

# Juggling options: Manipulation ease determines primate optimal fruit-size choice

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## Funding information

This work was supported by American Society of Primatologists, Columbus Zoo Conservation Fund, Sophie Danforth Conservation Fund, LSB Leakey Foundation (US), Leakey Fund (UK), Laurie Shapley, Margot Marsh Foundation, Oregon Zoo Conservation Fund, Percy Sladen Memorial Fund, Pittsburgh Zoo and Aquarium Conservation Fund, Primate Action Fund, Primate Conservation Inc., Roehampton University, Wildlife Conservation Society (all to AAB). Technical assistance was provided by Fundação Vitória Amazônica.

**Associate Editor:** Jennifer Powers

**Handling Editor:** Eike Neuschulz

## Abstract

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

## KEYWORDS

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

## 1 | INTRODUCTION

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

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

The golden-backed uacari (*Cacajao ouakary* (Spix, 1823): Pitheciinae, Pitheciidae) is a medium-sized Neotropical primate (mean weight: 3.5 kg, mean body length: 389 mm (♀) and 414 mm (♂): Hershkovitz, 1987), with a short, bushy, non-prehensile tail. Its principal habitat is the blackwater flooded forests (igapó) of the Rio Negro Basin, western Amazonia. In these areas, *C. ouakary* home range may exceed 2 km<sup>2</sup> (Bezerra, Barnett, Souto, & Jones, 2011). *Cacajao ouakary* shows group fission–fusion behavior as a strategy

to avoid scramble competition for resources. Therefore, they often travel and forage in small bands (2 to 26 individuals) the size of these varies seasonally (Barnett, 2010). These primates feed, mainly, on immature seeds (Barnett, Bowler, Bezerra, & Defler, 2013; Barnett, de Castilho, Shapley, & Anicácio, 2005). For such items, outer layers of the husk are removed with procumbent incisors and harder layers (if present) then punctured with hypertrophied canines, a process known as sclerocarpic foraging (sensu Kinzey, 1992).

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

## 2 | METHODS

### 2.1 | Study area and subjects

We conducted our study in the blackwater seasonally flooded forest (igapó, sensu Prance, 1979) in Jaú National Park (1°53'15"S, 61°41'25"W), a 2.3 million ha protected area in central Brazilian Amazonia, situated some 220 km west of the city of Manaus on the south bank of the Rio Negro, Amazonas State (Figure S1). Igapó has an annual monomodal flood pulse, that is both of high amplitude (it may exceed 12 m) and long duration (up to 9 months) (Junk et al., 2011). Igapó has low plant species richness, and fruit production synchronized to the flood pulse (Ferreira & Parolin, 2007), with most species being hydro- or ichthyochorous (Correa, Winemiller,

Lopez-Fernandez, & Galetti, 2007). Phenological synchrony is high, both within and between species. Accordingly, igapó fruit production peaks between March and June, that of leaves between July and October, at which time tree canopy fruit availability is low, and during November–February neither fruit nor young leaves are available in igapó (Barnett, 2010). The current work is part of a broader study of golden-backed uacari foraging ecology (Barnett, 2010; Barnett, Almeida, et al., 2012; Barnett et al., 2013, 2016; Barnett & Shaw, 2014; Bezerra et al., 2011) conducted between October 2006 and April 2008 in Jaú National Park.

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

In the *C. ouakary* diet, 77% of all recorded fruits are ingested in the immature state and thus eaten after direct removal from the parent tree (Barnett, 2010). Almost all fruits eaten when ripe are small soft berries (e.g., *Eugenia* and *Calypttranthes*: Myrtaceae). The sole large hard fruit eaten when mature are from *A. latifolia*. We never recorded these being eaten when immature, even though they mature contemporaneously with species whose immature seeds are common in the uacari diet, such as *Micropholis venulosa* (Mart. & Echlér) Pierre (Sapotaceae) and *Eschweilera tenuifolia* (O. Berg) Miers (Lecythidaceae) (Barnett, 2010). Moreover, and unlike any other item in the uacari diet, eaten *Aldina* fruit are retrieved not from the canopy of their parent tree, but from the flooded igapó water surface, on which they are floating. During this period, *A. latifolia* trees no longer have fruits in their canopies; instead, the entire annual crop is floating on the water surface within the igapó forest (Figure S2a).

At the time of *A. latifolia* consumption, only trees of the genera *Maprounea*, *Casearia* Jacq. (Salicaceae), and *Ternstroemia* Mutis ex L. f. (Pentaphylacaceae) were recorded as fruiting in igapó; all were small trees (< 3 m canopy width), with low crop volumes (e.g., *Casearia*, 155 g/canopy; *Ternstroemia*, 72 g/canopy: Barnett, 2010). Given individual *Aldina* fruit masses (even the smallest are larger than most other igapó fruits) and their abundance (when trapped by floating impedimenta and by branches of partially submerged trees), *Aldina* fruit densities can reach up to 30 per m<sup>2</sup> (Barnett, unpublished data). These floating fruits likely represented the largest volume of fruit by species available in igapó at that time. Within the igapós of Jaú National Park, *A. latifolia* is abundant, ranking fourth for dominance and sixth in terms of importance index (Aguiar, 2015).

In the area of study, individuals of *A. latifolia* exceeded 20 m in height and more than 100 cm dbh and had a very large canopies (mean volume: 169.6 m<sup>3</sup>), with abundant fruit crops (mean number per canopy: 256 ± 166.5) (Barnett, 2010).

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

## 2.2 | Collection method

### 2.2.1 | Feeding behavior, biometry, and fruit penetrability

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

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

To quantify feeding observations, we used scan sampling interspersed with *ad libitum* observations (Altmann, 1974). This was based on blocks of 90 s consisting of two 30 s scans, separated by 30 s of *ad libitum* observation. This mixed sampling strategy maximized collected data representativeness (Fragaszy, Boinski, & Whipple, 1992). Deployment of this strategy was helped by the fact that, at this time of year, fruit resources were scarce, and the uacaris foraged singly or in small groups (2–4 animals). We recorded manipulation time (retrieval, de-husking, and seed processing) by direct observation, recording times them with an electronic stopwatch. We operationally

defined these categories as follows: i) retrieval: the time from when the animal initially removed the floating fruit the water surface and, having carried the fruit to a specific location, sat to process it, ii) de-husk: the time from when the uacari held the fruit to its mouth and began to bite the husk until the husk covering was reduced sufficiently that the seed could be extracted, and iii) seed processing: the time required for the seed to be removed from the remains of the husk, and then processed dentally, timing terminating when the seed (or parts thereof) were swallowed. Note: *Aldina latifolia* fruits have a smooth surface and do not require any additional actions, such as removal of spines or hairs, to prepare them for dental processing.

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

We could not collect eaten seed weights directly but because the primates often ate most of it (Balcomb & Chapman, 2003; Barnett, Boyle, et al., 2012), but we were able to derive eaten seed size from fruit lumen volumes. The size of the reassembled seed space was then measured, and the volume was calculated, and from this the weight, using mean densities of entire seeds. To test whether relative seed volume affected fruit-size choice, we measured seeds separately, and then treating the seed as a prolate triaxial ellipsoid, we calculated seed volume ( $V$ ) using the formula:

$$V = 4/3 \pi ab^2$$

where the value for the central diameter is the mean of two measurements from the center of the ellipse to the most distant point on the pod, being (a) is the half of length of the longest axis (seed length) and (b) the half of the shorter axis (seed width). This was used to calculate volumes for 65 seeds (44 uneaten and 21 eaten fruits: Table S1).

To ensure maximum comparability, we collected eaten and uneaten fruits from the same area and in the same time period. We aimed get a perfect balanced design, but given the nature of the data, we were not able to retrieve all information for every fruit (some eaten fruits were impossible to be pieced together to measure all variables). We measured fruit pericarp penetrability separately at points diametrically opposite on the medial circumference of the fruit surface in 8 eaten and 25 uneaten fruits (total 33 fruits). We also measured minimum and maximum husk thickness in 43 eaten and 53 uneaten fruits (total 96 fruits). To obtain the penetrability measures for these fruits, we used a prosthetic uacari canine (weight

4.5 g, height 4.2 mm, tip diameter 1 mm<sup>2</sup>) mounted on a standard fruit penetrometer (Facchini FT 011 Fruit Firmness Tester, marketed by International Ripening Company, Norfolk, VA 23502–2095: see Barnett, Santos, Boyle, & Bezerra, 2015 for details) and measured penetrability at the fruit midpoint. To ensure repeatability, the penetrometer was mounted in a Fridley Fruit Tester (see Figure 3, Barnett, Santos, et al., 2015). A prosthetic uacari canine was used in place of the standard penetrometer head because previous studies (Barnett, Santos, et al., 2015) had shown that the standard penetrometer head substantially overestimates force required for husk penetration.

### 2.2.2 | Hand allometry

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

### 2.2.3 | Data analysis

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

For the subset of observations for which fruit processing times were available ( $n = 21$ ), we individually regressed fruit length (mm) against time spent: (i) retrieving fruit from the water, (ii) de-husking, and (iii) eating the seed.

To test for possible fruit selection by uacaris, we performed an *F* test to compare variances of total length, width, and maximum and minimum husk thickness between eaten and uneaten *A. latifolia* fruits. The null hypothesis for this test was that the ratio of the variances of the eaten and uneaten fruits would be equal to 1. To control for possible bias within an unbalanced sampling design (eaten = 56, uneaten fruits = 105), we used a bootstrap procedure (permutation with replacement). In each run, the eaten and uneaten fruit measures were randomized and *F* test variance computed. We then compared the statistics of the 999 permutations with the observed value to calculate the probability that the observed value was larger than random. Descriptive statistics and frequency of hand measurements were performed to obtain minimum, maximum, and average sizes. All analyses were made in R (R Core Team, 2016).

### 3 | RESULTS

#### 3.1 | Fruit measurements

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

#### 3.2 | Observations

The three uacaris selected 21 fruits and abandoned six (Table S3). Once retrieved from the water surface, individual fruit were taken to

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

There was no relationship between retrieval time and fruit size ( $R^2 < 0.01$ ,  $F_{1,19} = 0.003$ ,  $p = .951$ ; Figure 1a), but there was an increase in time taken to de-husk the fruit ( $R^2 = 0.25$ ,  $F_{1,19} = 7.681$ ,  $p = .012$ ; Figure 1c), and time required to process seeds from larger fruits ( $R^2 = 0.23$ ,  $F_{1,19} = 7.202$ ,  $p = .014$ ; Figure 1b). Once fruits are removed from the surrounding husk, the relationship between time taken to process a seed and its volume (in  $\text{cm}^3$ ) shows a very clear linear relationship ( $R^2 = 0.96$ ,  $p < .001$ : Figure 1d). In addition, it was observed a proportional increase in seed size as much as in fruit size (Figure 2a) and weight (Figure 2b) increased ( $R^2 = 0.71$ ,  $F_{1,55} = 132.1$ ,  $p < .001$ ; and  $R^2 = 0.61$ ,  $F_{1,47} = 78.06$ ,  $p < .001$ , respectively). Smaller and lighter fruits tended to have disproportionately thicker husks, compared to larger and heavier fruits ( $R^2 = 0.61$ ,  $F_{1,77} = 124.2$ ,  $p < .001$ ; and  $R^2 = 0.55$ ,  $F_{1,56} = 72.53$ ,  $p < .001$ , respectively). In both cases, the asymptotic model had a better fit compared to a linear model (Delta AIC > 2).

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

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

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

<sup>a</sup>Sum of palm length and D2 length.

<sup>b</sup>Width value multiplied by two.

<sup>c</sup>Total hand length multiplied by two.



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

<sup>a</sup>measured indirectly from reconstituted lumen volumes.

Penetrometer values were obtained from 25 uneaten and 8 eaten *A. latifolia* fruits. The mean penetrability value for the exocarp (outer husk) was 3.94 kg/mm<sup>2</sup> (range 3.5–4.3, *SD*  $\pm$  0.23), with a maximum thickness that varied from 1.50 to 3.32 mm (mean 2.43, *SD*  $\pm$  0.74). However, the very much thicker mesocarp (inner husk: up to 23 mm) was spongy and had a very low penetration resistance (mean 1.29 kg/mm<sup>2</sup>, range 1.14–1.46, *SD*  $\pm$  0.14, *n* = 11).

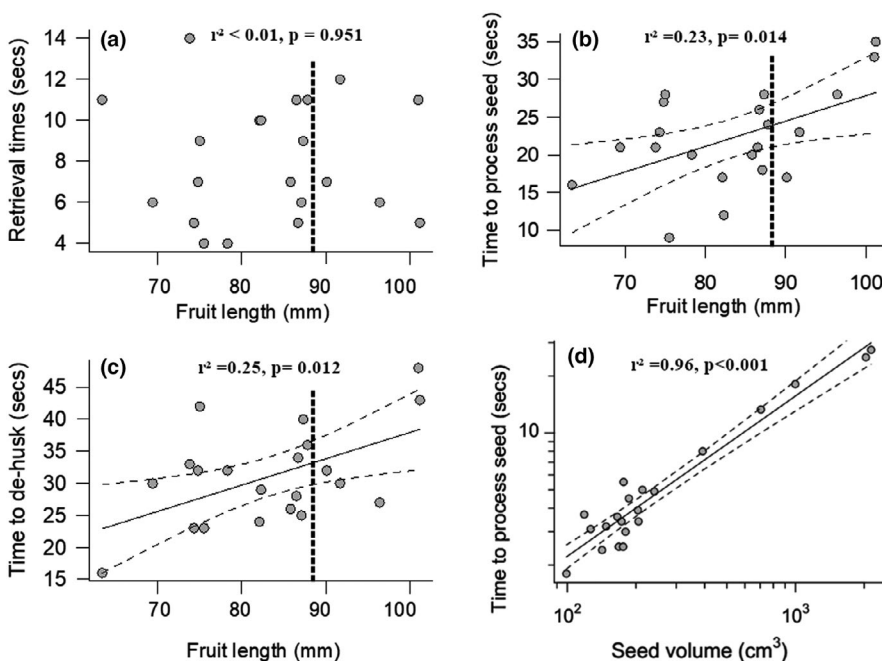
#### 4 | DISCUSSION

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

current data appear to support the size spectrum hypothesis of Scott and Murdoch (1983), where exploited prey size depends on the available prey size range relative to those sizes a predator can harvest most effectively.

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

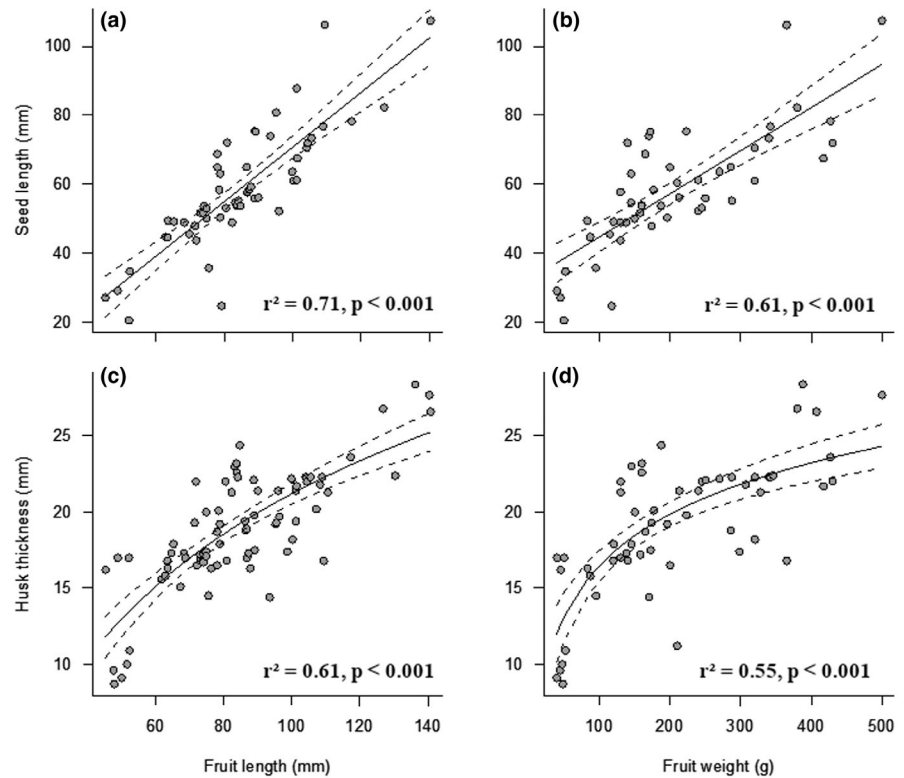
Studies of how human hands grip a cylinder show that the greater the diameter, the smaller the contact area of the hand, leading to grip strength reduction due to reduced palm skin contact



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

**FIGURE 1** Time to retrieve (a), de-husk (b), and process seeds (c) in seconds, related to fruit length (mm) for 21 direct feeding observations. Relation between volume of individual *Aldina latifolia* seeds (cm<sup>3</sup>) and time (seconds) required to process the seed (d). Solid lines represent the model, while ticked lines show 95% confidence intervals. The dashed line represents the average *Cacajao ouakary* hand size (88.26  $\pm$  6.35).

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



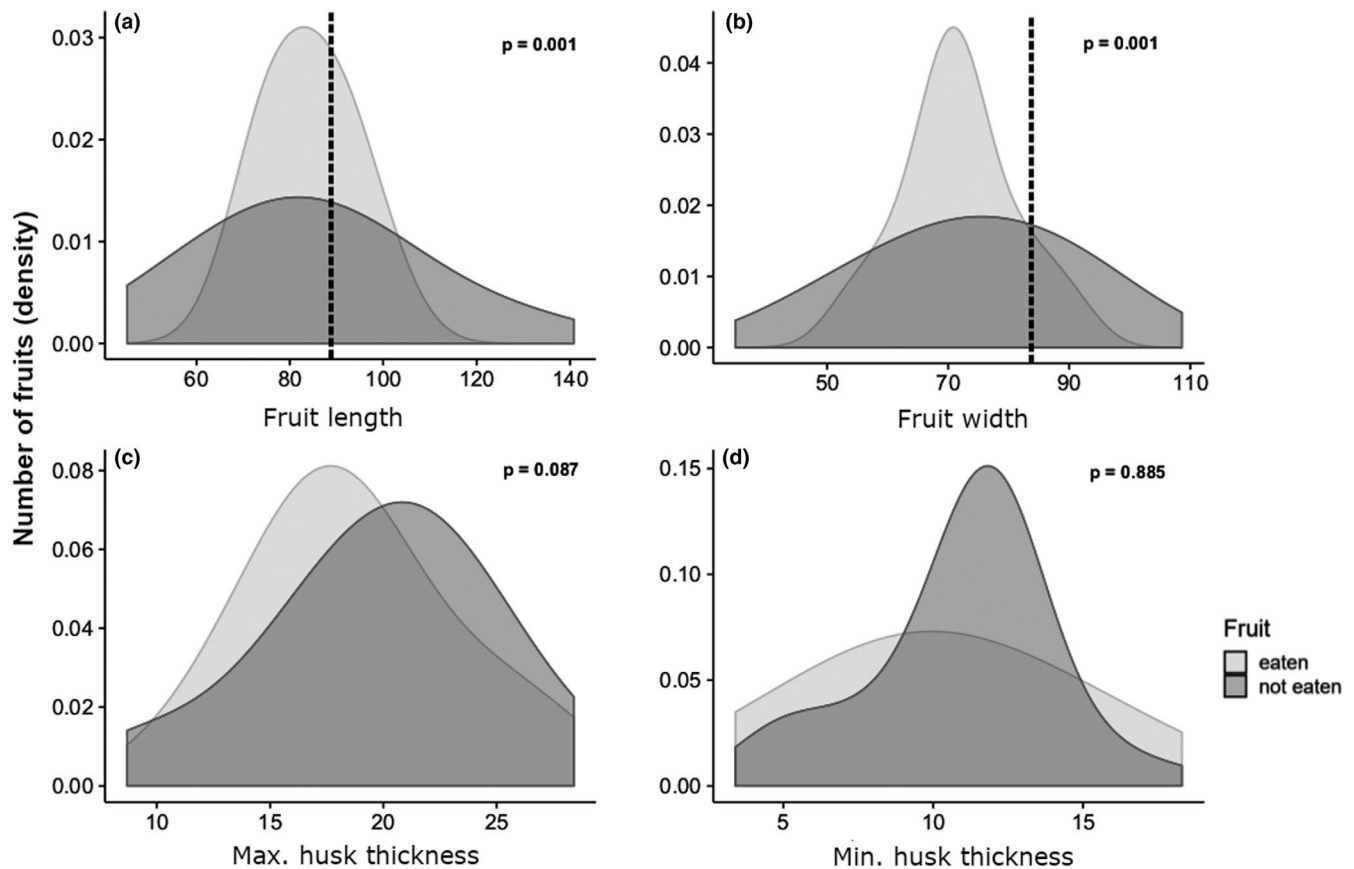
with the object (Edgren, Radwinx, & Irwin, 2004; Grant, Habes, & Steward, 1992). Additionally, young chimpanzees have better grabbing action when food items are small than when they are large (Seo & Armstrong, 2008), while adult male chimps have, on average, larger hands than females and show greater difficulty in manipulating small objects than do females (Hopkins, Cantalupo, Wesley, Hostetter, & Pilcher, 2002). Therefore, fruits much smaller or larger than the hand would be difficult to handle. The size of fruits selected, therefore, may be linked to the physical limits of hand size. The overlap in size between the favored subset of fruit sizes and uacari full hand sizes supports this hypothesis. That uacaris apparently either test their limits, or sometimes make mistakes, is shown by the sizes of six abandoned fruits, where all but one was either notably larger or smaller than the eaten fruits. Selection of medium-sized *A. latifolia* fruits by *C. ouakary* represents an apparent example of a primate selecting a sub-sample from the available weight-size continuum, a selectivity that presumably maximizes the trade-off between the energy that may be derived from a seed, and the time and energy expended in processing the fruit to access this, either in terms of the nutritional value of the seed, or in terms of the time invested.

Studies investigating aspects of seed- or fruit-size preference in primates are infrequent, with many involving between-species rather than within-species comparisons (e.g., Catherine, 1996; Chapman & Chapman, 1996; Gross-Camp, Mulindahabi, & Kaplin, 2009; Janson, Stiles, & White, 1986; Lambert, 2002; Sourd & Gautier-Hion, 1986) or considering other aspects, such as multi-species interactions (Gathua, 2000; Howe, 1980), the presence of irritant hairs (Lucas et al., 2001; Tutin, Parnell, & White, 1996), or defensive chemicals

(Lucas et al., 2001; Wrangham & Waterman, 1981, 1983). The majority of size-based selection studies so far, consider the size of the fruit in relation to that of the body, the pulp ratio by seed size, crop volume (e.g., *Lagothrix lagothricha* (Humboldt, 1812): Stevenson et al., 2005; *Macaca fascicularis* (Raffles, 1821): Corlett & Lucas, 1990; *Ateles paniscus* (Linnaeus, 1758): Russo, 2003; *Saguinus* spp: Garber & Kitron, 1997), or all these factors together (e.g., *Pongo pygmaeus* (Linnaeus, 1,760): Leighton, 1993).

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

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



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

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

We cannot affirm that the optimal foraging behavior of the group observed in the present study is practiced by the other groups of *C. ouakary*, but there is a potential for this to occur. Specific behavior that occurs within a group can be of great importance to the

population. The most efficient foraging strategies will be favored by natural selection and will spread to a population at the expense of those less efficient. Social facilitation occurs in many species of primates and other animals living in groups can learn from each other's behavior (Clayton, 1978; Galef Jr. & Giraldeau, 2001; Galef & Whiskin, 2000; Giraldeau & Caraco, 2000; Melin et al., 2014). But this has yet to be studied in *Cacajao* species. However, Barnett (2010) observed juveniles close to feeding adults, imitating the behaviors they used to extract seeds from large, hard fruits, even if the younger animals processed such fruits without success.

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



studies using a larger number of animals and looking at both hand size and fruit size in relation to uacari maximum gape could also be highly informative, as could studies that consider the impact of such limitations on foraging by uacaris.

## ACKNOWLEDGMENTS

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

## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## DATA ACCESSIBILITY

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

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Dias da Silva RHP, Castro Sa MJ, Baccaro FB, Tománek P, Barnett AA. Juggling options: Manipulation ease determines primate optimal fruit-size choice. *Biotropica*. 2020;52:1275–1285. <https://doi.org/10.1111/btp.12835>