower (e.g., *Annona*, 1.4%: Villela et al., 2013; *Bactris*, 1.8%–2.7%, Yuyama et al., 2003; *Spondias*, 1.6%, Tiburski et al., 2011).

Thus, feeding from *Polybia* nests yields a mean of 33.2% more energy gram than an equivalent mass of fruit (SD ± 23.37, range 16.4–86.3, $N = 9$) for *C. albifrons*, while *S. collinsi* will have gained a mean of 41.9% (SD ± 29.1, range 18.5–95.1, $N = 5$) from feeding from *Mischocyttarus* nests. This supports Prediction 1, that energy yields from nests would be high compared to other food types available.

Primate nest feeding behaviour in relation to wasp defence intensity

Variation exists between wasp species in both aggression levels and sting pain intensity, with more aggressive species having more painful stings (Table 4). Wasp aggression and sting intensity, as well as nest size, were related to primate feeding behaviours and duration of foraging at wasp nests, with predation strategies adopted vary to reduce the time a primate spends in proximity to a nest as aggression and sting-pain increase.

This diversity of behaviours (see also Appendix S1), supports Prediction 2, that individual primates will deploy strategies that minimize risk of prey attack.

Differences in raiding primate age and sex

We observed 47 raids on wasp nests (all primate and wasp species combined), of which 44 were successful attacks by adults, involving 46 individual primates. The sex of 1 adult was not determined while of the remaining 45, 19 were females and 26 were males ($\chi^2 = 1.088$, NS).

For age-classes, attacks did not occur in proportion to group age-classes composition. When the adult/juvenile ratios of *C. albifrons*, *S. collinsi* and *S. sciureus* were averaged, the expected number of attacks by younger individuals was 16 of the 49 observed events (all adult and juvenile, successful and aborted, attacks combined: see Appendix S1). However, we recorded only three such events ($\chi^2 = 15.68$, $p < 0.0001$), only one of which

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

Primate species (BMR)	Wasp species[a]	Larval mass captured (g) per 100 cells consumed	Energy yield (metabolizable energy) (kJ)	Chocolate bar equivalent %[b]	% BMR (Ross; Stahl)	Hours of resting time supported by the energy gained	Feeding bout length (min)
Cebus albifrons (585 kJ[c] [Ross] 752 [Stahl] kJ/day[d])	*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[c] − 392.7 kJ/day[d])	*Mischo-cyttarus* sp.	5.7	21.1	2.8	7.08; 5.4	1.68–1.28	5 (including processing)

[a]Due to small sample size (N = 1), and possible loss of material prior to sampling, calculations were not possible for *Apoica thoracica*.
[b]Based on 36 g Snickers® bar (Mars Inc). (741 kJ: https://www.snickers.com).
[c]logBMR vs. logMass regression.
[d]Using Stahl's equation, which relates BMR (millilitres CL per hour) to body weight (M in kg).

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

Diet item	Energy value per 100 g kJ (kcal)[a]	Energy yield of item as percentage of yield for 100 g wasp larva tissue[b,c]	Reference
Cebus albifrons Polybia			
Spondias mombin (Anacardiaceae) fruit pulp	273.7 (65.42)	17.8	Tiburski et al. (2011)
Annona sp. (Anonaceae) fruit pulp	296.7 (70.91)	19.3	Villela et al. (2013)[d]
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 and 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)[e]
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)[f]
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)[f]

[a]Given in literature as kcal, and converted here to kJ for consistency (kcal value in parentheses: 1 kcal = 4.184 kJ).

[b]Using values for fully hydrated food items as this is how they would be ingested by the primates.

[c]Values (calculated from Table 2) = 369.7 for 100 g of *Polybia quadricincta* larval tissue, 369.52 for *Mischocyttarus* sp.

[d]For *Annona crassifolia*.

[e]For *Passiflora glandulosa*, *Passiflora alata* and *Passiflora edulis*.

[f]For *Pouteria caimito*.

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

Wasp species	Aggression level[a]	Sting pain intensity[a]	Primate attack behaviour[b]	Energy yield per unit time (kJ/min)[c]
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

[a]Based on field experience of JW and other experienced fieldworkers on Neotropical wasps (see Acknowledgements).

[b]Table 1 contains details.

[c]Based on duration of attacks (Table 1), and energy yields per nest type (Table 2).

was successful (a juvenile *C. albifrons*; Appendix S1, Event 13), while two (events 40 and 41) involved a juvenile *S. collinsi*, who withdrew after being badly stung, and without reaching the nest. Therefore, we found support for Prediction 3 (raids on wasp nests will be conducted by adults).

Of the 45 raids conducted by adults, we could not determine the sex of 1 adult, but of the remaining 44, 19 were females and 25 were males ($\chi^2 = 1.088$,

$p > 0.05$). For relationships between level of risk and sex of raiding adult, the number of males and females raiding the low-risk *Mischocyttarus* nests did not differ significantly; *S. collinsi* ($\chi^2 = 0.89$, $p = 0.96$), or were at parity for *S. sciureus*. For *C. albifrons* raiding the medium-risk *Polistes* nests, eight of nine records were from females ($\chi^2 = 5.44$, $p = 0.019$), while all eight attacks (*C. albifrons* and *S. apella* combined) on high-risk nests (*Apoica* and *Chartaegus* combined) involved adult males ($\chi^2 = 8.00$, $p = 0.004$). These findings provide support for Prediction 4, that risky foraging behaviours will be less common in adult females than in males.

DISCUSSION

Our predictions received full or partial support. While wasp nests yield more energy per gram than plant-based food, they must be accessed with specific strategies depending on the nature of the wasp species defence.

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

Mischocyttarus and *Polybia* wasp larvae energy values were high. An incomplete data set meant it was not possible to calculate energy yield per-unit-time for *Apoica* and *Chartergus*. However, given the larger number of larvae-containing cells in their nests, it is likely that yields were proportionally higher for *Apoica* and *Chartergus* predation events. Consequently, such risker events would yield higher pay-offs.

Vespid Hymenoptera are abundant in Amazonia, with 50–60 species in any one area of *terra firme* forest (Silva & Silveira, 2009; Somavilla et al., 2015). Thus, widely ranging and foraging primates, such as *Cebus* and *Saimiri* (Kinzey, 1997), will encounter wasp nests frequently. Larvae provide a higher nutrient to mass ratio than adult insects, are more easily assimilated as thinner less-sclerotized exoskeletons are more quickly digested and lack legs and wings which both fill the gut lumen and are indigestible (Janssen et al., 2017).

Other dangerous, but potentially high-yield foods, like scorpions and large centipedes, though often abundant, may simply be avoided because of their lethality (such venom can kill small mammals swiftly: Molinari et al., 2005). Their predation requires investment in learning-based behaviour, only becoming energetically viable in scorpion-specialists, (meerkats: Thornton & McAuliffe, 2006). Despite their high energy content, such potential prey become too dangerous for generalists such as *Cebus* and *Saimiri* (Mukherjee & Heithaus, 2013).

Prediction 2 (primates would use specialized handling strategies to minimize risk of being stung)

We found partial support for this prediction. We expected nests of each wasp species to be treated differently, as they vary in defensive response vigour, and (as perceived by humans) sting power and duration. Though *Polybia* (including *P. quadricincta*) have a powerful sting (McCann et al., 2013), monkeys showed no signs of being stung (Figure 1a), and no wasps were observed to attack them while they consumed nest contents (Figure 1b,c). This may be due to the absconding swarm strategy (O'Donnell & Jeanne, 2002; Sazima, 2014; Sonnentag & Jeanne, 2009) being an additional anti-predator mechanism to sting-based next defence. The importance of the strategy deployed by adult *Saimiri* when feeding

on *Mischocyttarus* of knocking down nests and waiting for adult wasps to leave (i.e., abscond) can be seen from the results of events 40 and 41 (Appendix S1) where young animals were badly stung.

Apoica wasps are regarded with immense caution by rural Amazonians and researchers, due to intense and long-lasting pain caused by their sting (Robert Jeanne, Fernando Noll, and Sean O'Donnell, pers. comms.), and specologists consider them one of the most dangerous wasps (Robert Jeanne, pers. comm.), which may explain why *Saimiri* actively avoided such nests (Event 49, Appendix S1). The attack on an *Apoica* nest by three adult male *C. albifrons* was the only predation event where more than one individual was involved and may have had a risk-spreading function (Mukherjee & Heithaus, 2013).

The *Chartergus* predation-events demonstrated the coordinated and vigorous nest defence considered typical of polistine wasps (Chadab, 1979). Monkeys raiding *Chartergus* nests fled actively and appeared to receive stings, similar to events reported by Fragaszy et al. (2004). The wasp genus is so aggressive that icteriid birds (*Cacicus*, *Gymnostinops* and *Psarocolius* spp.) suspend their nests beside them for protection (Quinn & Ueta, 2008; Robinson, 1985: Figure 3b). Our data indicate that large nest-cell size, and consequent high energy yields, justified the smash-grab-and-flee approach for the primate, indicating the presence of alternative foraging strategies within the overall rubric of insectivory and nest-based larval wasp predation. However, the active avoidance by a group of *S. sciureus* of a *Chartergus* in their home range (Event 52, Appendix S1) shows not all primate species have this capacity.

Though painful (A. I. Stone, pers. exp.), a *Mischocyttarus* sting is less powerful than *Polistes* (J. W. Wenzel, pers. exp.; Schmidt, 2019). Additionally, *Mischocyttarus* wasps are rarely aggressive, quickly deserting a threatened nest. However, many *Mischocyttarus* spp. appear as Batesian mimics of other genera, more bellicose and/or with more powerful stings, including: *Agelaia* (O'Donnell & Joyce, 1999; Starr, 1985 [as *Stenopolybia*]), and *Polybia* (Garcete-Barrett, 2014), with the deception being sufficient to promote avoidance in visually oriented predators (dragonflies: O'Donnell, 1996; Rashed et al., 2005). *Saimiri* monkeys used a different technique than *Cebus* and *Sapajus* capuchins to attack wasp nests, knocking them to the ground and awaiting desertion by adult wasps (which takes 2–5 min). Use of this technique indicates even though *Polistes* wasps are non-aggressive, *Saimiri* exercise caution and risk-avoidance. It may also be a standard response by *Saimiri* to wasp nests, since *S. oerstedi* display similar behaviour with *Polistes* wasps (Boinski & Timm, 1985).

Risk assessment occurs even when a species is fully or partially immune to the potential prey's venom (Rowe & Rowe, 2006). For *Saimiri*, risk assessment may be a mixture of actual and, due to *Apoica*-mimicry by *Mischocyttarus*, perceived risk *Apoica* nest avoided: see Appendix S1. *Saimiri* exploited only nests of wasp species either physiologically (*Polistes*) or behaviorally (*Mischocyttarus*) low-risk. Both *Mischocyttarus* and *Polistes* are abundant (providing, 20 and 24 respectively, of the 63 species inventoried by Silva & Silveira, 2009). Thus, encounters with these less-dangerous insects may be sufficiently frequent to provide energy and nutritional supplements for the smaller *Saimiri*, leaving the higher-risk, but higher-yield, species for the larger *Cebus*.

Prediction 3 (that adults would mostly predate nests)

We found support, 93.8% of predation events involved adults. Juveniles comprise almost 50% of social groups of *S. collinsi* (Stone, 2007a, 2007b);

however, juvenile squirrel monkeys were not engaged in wasp nest predation, except of those that adults had discarded (Events 14–21, 47, 48, 53; Appendix S1). Both juvenile *Cebus* and *Saimiri* watched, rather than participated (*Cebus* juveniles initiated 1: Event 13), indicating risky actions often require experience (two young *S. collinsi* were badly stung when approaching nests: Events 40, 41, Appendix S1). These observations might be expected when predation is difficult and high-risk, requiring speed, coordination and dexterity (Gunst et al., 2008; Gunst, Boinski, et al., 2010; Gunst, Leca, et al., 2010; Stone, 2006; Westergaard et al., 1997). Soley et al. (2017) reported greater success with a hard-to-process resource with painful defence capacity (hermit crabs) for *C. capucinus*. In this context, it is interesting to note that the high-risk, high-speed attacks on *Chartergus* require experience and coordination, yet in no case was another animal seen observing the raider. It remains uncertain how experience is gained.

Foraging theory predicts individuals most likely to take risks and engage dangerous prey will be younger, lower in social rank, hungry, and/or less-experienced (Elbroch et al., 2017; Mukherjee & Heithaus, 2013). However, wasp nest defences can only be minimized or avoided with guile and speed, which come with practice. Wasp nest predation appears to be the purview of adult *Cebus* and *Saimiri*, and like such items, can only be processed by watching proficient individuals (Ottoni et al., 2005; Figure 1e), like the successful use of stones and anvils in capuchins (De Resende et al., 2008). Gaining capacity to attack wasp nests has parallels with how chimpanzees learn how to fish for termites (Lonsdorf, 2006), and process fruits (Bray et al., 2018; Corp & Byrne, 2002), as well as the ontogenetic enhancement of manual dexterity facilitating this (Boesch et al., 2019).

Prediction 4 (risky foraging would be more common in males)

We found support for this prediction. While six of the seven observed *Polybia* predation events involved adult female *C. albifrons*, all predation on *Chartergus* and *Apoica* involved males. For *S. collinsi* feeding on *Mischocyttarus*, 40% of events involved adult females. These wasps are non-aggressive, therefore little direct risk would be associated with predation. Females with dependent young were not seen to attack nests (Events 14–41, 42–40, Appendix S1), which may explain reduced female participation.

Other studies have found a strong male-bias in capuchin monkey wasp-nest predation (Fragaszy et al., 2004; WR Spironello, unpublished data: 13 events in 13 months), with similar bias recorded for other primates (Dufour, 1987; Paoletti & Dreon, 2005). This pattern is notable given lactating females have higher demands for protein and fat (Herrera & Heymann, 2004), and greater insect consumption (McCabe & Fedigan, 2007). Lactating females may not exploit this resource due to the risk of infants being stung, who do not leave their mother's body surface until several months after birth (*Cebus*: Young & Heard-Booth, 2016; *Saimiri*: Byrne & Suomi, 1995; Tardif, 1994). The low numbers of adolescents among those raiding nests (6.7% *Cebus*; 6.9% both *Saimiri* combined: Appendix S1) is also notable, since young *C. albifrons* have 2.5% higher protein requirements than adults (Ausman & Hegsted, 1980), emphasizing that considerable restraint is exercised by adolescents. Observation of predation technique to mitigate risk of sting by inexperienced individuals (Appendix S1; Figure 1e) parallels the attention given by juveniles to other complex foraging tasks, such as nut-cracking (De Resende et al., 2008; Visalberghi, 1987).

Perhaps wasps are favoured primarily because of their taste, so that the primates running risks to access them are not energy accountants, but gourmands. Taste preference for pleasure alone is a rarely explored aspect of primate foraging ecology, as when the role of taste perception is assayed it is in the context of the capacity of this sense to inform or fore-warn about the composition of a potential foodstuff (Dominy et al., 2001; Hellekant et al., 1993; Simmen et al., 2006; Simmen & Sabatier, 1996). This possibility could be investigated with in-field choice tests that presented wasp larvae and other insects of equal energy yield using feeding plat-forms as used by Bicca-Marques and Garber (2003). The importance of micro-nutrients, such as vitamins and minerals (Bryer et al., 2015), also needs investigation.

CONCLUSIONS

Individual primate behavioural sequences were notably uniform during *Chartagus*, *Mischocyttarus* and *Polybia* predation-events. Nevertheless, how primates processed nests of each genus varied greatly. From this we conclude that, despite being a vigorously defended resource (in many cases by exceptionally powerful stings), when successful, exploitation of nest-based wasp larvae has a high energy pay-off. Our results suggest that the occasional energy bonanza derived from exploiting such challenging foods exceeds that derived from more tractable items, such as fruit. Thus, such a form of exploitation is a viable strategy if the predating primate has the dexterity and speed to achieve it successfully, while simultaneously minimizing the risk of pain and injury.

As such, wasp-nest predation should be seen in the larger context of risky and demanding items exploited by these primates. For example, *Saimiri* employ an "oven mitt" technique when handling urticaceous cater-pillars; cushioning their hand with the tuft of fur at the end of their tail while grabbing the prey, then rubbing the caterpillar vigorously against a branch or tail-fur to remove irritant hairs (Boinski & Fragaszy, 1989; Stone, 2006).

Insectivory is generally considered the purview of smaller primates (Atsalis, 2008; McGrew, 2001), and arthropods compose some 70% of the diet of *S. collinsi* (Stone, 2007a), while Hymenoptera account for 40% of *S. collinsi* arthropod prey in some months (Stone, 2004). However, in-sects can comprise 46% of the *Cebus* monthly diet (Mallott et al., 2017; McCabe & Fedigan, 2007), and wasp larvae 15%–36% (Mallott et al., 2017; Perry & Jiménez, 2007). The high energy values revealed here (compare Tables 2 and 3), allied with the possession of chitinases by *Cebus* (Janiak 2016; Janiak et al., 2018), and the thin chitin coverings of wasp larvae, may explain the apparent contradiction of how a comparatively large primate like *Cebus* can be so highly insectivorous for extended periods of the year.

AUTHOR CONTRIBUTIONS

Adrian A. Barnett: Conceptualization (lead); data curation (lead); formal analysis (equal); investigation (lead); methodology (lead); project admin-istration (equal); writing – original draft (lead); writing – review and edit-ing (equal). **Anita I. Stone:** Conceptualization (supporting); data curation (supporting); formal analysis (equal); methodology (equal); writing – origi-nal draft (supporting); writing – review and editing (equal). **Peter Shaw:** Formal analysis (lead); methodology (equal); writing – review and editing (equal). **Beatriz Ronch-Teles:** Investigation (supporting); methodology (supporting); resources (equal); writing – review and editing (equal). **Tereza dos Santos-Barnett:** Data curation (supporting); formal analysis (support-ing); investigation (supporting); methodology (supporting); visualization

DATA AVAILABILITY STATEMENT
The datasets analysed during the current study are available from the corresponding author on reasonable request.

ETHICAL APPROVAL
All research complied with Brazilian law. We adhered to Association for the Study of Animal Behaviour guidelines for research animal treatment

(Buchanan et al., 2012), to the Code of Best Practices for Field Primatology of the American Society of Primatologists and International Primatological Society (www.asp.org/resources/docs/Code20of_Best_Practices20Oct202014.pdf). We did not trap or handle study animals and maintained a minimum 2 m distance from individuals to minimize stress.

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SUPPORTING INFORMATION

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