UNIVERSIDADE FEDERAL DO AMAZONAS - UFAM

INSTITUTO DE CIÊNCIAS BIOLÓGICAS - ICB
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA – PPGZOO

FAZENDO A FEIRA: PRIMATAS UACARIS (*CACAJAO*, PITHECIIDAE) SELECIONAM FRUTOS DE TAMANHO IDEAL PARA UMA REFEIÇÃO PARCIMONIOSA.

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Manaus, Amazonas
Janeiro, 2020.

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Sinopse:

Estudou-se a aplicação da teoria do forrageamento ótimo, a qual prediz que animais buscam, simultaneamente, minimizar o tempo gasto na alimentação e maximizar o ganho energético por meio da seleção de tamanho dos frutos e sementes consumidos em relação ao tempo de manuseio, peso do fruto, espessura do pericarpo, assim como aspectos biométricos limitantes como tamanho da mão e abertura da boca dos primatas.

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RESUMO GERAL

A teoria do forrageamento ótimo prediz que animais buscam, simultaneamente, minimizar o tempo gasto no processamento do alimento e maximizar o ganho energético obtido pelo alimento. Para testar essa premissa, no capítulo um monitoramos e analisamos o forrageio de um primata especializado em sementes de frutos imaturos, o uacari-de-costa-dourado (*Cacajao ouakary,* primata da família Pitheciideae) ao predarem drupóides grandes monospérmicas de cascas grossas e tamanho variável de macucu (*Aldina latifolia*, Fabaceae). Utilizamos para isso, amostragem por varredura "scan-sampling" e *ad libitum* para registrar as observações de alimentação, medidas dos frutos consumidos e não-consumidos, a penetrabilidade da casca destes, e o tamanho das mãos de *C. ouakary* taxidermizados. Para testar se os uacaris estavam selecionado frutos com as melhores características, comparamos 8 métricas de 75 comidas e 105 sementes/frutos não consumidos coletados. Nossa hipótese é que uacari-de-costa-dourada consumirá frutos da classe de tamanho e com características que exige menos tempo para obter, manipular e ingerir, devido à dificuldade de manipulação de objetos maiores que a palma da mão deste primata. Seguindo nossas premissas, *Cacajao ouakary* seleciona frutos de *Aldina latifolia* com tamanho e peso médios desproporcionais à sua abundância, minimizando o tempo gasto no processamento do alimento e maximizando o ganho energético. Em termos de rendimento energético por unidade de tempo, a escolha de vagens de tamanho médio se encaixa na teoria do forrageamento ótimo. O maior tempo gasto no processamento de drupóide grandes de *A. latifolia* para *C. ouakary* também podem ser atribuídos a dificuldades em manipular objetos de cinco a sete vezes o tamanho da palma da mão do animal e um sexto do seu próprio peso corporal. Este resultado nos levou ao segundo capítulo desta dissertação.

Os vertebrados são frequentemente limitados pelo tamanho do alimento, pois estes não correspondem à capacidade limite de abertura da boca e ao tamanho corpóreo, além de demandar maior tempo e habilidade de manuseio. A anatomia das mãos e boca de primatas frugívoros pode, portanto, limitar o consumo de frutos superiores à capacidade de encaixe na boca, o que, no caso, pode tornar o processo energicamente desgastante pelo aumento no esforço aplicado no manuseio, abertura e mastigação do fruto. Diante do exposto, o objetivo do segundo capítulo foi analisar a empunhadura e a capacidade máxima de encaixe da boca no fruto e determinar se estes parâmetros são critérios na seleção de frutos na dieta alimentar do gênero *Cacajao*. Desta forma, testamos a significância da biometria do tamanho da mão e abertura máxima da boca (gape) de quatro taxa de *Cacajao*, cujos espécimes são provenientes de coleções zoológicas, em relação à lista de espécies de árvores na área de vida dos primatas, categorizando os frutos em consumidos e não-consumidos. A hipótese levantada para esta questão é que primatas do gênero *Cacajao* minimizarão os gastos energéticos na obtenção do alimento, ao escolherem frutos de fácil empunhadura (grip), fácil encaixe na abertura máxima da boca (gape) e que também apresentem sementes com dimensões inferiores à distância entre caninos. Salvo *C. melanocephalus*, os uacaris, no processo de escolha das espécies que irão compor sua dieta, não consideram o nível de dificuldade de manuseio com base no tamanho do fruto. *Cacajao c. calvus, C. c. ucayalii* e *C. ouakary* apresentam em sua dieta mais espécies de frutos de "fácil" manuseio, seguido dos "manuseáveis" e de "fácil" encaixe entre os caninos. Em relação ao *C. melanocephalus*, mesmo tendo disponível mais espécies de frutos de "fácil" manuseio e encaixe entre os caninos, optou pelas espécies com frutos "manuseáveis", de "difícil" encaixe e menor frequência, além de consumir quase todas as espécies com frutos "difíceis" disponível em sua área de vida. Os frutos consumidos pelo primata foram, em média, significativamente maior do que os não consumidos. As diferenças encontradas na seleção de frutos da dieta de *C. melanocephalus* em relação aos demais primatas foram atribuídas ao seu tamanho corpóreo e habitat.

SUMÁRIO

1 INTRODUÇÃO GERAL

A teoria do forrageamento ótimo, proposta por MacArthur e Pianka (1966), permite compreender as decisões do forrageio tomadas pelos predadores, mas não especifica, precisamente, como o forrageador deve tomar tais decisões. A teoria aborda que predadores gastam tempo e energia na obtenção do alimento, desde a busca à manipulação da presa, pressionando o predador a desenvolver estratégias na obtenção de maior número de itens alimentares que maximizem o ganho energético (MacArthur & Pianka 1996).

As presas desenvolvem, portanto, estratégias comportamentais ou mecanismos de defesa que dificultam a eficiência dos predadores (Futuyama 1983; Arbour & Zanno, 2018), e no caso de frutos e sementes, a variação no tamanho destes (Michaels et al. 1988) também pode influenciar no sucesso da predação (Galetti et al. 2013). A eficácia do forrageamento, no entanto, não é limitado somente pelas restrições estruturais do predador (e.g. *Esox lucius*: Nilsson & Brönmark 2000). Dentre as presas disponíveis, mesmo que as características entre elas sejam semelhantes, o indivíduo deverá selecionar aquela(s) que minimizem o tempo de manuseio e maximizem o rendimento energético (Stephens e Krebs 1986; Tsujita et al. 2008).

Em específico para frugívoros, estes tomam decisões de forrageamento em, pelo menos, três níveis: escolhendo entre (i) frutos de diferentes espécies, seguido de (ii) frutos de indivíduos da mesma espécie e, então, (iii) frutos disponíveis na mesma planta (Leighton 1990; Sallabanks 1993; Wheelwright 1993). Essa seleção hierárquica e sequencial é geralmente baseada no tamanho do fruto ou de características afins como a proporção de polpa por fruto, peso do fruto ou restrições anatômicas dos frugívoros (Jordano 1995; Mello et al. 2005; Hartstone-Rose & Perry 2011).

Ao forragearem, primatas frugívoros enfrentam uma série de adversidades que frequentemente resultam em grandes áreas de vida, longos tempos de viagem e distribuição do tempo altamente restrita para cada atividade (Chaves, Stoner, & Arroyo-Rodríguez, 2011), sendo necessário aumentar a eficiência energética na alimentação. A maioria dos primatas, portanto, selecionam frutos que contenham polpa (Lambert 1998), uma vez que estes são suaves, flexíveis e geralmente separados do ambiente externo por uma casca fina, fazendo com que este alimento seja relativamente simples e rápido de processar (Stevenson et al. 2005).

Primatas que se alimentam de frutos imaturos, no entanto, podem enfrentar uma variedade de mecanismos de defesas químicas e físicas que impedem o acesso às sementes (Mack 2000; Hanley et al. 2007). Estes mecanismos podem, por conseguinte, aumentar o tempo de escolha dos itens alimentares e/ou prolongar o tempo de manuseio, exigindo a necessidade de técnicas de processamento eficientes.

De forma a romper as barreiras físicas e obter acesso às sementes, os primatas desenvolveram algumas estratégias físico-mecânicas de ferramentas, como o uso de pedras, ostras, gravetos, troncos e outras de origem vegetal (Haslam et al. 2016; Rocha, Reis, & Sekiama 1998; Fernandes 1991; lzaw & Mizuno 1977; Struhsaker & Leland 1977); e adaptações morfológicas bucais, como as encontradas em primatas do gênero *Cacajao* e outros de sua clade (*Pithecia* e *Chiropotes*). Todas estas ferramentas e adaptações são utilizadas por primatas para otimizar as estratégias de forrageio, visando, simultaneamente, a maximização dos ganhos e minimização dos gastos energéticos com o tempo de processamento e despesas musculares (Hemingway 1999; Herrel, Smet, Aguirre & Aerts 2008, Sayers 2008; Hohmann 2009, Shi et al. 2012).

A seleção dos frutos pelos primatas envolve fatores nutricionais e sensoriais como a cor, o cheiro (van Roosmalen 1985), o toque (Wrangham1977), a ausência de toxinas, o conteúdo nutricional, a dureza (Ayres 1987; Norconk & Veres 2011; Barnett et al. 2016) e tamanho (Flörchinger et al. 2010). O forrageio, portanto, não está relacionado apenas com a busca pelo alimento (Byrne 1996 abc). Dentre estes fatores, o tamanho do fruto é considerado, por alguns autores, como elemento primário no critério de seleção (Jordano 1995, 2000; Mello, Leiner, Guimarães, & Jordano 2005). Assim como a utilização de ferramentas para o acesso ao alimento, o tamanho dos frutos consumidos por primatas frugívoros pode limitar a ingestão das sementes devido à anatomia do animal.

Estudos realizados com aves (Darwin 1859, Wheelwright 1993, Arakaki 2011), répteis (Pianka & Vitt 2006), roedores (Gautier-Hion 1985) e mamíferos (e.g. Felidade-*Panthera onca*: Meachen-Samuels & Van Valkenburgh 2009), por exemplo, mostram que o tamanho do fruto ou presa corresponde à sua capacidade limite de abertura de boca. Quando o forrageamento não for simplesmente limitado pela abertura máxima da boca do animal (Nilsson & Brönmark 2000), este deve, então, selecionar itens alimentares que minimizem o tempo de manipulação e maximizem o rendimento energético, de acordo com sua aptidão física. O tamanho da pedra usada para a quebra de frutos, por exemplo, pode ser limitante para macacos jovens, uma vez que animais adultos têm maior êxito em quebrar as sementes por serem capazes de utilizar rochas mais pesadas que os juvenis (Rocha, Reis & Sekiama 1998).

Supondo que o primata Neotropical *Cacajao ouakary* (Pitheciidae) escolha os frutos pelos critérios de tamanho e peso (Dias-Silva et al., em prep.), a habilidade na manipulação destes deverá à (i) estrutura da mão, cuja seleção de frutos seria com base na eficiência do aperto de precisão (grip), e/ou no ii) encaixe da boca (gap), cuja seleção seria com base no tamanho máximo de abertura da mandíbula do primata.

2 JUSTIFICATIVA

O forrageamento é um tipo de observação de comportamento animal fundamental, nos possibilita entender como os animais interagem com as plantas e estas com os animais, elucidando os diversos aspectos ecológicos da fauna local e as estratégias de estabelecimentos e sobrevivência das plantas. Particularmente, estudos de interação animal-planta com primatas são vantajosos por apresentarem grande variabilidade de plantas na dieta. Estudos de forrageamento já foram realizados para uma variedade de grupos de vertebrados, entretanto, são raros em primatas, embora estudos sobre dieta e escolha de alimentos sejam comuns - estes raramente são estudados em termos de otimização. Apresentamos aqui um estudo que, a nosso conhecimento, é um dos poucos que já adotaram essa abordagem com primatas amazônicos. O presente trabalho analisa a otimalidade no comportamento de forrageamento dos primatas amazônicos pouco conhecidos, os uacaris (*Cacajao* spp.).

De todos os sete taxa de uacaris que ocorrem no Brasil, três são endêmicos. Uacaris são primatas raros das planícies da Amazônia e, isso se deve à restrição de área geográfica (Hershkovitz 1987) e à baixa densidade populacional. Em decorrência disso, a exploração de madeira, extração de recursos não madeireiros e a caça os tornam ainda mais frágeis (Ayres & Johns 1987; Aquino e Encarnación 1999; Bodmer et al. 2003). Ao contrário de *Cacajao ouakary* (*sensu* Ferrari et al. 2014), as subespécies de *Cacajao calvus* e *Cacajao honsomi* (= *Cacajao melanocephalus, sensu* Ferrari et al. 2014) estão atualmente classificadas como vulneráveis pela IUCN (2008), por apresentar 30% de redução da população nos últimos 30 anos, por consequência principalmente da caça e perda de habitat. Ecologia alimentar é um componente central da biologia das espécies, está relacionada com a sobrevivência, reprodução, dinâmica de produção, exigência de habitat e padrão de sociabilidade. Desta forma, é essencial entendermos os papéis ecológicos desempenhados por cada espécie para futuras estratégias de conservação.

REFERÊNCIAS

Aquino, R. & Encarnación, F. (1999). Observaciones preliminares sobre ladieta de *Cacajao calvus ucayalii* en el Nor-Oriente Peruano. Neotropical Primates, 7: 1-5.

Arbour, V.M.& Zanno, L. E. (2018). The evolution of tail weaponization in amniotes, *Proceedings of the Royal Society B,* **285 (1871)**.

Ayres, J.M. & Johns, A.D. (1987). Conservation of white uacaris in Amazonian várzea. Oryx, **21**: 74-80.

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

Bodmer, R. E. & Puertas, P. (2004). A brief history of the Yavari Valley. In: Pitman, Nigel and Vriesendorp, Corine and Moskovits, Debra, eds. *Peru*, *Yavari: rapid biological inventory*. The Field Museum, Chicago, pp. 172-177.

Byrne, R. W. (1996b). Machiavellian intelligence. *Evolutionary Anthropology*, **5**, 172–180.

Byrne, R. W. (1996c). Relating brain size to intelligence in primates. In: Mellars, P. A., Gibson, K. R. (Eds.), *Modelling the Early Human Mind* (pp. 49-56), Macdonald Institute for Archaeological Research, Cambridge.

Byrne, R.W. (1996a). The misunderstood ape: cognitive skills of the gorilla. In: Russon, A. E., Bard, K.A., & Parker, S. T. (Eds.). *Reaching into Thought: The Minds of the Great Apes* (pp 111-130). Cambridge: Cambridge University Press.

Chaves, Ó. M., Stoner, K. E., & Arroyo-Rodríguez, V. (2011). Seasonal differences in activity patterns of Geoffroy's Spider Monkeys (*Ateles geoffroyi*) living in continuous and fragmented forests in Southern Mexico. *International Journal of Primatology*, **32(4)**, 960-973.

Ferrari, S. F., Guedes, P. G., Figueiredo-Ready, W. M. B., & Barnett, A. A. (2014). Reconsidering the taxonomy of the Black-Faced Uacaris, *Cacajao melanocephalus* group (Mammalia: Pitheciidae), from the northern Amazon Basin. *Zootaxa*, **3866**, 353–370.

Flörchinger, M., Braun, J., Böhning-Gaese, K., & Schaefer, H.M. (2010). Fruit size, crop mass, and plant height explain differential fruit choice of primates and birds. *Oecologia*, **164(1)**, 151-161.

Futuyama, D.J. (1983). Evolutionary interaction among herbivorus insects and plants. *Coevolution*, 207-223.

Gautier-Hion, A., Duplantier, J. M., Quris, R., Feer, F., Sourd, C., Decoux, J. P., Dubost, G., Emmons, L., Erard, C., & Hecketsweiler, P. (1985b). Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia*, **65**, 324-337.

Galetti, M., Guevara, R., Cortes, M. C., Fadini, R., Von Matter, S., Leite, A. B., Jordano, P. (2013). Functional Extinction of Birds Drives Rapid Evolutionary Changes in Seed Size. *Science*, 340(6136), 1086–1090. doi:10.1126/science.1233774

Hanley, M. E., Lamont B. B., Fairbanks, M. M., & Rafferty, C. M. (2007). Plant structural traits and their role in anti-herbivore defense. Perspectives in *Plant Ecology, Evolution and Systematics*, **8**: 157-178.

Hartstone-Rose, A., & Perry, J. M. (2011). Intraspecific variation in maximum ingested food size and body mass in *Varecia rubra* and *Propithecus coquereli*. *Anatomy Research International*, **8**.

Herrel, A., De Smet, A., Aguirre, L.F., & Aerts, P. (2008). Morphological and mechanical determinants of bite force in bats: do muscles matter? *Journal of Experimental Biology*, **211(1)**, pp.86-91.

Jordano, P. (1995a). Frugivore-mediated selection on fruit and seed size: birds and St. Lucie's cherry, *Prunus mahaleb*. *Ecology* **76**:2627–2639.

Lambert, J. E. (1998). Primate digestion: interactions among anatomy, physiology, and feeding ecology. *Evolutionary Anthropology* 7:8-20.

Leighton, M. (1990). Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. *International Journal of Primatology* **14**:257-313.

MacArthur, R. H. & Pianka, E. R. (1966). On Optimal Use of a Patchy Environment. *The American Naturalist* **100**: 603-609

Mack, A. L. 2000. Did fleshy fruit pulp evolve as a defence against seed loss rather than as a dispersal mechanism? Journal of Biosciences 25:93-97.

Meachen-Samuels, J. & Van Valkenburgh, B. (2009). Craniodental indicators of prey size preference in the Felidae. *Biological Journal of the Linnean Society*, **96**, 784–799.

Mello, M. A. R., N. A. Leiner, P. R. Guimarães Jr. & P. Jordano. (2005). Size-based fruit selection of *Calophyllum brasiliense* (Clusiaceae) by bats of the genus *Artibeus* (Phyllostomidae) in a Restinga area, southeastern Brazil. *Acta Chiropterologica,* **7**:165-188.

Michaels, H. J., B. Benner, A. P. Hartgerink, T. D. Lee, S. Rice, M. F. Willson & R. I. Bertin (1988). Seed size variation: magnitude, distribution and ecological correlates. *Evolutionary Ecology* **2**:157-166.

Nilsson, P. A. & C. Brönmark 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos,* **88**:539-546.

Norconk, M. A. & Michael Veres. (2011). Physical Properties of Fruit and Seeds Ingested by Primate Seed Predators with Emphasis on Sakis and Bearded Sakis. *The Anatomical Record*, **294**, 2092–2111.

Pianka, E. R., Vitt, L. J. (2006). Lizards: Windows to the evolution of diversity (pp. 333). University of California Press.

Rocha, V. J., Reis, N. R. & Sekiama, M. L. (1998). Uso de ferramentas por *Cebus apella* (llnnaeus) (primates, cebidae) para obtenção de larvas de coleoptera que parasitam sementes de *Syagrus romanzoffianum* (cham.) Glassm. (Arecaceae). *Revista Brasileira de Zoologia*, **15**, 945 – 950.

Sallabanks, R. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology* 74: 1326-1336

Shi, J., Curtis, N., Fitton, L. C., O'Higgins, P., & Fagan, M. J. (2012). Developing a musculoskeletal model of the primate skull: predicting muscle activations, bite force, and joint reaction forces using multibody dynamics analysis and advanced optimisation methods. *Journal of Theoretical Biology*, **310 (1)**, 21-30.

Stephens, D. W. & J. R. Krebs (1986). *Foraging Theory.* Princeton University Press

Stevenson, P. R., M. Pineda & T. Samper (2005). Influence of seed size on dispersal patterns of woolly monkeys (*Lagothrix lagothricha*) at Tinigua Park, Colombia. *Oikos* 110: 435-440.

Tsujita, K., S. Sakai & K. Kikuzawa. 2008. Does individual variation in fruit profitability override color differences in avian choice of red or white *Ilex serrata* fruits? *Ecological Research* **23**:445-450.

Van Roosmalen, M. G. M. (1985). Habitat preferences, diet, feeding strategy and social organization of the black spider monkey *(Ateles paniscus paniscus* Linnaeus 1758) in Surinam. *Acta Amazônica,* **15**, 1-238.

Wheelwright, N.T. (1993). Fruit size in a tropical tree species: variation, preference by birds, and heritability. *Plant Ecology* **107**: 163-174.

Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys*, *and apes* (pp.503-38), ed. T.H. Clutton-Brock, London: Academic Press.

3 OBJETIVO GERAL E ESPECÍFICO

3.1. Capítulo I: Avaliar se *Cacajao ouakary* realiza o forrageamento ótimo ao escolher frutos de *Aldina latifolia* com espessura do pericarpo e tamanho ideal que proporcione menor tempo de obtenção, manuseio e ingestão.

3.1.1. Específicos

a) Caracterizar os frutos/sementes selecionados durante o forrageamento, avaliando os padrões alométricos dos frutos escolhidos.

b) Avaliar se o volume da semente, o tamanho dos frutos e espessura da casca influenciam no tempo de manuseio dos frutos (obtenção, descascamento e o processamento da semente).

c) Avaliar se o tamanho dos frutos, espessura da casca e tamanho da mão afetam na escolha do primata no momento do forrageio.

3.2. Capítulo II: Avaliar se o tamanho dos frutos consumidos na dieta dos uacaris apresenta melhor empunhadura e encaixe com a abertura da boca do que os não consumidos que são abundantes nas áreas de vida de seus respectivos habitats.

3.2.1. Objetivos Específicos

a) Caracterizar e classificar as dimensões dos frutos das plantas utilizados na dieta e dos presentes na área de vida de cada espécime, mas não utilizados.

b) Caracterizar as dimensões das mãos e da boca de 4 taxa do gênero *Cacajao*.

c) Avaliar se os frutos utilizados na dieta são fáceis ou difíceis de manusear e/ou ingerir quando comparados com aqueles presentes na área de vida de cada espécime, mas não utilizados.

CAPÍTULO I

Dias-Silva RHP, Castro Sa MJ, Baccaro F, Tománek P & Barnett AA. **Opções de malabarismo: seleção ótima da combinação tamanho-peso de drupóides de *Aldina latifolia* (Fabaceae) pelo primata *Cacajao ouakary* em floresta de igapó na Amazônia Central, Brasil.** Manuscrito publicado no periódico *Biotropica* (http://dx.doi.org/10.1111/btp.12835)

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Juggling options: manipulation ease determines primate optimal fruit size choice

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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 taxidermised *C. ouakary* hands. To test if 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.

Data Accessibility

The data used in the present study are available in the Dryad Digital Repository (2019) at http://doi.org/[doi], reference number [reference number].

Key words: *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, 1985; Norconk & Veres, 2011; Barnett et al., 2016), nutritional content (Felton et al., 2009; Rothman, Raubenheimer, & Chapman, 2011) and size (Flörchinger, Braun, Böhning-Gaese, & Schaefer, 2010; Corlett & Lucas, 1990**;** Stevenson, Pineda, & Samper, 2005). The size of the fruit, however, is considered as the primary selection criterion for many frugivorous species (Martin, 1985, Jordano, 1995a,b; Mello, Leiner, Guimarães, & Jordano, 2005; Jordano, 2014). 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 (Jordano, 1995b; Mello et al., 2005; Hartstone-Rose & Perry, 2011).

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 (Mack, 2000; Hanley, Lamont, Fairbanks, & Rafferty, 2007). 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, 2000).

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^2 (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, Castilho, Shapley, & Anicácio, 2005; Barnett, Bowler, Bezerra, & Defler, 2013). 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 (McArthur & 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, and (ii) reject fruits too large to be easily manipulated, held or bitten into; (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 if 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-June, that of leaves between July-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 et al., 2012a, 2013, 2016; Barnett & Shaw, 2014; Bezerra et al., 2011) conducted between October 2006 and April 2008 in Jaú National Park.

To test foraging model predictions, we used fruits of *Aldina latifolia* Spruce ex Benth. (Papilionoideae. Fabaceae), a common riverside tree in Rio Negro igapó (Parolin, Adis, Rodrigues, Amaral, & Piedade, 2004b; Ferreira & Parolin, 2007; Montero, Piedade, &

Wittmann, 2014; Aguiar, 2015). 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 et al., 2004a). The fruits have one (frequent) to two (rare, < 10%) ellipse-shaped seeds. After some 12 weeks afloat in the igapó, the fruit will dehisce and germinate (Figure S2b) (Barnett, unpublished data). With an average mass of 69 – 298.33 g, *A. latifolia* fruits are some of the largest and heaviest of any igapó tree (Barnett, 2010; Parolin, Wittmann, & Ferreira, 2013). They also show great variation in size and weight (Figure S2c) (see Table S4).

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

At the time of *A. latifolia* 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^2 (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: $169.6m^3$), with abundant fruit crops (mean number per canopy: 256 ± 166.5) (Barnett, 2010).

Accordignly, *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 surving through to the next season of diet item abundance.

2.2. Collection Method

2.2.1. Feeding behaviour, biometry and fruit penetrability

During this study we followed uacaris through their igapó habitat in wooden canoes. In a previous study (Barnett, Castilho, Shapley, & Anicácio, 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 apects 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 datail 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 is a mixture of direct observation and indirect evidence. Data was collected in the same area studied by Barnett & Castilho (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 & Castilho (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 seconds consisting of two 30 seconds scans, separated by 30 seconds of *ad libitum* observation. This mixed sampling strategy maximized collected data representativeness (Fragaszy, Boinski, & Whipple, 1992). Deployment of this strategy was helped by the fact that, at this time of year fruit resources were scarce, and the uacaris foraged singly or in small groups (2– 4 animals). We recorded manipulation time (retrieval, de-husking and seed processing) by direct observation, recording times them with an electronic stopwatch. We operationally defined these categories as follows: i) retrieval: the time from when the animal initially removed the floating fruit the water surface and, having carried the fruit to a specific location, sat to process it, ii) de-husk: the time from when the uacari held the fruit to its mouth and began to bite the husk until the husk covering was reduced sufficiently that the seed could be extracted, and iii) seed processing: the time required for the seed to be removed from the remains of the husk, and then processed dentally, timing terminating when the seed (or parts thereof) were swallowed. Note: *Aldina latifolia* fruits have a smooth surface and do not require any additional actions, such as removal of spines or hairs, to prepare them for dental processing.

Immediately following uacari foraging observations, any remaining *Aldina* fruits found under trees in which foraging had occurred were collected and measured. For the fruits that had their seeds consumed, the feeding debris, composed of large fallen fragments of freshly removed husk, were retrieved by a member of the field-team from beneath feeding trees immediately after the uacaris had left, then pieced together to reconstitute the lumen in which the single seed had rested. Retrieval was aided by the very slow current in flooded igapó (less than 0.2 m/h^{-1}: Barnett et al., 2015b), besides few fruits are consumed by tree. Size measurements were made with SPI dial callipers (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 et al., 2012b), 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 1mm^2) mounted on a standard fruit penetrometer (Facchini FT 011 Fruit Firmness Tester, marketed by International Ripening Company, Norfolk, VA 23502-2095: see Barnett, Santos, Boyle, & Bezerra, 2015a for details), and measured penetrability at the fruit midpoint. To ensure repeatability, the penetrometer was mounted in a Fridley Fruit Tester (see Figure 3, Barnett et al., 2015a). A prosthetic uacari canine was used in place of the standard penetrometer head because previous studies (Barnett et al., 2015a) had shown that the standard penetrometer head substantially over-estimates force required for husk penetration.

2.2.2. Hand allometry

We obtained measurements of uacaris hands from taxidermised 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 callipers, or if the hand had contorted, with a string (Figure S3d) which was then subsequently measured with callipers. We excluded specimens where palm and/or finger lengths could not be measured reliably, due to specimen damage or preperational inconsistency (e. g. hand with palm, but without fingers; hands with fingers, but with a torn palm; extremely contorted and dried-our hands).

2.2.3. Data analysis

To test if the ucaris 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 occassion, 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, 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 fruits 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 was performed to obtain minimum, maximum and average sizes. All analyses were made in R (R Core Team 2016).

3. RESULTS

Fruit measurements

Three golden-backed uacaris were observed feeding on 21 *A. latifolia* fruits (details: Table S1), and a further 48 fruits were collected from feeding debris (Table S4). We also collected six *A. latifolia* fruits that uacaris had begun to process but then abandoned (measurement given in

Table S3). Of these 75 fruits, greatest length, weight and pericarp thickness could be unambiguously obtained for 56. These were compared statistically with measures from 105 uneaten *A. latifolia* fruits found floating in the uacari feeding area (Table S4). Mean ranges and standard deviations for hand measurement are given in Table 1, and for fruits in Table 2.

Observations

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 seconds per fruit (mean 31.10 SD ± 7.65, n = 21), with a further nine to 35 seconds 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 ($R^2 < 0.01$, $F_{1,19} = 0.003$, $P = 0.951$; Figure 1a), but there was an increase in time taken to de-husk the fruit ($R^2 = 0.25$, $F_{1,19} = 7.681$, $P = 0.012$; Figure 1c), and time required to process seeds from larger fruits ($R^2 = 0.23$, $F_{1,19} = 7.202$, $P = 0.014$; Figure 1b). Once fruits are removed from the surrounding husk, the relationship between time taken to process a seed and its volume (in cm^3), shows a very clear linear relationship ($R^2 = 0.96$, $P < 0.001$: 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, $F_{1,55} = 132.1$, $P < 0.001$; and $R^2 = 0.61$, $F_{1,47} = 78.06$, $P < 0.001$, respectively). Smaller and lighter fruits tended to have disproportionally thicker husks, compared to larger and heavier fruits ($R^2 = 0.61$, $F_{1,77} = 124.2$, $P < 0.001$; and $R^2 = 0.55$, $F_{1,56} = 72.53$, $P < 0.001$, 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 ($P = 0.001$ in both cases) (Figure 3b). Neither maximum nor minimum fruit husk thickness had an influence on selection of individual *Aldina* fruit by uacaris ($P = 0.087$, 0.885, respectively) (Figure 3c-d).

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^2 (range 3.5-4.3, *SD* ± 0.23), with a maximum thickness that varied from 1.50-3.32 mm (mean 2.43, *SD* ± 0.74). However, the very much thicker mesocarp (inner husk: up to 23 mm), was spongy and had a very low penetration resistance (mean 1.29 kg/mm^2, range 1.14-1.46, *SD* ± 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 (Martin, 1985; Foster, 1990). 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 with the object (Grant, Habes, & Steward, 1992; Edgren, Radwinx, & Irwin, 2004). 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 favoured sub-set 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. Janson, Stiles, & White, 1986; Sourd & Gautier-Hion, 1986; Catherine, 1996; Chapman & Chapman, 1996, Lambert, 2002; Gross-Camp, Mulindahabi, & Kaplin, 2009) or considering other aspects, such as multi-species interactions (Howe, 1980; Gathua, 2000), the presence of irritant hairs (Tutin, Parnell, & White, 1996; Lucas et al., 2001), or defensive chemicals (Wrangham & Waterman, 1981, 1983; Lucas et al., 2001). 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, 1760): 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 mollusc 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.

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

We cannot affirm that the optimal foraging behaviour 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 behaviour that occurs within a group can be of great importance to the population. The most efficient foraging strategies will be favoured 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 behaviour (Melein et al., 2014; Clayton, 1978; Galef Jr. & Giraldeau, 2001; Galef Jr. & Whinskin, 200; Giraldeau & Caraco, 2000). But this, has yet to be studied in *Cacajao* species. However, Barnett (2010) observed juveniles close to feeding adults, imitating the behaviours 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 behaviour 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.

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

[a]Sum of palm length and D2 length [b]Width value multiplied by two [c]Total hand length multiplied by two

.

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

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

[a] measured indirectly from reconstituted lumen volumes

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^3) and time (seconds) required to process the seed (d). Solid lines represent the model, while ticked lines show 95% confidence intervals. The dashed line represents the average *Cacajao ouakary* hand size (88.26 ± 6.35).

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

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

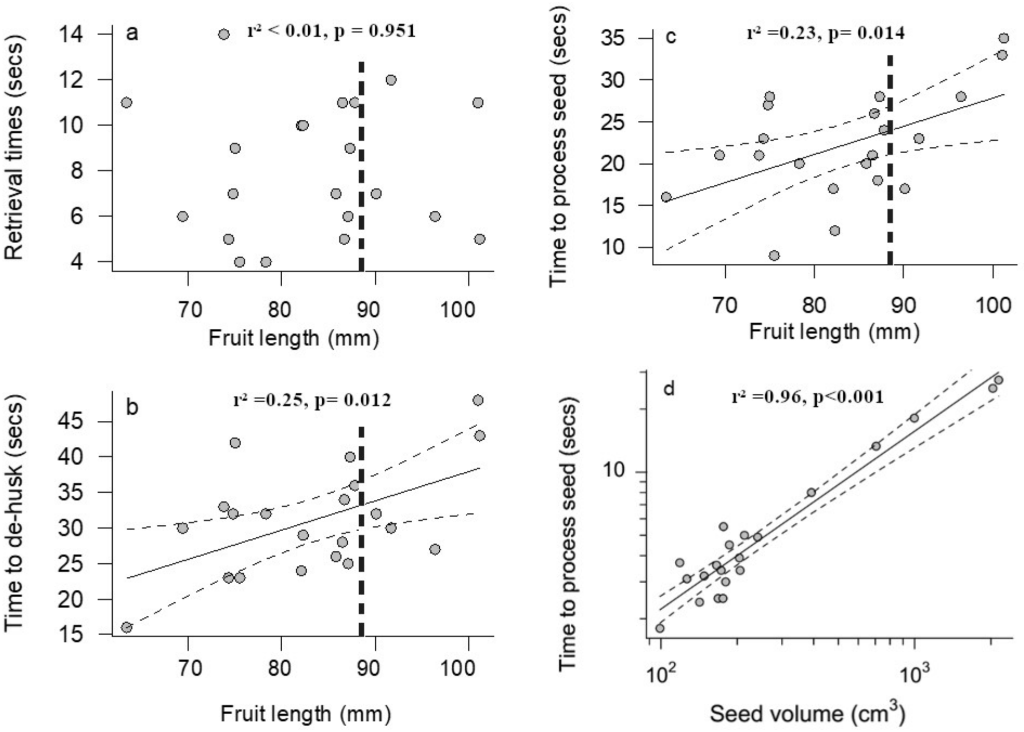
a
r² < 0.01, p = 0.951
Retrieval times (secs)
14
12
10
8
6
4
70
80
90
100
Fruit length (mm)
b
r² =0.25, p= 0.012
Time to de-husk (secs)
45
40
35
30
25
20
15
70
80
90
100
Fruit length (mm)
c
r² =0.23, p= 0.014
Time to process seed (secs)
35
30
25
20
15
10
70
80
90
100
Fruit length (mm)
d
r² =0.96, p<0.001
Time to process seed (secs)
10
10^2
10^3
Seed volume (cm³)

Figure 1

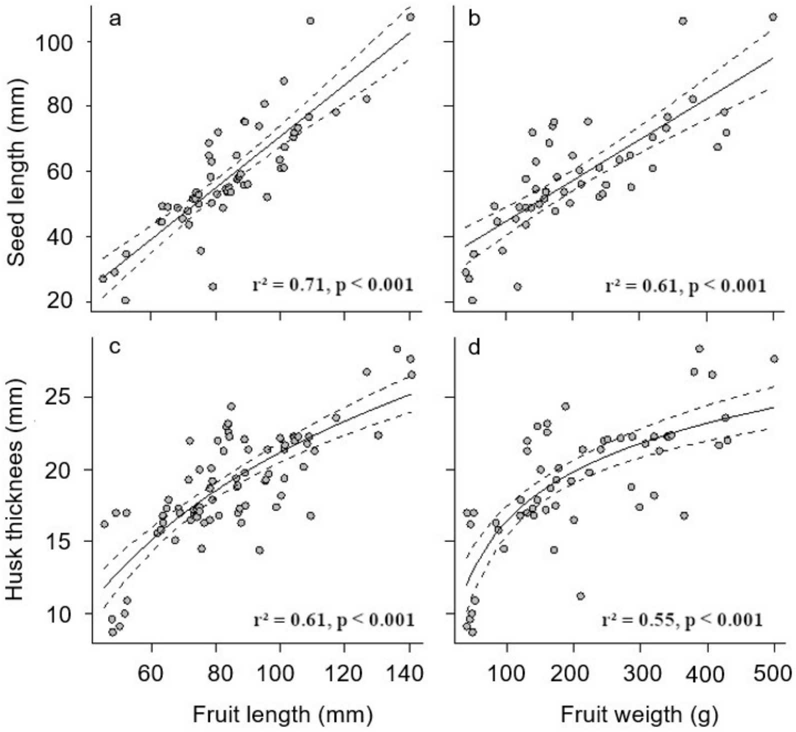
a
b
c
d
Seed length (mm)
100
80
60
40
20
Husk thicknees (mm)
25
20
15
10
r² = 0.71, p < 0.001
r² = 0.61, p < 0.001
r² = 0.61, p < 0.001
r² = 0.55, p < 0.001
60
80
100
120
140
100
200
300
400
500
Fruit length (mm)
Fruit weigth (g)

Figure 2

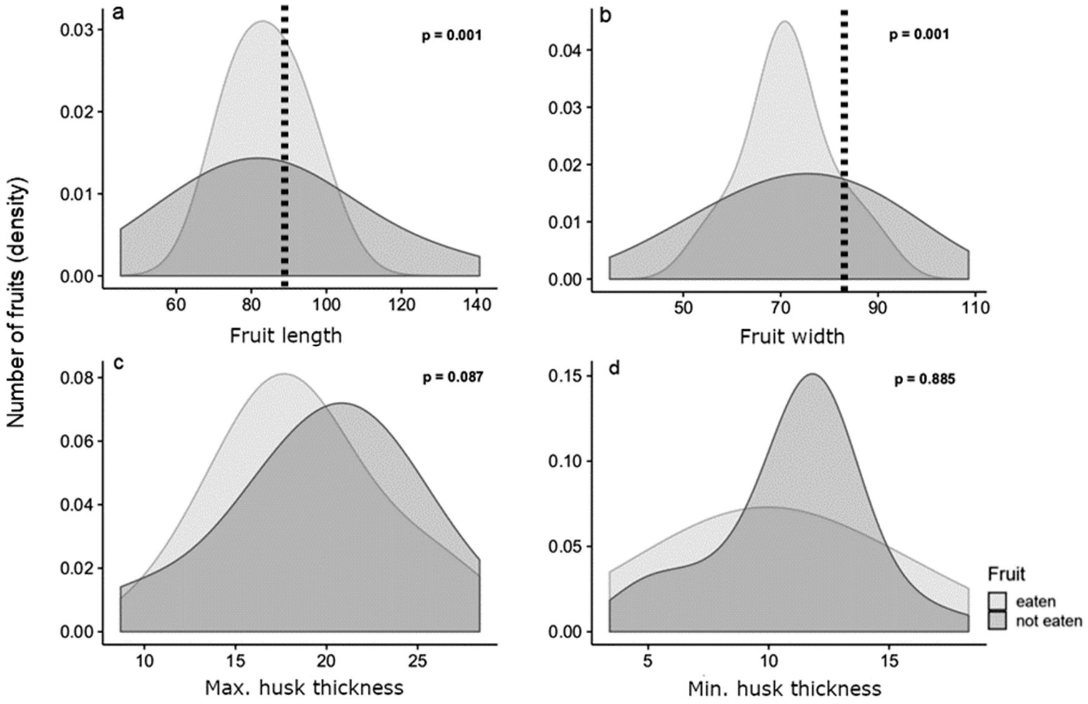
Number of fruits (density)
a
p = 0.001
0.03
0.02
0.01
0.00
60
80
100
120
140
Fruit length
b
p = 0.001
0.04
0.03
0.02
0.01
0.00
50
70
90
110
Fruit width
c
p = 0.087
0.08
0.06
0.04
0.02
0.00
10
15
20
25
Max. husk thickness
d
p = 0.885
0.15
0.10
0.05
0.00
5
10
15
Min. husk thickness
Fruit
eaten
not eaten

Figure 3

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

REFERENCES

Aguiar, D. P. P. de (2015). *Influência dos fatores hidro-edáficos na diversidade, composição florística e estrutura da comunidade arbórea de igapó no Parque Nacional do Jaú, Amazônia Central*. (Master dissertation, Instituto Nacional de Pesquisas da Amazônia).

Alcantara, J. M., & Rey, P. J. (2003). Conflicting selection pressures on seed size: evolutionary ecology of fruit size in a bird-dispersed tree, *Olea europaea*. *Journal of Evolutionary Biology*, **16(6)**, 1168–1176. doi:10.1046/j.1420-9101.2003.00618.x

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, **49(3)**, 227–266. doi:10.1163/156853974X00534

Armstrong, D. P., & Westoby, M. (1993). Seedlings from large seeds tolerated defoliation better: a test using phylogeneticaly independent contrasts. *Ecology*, **74(4)**, 1092–1100. doi:10.2307/1940479

Balcomb, S. R., & Chapman, C. A. (2003). Bridging the gap: influence of seed deposition on seedling recruitment in a primate–tree interaction. *Ecological Monographs*, **73(4)**, 625–642. doi:10.1890/02-4036

Barnett, A. A., Bezerra, B. M., Santos, P. J. P., Spironello, W. R., Shaw, P. J. A., MacLarnon, A., & Ross, C. (2016). Foraging with finesse: a hard-fruit-eating primate selects the weakest areas as bite sites. *American Journal of Physical Anthropology*, **160(1)**, 113–125. doi:10.1002/ajpa.22935

Barnett, A. A., Santos, P. J. P., Boyle, S. A., & Bezerra, B. M. (2015a). An improved technique using dental prostheses for field quantification of the force required by primates for the dental penetration of fruit. *Folia Primatologica*, **86(4)**, 398–410. doi:10.1159/000434677

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

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

Barnett, A. A., Bowler, M., Bezerra, B. M., & Defler, T. R. (2013). Ecology and behavior of uacaris (genus *Cacajao*). In L. M. Veiga, A. A. Barnett, S. F. Ferrari and M. A. Norconk (Eds.), *Evolutionary Biology and Conservation of Titis, Sakis and Uacaris* (1st ed., pp. 151–172). Cambridge: Cambridge University Press.

Barnett, A. A., Almeida, T., Spironello, W. R., Sousa Silva, W., MacLarnon, A., & Ross, C. (2012a). Terrestrial Foraging by *Cacajao melanocephalus ouakary* (Primates) in Amazonian Brazil: is choice of seed patch size and position related to predation risk. *Folia Primatologica*, **83(2)**, 126–139. doi:10.1159/000343591

Barnett, A. A., Boyle, S. A., Pinto, L. P., Lourenço, W. C., Almeida, T., Sousa Silva, W., … Spironello, W. R. (2012b). Primary seed dispersal by three Neotropical seed-predating primates (*Cacajao melanocephalus ouakary*, *Chiropotes chiropotes* and *Chiropotes albinasus*). *Journal of Tropical Ecology*, **28(6)**, 543–555. doi:10.1017/S0266467412000600

Barnett, A. A. (2010). *Diet, habitat, use and conservation ecology of the golden-backed uacari, Cacajao melanocephalus ouakary, in Jaú National Park, Amazonian Brazil* (Doctoral dissertation, University of Roehampton).

Barnett, A. A., Castilho, C. V. de, Shapley, R. L., & Anicácio, A. (2005). Diet, habitat selection and natural history of *Cacajao melanocephalus ouakary* in Jaú National Park, Brazil. *International Journal of Primatology*, **26(4)**, 949–969. doi:10.1007/s10764-005-5331-5

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

Bezerra, B. M., Barnett, A. A., Souto, A., & Jones, G. (2011). Ethogram and natural history of golden-backed uakaris (*Cacajao melanocephalus*). *International Journal of Primatology*, **32(1)**, 46–68. doi:10.1007/s10764-010-9435-1

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

Boyle, S. A., Thompson, C. L., Deluycker, A., Alvarez, S. J., Alvim, T. H. G., Aquino, R., … Barnett, A. A. (2016). Geographic comparison of plant genera used in frugivory among the pitheciids *Cacajao*, *Callicebus*, *Chiropotes*, and *Pithecia*. *American Journal of Primatology*, **78(5)**, 493–506. doi:10.1002/ajp.22422

Brewer, S. W. (2001). Predation and dispersal o f large and small seeds of a tropical palm. *Oikos*, **92(2)**, 245–255. doi:10.1034/j.1600-0706.2001.920206.x

Brown, S. C., Cassuto, S. R., & Loos, R. W. (1979). Biomechanics of chelipeds in some decapod crustaceans. *Journal of Zoology*, **188(2)**, 143–159. doi:10.1111/j.1469-

7998.1979.tb03397.x

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

Chapman, C. A., & Chapman, L. J. (1996). Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. *Journal of Tropical Ecology*, **12(04)**, 491–504. doi:10.1017/S026646740000972X

Correa, S. B., Winemiller, K. O., Lopez-Fernandez, H., & Galetti, M., (2007). Evolutionary perspectives on seed consumption and dispersal by fishes. *Bioscience*, **57(9)**, 748–756. doi: 10.1641/b570907

Corlett, R. T., & Lucas, P. W. (1990). Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (*Macaca fascicularis*). *Oecologia*, **82(2)**, 166–171. doi:10.1007/BF00323531

Cornejo, F., & Janovec, J. (2010). *Seeds of Amazonian plants* (Vol. 64). Princeton University Press.

Edgren, C. S., Radwinx, R. G., & Irwin, C. B. (2004). Gripforce vectors for varying handle diameters and hand sizes.*Human Factors*, **46(2)**, 244–251. doi:10.1518/hfes.46.2.244.37337

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

Felton, A. M., Felton, A., Wood, J. T., Foley, W. J., Raubenheimer, D., Wallis, I. R., & Lindenmayer, D. B. (2009). Nutritional Ecology of Ateles chamek in lowland Bolivia: How Macronutrient Balancing Influences Food Choices. *International Journal of Primatology*, **30(5)**, 675–696. doi:10.1007/s10764-009-9367-9

Ferrari, S. F., Guedes, P. G., Figueiredo-Ready, W. M. B., & Barnett, A. A. (2014). Reconsidering the taxonomy of the black-faced uacaris, *Cacajao melanocephalus* group (Mammalia: Pitheciidae), from the northern Amazon Basin. *Zootaxa*, **3866(3)**, 353-370. doi:10.11646/zootaxa.3866.3.3

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

Flörchinger, M., Braun, J., Böhning-Gaese, K. and Schaefer, H. M., (2010). Fruit size, crop mass, and plant height explain differential fruit choice of primates and birds. *Oecologia*, **164(1)**, 151-161. doi:10.1007/s00442-010-1655-8

Foster, M. S. (1990). Factors influencing bird foraging preferences among conspecific fruit trees. *Condor*, **92(4)**, 844-854. doi:10.2307/1368720

Foster, S. A. (1986). On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. *Botanical Review*, **52(3)**, 260–299. doi:10.1007/BF02860997

Fragaszy, D. M., Boinski, S., & Whipple, J. (1992). Behavioral sampling in the field: comparison of individual and group sampling methods. *American Journal of*

Primatology, **26(4)**, 259-275. doi:10.1002/ajp.1350260404

Garber, P. A., & Kitron, U. (1997). Seed swallowing in tamarins: evidence of a curative function or enhanced foraging efficiency? *International Journal of Primatology*, **18(4)**, 523–538. doi:10.1023/A:1026359105653

García-Lara, S., Bergvinson, D. J., Burt, A. J., Ramputh, A. I., Díaz-Pontones, D. M., & Arnason, J. T. (2004). The role of pericarp cell wall components in maize weevil resistance. *Crop Science*, **44(5)**, 1546-1552. doi:10.2135/cropsci2004.1546

Gathua, M. (2000). The effects of primates and squirrels on seed survival of a canopy tree, *Afzelia quanzensis*, in Arabuko-Sokoke Forest, Kenya. *Biotropica*, **32(1)**, 127–132. doi:10.1111/j.1744-7429.2000.tb00455.x

Grant, K. A., Habes, D. J., & Steward, L. L. (1992). An analysis of handle designs for reducing manual effort: the influence of grip diameter. *International Journal of Industrial Ergonomics*, **10(3)**, 199–206. doi:10.1016/0169-8141(92)90033-V

Hanley, M. E., Lamont, B. B., Fairbanks, M. M., & Rafferty, C. M. (2007). Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology, Evolution and Systematics*, **8(4)**, 157–178. doi:10.1016/j.ppees.2007.01.001

Hartstone-Rose, A., Perry, J. M. (2011). Intraspecific variation in maximum ingested food size and body mass in *Varecia rubra* and *Propithecus coquereli*. *Anatomy Research International,* **2011**, 1- 8. doi.org/10.1155/2011/831943

Hendrix, S. D. (1984). Variation in seed weight and its effects on germination in *Pastinaca* *sativa* L. (Umbelliferae). *American Journal of Botany*, **71(6)**, 795–802. doi:10.2307/2443470

Hershkovitz, P. (1987). Uacaries, new world monkeys of the genus *Cacajao* (Cebidae, Platyrrhini): a preliminary taxonomic review with the description of a new subspecies. *American Journal of Primatology*, **12(1)**, 1–53. doi:10.1002/ajp.1350120102

Hopkins, W. D., Cantalupo, C., Wesley, M. J., Hostetter, A. B., & Pilcher, D. L. (2002). Grip morphology and hand use in chimpanzees (*Pan troglodytes*): evidence of a left hemisphere specialization in motor skill. *Journal of Experimental Psychology*, **131**, 412–423. doi: 10.1037/0096-3445.131.3.412

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

Howe, H. F., & Vande Kerckhove, G. A. (1981). Removal of wild nutmeg (*Virola surinamensis*) crops by birds. *Ecology*, **62(4),** 1093–1106. doi:10.2307/1937007

Hughes, R. N., & Elner, R. W. (1979). Tactics of a predator, *Carcinus maenas*, and morphological responses of the prey, *Nucella lapillu***s. ***Journal of Animal Ecology*, **48(1)**, 65-78. doi:10.2307/4100

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

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

Janson, C. H., Stiles, E. W., & White, D. W. (1986). Selection on plant fruiting traits by brown capuchin monkeys: a multivariate approach. In *Frugivores and seed dispersal* (pp. 83-92). Springer, Dordrecht. doi:10.1007/978-94-009-4812-9

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

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

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

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

Junk, W. J., Piedade, M. T. F., Schöngart, J., Cohn-Haft, M., Adeney, J. M., & Wittmann, F. (2011). A classification of major naturally-occurring Amazonian lowland wetlands. *Wetlands*, **31(4)**, 623-640. doi: 10.1007/s13157-011-0190-7

Kinzey, W. G. (1992). Dietary and dental adaptations in the Pitheciinae. *American Journal* *of Physical Anthropology*, **88(4)**, 499–514. doi:10.1002/ajpa.1330880406

Kunz, B. K., & Linsenmair, K. E. (2007). The Disregarded West: Diet and behavioural ecology of olive baboons in the Ivory Coast. *Folia Primatologica*, **79(1)**, 31–51. doi:10.1159/000108384

Leighton, M. (1993). Modeling dietary selectivity by Bornean orangutans: Evidence for integration of multiple criteria in fruit selection. *International Journal of Primatology*, **14(2)**, 257–313. doi:10.1007/BF02192635

Leishman, M. R., Wright, I. J., Moles, A. T., & Westoby, M. (2000). The evolutionary ecology of seed size. *Seeds: the ecology of regeneration in plant communities*, **2**, 31-57.

Martin, T. E. (1985). Resource selection by tropical frugivorous birds: integrating multiple interactions. Oecologia, **66(4)**, 563-573. doi.org/10.1007/BF00379351

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, **100(916)**, 603-609. doi/10.1086/282454

Mack, A. L. (2000). Did fleshy fruit pulp evolve as a defence against seed loss rather than as a dispersal mechanism? *Journal of Biosciences*, **25(1)**, 93–97. doi:10.1007/BF02985186

Melin, A. D., Nevo, O., Shirasu, M., Williamson, R. E., Garrett, E. C., Endo, M., ... & Kawamura, S. (2019). Fruit scent and observer colour vision shape food-selection strategies in wild capuchin monkeys. *Nature communications*, **10(1)**, 2407. doi:10.1038/s41467-019-10250-9

Mello, M. A. R., Leiner, N. O., Guimarães, P. R., & Jordano, P. (2005). Size-based fruit selection of *Calophyllum brasiliense* (Clusiaceae) by bats of the genus *Artibeus* (Phyllostomidae) in a Restinga area, southeastern Brazil. *Acta Chiropterologica*, **7(1)**, 179–182. doi:10.3161/1733-5329(2005)7[179:SFSOCB]2.0.CO;2

Michaels, H. J., Benner, B., Hartgerink, A. P., Lee, T. D., Rice, S., Willson, M. F., & Bertin, R. I. (1988). Seed size variation: magnitude, distribution, and ecological correlates. *Evolutionary Ecology*, **2(2)**, 157–166. doi:10.1007/BF02067274

Moles, A. T., & Westboy, M. (2004). Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology*, **92(3)**, 372–383. doi:10.1111/j.0022-0477.2004.00884.x

Montero, J. C., Piedade, M. T. F., & Wittmann, F. (2014). Floristic variation across 600 km of inundation forests (igapó) along the Negro River, Central Amazonia. *Hydrobiologia*, **729(1)**, 229–246. doi:10.1007/s10750-012-1381-9

Nevo, O., Garri, R. O., Salazar, L. T. H., Schulz, S., Heymann, E. W., Ayasse, M., & Laska, M. (2015). Chemical recognition of fruit ripeness in spider monkeys (*Ateles geoffroyi*). *Scientific reports*, **5**, 14895. doi:10.1038/srep14895

Nilsson, P. A., & Bronmark, C. (2000). Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos*, **88(3)**, 539–546. doi:10.1034/j.1600-0706.2000.880310.x

Norconk, M. A. & Veres, M. (2011). Physical Properties of Fruit and Seeds Ingested by Primate Seed Predators with Emphasis on Sakis and Bearded Sakis. *The Anatomical*

Record: Advances in Integrative Anatomy and Evolutionary Biology, **294(12)**, 2092–2111. doi: 10.1002/ar.21506

Norconk, M. A., & Kinzey, W. G. (1994). Challenge of neotropical frugivory: travel patterns of spider monkeys and bearded sakis. *American Journal of Primatology*, **34(2)**, 171–183. doi:10.1002/ajp.1350340208

Parolin, P., Wittmann, F., & Ferreira, L. V. (2013). Fruit and seed dispersal in amazonian floodplain trees: a review. *Ecotropica*, **19(1/2)**, 15–32.

Parolin, P., De Simone, O., Haase, K., Waldhoff, D., Rottenberger, S., Kuhn, U., Kesselmeier, J., Kleiss, B., Schmidt, W., Piedade, M. T. F., & Junk,W. J. (2004a). Central Amazonian floodplain forests: tree adaptations in a pulsing system. *Botanical Review*, **70(3)**, 357–380. doi:10.1663/0006-8101(2004)070

Parolin, P.; Adis, J.; Rodrigues, W.A.; Amaral, I.; Piedade, M.T.F. (2004b). Floristic study in na igapó floodplain Forest in Central Amazônia, Brazil (Tarumã-Mirim, Rio Negro). *Amazoniana*, **18 (1/2)**: 29-47. http://hdl.handle.net/11858/00-001M-0000-000F-DA53-3

Parolin, P. (2002). Submergence tolerance vs. escape from submergence: two strategies of seedling establishment in Amazonian floodplains. *Environmental and Experimental Botany*, **48(2)**, 177–186. doi:10.1016/S0098-8472(02)00036-9

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

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

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

Rothman, J. M., Raubenheimer, D., & Chapman, C. A. (2011). Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. *Biology letters*, *7*(6), 847-849. doi.org/10.1098/rsbl.2011.0321

Russo, S. E. (2003). Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia*, **136(1)**, 80–87. doi:10.1007/s00442-003-1239-y

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

Scott, M. A., & Murdoch, W. W. (1983). Selective predation by the backswimmer, *Notonecta*. *Limnology and Oceanography*, **28(2)**, 352–366. doi:10.4319/lo.1983.28.2.0352

Seo, N. J., & Armstrong, T. J. (2008). Investigation of grip force, normal force, contact area, hand size, and handle size for cylindrical handles. *Human Factors,* **50(5)**, 734–744. doi:10.1518/001872008X354192

Smith, J. M. (1966). Sympatric speciation. *American Naturalist*, **100(6)**, 637–650. doi:10.1086/282457

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

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

Toju, H. (2008). Fine-scale local adaptation of weevil mouthpart length and camellia pericarp thickness: altitudinal gradient of a putative arms race. *Evolution*, **62(5)**, 1086–1102. doi:10.1111/j.1558-5646.2008.00341.x

Traveset, A., Willson, M. F., & Gaither, J. C. (1995). Avoidance by birds of insect-infested fruits of *Vaccinium ovalifolium*. *Oikos*, **73(3)**, 381-386. doi:10.2307/3545962

Tsujita, K., Sakai, S., & Kikuzawa, K. (2008). Does individual variation in fruit profitability override color differences in avian choice of red or white *Ilex serrata* fruits? *Ecological Research*, **23(2)**, 445–450. doi:10.1007/s11284-007-0396-6

Tutin, C. E. G., Parnell, R. J., & White, F. (1996). Protecting seeds from primates: examples from *Diospyros* spp. in the Lopé Reserve, Gabon. *Journal of Tropical Ecology*, **12(3)**, 371–384. doi:10.1017/S0266467400009573

Van der Pijl, L. (1982). Principles of Dispersal in Higher Plants (3rd edn)–Springer. *Berlin Heidelberg New York*. doi:10.1007/978-3-642-87925-8

Van Schaik, C. P., & Knott, C. D. (2001). Geographic variation in tool use on *Neesia* fruits in orangutans. *American Journal of Physical Anthropology*, **114(4)**, 331–342. doi:10.1002/ajpa.1045

Venable, D. L. (1992). Size-number trade-offs and the variation of seed size with plant resource status. *American Naturalist*, **140(2)**, 287–304. doi:10.2307/2462610

Wittmann, A. D. O., Lopes, A., Conserva, A. D. S., Wittmann, F., & Piedade, M. T. (2010). Seed germination and seedling establishment of Amazonian floodplain trees. In *Amazonian Floodplain Forests* (pp. 259-280). Springer, Dordrecht. doi:10.1007/978-90-481-8725-6_13

Wrangham, R. W., & Waterman, P. G. (1981). Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea*: with special reference to reproductive strategies and tannin production. *Journal of Animal Ecology*, **50(3)**, 715-731. doi:10.2307/4132

Wrangham, R. W., & Waterman, P. G. (1983). Condensed tannins in fruits eaten by chimpanzees. *Biotropica*, **15(3)**, 217-222. doi:10.2307/2387832

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

Wright, B. (2005). Craniodental biomechanics and dietary toughness in the genus *Cebus*. *Journal of Human Evolution*, **48(5)**, 473–492. doi:10.1016/j.jhevol.2005.01.006

SUPPLEMENTARY MATERIAL

Table S1 Handling times and estimated fruit and seed volumes of 21 observed feeding bouts.

Handling Time			Size (mm)			Access time (remove husk + process seed) per cm^3 of seed[a]
Collect fruits in the water	Remove Husk	Process Seed	Whole fruit (length)	Seed (length x width)	Volume of seed (mm^3)	
12	30	23	91.7	71.9 x 48.4	88.0	1.66
10	24	17	82.1	53.6 x 28.8	22.00	0.54
11	48	33	101	86.4 x 75.0	247.72	3.06
4	32	20	78.3	57.9 x 29.0	25.45	0.49
6	27	28	96.4	78.8 x 55.0	124.18	2.58
11	28	21	86.5	61.8 x 30.5	29.9	0.61
9	42	28	75	54.7 x 27.7	21.77	0.31
7	26	20	85.8	56.8 x 26.4	20.73	0.45
4	23	9	75.5	55.7 x 27.5	21.86	0.68
6	25	18	87.1	63.2 x 28.4	18.24	0.42
6	30	21	69.4	46.8 x 29.7	12.29	0.25
5	23	23	74.3	57.0 x 24.9	18.35	0.40
10	29	12	82.3	52.5 x 24.0	15.80	0.39
7	32	17	90.1	68.4 x 37.0	49.02	1.01
5	43	35	101.2	87.8 x 76.4	268.34	3.44
5	34	26	86.7	57.7 x 27.3	22.40	0.37
11	36	24	87.8	59.1 x 28.8	25.72	0.43
7	32	27	74.8	53.0 x 25.3	17.90	0.31
14	33	21	73.8	51.7 x 21.4	12.42	0.23
9	40	28	87.3	58.5 x 26.2	21.06	0.31
11	16	16	63.4	44.6 x 25.2	14.59	0.46

[a] volume calculated as a prolate triaxial ellipsoid.

Table S2 Details of *Cacajao ouakary* specimens used in current study for palm and digit length measurements. Taxonomy follows (Ferrari, Guedes, Figueiredo-Ready and Barnett 2014), n =13.

Taxon	**Sex**	**Age**	**Collection Number**	**Collector**	**Location**	**Date of Collection**	**Museum**
Cacajao ouakary	M	AD	26.5.5.18	W. Ekrhard	Castanheiro Miri, Solimoes	19/08/1925	NHML
	F	?	5238	Marc Van Roosmalen	River Solimões, Lago Amanã, ca.100km acima de Manacapuru, Am, Brasil	18/06/1996	INPA
	M	?	5239	Marc Van Roosmalen	River Solimões, Lago Amanã, ca.100km acima de Manacapuru, Am, Brasil	18/06/1995	INPA
	F	AD	5240	Marc Van Roosmalen	River Solimões, margem esquerda, Manacapuru	26/06/1998	INPA
	F	AD	36615	João Valsecchi	Maraã, Amazonas, Comunidade Boa Esperança, Igarapé da Seringa - RDSA	11/06/2004	MPEG
	F	AD	36635	João Valsecchi	Maraã, Amazonas, Comunidade Boa Esperança, Igarapé Juá Grande - RDSA	15/06/2004	MPEG
	M	AD	36630	João Valsecchi	Maraã, Amazonas, Comunidade Boa Esperança, Igarapé Juá Grande - RDSA	14/06/2004	MPEG

	F	AD	36649	João Valsecchi	Maraã, Amazonas, Setor Coraci, River Coracizinho-RDSA	18/06/2004	MPEG
	M	AD	36644	João Valsecchi	Maraã, Amazonas, Setor Coraci, River Coracizinho- RDSA	17/06/2004	MPEG
	F	AD	36638	João Valsecchi	Maraã, Amazonas, Setor Coraci, River Coracizinho RDSA	17/06/2004	MPEG
	F	AD	36650	João Valsecchi	Maraã, Amazonas, Setor Coraci, River Coracizinho- RDSA	18/06/2004	MPEG
	F	JUV	36651	João Valsecchi	Maraã, Amazonas, Setor Coraci, River Coracizinho- RDSA	18/06/2004	MPEG
	M	AD	36637	João Valsecchi	Maraã, Amazonas, Setor Coraci, River Coracizinho- RDSA	17/06/2004	MPEG

Nota: NHML- Natural History Museum London, INPA-Instituto Nacional de Pesquisas da Amazônia and MPEG-Museu Paraense Emilio Goeldi. Sex: M- Male; F- Female; Age: AD- Adult; JUV- Juvenile.

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Table S3 Lengths and weights of abandoned *Aldina latifolia* (Fabaceae) fruits from igapó forest, central Amazonian Brazil.

Dimension Fruit (mm)				**Dimension Seed (mm)**		
Size (length x width)	**Weight (g) (fruit+seed)**	**Husk thickness max -min**	**Husk penetrability (kg)**	**Size (length x width)**	**Weight (g)**	**Ratio total/ weight**
69.8 x 58.30	110	14.4 − 10.6	3.7	41.4 x 37.2	83	78.18
111.4 x 90.4	385	23.1 − 13.6	4.2	109.4 x 85.9	329	85.46
107.3 x 89.5	362	17.1 − 10.6	4	98.5 x 78.6	298	82.32
52.1 x 53.1	47	14 − 8.8	3.6	38.7 x 12.9	37	78.72
104.8 x 82.4	358	19.1 − 14.2	3.8	92.2 x 73	309	86.31
98.1 x 82	345	23.3 − 14	3.7	87.6 x 74.2	210	60.86

Table S4 Lengths and weights of eaten and uneaten *Aldina latifolia* (Fabaceae) fruits from igapó forest, central Amazonian Brazil.

Non-eaten (N=105)				**Eaten (N=48)**			
Size Fruit (mm) (length x width)			**Weight (g)**	**Size Fruit (mm) (length x width)**			**Weight (g)**
105.60	x	93.00	345.00	96.00	x	82.50	240.00
103.60	x	94.70	350.00	86.80	x	74.60	130.00
95.30	x	88.50	255.00	100.20	x	90.20	320.00
114.60	x	119.00	460.00		x	72.40	210.00
79.80	x	75.80	145.00	93.50	x	62.20	170.00
90.80	x	91.60	235.00		x	60.50	-
104.10	x	92.30	320.00	74.40	x	70.00	-
126.80	x	97.30	380.00		x	65.40	-
74.80	x	63.30	150.00	74.00	x		-
109.40	x	87.30	365.00		x	66.10	-
84.10	x	85.30	287.50		x	53.60	-
71.80	x	83.10	130.00		x	67.00	-
84.70	x	73.70	187.50		x	55.00	-
57.50	x	57.00	65.00	91.70	x	79.40	-
66.00	x	50.90	100.00	82.10	x	72.70	-
90.20	x	78.80	210.00	76.00	x	69.60	-
54.80	x	47.00	52.50	101.00	x	91.10	-
83.20	x	73.50	145.00	92.90	x	81.60	-
76.40	x	75.30	195.00	86.40	x	74.40	-
65.90	x	65.90	130.00	78.30	x	70.20	-
69.80	x	60.30	115.00	72.80	x	68.50	-
92.60	x	91.60	345.00	96.40	x	83.60	-
82.30	x	61.30	130.00	88.60	x	72.80	-
88.80	x	86.40	250.00	86.50	x	71.10	-
83.80	x	67.40	160.00	84.10	x	73.70	-

91.80	x	83.40	225.00	75.00	x	71.40	-
88.90	x	88.30	223.00	85.80	x	74.50	-
55.00	x	85.00	175.00	93.20	x	84.80	-
104.40	x	89.90	430.00	75.50	x	71.30	-
78.00	x	73.10	165.00	83.60	x	73.80	-
70.20	x	69.10	120.00	97.70	x	88.60	-
90.80	x	76.00	205.00	87.10	x	70.20	-
61.00	x	48.90	70.00	69.40	x	54.00	-
105.50	x	89.00	340.00	74.30	x	70.10	-
83.70	x	80.00	160.00	76.20	x	68.70	-
101.00	x	87.90	320.00	82.30	x	74.30	-
79.20	x	76.80	117.50	90.10	x	80.00	-
90.50	x	86.50	180.00	101.20	x		-
78.00	x	78.00	200.00	86.70	x		-
78.80	x	69.10	145.00	87.80	x		-
80.80	x	61.80	140.00	74.80	x		-
89.10	x	69.10	172.50	73.80	x		-
99.90	x	77.80	270.00	87.30	x		-
68.90	x	68.30	127.50	63.40	x		-
69.50	x	61.20	130.00	86.20	x	62.00	-
64.40	x	58.00	80.00	74.80	x	58.90	-
62.50	x	50.00	85.00	76.30	x	67.10	-
48.80	x	38.60	40.00	72.10	x	67.20	-
75.50	x	55.40	95.00	-	-	-	-
45.20	x	49.20	45.00	-	-	-	-
52.10	x	55.10	50.00	-	-	-	-
140.40	x	98.80	500.00	-	-	-	-
80.50	x	93.00	245.00	-	-	-	-
101.20	x	74.50	240.00	-	-	-	-
79.20	x	65.60	194.00	-	-	-	-
83.20	x	72.10	171.00	-	-	-	-

107.60	x	94.10	314.00	-	-	-	-
100.10	x	86.20	296.00	-	-	-	-
106.70	x	88.60	386.00	-	-	-	-
104.40	x	88.60	336.00	-	-	-	-
100.70	x	84.70	301.00	-	-	-	-
93.70	x	76.20	246.00	-	-	-	-
94.40	x	73.70	237.00	-	-	-	-
76.80	x	67.30	197.00	-	-	-	-
46.20	x	36.20	121.00	-	-	-	-
81.90	x	72.40	159.00	-	-	-	-
73.80	x	70.00	178.00	-	-	-	-
45.90	x	34.90	120.00	-	-	-	-
72.40	x	62.80	172.00	-	-	-	-
88.80	x	76.40	217.00	-	-	-	-
110.20	x	89.20	417.00	-	-	-	-
111.40	x	92.70	415.00	-	-	-	-
86.60	x	78.20	210.00	-	-	-	-
90.00	x	71.40	200.00	-	-	-	-
96.20	x	77.00	261.00	-	-	-	-
101.30	x	89.60	100.00	-	-	-	-
70.40	x	62.70	167.00	-	-	-	-
58.60	x	48.30	178.00	-	-	-	-
91.20	x	74.20	207.00	-	-	-	-
86.30	x	71.70	212.00	-	-	-	-
78.40	x	64.70	191.00	-	-	-	-
59.20	x	60.10	174.00	-	-	-	-
80.90	x	70.60	214.00	-	-	-	-
63.70	x	56.70	182.00	-	-	-	-
73.10	x	65.30	180.00	-	-	-	-
66.80	x	58.70	179.00	-	-	-	-
106.80	x	87.40	428.00	-	-	-	-

131.80	x	98.80	478.00	-	-	-	-
64.20	x	54.30	176.00	-	-	-	-
127.90	x	96.00	438.00	-	-	-	-
121.30	x	94.30	439.00	-	-	-	-
55.80	x	47.20	174.00	-	-	-	-
131.70	x	101.20	466.00	-	-	-	-
79.10	x	75.80	188.00	-	-	-	-
130.40	x	100.00	346.00	-	-	-	-
110.60	x	98.30	328.00	-	-	-	-
108.30	x	96.30	307.00	-	-	-	-
98.70	x	83.20	298.00	-	-	-	-
140.80	x	107.60	407.00	-	-	-	-
136.30	x	108.60	388.00	-	-	-	-
47.80	x	47.80	48.10	-	-	-	-
50.00	x	52.30	39.70	-	-	-	-
51.50	x	46.20	47.20	-	-	-	-
73.20	x	72.00	119.40	-	-	-	-
47.60	x	46.40	44.20	-	-	-	-

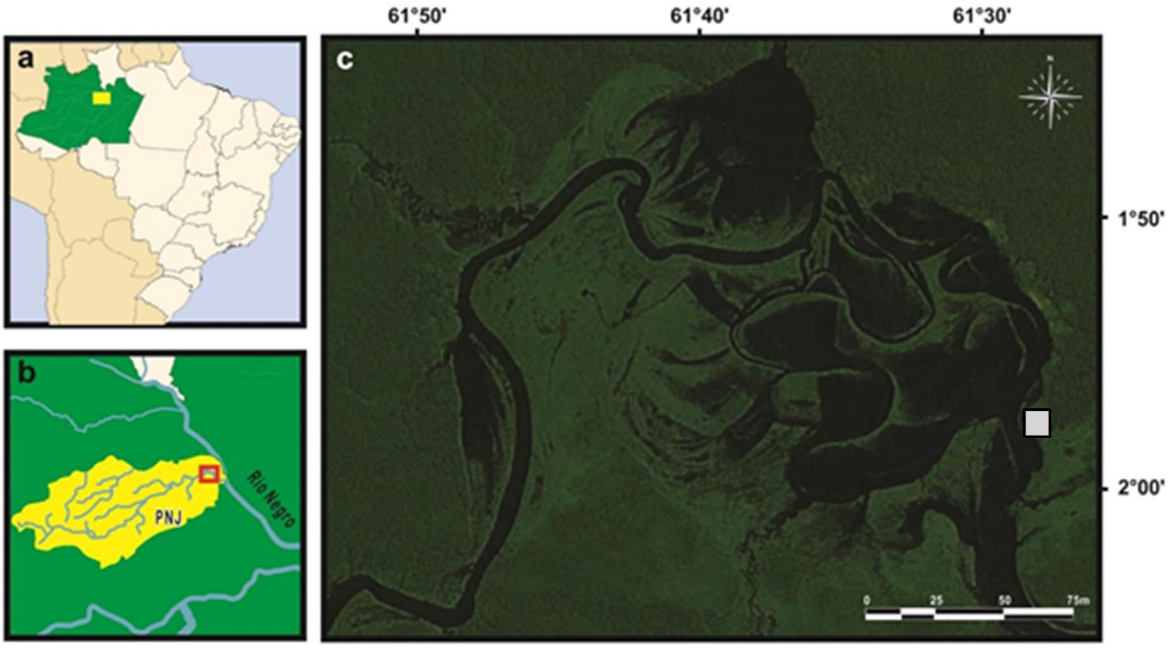

Figure S1 Location of study site within Jaú National Park Amazonian Brazil (a-b), and c) igapó forest of the “Seringalzinho” region, showing the 2006-2008 study support base (pale blue square). Map: Matheus J. Castro Sa.

Figure S2 Hydrochoric fruits of *Aldina latifolia* (Fabaceae) floating in water (red arrows) (A) still-floating seed germinating after 12 weeks afloat (B). In the image (C) collected fruits belonging to the same maturation stage (mature), with substantial variation in size and weight: small fruit (left), medium (center) and large (right) fruit. Photo: Alessandro Rocha (b), Adrian Barnett (a, d).

Figure S3 Measuring uacaris hands (Taxon INPA 5240) (A), palm length from the wrist crease to the midline of palmar digital crease of middle digit (D3) (B); palm width, taken at widest part of palm (C); measurement of the longest digit (D2 in *Cacajao*), from base to tip, with calipers (D). Use of string to measure length when D2 contorted (Taxon 26.5.5.18 NHML) (E). Photos: Renann H. P. Dias da Silva (a,b-d), Adrian Barnett (e).

CAPÍTULO II

Dias da Silva R. H. P, Menezes, J.C.G., Castro Sá, M.J., Baccaro, F., & Barnett, A. A. **Fazendo a feira: primatas uacaris (C*acajao*, Pitheciidae) seleciona frutos de tamanho ideal para uma refeição parcimoniosa.** Projeto de mestrado submetido ao Programa de Pós-Graduação em Zoologia, do Instituto de Ciências Biológicas da Universidade Federal do Amazonas–UFAM. Manuscrito formatado de acordo com as normas do periódico *Physycal Anthropology*.

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Running Header *Dias-Silva et al. Primate fruit choice hand and gape size*

Handling limits and fruit choice: the role of gape- and hand-size in fruit species choice in a specialist seed-predating primate genus (*Cacajao*, Pitheciidae)

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[1] **Authors' Contributions**
RHP data analysis and study design, drafted the manuscript and collected data on Cacajao hand size; FB advised on sample design and carried out statistical analyses; JCGM and MCS assisted with study design and helped draft the manuscript. AAB studydesign, hand size data collection and manuscript editing. All authors contributed to the manuscript, approved the final version and are accountable for the work.

ABSTRACT

Vertebrate food items rarely occur in uniform sizes. Animals are, therefore, often limited by food item sizes exceeding gape size, or which are either difficult or time-consuming to handle. Frugivorous primate anatomy may therefore limit consumption of fruits large in relation to the size of the hands and mouth, as processing them can result in larger energetic demands via the increased effort required when handling, opening and chewing such fruit. Given the above, the objective of this study was to analyse the grip and the maximum capacity of the mouth to accommodate fruit, and determine whether such parameters form selection criteria in determining fruits types eaten by of members of the genus *Cacajao*. To test this, four uacari (Pitheciidae) taxa were used (*Cacajao c. calvus* [Geoffroy Saint-Hilaire, 1847], *C. c. ucayalii* [Thomas, 1928], *C. melanocephalus* [Humboldt, 1812] and *C. ouakary* [Spix, 1823]), and study area species, including eaten and non-eaten fruit species, and compared these with hand and gape sizes from specimens in zoological collections, divided into three categories (*easy*, *manageable* and *difficult* handling/ingesting), and tested using a contingency table with Chi-square statistics. Except for *C. melanocephalus*, uacaris, when choosing diet species, appear not to use size of fruit-based levels of difficulty as selection criteria. Diets of *C. c. calvus*, *C. c. ucayalii* and *C. ouakary* large proportions of easy-to-handle fruit species in their diet, followed by *manageable* and those in the between-canines *easy-fit* categories. In contrast, the *C. melanocephalus* diet was dominated by hand *manageable* and between-canines *difficult-fit* categories. Fruit category selection differences between *C. melanocephalus* and the other taxa analysed were attributed to body size and habitat composition.

Key words: Handling, gape limited, precision grip, fruit size, Amazon

1. INTRODUCTION

Although Neotropical primates have a variety of potential fruit-based food resources, not all of these are easily accessible (Norconk, Wright, Conklin-Brittain, & Christopher, 2009). The foraging process that decides which species are included in a primate diet, and in what proportions, is composed of many decisions, including where to search for food, how to move between locations, and, once food is found, how to select and process it (preparing, chewing, ingesting, and digesting) (Norconk et al., 2009). These challenges are influenced both by food availability in the environment (in other words, forest productivity and seasonality), and the ease with which energy can be gained from the fruit and leaves available at a particular temporo-spatial point within the home range (a trade-off between physicochemical aspects of the plant and the anatomical and physiological capacities of the primate) (Milton, Giacalone, Wright, & Stockmayer, 2005).

Primates of the genus *Cacajao* (Pitheciinae: Pitheciidae) have diets dominated by seeds and fruits, although a variety of other food items, including flowers, leaves, nectar, and insects are also consumed. Fruit consumption represents 90% of the annual diet of *Cacajao c. calvus*, while for *Cacajao c. ucayalli*, *Cacajao melanocephalus* and *Cacajao ouakary*, fruit represents 88%, 91%, and 61.8%, respectively. Unusually among primates, members of this genus show a strong preference for immature seeds, and these comprise the greatest part of the diet in all taxa analysed so far (*Cacajao c. calvus*, 66%: Ayres, 1986; *C. melanocephalus,* 63.8%: Boubli, 1997; *C. c. ucayalii,* 50.6%: Bowler, 2007; 50.2%, *C. ouakary*: Barnett, 2010). In the Neotropics this tendency is shared primarily by *Chiropotes* and *Pithecia* species (Kay, Meldrum, & Takai, 2013), which, like *Cacajao* are members of the Pitheciidae subfamily Pitheciinae.

Cacajao and other pitheciines are not the only primates to feed extensively on immature fruits (e.g. *Papio* spp.: Kunz & Linsenmeier, 2008; *Colobus* spp.: Wasserman

& Chapman, 2003; *Pongo* spp.: Ungar 1995; *Propithecus*: Hemingway, 1996). They are, however, the only primates that have immature seeds as the main item in their diets (Kay, Meldrum, & Takai, 2013). In such fruits, developing seeds commonly contain high levels of, frequently toxic, secondary compounds (Freeland & Janzen, 1974; Lucas et al., 2001), or are surrounded by physical barriers that hamper predation, such as spines, hard or thick fruit walls, and/or exudates (Kinzey & Norconk, 1990, 1993; Lucas et al., 2001). Nevertheless, primates of the genus *Cacajao,* and other members of the Pitheciinae, have developed behavioral strategies and dental and cranial morphological adaptations to overcome these barriers and gain access to the seeds inside immature fruits (Kay, 2013, Kinzey, 1992; Barnett, Santos, Boyle, & Bezerra, 2015). It has been proposed (van Roosmalen & van Roosmalen, 2016) that *Cacajao* has intestinal adaptions to neutralize such toxins, alhough the mechanism was not explained.

The use of materials derived from geophagy to mediate the effects of secondary compounds from seeds and leaves is widely reported for primates (*Macaca mulata*: Gurian et al., 1992; *Procolobus kirkii:* Cooney & Struhsaker, 1997: reviewed by Krishnamani & Mahaney, 2000 and by Ferrari et al., 2008). Though it has yet to be observed in *Cacajao,* this strategy has been recorded for other pitheciins (*Chiropotes*: Veiga & Ferrari, 2007; *Pithecia*: Setz et al., 1999). An additional mechanism with which to avoid intoxication by immature fruits and seeds secondary compounds, one of the strategies used by some Pitheciines (including *Cacajao* spp.) is to dilute the toxicity of a species-specific suite of chemicals by feeding on small portions of seeds of a series of plant species in sequence (as opposed to the extended feeding bouts on a single species practiced by eaters of toxin-free pulp, such as *Atele*s spp.: Barnett & Dias-Silva, in prep.). However, such seeds are rich in lipids, and carbohydrates, and with low tannin content (Ayres, 1981; Boubli, 1998; Bowler, 2008; Barnett, 2010; Norconk & Veres, 2011).

In terms of morphological adaptations, members of the pitheciine clade have strong, deep, jaws, procumbent incisors and robust hypertrophied canines (Kay, 2013; Kinzey, 1992; Barnett, Santos, Boyle, & Bezerra, 2015) to break thick and rigid pericarps (e.g. Lecythidaceae pixidia) that surround such food sources. In addition to their anatomical characteristics, these primates commonly use both hands to manipulate fruit (Barnett, *unpublished data*) and bite strategically, tactically positioning a canine on the sulcus of dehiscent diet fruits, and the thinnest part of the pericarp of indehiscent ones, to minimize the force that needs to be applied and to avoid breaking their teeth (Barnett et al., 2016). Moreover, medium-sized fruits are preferred by *C. ouakary* (Dias-Silva et al., submitted), possibly because this eases pre-bite manipulation and, once in the mouth, facilitates the application of the pressure necessary to rupture the husk.

All of the above-mentioned strategies and adaptations are used to optimize foraging, so maximizing gains while simultaneously minimizing energy costs associated with processing time and muscle expenditure (Emlen, 1966; Milton, 1979, 1980, 1984; Chivers, Wood, & Bilsborugh, 1984; Garber, 1987; Hemingway, 1999; Sayers, 2008; Hohmann, 2009). However, not all age-classes can make use of these strategies: though *Aldina latifolia* fruits are eaten by adult *C. ouakary*, juveniles apparently find them too large and heavy to manipulate (Barnett, 2010). This parallels the situation where Capuchin-monkey (*Sapajus apella*) (Rocha, Reis, & Sekiama,1998) selection of rocks of favourable weight, resistance, and size (Haslam et al., 2016) for precision grip and best handling (Hopkins, Cantalupo, Wesley, Hostetter, & Pilcher, 2002), is related to the size, strength and developmental stage of the animal involved.

A close relationship between gape and body size, where fruit or prey sizes correspond to the maximum extent of mouth opening and body size, has been recorded across a great variety of vertebrates, including many species of fish, amphibians and birds

(Schmitt & Holbrook, 1984: *Embiotoca*, Embiotocidae; Hambright, 1991: *Micropterus salmoides*, Centrarchidae; Jaeger, & Rubin, 1982: *Plethodon cinereus*, Plethodontidae; Wheelwright, 1985: Cotingidae and other tropical birds; Wheelwright, 1993, for birds and fruits of the lauraceous neotropical tree *Ocotea tenera*; McPherson, 1989: *Bombycilla cedrorum,* Bombycillidae, overall winter diet fruits), for small seed-eating mammals (e.g. Garb, Koltler, & Brown, 2000: *Gerbillus* spp.) or eggs (e.g. Blight, Ryder, & Bertram, 1999: *Peromyscus keeni* and eggs of rhinoceros auklet, *Cerorhinca monocerata*), for bats (*Artibeus* spp. and fruits) of *Calophyllum brasiliense,* Calophyllaceae: Mello, Leiner, Guimarães, & Jordano, 2005), reptiles (Pianka & Vitt, 2006), rodents (Gautier-Hion et al., 1985) and felines (e.g. *Panthera onca*: Meachen-Samuels & Van Va Lkenburgh, 2009). In cases where foraging does not simply involve the opening of the mouth to the maximum possible extent (Nilsson & Brönmark, 2000), and the animal should then select food items that minimize handling time and maximize energy yield, according to their abilities (Elner & Hughes, 1978; Hughes & Elner, 1979).

Cacajao ouakary is known to chooses fruits by size and weight, with demonstrated preference for heavy-medium sized fruits over light-small fruits with thick husks, as the latter require longer handling times and provide a lower energy return (Dias-Silva et al., submitted). However, this analysis considered only one (rather large) fruit type.

Given the above considerations, it is possible that food choice by primates of the genus *Cacajao* may be related to its anatomical features, across a range of diet item sizes. The maximum mouth opening aperture for a primate sets a size limit for objects that can fit into the mouth, without dislocating the jaw. In addition, hand size may be a potential limiting and influential factor in the diet item choice process, as it may be difficult to establish a good grip on large fruits, leading to greater handling times. In much the same way, very small fruits may also be hard to manipulate with precision (Jones-Engel & Bard, 1996; Rocha, Reis, & Sekiama, 1998).

Thus, when foraging, a primate may encounter a wide variety of challenges related to handling ability. We hypothesize that the anatomy of bald (*Cacajao calvus calvus* and *C. c. ucayalli*) and black-faced uacaris (*C. melacocephalus* and *C. ouakary*) limits the consumption of fruits exceeding ergonomically viable handling capacity and maximum gape. Accordingly, the goal was to evaluate whether the size of fruits eaten by four *Cacajao* taxa of (*C. c. calvus*, *C. c. ucayallii*, *C. melacocephalus,* and *C. ouakary*) showed better correspondence to grip-capacity and gape-size than fruits that were abundant but uneaten.

2. MATERIAL AND METHODS

2.1. Sampling methods

For four *Cacajao* taxa (*C. c. calvus, C. c. ucayalii, C. melanocephalus* and *C. ouakary*) we used five lists of diet fruits (Ayres, 1986; Boubli, 1998; Bowler, 2008 and Barnett, 2005, 2010), from different study areas and environments (varzea, chavascal, igapó, borokotó, campina and terra-firme, see Barnett et al. [2015] for more details of these habitat types). Together, these were combined into a database that characterized fruits and seeds available by habitat, physical characteristics and whether they were eaten or uneaten. The distribution, feeding habits, body size, daily movement patterns and group size of the congeneric primates was assumed to be functionally identical (Table S1). In order to avoid multiple representations by synonymous taxa and to ensure all analysis was conducted using the current accepted taxonomy, the names of all plant species on the fruit lists were checked using the online platforms iPlant Collaborative.org

- Taxonomic Name Resolution Service v4.0 (2016), The Plant List (2016), and Tropicos.org (2016).

Fruit and seed sizes were obtained from the following sources: Van Roosmalen (1985, 2013); Gentry (1996); Wittmann et al. (2010); Ribeiro et al. (1999); Cornejo & Janovec (2010); Flora Neotropica; Herbarium NYBG (Section "*Monograph Details*"); *Seed Information Database Kew;* Flora de Nicarágua; Flora do Peru; Flora do Ecuador; Flora Neotropica; Flora das Reservas Biológicas de Iquitos, Peru; Flora of the Venezuelan Guayana; Flora Brasiliensis, Guia Reserva Florestal Ducke; Biodiversity Heritage Library – BHL and Internet Archive (https://archive.org/). Whenever data concerning the accepted name of the species could not be found in any of the sources used, we either either deployed species synonyms data (e.g. accepted name: *Salacia spectabilis,* synonym: *Salacia cordata*) or accessed other online sources, such as descriptions in online herbarium records and Species Link, articles found through Google Scholar, Web of Science, and Mendeley, using the genus and/or botanical species of interest as keywords. Seed size was classified according to Cornejo & Janovec (2010).

The use of average values for length, width and thickness of fruits and seeds and using measurements derived from the literature, is a canonical method (e. g. Hawes & Peres, 2014), Its validity lies in that fact that, while fruit morphology and seed size are highly conserved and show consistent uniformity across tree genera and woody lianas in the Amazon, such traits tend to vary more between genera (Casper, Heard, & Apanius, 1992; Kelly, 1995; ter Steege & Hammond, 2001). Plants unidentified at the genus and/or species level were allocated average fruit and seed length values derived from the literature for the family in question.

Hand measurement samples were obtained from 103 individuals from different field locaities and musuem collections (Table S2) represented by 7 taxa (4 subspecies and

4 species) of *Cacajao*: *C. calvus calvus* (n=21), *C. calvus rubincundus* (n=38), *C. calvus ucayalli* (n=11), *C. calvus noavaesi* (n=4), *C. ouakary* (n=5), *C. melanocephalus* (n=21) and *C. ayresi* (n=3). Of the 103 animals sampled, 46 were female, 42 were male and 15 sex undefined. While published lists of diet items exist, to date, for only four uacari taxa (*C. c. calvus*, *C. c. ucayalli*, *C. melanocephalus* and *C. ouakary*), the other three taxa known for the genus (i.e. *C. c. rubicundus*, *C. c. novasei* and *C. ayresi*), all have representatives in zoological collections. These were added to the data set using geographic distributions in Silva Júnior et al. *apud* Veiga, Barnett, Ferrari, and Norconk (2013). Therefore, *C. c. rubicundus* was added to the *C. c. ucayalli* dataset, *C. c. novasei* to the *C. c. calvus* (Figueredo-Ready et al., 2013), and *C. ayresi* to that of *C. melanocephalus* (Ferrari, Guedes, Figueiredo-Ready, & Barnett, 2014). Classification of *C. ouakary* and *C. melanocephalus* follows Ferrari, Guedes, Figueiredo-Ready, and Barnett (2014).

All samples were obtained from taxidermized animals or dried skins of museum specimens with undamaged hands (Figure 1f), available at the four institutions visited: Museu Paraense Emilio Goeldi, Belem, Brazil (MPEG); Natural History Museum, London, England (NHML); Museum of Zoology, University of São Paulo, Sao Paulo, Brazil (MZUSP); Zoological Collection of the National Institute for Amazonian Research, Manaus, Brazil (INPA).

Measurements of palm length were made from the wrist crease to the interpalangeal palmar region (digito-palmar crease) towards the middle finger, while width was obtained from the widest part of the base of the palm. The total hand area was obtained by adding the length and width measurements with the largest finger length measurements (in this case, the ring finger) from the base to the apex of the finger. Measurements were obtained with a line of string, which allowed the dried, contorted, fingers and hands of taxidermized animals to be measured with accuracy (Figure S1a-f). For specimens with fully extended hands, callipers were used. Whenever possible the right hand was measured, as primates tend to demonstrate greater ability with this hand when handling objects and food (Hopkins, Cantalupo, Wesley, Hostetter, & Pilcher, 2002).

To estimate maximum mouth aperture (gape) from specimen skulls, we took four measurements. All may be subject to overestimation, since their form assumes that there are no adductor chewing muscles (masseter, temporal and middle pterygoid muscles) and associated ligaments to limit jaw extention A description for each method used to estimate gape is given in Table 1. Skull structures mentioned in the description are shown in Figure S2.

After controlling for the different mouth opening angles, gape measurements were performed: i) maximum distance between upper and lower incisors (DII) (Figure S3a) at different angles, and ii) maximum distance between upper and lower canine tips (DCC) (Figure S3b). For skull-dental anatomy, distances between the tips of the upper and lower canines (Figure S3cd) were measured only for specimens with a full set of canines. This measure gave an estimate of which potential diet items would be excluded by the inability to pass through the buccal aperture due to limiting presence of the hypertrophied canines.

2.2. Data Analysis

The sample of taxidermized individuals of the genus *Cacajao* contained 98 specimens (five individuals were removed from the 103, for being very young), of these were 44 females, 39 males and 15 of undefined sex. Biometric hand measurements were collected from a total of 73 specimens (*C. c. calvus* N=18, *C. ucayalii* N=33*, C.*

melanocephalus N=9, and *C. ouakary* N=13). Gape measurements (Figure 3) were obtained for 58 individuals (*C. c. calvus* N=10, *C. c. ucayalii* N=35, *C. melanocephalus* N=8, and *C. ouakary* N=5). Distance measurements between upper and lower canines were obtained from 64 specimens (*C. c. calvus* N=12, *C. ucayalii* N=38, *C. melanocephalus* N=9, and *C. ouakary* N=5).

Differences in the number of specimens measured for the different metrics is due to the quality of the material found in the museums, with some specimens incomplete or deteriorated in the relevant area (e.g. Figure 1f). When this occurred, missing values for each metric were estimated from linear regressions with the same metric derived from other, complete, specimens. In order to obtain the smallest measurement error with gape estimationds, a Pearson correlation analysis was performed. The selected variable was then used in the contingency table following a descriptive statistical analysis.

Descriptive statistical analysis was performed for each of the variables measured from eaten and uneaten fruits and seeds, hand and buccal gape metric for each *Cacajao* taxon. To analyze whether differences for these variables existed between the sampled primate taxa, a Kruskal-Wallis test was used, followed by a Nemenyi *post-hoc* Test for a multiple comparison between *Cacajao* taxa, with data distribution normality verified with a Shapiro-Wilk test. Wilcoxon and Mann-Whitney Tests for independent samples were used to test for differences between the lengths and widths of eaten and uneaten fruits/seeds in the diet and habitat of each sampled *Cacajao* taxon.

To determine whether uacaris were choosing seeds by size class in the same proportion as their availability, we compared seeds of the plant species consumed (number of seeds per size class) and availability (number of species of plants with uneaten seeds in the home range per size class), with a contingency test using Chi-square (χ^2)

statistics. Seed size classification followed Cornejo & Janovec (2010): i) tiny (<5mm), ii) small (5 to 10mm), iii) medium (10 to 20mm) and iv) large (> 20mm).

To test whether eaten fruits provided better grips and fitted more easily into the mouth than did uneaten fruits of plant species available in the home range of each primate, we compared the relationship between the size of eaten and uneaten fruit and seeds, with hand size, mouth gape extent, and distance between canine tips, and created a three-level classification of handling difficulty (i.e. *easy*, *manageable*, and *difficult*), and two levels for gape samples (i.e. easy and difficult), with analysis occurring via a contingency table using the chi-square statistic (χ^2). Fruits and seeds were categorized as follows:

a) Fruits that are easy-to-handle and/or ingest: fruit diameter equal to or less than the average length of the palm and maximum gape size;

b) Fruits of medium difficulty to handle (*manageable*) and/or ingest: fruit diameter equal to or smaller than average hand size and equal to the maximum gape size;

c) Fruits difficult to handle and/or ingest: fruit diameter larger than average hand size and maximum gape size (in this case they need to use both hands).

d) Seeds easy to eat: seed diameter smaller than the space between the upper canines;

e) Seeds difficult to ingest: seed diameter equal to or greater than the space between the upper canines.

All analyzes were processed in the R program (R Core Team 2016), with the *pmcmr* package used for the Nemenyi *post-hoc* Test.

3. RESULTS

In total the five lists of plants eaten and uneaten fruits by uacaris within their home study ranges contained 1299 distinct plant species: (*C. c. calvus*: 195, *C. c. ucayalii*: 458, *C. melanocephalus*: 291 and *C. ouakary*: 355. Of these, *C. c. calvus* consumed 74 (37.95%), *C. c. ucayalii* 139 (30.35%), *C. melanocephalus* 117 (40.21%), and *C. ouakary* 144 (39.24%). Of these, in all four cases, large percentages were not eaten: *C. c. calvus*: 121 (62.05%), *C. c. ucayalii*: 319 (69.65%), *C. melanocephalus*: 174 (59.79%) and *C. ouakary*: 223 (60.76%). Mean values and standard deviation for all hand and gape metrics for the studied taxa are given in Table 2.

Gape measurements

We used regression analyses to predict gape measurements data for the skull samples that did not have all teeth present, based on data from the 98 specimens that had all canine and incisive teeth (gpii: R^2= 0.57, n= 57; gpcc: R^2= 0.62, n= 58), raising the total of incisor-incisor and canine-canine to 92 gape measurements (*C.c. calvus*, N=20; *C. c. ucayalii*, N= 46; *C. melanocephalus,* N=13 and *C. ouakary,* N=13).

Results of Pearson's correlation test indicated *total maximum opening* as the metric with the best correlation between incisor-incisor and canine-canine distances (p=0.94, n=92), for all four mouth gape measurements (Figure 1). The distance between the superior and inferior canine also showed a high correlation (p=0.87, n= 92), therefore we decided to use only one measurement between canines in subsequent chi-square analyses.

There was no significant difference between *Cacajao* species, neither for the distance of incisor-incisor gap (Kruskal-Wallis, χ^2= 2.3914, *df* = 3, *p*= 0.4952) nor for canine-canine gap (Kruskal-Wallis, χ^2= 2.3751, *df* = 3, *p*= 0.4983) (Figure 2). Among the mouth opening methods selected, *C. c. calvus* was the one that had, on average, the greatest capacity for incisor-incisor and canine-canine opening mouth, followed by *C. c. ucayalli* (Table 2). *Cacajao ouakary* and *C. melanocephalus* were the lowest (Table 2).

The mean distance between the upper canines (upp) was different among the primates (Kruskal-Wallis, χ^2= 11.79, *df*= 3, *p*= 0.008) (Figure 3), but the distance between the lower canines did not show significant differences (Kruskal-Wallis, χ^2= 5.94 , *df*= 3, *p*= 0.115). This difference is because *Cacajao melanocephalus* was significantly smaller than *C. c. ucayalli* (*p*= 0.0045) and *C. c. calvus* (*p*= 0.0313) (Figure 3). *Cacajao c. calvus* had the highest mean inter-canine distance, followed by *C. c. ucayalii* (Table 2), though the difference between them was not statistically significant (*p*= 0.9946). Among the black-faced uacaris, the *C. ouakary* showed canines distances close to that of *C. melanocephalus*, with no significant differences (*p*= 0.4495). In addition, *C. oukary* was not significactly different from between *C. c. ucayalii* (*p*= 0.8393) and *C. c. calvus* (*p*= 0.9269).

Hand measurements

Biometric measurements of the hand size of primates did not vary significantly between sexes (Table 3), although females show a tendency to have palm width and palm length, respectively, larger and smaller than males of the same species (Table 3).

Hand and palm metrics for members of the genus *Cacajao*, gave a mean hand length of $\bar{x}$ = 91.37 ± 10.13 mm (range 68.7 - 118.9 mm), while the of palm width palm length metrics were $\bar{x}$ = 34.33 ± 3.65 mm (range 23 - 51 mm) and $\bar{x}$ = 45.91 ± 4.75 mm (range 36 - 60 mm), respectively. Overall hand size was statistically different between the analyzed taxa (Kruskal-Wallis, χ^2= 9.8969, df= 3, p= 0.01946) (Figure 4). In terms of species, *C. melanocephalus* and *C. ouakary* were not significantly different (p= 0.19) and have the smallest hands (Table 2), and were significantly different from *C. c. rubicundus* (*Cm.*: p= 0.01; *Co*: p= 0.02) which had the largest hand, but not very different from *C. c. calvus* (p= 0.18) (Figure 6). The size of *C. c. calvus* hands was like of *C. ouakary* (p= 0.21) and different from *C. melanocephalus* (p= 0.04) (Table 2).

For palm length (Figure 4b), *C. calvus* and *C. ucayalii* had significantly similar sizes (p= 0.70), as did *C. melanocephalus* and *C. ouakary* (p= 0.24). In general, there was no significant difference in hand size among the taxa (Table 2), although *Cacajao ucayalli* had a palm length virtually bigger than *C. melanocephalus* (p= 0.096). However, the palm width was different among the primates (Figure 4a), in which *C. ucayalli* showed a significant difference from *C. c. calvus* (p= 0.012) and virtual of *C. melanocephalus* (p= 0.073), but not significantly bigger than that of *C. ouakary* (p= 0.2139). *Cacajao ouakary* did not differ from *C. melanocephalus* (p= 0.18), and *C. calvus* (Cm ~ Cc: p = 0.6114; Co ~ Cc: p= 0.88).

Fruits and seed sizes

Diet fruits sizes varied significantly between the studied uacari taxa, for both length (Kruskal-Wallis, χ^2= 13.23, df= 3, p= 0.0042), and ~~in~~ width (Kruskal-Wallis, χ^2= 22, df= 3, p <0.05), with fruits eaten by *C. melanocephalus* having the greatest length ($\bar{x}$= 65.38 ± 64.38) (Figure 5). In general, *C. c. calvus* ($\bar{x}$= 58.98 ± 62.34; p= 0.1795), *C. c. ucayalii* ($\bar{x}$= 55.32 ± 61.89; p= 0.0066) and *C. ouakary* ($\bar{x}$= 60.72 ± 71.30; p= 0.0088), selected fruits of approximatly similar length (Figure 5a) (range 2 mm to 400 mm, with an average of 57 x 30 mm in length. The same pattern occured for fruit width, where *C. melanocephalus* ($\bar{x}$= 38.79 ± 24.13) selected fruits with widths significantly greater than *C. c. ucayalii* ($\bar{x}$= 27.22 ± 18.14; p<0.05), *C. ouakary* ($\bar{x}$= 37.34 ± 50.89; p= 0.0031), or *C. c. calvus* ($\bar{x}$= 30.37 ± 19.49; p= 0.0569).

For size of the fruits of plant species present in the home ranges of the analysed *Cacajao* taxa, but not eaten by them, showed no significant difference for either fruit length (Kruskal-Wallis, χ^2 = 5.37, *df*= 3, p= 0.1465) or width (Kruskal-Wallis, χ^2= 0.25, *df*= 3, p= 0.97) (Figure 5ab). Although not significant, *C. ouakary* uneaten fruits length ($\bar{x}$= 44.86 ± 50.20) was, in terms of absolute mean values, lower than *C. c. ucayalii* ($\bar{x}$= 61.37 ± 71.79; p= 0.20), *C. c. calvus* ($\bar{x}$= 63.91 ± 73.69; p= 0.24) or *C. melanocephalus* ($\bar{x}$= 51.74 ± 56.01; p= 0.37).

When diet data was combined for all *Cacajao* taxa, there was no significant difference in the sizes ranges of eaten and uneaten fruit classes. For the primate taxa themselves, neither *C. c. calvus* nor *C. c. ucayalli* showed significant differences for either length (Cc: W= 4490, p = 0.2892; Cu: W= 17978, p= 0.3321) or width (Cc: W= 2115, p= 0.3137; Cu: W= 8472, p= 0.6571) of eaten and uneaten fruits. However, both *C. melanocephalus* and *C. ouakary* showed significant differences in the size of eaten and uneaten fruits (Figure 5ab). Fruits eaten by *C. melanocephalus* had both greater length (W= 12329, p= 0.00014) and width (W= 10786, p= 0.001), than those uneaten. While for *C. ouakary*, eaten fruits were significantly longer than uneaten ones (W= 16200; p= 0.02335), though not greater in width (W= 8812, p= 0.1911).

The length of the seeds consumed is also different between *Cacajao* taxa (Kruskal-Wallis, χ^2= 12.015, *df*= 3, p= 0.0073), as was width (Kruskal-Wallis, χ^2= 16.859, *df*= 3, p= 0.0007). This occurred because *C. melanocephalus,* consumed seeds both longer

($\bar{x}$= 22.35 ± 11.11) than *C. c. ucayalii* ($\bar{x}$= 19.22 ± 13.05; p= 0.0397), *C. ouakary* ($\bar{x}$= 20.37 ± 17.82; p= 0.007), or *C. c. calvus* ($\bar{x}$= 19.65 ± 13.18; p= 0.0333), as well as wider (Cm: $\bar{x}$= 14.96 ± 8.24) (Cc: $\bar{x}$= 12.38 ± 9.54, p= 0.07802; Cu: $\bar{x}$= 11.42 ± 9.52, p= 0.00068; Co: $\bar{x}$= 14.15 ± 16.19, p= 0.01481). The other uacaris consumed seeds significantly similar in length and width (Figure 6).

For uneaten seeds, there was no significant differences between uacari taxa for seed length (Kruskal-Wallis, χ^2 = 7,638, df= 3, p= 0.05412), seed width (Kruskal-Wallis, χ^2 = 4.8682, df= 3, p= 0.1817) (Figure 6), and between *Cacajao* species: *C. c. calvus* (length: $\bar{x}$= 16.92 ± 14.04; width: 11.79 ± 11.95), *C. melanocephalus* (length: $\bar{x}$= 20.73 ± 15.47; width: 13.16 ±11.90), *C. ouakary* (length: $\bar{x}$= 20.69 ± 17.01; width: 13.93 ±10.21), *C.c. ucayalli* (length: $\bar{x}$= 17.83 ± 15.69; width: 12.78 ±10.19).

For individual *Cacajao* taxa, there were significant differences between eaten and uneaten seeds only for *C. c. ucaylii* seed length (W= 10889; p= 0.04217) and for both seed length and width for *C. melanocephalus* (length: W= 6480; p= 0.01918, width: W= 5564; p=0.002505). The remaining relationships between seed length and/or width was not significant: *C. c. ucayalli* (width: W=1698, p= 0.8509), *C. c. calvus* (length: W= 2938, p= 0.0788, width: W= 2167, p= 0.1909) and *C. ouakary* (length: W= 6139, p= 0.7601, width: W= 1698, p= 0.8509) (Figure 6).

Diet and fruit selection

We performed separate analyses for each of the handling and gape-size capacities for each of the analyzed *Cacajao* taxa. For fruit handling ease based on hand length and width, only *C. melanocephalus* showed a significant difference among the three levels of difficulty, doing so for both metrics (length: χ^2= 15.058, df= 2, p= 0.00054; width: χ^2=

11.469, *df*= 2, *p*= 0.00323), which in these metrics, the category *manageable* had the highest frequency for eaten compared to uneaten fruits.

The same occurred for fruits of sizes that fitted between canines. Again, only *C. melanocephalus* showed statistical differences between eaten and uneaten fruits. The level of commonest class for fitting the fruits between canines was *difficult,* a result which differed from the expected (Table 7). For length, fruits between canines class *difficult* were more commonly eaten than *easy* in terms of absolute values and showed observed frequencies of eaten fruits higher than expected (Table 7) (χ^2= 10.754, *df*= 1, *p*= 0.00104). By contrast, for width fitting capacity, fruits in the *easy* category occurred at a frequency higher than expected (χ^2= 6.398, *df*= 1, *p*= 0.01143). Despite the capacity to fit fruit between incisor-incisor and canine-canine relating to the same end, incisor-incisor fitting showed no statistical difference between eaten and uneaten fruits for any of the analyzed *Cacajao* taxa.

For seed passage between the upper canines, only *C. melanocephalus* ate seeds in a way that differed from the expected. It did this for both length (χ^2= 13.582, *df*= 1, *p*= 0.00023) and width (χ^2= 11.81, *df*= 1, *p*= 0.000589). In this case, the overall frequency of eaten seeds of these species was for *difficult* to pass between the canines, instead of the category *easy*.

For all other *Cacajao* taxa, there was no difference for eaten and uneaten fruits or seeds in any of the measured handling and gape-fitting capacities. *Cacajao c. calvus*, *C. c. ucayalli* and *C. ouakary* (Tables 4-6) all preferred easy-to-handle fruits over those *medium* and *difficult* categories. However, for passage of seeds between upper canines, these three taxa consumed seeds in the *easy* and *difficult* categories with equal frequency, this being close to 50-50%.

According to handling classes, the mean size of fruits (Table 8) eaten by the studied *Cacajao* taxa was higher than the uneaten within the easy to manipulate category, while for handle category, the uneaten fruits were, on average, larger than eaten fruits within same class. The difficult to manipulate category showed differences between the species, with the uneaten fruits being larger than eaten ones for *C. melanocephalus* and *C. ouakary,* while the opposite was true for *C. c. calvus* and *C. c. ucayalii* (Table 8).

For seed sizes (Cornejo & Janovec 2010), *C. oukary* consumed more species of plants with medium-sized seeds, while the other uacari taxa consumed more plants with large-sized seeds (Table 12). For the proportions of seeds eaten and uneaten for each size class, there was a significant association between consumption and size class for *C. melanocephalus* (χ^2 = 20.535, *df*= 3, *p*= 0.0001315) and *C. c. ucayalii* (χ^2 = 56.756, *df*= 3, *p*= 2.898e-12).

Consumption by *C. melanocephalus* involved fewer small and medium-sized seeds than expected, but far more large seeds than expected (Tables 9 and 10). For *C. c. calvus* (χ^2= 5.5789, *df*= 3, *p*= 0.134) and *C. oukary* (χ^2= 4.07, *df*= 3, *p*= 0.254), there was no significant association between consumption and size class (Tables 9 and 10). Despite *C. calvus* apparently consuming more large seeds (43.86%) than expected (25.84%), the difference was not statistically significant. This taxon also forages a high frequency on plant species with medium seeds (33.33%), which were frequent in the area studied (44.94%). *Cacajao ouakary* consumed seeds in the same proportion as was expected from their frequency in the environment (Tables 9 and 14).

4. DISCUSSION

With the exception of *C. melanocephalus*, fruit selection by uacaris does not appear to be related to the size of available fruits. In terms of size-based ease-ofmanipulability categories, *C. c. calvus, C. c. ucayalii* and *C. ouakary* all showed a preference for *easy* fruits, followed by *manageable* ones. In this context it is worth noting that, as the three-dimensional shape of the fruit was considered, even if the length of a fruit made if difficult-to-handle, it could often be easily manipulated by virtue of its width. However, unlike the other taxa, *C. melanocephalus*, despite easy-to-handle fruit species being available in larger numbers at the study site, opted to consume more species with fruits in the *manageable* size class. It did this even though these were proportionally less frequent. It also disproportionately selected species with difficult-to-handle fruits, feeding on almost all species in the area that produced fruits in this size class. Fruits consumed by this taxon were, on average, significantly larger than those not consumed.

Why the species selected by *C. melanocephalus* for its diet differ so markedly from the other analysed taxa may be a consequence of either study group habitat or their body size. Contrary to the opinion of Hershkovitz (1987) that occupied habitats are very similar across the range of the genus, *Cacajao* taxa occupy and exploit a range of habitats outside the seasonally-flooded forests for which they are well known (Barnett, Bowler, Bezerra, & Defler, 2013a). However, as analysed here, the average size of fruits and seeds available in the various exploited habitats are very similar.

However, in the area inhabited by the *C. melanocephalus* population studied by Boubli (1997, 1999), and used in the current study, has a very unusual botanical composition (Boubli, 2002) compared to the habitats occupied by the other *Cacajao* taxa (Barnett et al., 2013a), as it dominated by relatively few, highly agglomerated, species which produce fruits for long periods, from eight to nine months, while many others produce fruits more than once a year (Boubli, 1997). In addition, there is to a relative absence of competitors for preferred food resources (unlike many other habitats, where competition may come from sciurids and psittacids: Barnett et al., 2005, 2015). This low degree of seasonal fluctuation in resource abundance does not require seasonal migration

(Barnett et al., 2013a), and so may allow more time to specialize on difficult-to-handle species, where abundance offsets increased energetic handling costs. Such effects may be enhanced by the fact that *C. melanocephalus* is the smallest of the taxa in the current study (e. g. hand sieze: *C. c. calvus*, 91.2 mm; *C. c. ucayalii*, 94,8 mm; *C. melanocephalus*, 86.32 mm *C. ouakary*, 88.6 mm). According to Hershkovitz (1987), uacaris of the black-headed clade are, overall, smaller than those of the bald-headed clade.

Studies of *Cacajao ouakary* have shown forms of within-species fruit selectivity that minimizes time or energy when obtaining food (Dias-Silva et al., submitted), choosing fruits of a size that is easy to grip and medium-sized seeds and which maximize the time/energy trade-off. Such aspects involve dental processing, which is to some extent limited gape-limited due to biomechanical limitations of effective bite force, but mediated by the use of sutures and thinnest points in the pericarp to facilitate access.

In the diet of other analysed uacari taxa, easy-to-handle fruits were most commonly chosen, followed by those in the *manageable* class, with a few classified as *difficult* (although they could easily be held with two hands). In general, average size of fruits in the diet of a primate species is smaller than the average size of their hands. According to Yakou, Yamamoto, Koyama, and Hyodo (1997), the "optimum grasping diameter" is when the object is in contact with the entire palm area and with the fingertips, so that many of the species of fruits that appear in primate diets are generally of sizes that allow handling with a precision grip. Uacaris lack the ability to bring the thumb to touch the index finger (Napier, 1960), but the first two digits of the hand are opposed to the others (schizodactylous, *sensu* Youlatos, 1999), making a form of precision grip possible.

Regardings the average size of the fruits classified as difficult, these could was easily manipulated with both hands, considered primates are characterized by a their use of a curved hand, lacking claws, that is used to grab food items (Toussaint et al., 2013), manipulate fruits/seeds and tools (Rocha et al., 1998), and is adapted to hold on to the branches (Youlatos, 1999; Toussaint et al., 2013). These fruit handling strategies modify the relationship between the size of the frugivorous body and the size of the seed (Corlett & Lucas, 1990; King, 1986).

However, uacaris are sclerocarpic foragers, specialists in using their robust canines to break through the husks of a variety of fruits to reach the seeds inside (Kinzey, 1992, Rosenberger & Kinzey, 1976), often using weakness of natural sutures to do so (Barnett et al., 2017). Functionally, canines positioned outside the contour of the dental arch, allow uacaris to open fruits that exceed the width of their gape and increase the ability to pierce objects "with considerable force" (Kinzey, 1992), while the procumbent incisors are used as tweezers to access the seeds (Kinzey, 1992), to scrape or remove the soft mesocarp from the inside of the fruit or to scrape the pericarp (outer covering) of the fruits that are very large or difficult to perforate with the canines (for example, *Gustavia augusta* and *Lecythis idatimon*, Lecythidaceae: Norconk & Veres, 2011).

However, there is an indirect biomechanical interaction between grip and bite forces since, using fruit that are *easy* to hold aids the precision grip, so guaranteeing that the hand functions as a firm support base, which allowing a more precise application of canine strength since the fruit will be less likely to fall when the bite force is applied. Fruit size and mass have been widely considered to be a key influence on frugivorous patterns, since feeding through handling time costs can influence the speed at which energy and nutritional rewards are obtained (Foster, 1990; Wheelwright, 1993; Mello, 2005). However, while studies of diet and food choice are common for primates, they rarely do so in terms of handling optimality. Here we have compared an extensive data base of fruit sizes, one that includes both those fruit available to uacaris for consumption and those actually eaten. This was combined with museum-derived data on hand and gape size, together, this allowed the predictions of manipulation and processing to be tested.

In the current study, species with difficult-to-manipulate fruits, those which would be large in proportion to the size of an individual uacari, were infrequent components of the diet for three of the four studied taxa, showing size to be a potentially limiting factor at the time of fruit collection and during handling. Such choices extend to within-species selectivity; a study with *C. ouakary* found preferential consumption of medium-sized fruits. These not only fitted the hand better, but also had lower handling times than larger fruits and gave better per-unit yields than smaller ones (Dias-Silva et al., submitted).

The choice of easy-to-manipulate fruits by the uacaris can be explained by the characteristics of their schizodactylous hands, which facilitates branch grasping (Youlatos 1999), but complicates fine digit-based object manipulation (Candland & Bush, 1995; Christel & Fragaszy, 2000).

Large fruits are considered to be those measuring 100-500mm. However, most consumed fruits with such measurements belong to the Fabaceae or Apocynaceae, and so have a pod like form, where one measurement is substantially less than the other: e.g. *Inga* spp. (± 500mm length), *Acacia tenuifolia* (200 x 40mm), *Eperua leucantha* (300 x 80mm), *Alexa imperatricis* (160 x 25mm), *Hidrochorea marginata* (110 x 18mm), *Parkia igneiflora* (300 x 45 mm) and *Macrolobium angustifolium* (105 x 58mm) (all Leguminosae), as well as Apocynaceae like *Malouetia* spp. (300 x7 mm), *Mucoa duckei* (100 x 12mm) and *Paranchornia peruviana* (100 x 13.2mm). Consequently, the fact must be considered that, irrespective of the length of such fruits, their width corresponds well to the adult uacari hand width (86-94mm) and so allows for a firm grip, and hence manipulation, to be achieved.

Despite consuming fruits that are easy-to-manipulate, on average the fruits consumed were larger than those not consumed, which differed from what was expected. This has also been reported by Ayres (1986) for *C. c. calvus*, Boubli (1998) for *C. melanocephalus*, and Bowler (2008) for *C. c. ucayalli* (2008). Medium-sized and large fruits may be preferred because they allow better grip strength and greater precision for a given hand size, as uacari are considered medium-sized primates (Hershkovitz, 1987).

Seeds classified as small and tiny using the categories of Cornejo & Janovec (2010) were little used by the animals studied in the current work. Tiny and small seeds were not preferred, possibly because such fruits do not provide a surface of good grip strength and precision (Jones-Engel & Bard, 1996, Hopkins, Cantalupo, Wesley, Hostetter, & Pilcher, 2002) given the hand size of uacaris, which are medium-sized primates (Hershkovitz, 1987), as well as because of their lower per-unit energy content (Milton, 1999; Chapman et al., 2012). As a result of the large volumes of secondary compounds in their diet, uacaris may need to consume more grams of protein per day than would be predicted by body weight (Milton, 1980). Linked to this, for *Inga* spp. seeds consumed by *C. c. calvus,* the largest had lower concentrations of phenolic compounds and condensed tannins than the smaller ones, in addition to having higher levels of lipids (Ayres, 1986). Thus, size choice may be nutrient-related in some cases.

The current study found consumed species had larger fruits than those that were not consumed, and that most consumed fruits were in then medium size range. The choice for medium-sized foods that are easy-to-handle but, nevertheless, difficult to fit between the canines can also be explained by the presence of such physical defences as the endocarp and testa around the seed, which serve to deter non-specialist potential predators (Hulme & Benkman, 2002), and increase with seed size between species (Moles, Warton, & Westoby, 2003).

Morphological specialization to allow one-handed grip (prehension) and object manipulation are considered key adaptations in the evolution of primates (Jones, 1916; Haines, 1955; Napier, 1960, 1961; Cartmill, 1974 ab; Godinot & Beard, 1991, 1993; Jouffroy, Godinot, & Nakano, 1991; Godinot, 1992; Lemelin, 1996; Hamrick, 2001, 2007; Bloch & Boyer, 2002; Kirk et al., 2008). Primate studies show that hand and body size is a limiting factor in foraging in relation to branch thickness and support capacity (Shapiro & Young, 2010; Remis, 1995, 1999). Hand size can also be a limiting factor in foraging, and therefore further studies of the effect of hand morphology of uacaris and other primates on foraging capacity should be investigated in the context of diet comparison. It is likely that this is an important limiting factor (Christel & Fragaszy, 2000b; Dominy, Lucas, Wrangham, & Ramsden, 2004; Fragaszy & Crast, 2004), and one that operates in addition to well-established the physical and chemical barriers (Clauss, 2003; McGraw & Daegling, 2012), and limiting factors of nutritional content (Felton et al., 2009), abundance and seasonality (Hemingway & Bynum, 2005) already well documented for primates.

Cacajao melanocephalus aside, the uacaris studied did not appear to use size-related difficulty of handling fruit as a criterion for including or excluding a species in the diet. *Cacajao c. calvus*, *C. c. ucayalii* and *C. ouakary* all had diets with a high percentage of fruit species in the easy-to-handle category, followed by *manageable*, and those that fit easily between canines. For *C. melanocephalus*, even though more species of fruits were available in the environment in the *easy* category for both handling and fitting between canines, the diet contained a disproportionately high number of species with *manageable* fruits, and of *difficult* to fit between canines, same which in lowest frequency in the environment, as well as consuming almost all species in the *difficult* category available in its home range. Fruits consumed by this primate were, on average, significantly larger than those not consumed. Differences found in *C. melanocephalus* diet fruit selection compared to the congeneric taxa analysed were attributed to their body size and habitat. Thus, while size is important in some aspects of selectivity, it is clear that others factors, most likely abundance and the presence of chemical and physical defences are also responsible for diet choice in these species, which have evolved to exploit the maximum range of resources across a wide size spectrum of available sizes in a series of highly challenging environments.

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6. BIBLIOGRAPHIC REFERENCES

Akosim, C., Joseph, J., & Egwumah, P.O., (2010). Assessment of Feeding Behavoir of Olive Baboon (*Papio anubis*) in Hong Hills Adamawa State Nigeria. *Journal of Research in Forestry, Wildlife and Environment*, **2(1)**: 60-72.

Amirsheybani, H. R., Crecelius, G. M., Timothy, N. H., Pfeiffer, M., Saggers, G. C., & Manders, E. K. (2000). The natural history of growth of hand. Part II: Hand length as a treatment guide in paediatric trauma patients. *The Journal of Trauma*, **49(3)**, 457 – 460. doi: 10.1097/00005373-200009000-00012

Ayoub, M. M., & Lo Presti, P. (1971). The determination of an optimum size cylindrical handle by use of electromyography. *Ergonomics*, **14(4)**, 509–518. doi: 10.1080/00140137108931271

Ayres, J. M. (1986). *Uakaris and Amazonian Flooded Forest.* Doctoral dissertation, University of Cambridge, Great Britain.

Barnett, A. A., Ronchi-Teles, B., Sousa Silva, W., Almeida, T., Bezerra, B., Gonçalves de Lima, M., Spironello, W. R., MacLarnon, A., Ross, C., & Shaw, P. J. A. (2017). Covert carnivory: a seed-predating primate, the golden-backed uacari, selects insect-infested fruits. *Journal of Zoological Research* **1(1)**: 16-31

Barnett, A. A., Bezerra, B. M., Spironello, W. R., Shaw, P., Ross, C. & MacLarnon, A. (2016). Foraging with finesse: a hard-fruit-eating primate selects weakest areas as bite sites. *American Journal of Physical Anthropology*, **160(1)**, 113-125. doi: 10.1002/ajpa.22935

Barnett, A. A., Almeida, T., Andrade, R., Boyle, S., Gonçales-Lima, M., Sousa Silva, W., Spironello, W. R., & Ronchi-Teles, B. (2015a). Ants in their plants: *Pseudomyrmex* ants reduce primate, parrot and squirrel predation on *Macrolobium acaciifolium* (Fabaceae) seeds in Brazilian Amazonia. *Biological Journal of the Linnean Society,* **114(2)**: 260-273. doi: doi.org/10.1111/bij.12425

Barnett, A. A., Santos P. J. P., Boyle S.A., & Bezerra B.M. (2015b). An improved technique using dental prostheses for field quantification of the force required by primates for the penetration of fruit. *Folia Primatologica* **86(4)**, 398-410. doi: 10.1159/000434677

Barnett, A. A., Bowler, M., Bezerra, B. M., & Defler, T. R. (2013a). *Ecology and behaviour of uacaris* (Cacajao). L. Veiga, A. A. Barnett, S. Ferrari, & M. Norconk (Eds.) Chapter 14: Evolutionary Biology and Conservation of Titis, Sakis and Uacaris, Cambridge University Press.

Barnett, A. A., Ronchi-Teles, B., Almeida, T., Sousa Silva, W., Bezerra, B., Deveny, A., Schiel-Baracuhy, V., Spironello, W., Ross, C., & MacLarnon, A. (2013b). Arthropod predation by the golden-backed uacari, *Cacajao melanocephalus ouakary* (Pitheciidae), in Jaú National Park, Brazilian Amazonia. *International Journal of Primatology* **34(3)**: 470-485. doi: 10.1007/s10764-013-9673-0

Barnett, A. A. (2010). *Diet, habitat use and conservation ecology of the golden-backed uacari,* Cacajao melanocephalus ouakary*, in Jaú National Park, Amazonian Brazil.* Doctoral thesis, Centre for Research in Evolutionary Anthropology, Roehampton University, London, Great Britain.

Barnett, A. A., de Castilho, C. V., Shapley, R. L., & Anicácio, A. (2005). Diet, habitat selection, and natural history of the golden-backed uacari, *Cacajao melanocephalus ouakary,* in Jaú National Park, Brazil. *International Journal of Primatology,* **26(4)**, 949-961. doi: 10.1007/s10764-005-5331-5

Beckman, N. G. (2013). The distribution of fruit and seed toxicity during development for eleven Neotropical trees and vines in Central Panama. *PloS One*, **8(7)**, e66764. doi: 10.1371/journal.pone.0066764.

Blight, L. K., Ryder, J. L., & Bertram, D. F. (1999). Predation on Rhinoceros Auklet eggs by a native population of *Peromyscus*. *The Condor*, **101(4)**, 871-876. doi: 10.2307/1370079

Bloch, J. I., Silcox, M. T., Boyer, D. M., & Sargis, E. J. (2007). New Paleocene skeletons and the relationship of plesiadapiforms to crownclade primates. *Proceedings of the National of Science of the United State of America*, **104(4)**, 1159–1164. doi:10.1073/pnas.0610579104

Boesch, C., Boesch, H. (1990).Tool use and tool making in wild chimpanzees. *Folia Primatologica*, **54(1-2)**, 86-99. doi: 10.1159/000156428

Boubli, J.P. & Ditchfield, A. D., (2000). The time of divergence between the two species of uacari monkeys: *Cacajao calvus* and *Cacajao melanocephalus*. *Folia Primatologica*, **71(6)**, 387-391. doi: 10.1159/000052735

Boubli, J. P., & Couto dos Santos, F. R. (2007). Phenology of canopy trees in the ever-wet lowland forest mosaic of Pico da Neblina National Park, Amazonas, Brazil. *Ecotropica* **13**: 17-26.

Boubli, J. P., (2005). *Floristics, primary productivity and primate diversity in Amazonia: contrasting a eutrophic varzea forest and an oligotrophic caatinga forest in Brazil.* J. L. Dew, & J. P. Boubli (Eds.) Tropical Fruits and Frugivores. Springer, Dordrecht.

Boubli, J. P. (1997). *Ecology of the black uakari monkey,* Cacajao melanocephalus melanocephalus, *in Pico da Neblina National Park, Brazil.* Doctoral dissertation, University of California, Berkeley, USA.

Bowler, M. (2007). *The Ecology and Conservation of the Red Uakari Monkey on the Yavari River,* Peru. Doctoral dissertation, University of Kent, Canterbury, Great Britiain.

Byrne, R.W. (1996a). *The misunderstood ape: cognitive skills of the gorilla*. A. E. Russon, K. A. Bard, & S. T. Parker (Eds.). Reaching into Thought: The Minds of the Great Apes. Cambridge: Cambridge University Press.

Byrne, R. W. (1996b). Machiavellian intelligence. *Evolutionary Anthropology*, **5(5)**, 172–180. doi: 10.1002/(SICI)1520-6505(1996)5:5<172::AID-EVAN6>3.0.CO;2-H

Byrne, R. W. (1996c). *Relating brain size to intelligence in primates*. P. A. Mellars, K. R. Gibson (Eds.) Modelling the Early Human Mind, Cambridge: Macdonald Institute for Archaeological Research.

Byrne, R. W. (1999). *Cognition in great ape ecology. Skill-learning ability opens up foraging opportunities*. H. Box, & K. R. Gibson (Eds.), Mammalian social learning: comparative and ecological perspectives. Cambridge University Press.

Candland, D. K., & Bush, S. L. (1995). *Primates and behaviour*. E. F. Gibbons, B. S. Durrant, & A. J. Demarest (Eds). Conservation of endangered species in captivity: an interdisciplinary approach. Albany, NY: State University of New York Press.

Cartmill, M. (1974a). *Pads and claws in arboreal locomotion*. F. A. Jenkins (Eds.), Primate locomotion. New York, NY: Academic Press. doi: 10.1016/B978-0-12-384050-9.50007-6

Cartmill, M. (1974b). Rethinking primate origins. *Science*, **184(4135)**, 436–443. doi: 10.1126/science.184.4135.436

Casper, B. B., Heard, S. B., & Apanius, V. (1992). Ecological correlates of single-seededness in a woody tropical flora. *Oecologia*, **90(2)**, 212–217. doi: 10.1007/BF00317178

Chapman, C. A., Rothman, J. M., & Lambert, J.E. (2013). *Food as a selective force in primates*. J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, & J. B. Silk (Eds) The evolution of primate societies. The University of Chicago Press, Chicago, US.

Chivers, D. J., Wood, B. A., & Bilsborough, A. (1984). *Food acquisition and processing in primates*. Dordrecht, Netherlands: Springer.

Christel, M. I., & Fragaszy, D. (2000a). Manual function in *Cebus apella*. Digital mobility, preshaping, and endurance in repetitive grasping. *International Journal of Primatology*, **21(4)**, 697-701 doi: 10.1023/A:1005521522418

Christel, M. I. & Fragaszy, D. (2000b). Endurance as a measure of manual dexterity and performance asymmetry in *Cebus apella*. *Folia Primatologica,* **7**, 190-101. doi: 0164-0291/00/0800-0697$18.00/0.

Clauss, M. (2003). Tannins in the nutrition of wild animals: a review. *Zoo Animal Nutrition*, **2**, 53-89. doi: 10.5167/uzh-3509

Corlett, R. T., & Lucas, P. W. (1990). Alternative seed-handling strategies in primates: Seed-spitting by longtailed macaques (*Macaca fascicularis*). *Oecologia*, **82(2)**, 166–171.

Cornejo, F. & Janovec, J. (2010). *Seeds of Amazonian plants*. Princeton University Press, Princeton.

Corso, J., Bowler, M., Heymann, E. W., Roos, C., & Mundy, N. I. (2016). Highly polymorphic colour vision in a New World monkey with red facial skin, the bald uakari (*Cacajao calvus. calvus*). *Proceedings of The Royal Society*, **283(1828)**, 20160067. doi: 10.1098/rspb.2016.0067

Costello, M., & Fragaszy, D. (1988). Prehension in *Cebus* and *Saimiri*: I. Grip type and hand preference. *American Journal of Primatology,* **15(3)**, 235–245. doi: 10.1002/ajp.1350150306

Defler, T. R. (2001). *Cacajao melanocephalus ouakary* densities on the lower Apaporis River, Colombian Amazon. *Primate Report* **61**: 31-36. doi: 10026726748/

Dominy, N. J., Lucas, P. W., Wrangham, R.W., & Ramsden, L. (2004). The potential importance of fruit texture for the evolution of digital dexterity. *Folia Primatologica,* **75**, 189.

Edgren, C. S., Radwin, R. G., & Irwin, C. B. (2004). Grip force vectors for varying handle diameters and hand sizes. *Human Factors*, **46(2)**, 244–251. doi: 0.1518/hfes.46.2.244.37337.

Emlen, J. M. (1966). The role of time and energy in food preference, *American Naturalist*, **100(916)**, 611-617.

Felton, A. M., Felton, A., Lindenmayer, D. B., & Foley, W. J. (2009). Nutritional goals of wild primates. *Functional Ecology*, **23(1)**, 70–78. doi:10.1111/j.1365-2435.2008.01526.x

Fernandes, M. E. B. (1991). Tool use and predation of oysters *(Crassostrea rhizophorae)* by the tufted capuchin, *Cebus apella,* in brackish water mangrove swamp. *Primates*, **32(4)**, 529-531. doi: doi.org/10.1007/BF02381944

Ferrari, S. F., Guedes, P. G., Figueiredo-Ready, W. M. B., & Barnett, A. A. (2014). Reconsidering the taxonomy of the Black-Faced Uacaris, *Cacajao melanocephalus* group (Mammalia: Pitheciidae), from the northern Amazon Basin. *Zootaxa*, **3866**, 353–370.

Ferrari, S. F., Veiga, L. M., & Urbani, B. (2008). Geophagy in New World monkeys (Platyrrhini): ecological and geographic patterns. *Folia Primatologica*, **79(5)**, 402-415. doi:10.1159/000141901

Flörchinger, M., Braun, J., Böhning-Gaese, K., & Schaefer, H. M. (2010). Fruit size, crop mass, and plant height explain differential fruit choice of primates and birds. *Oecologia*, **164(1)**, 151–161. doi:10.1007/s00442-010-1655-8

Foster, M. S. (1990). Factors influencing bird foraging preferences among conspecific fruit trees. *The Condor*, **92(4)**, 844-854. doi: 10.2307/1368720

Fragaszy, D., & Crast, J. (2004). Intrinsic movements of the hand contribute to dexterity in capuchin monkeys. *American Journal of Primatology,* **62(1)**, 108-109

Freeland, W. J., & Janzen, D. H. (1974). Strategies in herbivory by mammals: the role of plant secondary compounds. *The American Naturalist*, **108(961)**, 269-89. doi: 10.1086/282907

Garb, J., Kotler, B. P., & Brown, J. S. (2000). Foraging and community consequences of seed size for coexisting Negev desert granivores. *Oikos*, **88(2)**, 291–300. doi: 10.1034/j.1600-0706.2000.880207.x

Garber, P. A. (1987). Foraging strategies among living primates. *Annual Review Anthropology*, **16(1)**, 339–364. doi:10.1146/annurev.an.16.100187.002011

Gartlan, J. S., McKey, D. B., Waterman, P. G., & Struhsaker, T. T. (1980). A comparative study of the phytochemistry of two African rain forests. *Biochemical Systematics and Ecology*, **8(4)**, 401-422. doi: 10.1016/0305-1978(80)90044-7

Gautier-Hion, A., Duplantier, J. M., Quris, R., Feer, F., Sourd, C., Decoux, J. P., Dubost, G., Emmons, L., Erard, C., & Hecketsweiler, P. (1985). Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia*, **65(3)**, 324-337. doi: 10.1007/bf00378906

Gentry, A. H. (1993). *A field guide to the families and genera of woody plants of Northwest South America (Colombia, Ecuador, Peru) with supplementary notes on herbaceous taxa*. Chicago: The University of Chicago Press.

Godinot M., & Beard K. C. (1993). *A survey of fossil primate hands*. H. Preuschoft & D. J. Chivers (Ed.) Hands of primates. New York, NY: Springer-Verlag. doi: 10.1007/978-3-7091-6914-8_23

Godinot M. (1991). Approches fonctionnelles des mains de primates paléogènes. *Geobios,* **24**, 161–173. doi: 10.1016/S0016-6995(66)80021-9

Godinot, M. (1992). Early euprimate hands in evolutionary perspective. *Journal of Human Evolution*, **22(4-5)**, 267–283. doi: 10.1016/0047-2484(92)90059-I

Gómez, J. M., & Verdú, M. (2012). Mutualism with plants drives primate diversification. *Systematic Biology*, **61(4)**, 567–577. doi: 10.1093/sysbio/syr127

Haines, R. W. (1955). The anatomy of the hand of certain insectivores. *Journal of Zoology*, **125(3-4)***,* 761-777. doi: 10.1111/j.1096-3642.1955.tb00626.x

Hambright, K. D. (1991). Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American*

Fisheries Society, **120(4)**, 500–508. doi:10.1577/1548-8659(1991)120<0500:eaopsb>2.3.co;2

Hamrick, M. (2007). *Evolvability, limb morphology, and primate origins*. M. Dagosto, M. J. Ravosa, (Eds.). Primate origins: adaptations and evolution. New York, NY: Plenum Press. doi: 10.1007/978-0-387-33507-0_11

Hamrick, M.W. (2001). Primate origins: evolutionary change in digit ray patterning and segmentation. *Journal of Human Evolution*, **40(4)**, 339-351. doi: 10.1006/jhev.2001.0467

Handley Jr, C. O. (1978). Mammals of the Smithsonian Venezuelan project. *Brigham Young University Science Bulletin, Biological Series*, **20(5)**: 1-88. doi: http://doi.org/10.5962/bhl.part.5667

Haslam, M., Luncz, L. V., Staff, R. A., Bradshaw, F., Ottoni E. B., & Falótico, T. (2016). Pre-Columbian monkey tools. *Current Biology*, **26(13)**, 521–522. doi: 10.1016/j.cub.2016.05.046.

Hawes, J. E., & Peres, C. A. (2014). Fruit–frugivore interactions in Amazonian seasonally flooded and unflooded forests. *Journal of Tropical Ecology*, **30(5)**, 381–399. doi:10.1017/S0266467414000261

Hemingway, C. A. (1998). Selectivity and variability in the diet of Milne-Edwards' sifakas (*Propithecus diadema edwardsi*): Implications for folivory and seed-eating. *International Journal of Primatology*, **19(2)**, 355-377. doi:10.1023/A:1020344018670.

Hemingway, C. A., & Bynum, N. (2005). *The influence of seasonality on primate diet and ranging*. D. P. Brockman, & C. P. van Scheik (Eds.) Seasonality in Primates. Cambridge University Press, Studies in Biological and Evolutionary Anthropology. doi:10.1017/cbo9780511542343.004

Hershkovitz, P. (1987). Uacaries, New World Monkeys of the genus *Cacajao* (Cebidae, Platyrrhini): a preliminary taxonomic review with the description of a new subspecies. *American. Journal of Primatology,* **12(1)**, 1-53. doi: http://doi.org/10.1002/ajp.1350120102

Heymann, E. W. (1990). Further field notes on the red uacari, *Cacajao calvus ucayalii*, from the Quebrada Blanco, Amazonian Peru. *Primate Conservation*, **11**, 7–8.

Hohmann, G. (2009). *The diets of non-human primates: frugivory, food processing, and food sharing*. J. J. Hublin, M. P. Richards (Eds.). The evolution of hominin diets: integrating approaches to the study of Palaeolithic subsistence. Dordrecht, Netherlands: Springer. Vertebrate Paleobiology and Paleoanthropology series. doi: 10.1007/978-1-4020-9699-0_1

Hohmann, G., Robbins, M. M., & Boesch, C. (Eds.). (2006). *Feeding ecology in apes and other primates: ecological, physiological and behavioural aspect*. Cambridge: Cambridge University Press

Hopkins, W. D., Cantalupo, C., Wesley, M. J., Hostetter, A. B., & Pilcher, D. L. (2002). Grip morphology and hand use in chimpanzees (*Pan troglodytes*): Evidence of a left hemisphere specialization in motor skill. *Journal of Experimental Psychology General*, **131(3)**, 412–423. doi: 10.1037/0096-3445.131.3.412

Hulme, P., & Benkman, C. (2002). *Granivory*. C. Herrera, O. Pellmyr (Eds.). Plant-Animal Interactions: An Evolutionary Approach. Oxford, UK: Blackwell Publishing.

Hunt, K. D. (1992) Positional behavior of *Pan troglodytes* in the Mahale mountains and Gombe Stream National Parks, Tanzania. *American Journal Physical. Anthropology*, **87(1)**, 83-105. doi: 10.1002/ajpa.1330870108

Izawa, K., & Mizuno, A. (1977). Palm fruit cracking behavior of wild black-capped capuchin (*Cebus apella*). *Primates*, **18(4)**, 773-792. doi: 10.1007/BF02382930

John, A. (1972). The evolution of the use of tools by feeding animals. *Evolution*, **26(3)**, 464-473. doi: 10.2307/2407020

Jones, F. W. (1916). Arboreal man. Longmans. London: Arnold.

Jones-Engel, L. E., & Bard, K. A. (1996). Precision grips in young chimpanzees. *American Journal of Primatology,* **39(1)**, 1–15. doi: 10.1002/(SICI)1098-2345(1996) 39:1<1::AID-AJP1>3.0.CO;2-2

Jordano, P. (2000). *Fruits and frugivory*. M. Fenner (Ed. 2). Seeds: the ecology of regeneration in plant communities, CABI Publ., Wallingford, UK.

Jordano, P. (1995). Frugivore-mediated selection on fruit and seed size: birds and St. Lucie's cherry, *Prunus mahaleb. Ecology*, **76(8)**, 2627–2639. doi: 10.2307/2265833

Jouffroy, F. K., Godinot, M., & Nakano, Y. (1991). Biometrical characteristics of primate hands. *Journal of Human Evolution*, **6(4)**, 269–306. doi: 10.1007/BF02437254

Kay, R. F., Meldrum, D. J., & Takai, M. (2013). *Pitheciidae and other platyrrhine seed predators*. L. M. Veiga, A. A. Barnett, S. F. Ferrari, & M. A. Norconk (Eds.) Evolutionary biology and conservation of titis, sakis and uacaris. Cambridge: Cambridge University Press.

Kelly, C. K. (1995). Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. *Oecologia*, **102(3)**, 377–388. doi: 10.1007/BF00329805

King, B. J. (1986). Extractive foraging and the evolution of primate intelligence. *Human Evolution*, **1(4)**, 361–372. doi: 10.1007/BF02436709

Kinzey, W. G., & Cunningham, E. P. (1994). Variability in platyrrhine social organization. *American Journal of Physical Anthropology*, **34(2)**, 185–198. doi:10.1002/ajp.1350340209.

Kinzey, W. G., & Norconk, M. A. (1990). Hardness as a basis of fruit choice in two sympatric primates. *American Journal of Physical Anthropology*, **81(1)**, 5-15. doi: 10.1002/ajpa.1330810103

Kinzey, W. G., & Norconk, M. A. (1993). Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Suriname and Venezuela. *International Journal of Primatology,* **14(2)**, 207–227. doi: 10.1007/BF02192632

Kinzey, W. G. (1992). Dietary and dental adaptations in the Pitheciinae. *American Journal of Physical Anthropology*, **88(4)**, 499-514. doi: 10.1002/ajpa.1330880406

Kirk, E. C., Lemelin, P., Hamrick, M. W., Boyer, D. M., & Bloch, J. I. (2008). Intrinsic hand proportions of euarchontans and other mammals: implications for the locomotor behavior of plesiadapiforms. *Journal Human Evolution*, **55(2)**, 278–299. doi: 10.1016/j.jhevol.2008.02.008

Kubitzki, K. (1987). The ecogeographical differentiation of Amazonia inundation forests. *Plant Systematics and Evolution*, **162(1-4)**, 285-304. doi: 10.1007/bf00936922

Kühl, H. S., Kalan, A. K., Arandjelovic, M., Aubert, F., D'Auvergne, L., Goedmakers, A., Boesch, C.,…& Ton, E. (2016). Chimpanzee accumulative stone throwing. *Scientific Reports*, **6 (22219)**, 1-6. doi:10.1038/srep22219.

Kuhlmann, M. (2012). *Frutos e sementes do Cerrado atrativos para fauna: guia de campo*. Brasília, Editora Rede de Sementes do Cerrado

Kunz, B. K., & Linsenmair, K. E. (2008). The disregarded west: diet and behavioural ecology of olive baboons in the Ivory Coast. *Folia Primatology*, **79(1)**, 31–51. doi: 10.1159/000108384

Kunz, B. K., & Linsenmeier, K. E. (2007). Changes in baboon feeding behavior: maturity-dependent fruit and seed size selection within a food plant species. *International Journal of Primatology*, **28(4)**, 819-835. doi:10.1007/s10764-007-9160-6

Ledogar, J. A., Luk, T. H., Perry, J. M., Neaux, D., & Wroe, S. (2018). Biting mechanics and niche separation in a specialized clade of primate seed predators. *PloS One*, **13(1)**, e0190689. doi: 10.1371/journal.pone.0190689

Lehman, S. M., Robertson, K. L. (1994). Preliminary survey of *Cacajao melanocephalus melanocephalus* in southern Venezuela. *International Journal of Primatology,* **15(6)**, 927–934.

Lehman, S. M. (2013). *Evolutionary ecology of the pitheciinae: evidence for energetic equivalence or phylogenetically structured environmental variation?*. M. Veiga, A. A. Barnett, S. F. Ferrari, & M. A. Norconk (Eds). Evollutionary Biology and Conservation of Titis, Sakis and Uacaris. Cambridge University Press.

Lemelin, P. (1997). *The evolution of manual prehensility in primates: A comparative study of prosimians and didelphid marsupials*. Doctoral dissertation. State University of New York at Stony Brook., Stony Brook, USA.

Lucas, P. W., Beta, T., Darvell, B. W., Dominy, N. J., Essackjee, H. C., Lee, P. K. D., Osorio, D., Ramsden, L., Yamashita, N., & Yuen, T. D. B., (2001). Field kit to characterize physical, chemical and spatial aspects of potential primate foods. *Folia Primatology*, **72(1)**, 11-25. doi: 10.1159/000049914

Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., & Hamada, Y. (2007). Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology*, **69(2)**, 227-233. doi: 10.1002/ajp.20342

Marzke, M. W. & Wullstein, K. L. (1996) Chimpanzee and human grips: a new classification with a focus on evolutionary morphology. *International Journal of Primatology,* **17(1)**, 117–139. doi:10.1007/BF02696162

McGraw, W. S., & Daegling, D. J. (2012). Primate feeding and foraging: integrating studies of behavior and morphology. *Annual Review of Anthropology*, **41**, 203-219. doi: 10.1146/annurev-anthro-092611-145801

McKey, D. (1978). *Soils, vegetation, and seed-eating by black colobus monkeys*. G. G. Montgomery (Eds). The Ecology of Arboreal Folivores, Washington, D.C.: Smithsonian Institution Press.

McPherson, J. M. (1989). A field study of winter fruit preferences of cedar waxwings. *The Condor*, **89(2)**, 293-306. doi: 10.2307/1368482

Meachen-Samuels, J., & Van Valkenburgh, B. (2009). Craniodental indicators of prey size preference in the Felidae. *Biological Journal of the Linnean Society*, **96(4)**, 784–799. doi: 10.1111/j.1095-8312.2008.01169.x

Mello, M. A. R., Leiner, N. A., Guimarães Jr. P. R., & Jordano, P. (2005). Size-based fruit selection of *Calophyllum brasiliense* (Clusiaceae) by bats of the genus *Artibeus* (Phyllostomidae) in a Restinga area, southeastern Brazil. *Acta Chiropterologica*, **7(1)**, 179-182. doi: 10.3161/1733-5329(2005)7[179:SFSOCB]2.0.CO;2

Milton K, Van Soest PJ, & Robertson J. (1980). Digestive efficiencies of wild howler monkeys. *Physiological Zoology*, **53(4)**, 402-409. doi: 10.2307/30157878

Milton K. (1979). Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *American Naturalist*, **114(3)**, 362–378. doi: https://doi.org/10.1086/283485

Milton K. (1980). *The foraging strategy of howler monkeys: a study in primate economics*. New York, NY: Columbia University Press.

Milton, K. (1984). *The role of food-processing factors in primate food choice*. P. S. Rodman, & J. G. H. Cant (Eds). Adaptation for foraging in nonhuman primates, New York, NY: Columbia University Press.

Milton, K. (1999). Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us? *Nutrition*, **15(6)**, 488-498. doi: 10.1016/s0899-9007(99)00078-7

Milton, K., Giacalone, J., Wright, S. J., & Stockmayer, G. (2005). *Do frugivore population fluctuations reflect fruit production? Evidence from Panama*. J. Lawrence Dew, & J. P. Boubli (Eds.) Tropical Fruits and Frugivores: the search for strong interactors, Netherlands: Springer Printed. doi:10.1007/1-4020-3833-x_2

Moles, A. T., Warton, D. I., & Westoby, M. (2003). Do small-seeded species have higher survival through seed-predation than large-seed species? *Ecology*, **84(12)**, 3148–3161. doi: 10.1890/02-0662

Napier, J. R. (1960). Studies of the hands of living primates. *Proceedings of the Zoological Society of London*, **134(4)**, 647-657. doi: 10.1111/j.1469-7998.1960.tb05606.x

Napier, J. R. (1961). Prehensility and opposability in the hands of primates. S*ymposia of the Zoological Society of London*, **5**, 115–132. doi: 10.1007/978-1-4939-3646-5_2

Netter, F. H. (2011). *Atlas de Anatomia Humana*. Rio de Janeiro. Editora Elsevier.

Nilsson, P. A., & Brönmark, C. (2000). Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos*, **88(3)**, 539-546. doi: 10.1034/j.1600-0706.2000.880310.x

Norconk, M. A., & Michael Veres. (2011). Physical properties of fruit and seeds ingested by primate seed predators with emphasis on sakis and bearded sakis. *Anatomical Record*, **294(12)**, 2092–2111. doi: 10.1002/ar.21506

Norconk, M. A., Wright, B. W., Conklin-Brittain, N. L., & Vinyard, C. J. (2009). *Mechanical and nutritional properties of food as factors in platyrrhine dietary* *adaptations.* P. A. Garber, A. Estrada, J. C. Bicca-Marques, E. W. Heymann, K. B. Strier (Eds.). South American Primates, New York, NY: Springer. doi:10.1007/978-0-387-78705-3_11

Parolin, P. (2000). Seed mass in Amazonian floodplain forests with contrasting nutrient supplies. *Journal of Tropical Ecology*, **16(3)**, 417-428. doi: 10.1017/S0266467400001486

Parolin, P., Waldhoff, D., & Piedade, M. T. F. (2010). *Fruit and seed chemistry, biomass and dispersal*. W. J. Junk et al. (Eds.) Amazonian floodplain forests: ecophysiology biodiversity and sustainable management, Springer, Dordrecht. doi: 10.1007/978-90-481-8725-6_12

Pianka, E. R., & Vitt, L. J. (2006). *Lizards: Windows to the evolution of diversity*. University of California Press. doi: 10.1525/j.ctt1pp0q8

Pouydebat, E., Coppens, Y., & Gorce, P. (2006). Evolution de la prehension chez les primates humains et non humains: la precision et l'utilisation d'outils revisitees. *L'anthropologie* **110(5)**, 687–697. doi: 10.1016/j.anthro.2006.10.002

Pouydebat, E., Gorce, P., Coppens, Y., & Bels, V. (2009). Biomechanical study of grasping according to the volume of the object: Human versus non-human primates. *Journal of Biomechanics*, **42(3)**, 266–272. doi: 10.1016/j.jbiomech.2008.10.026

Püschel, T. A., Marcé-Nogué, J., Kaiser, T. M., Brocklehurst, R. J., & Sellers, W. I. (2018). Analyzing the sclerocarpy adaptations of the Pitheciidae mandible. *American Journal of Primatology*, **80(5)**, e22759. doi: 10.1002/ajp.22759

Remis, M. J. (1999). Tree structure and sex differences in arboreality among western lowland gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *Primates*, **40(2)**, 383-396. doi: 10.1007/BF02557560

Remis, M., (1995). Effects of body size and social context on the arboreal activities of lowland gorillas in the Central African Republic. *American Journal of Physical Anthropology*, **97(4)**, 413-433. doi: 10.1002/ajpa.1330970408

Ribeiro, J. E. L. da S., Hopkins, M. J. G., Vicentini, A., Sothers C. A., Costa, M. A. D. A S., Brito, J. M. De, Souza, M. A. D. De, Martins, L.H.P., Lohman, L. G., Assuncão, A. O., Pereira, E. Da C., Silva, C. F. Da, Mesquita, M. R., & Procopio, L. C. (1999). *Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônia central*. INPA-DFID, Manaus, Brazil.

Rocha, V. J., Reis, N. R., & Sekiama, M. L. (1998). Uso de ferramentas por *Cebus apella* (Linnaeus) (Primates, Cebidae) para obtenção de larvas de coleoptera que parasitam sementes de *Syagrus romanzoffianum* (Cham.) Glassm. (Arecaceae). *Revista Brasileira de Zoologia*, **15(4)**, 945–950. doi: 10.1590/S0101-81751998000400012

Rosenberger, A. L., & Kinzey, W. G. (1976). Functional patterns of molar occlusion in platyrrhine primates. *American Journal Physical Anthropology*, **45(2)**, 281–297. doi: 10.1002/ajpa.1330450214

Sayers, K. A. (2008). *Optimal Foraging on the Roof of the World: a field study of Himalayan langurs*. Doctoral thesis, OH: Kent State University.

Schimitt, R. J., & Holbrook, S. J. (1984). Gape-limitation, foraging tactics and prey size selectivity of two microcarnivorous species of fish. *Oecologia*, **63(1)**, 6-12. doi: 10.1007/BF00379778

Shapiro, L. J., & Young, J. W. (2010). Is primate-like quadrupedalism necessary for fine-branch locomotion? A test using sugar gliders (*Petaurus breviceps*). *Journal of Human Evolution*, **58(4)**, 309-319. doi: 10.1016/j.jhevol.2009.12.002

Spinozzi, G., Truppa, V., & Lagana, T. (2004). Grasping behavior in Tufted Capuchin monkeys (*Cebus apella*): grip types and manual laterality for picking up a small food item. *American Journal of Physical Anthropology*, **125(1)**, 30–41. doi: 10.1002/ajpa.10362

Struhsaker, T.T., & L. Leland. (1977). Palm-nut smashing by *Cebus apella* in Colombia. *Biotrópica*, **9(2)**, 124-126. doi: 10.2307/2387666

Ter Steege, H., & Hammond, D. S. (2001). Character convergence, diversity, and disturbance in tropical rain forest in Guyana. *Ecology,* **82(11)**, 3197–3212. doi: 10.1890/0012-9658(2001)082[3197:CCDADI]2.0.CO;2

The Plant List. (2013). Version 1.1. Published on the Internet; http://www.theplantlist.org/ (accessed 2017).

The Taxonomic Name Resolution Service [Internet]. iPlant Collaborative. (2017). Available from: http://tnrs.iplantcollaborative.org.

Tonooka, R., & Matsuzawa, T. (1995). Hand preferences in captive chimpanzees (*Pan troglodytes*) in simple reaching for food. *International Journal of Primatology,* **16(1)**, 17–34. doi: 10.1007/BF02700151

Toussaint, S., Reghem, E., Chotard, H., Herrel, A., Ross, C. F., & Pouydebat., E. (2013). Food acquisition on arboreal substrates by the grey mouse lemur: implication for primate grasping evolution. *Journal of Zoology*, **291(4)**, 235–242. doi:10.1111/jzo.12073

Tropicos.org.Missouri Botanical Garden. (2017). http://www.tropicos.org.

Ungar, P. S. (1995). Fruit preferences of four sympatric primate species at Ketambe, northern Sumatra, Indonesia. *International Journal of Primatology*, **16(2)**, 221-323. doi: 10.1007/BF02735479

Van Lawick-Goodall, J. (1971). Tool using in primates and other vertebrates. *Advances in the Study of Behavior*, **3**, 195-249. doi: 10.1016/S0065-3454(08)60157-6

Van Roosmalen, M. G. M. (1985). *Fruits of the Guianan flora*. Institute of Systematic Botany, Utrecht University, Utrecht.

Van Roosmalen, M. G. M. (1985). Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* [Linnaeus, 1758]) in Surinam. *Acta Amazônica,* **15**, 7-238. doi: 10.1590/1809-43921985155238

Van Roosmalen, M. G. M. (2013). *Wild fruits from the Amazonia*. Independent production. Amazon Digital Services LLC, Volume 1.

Veiga, L. M., & Ferrari, S. F. (2007). Geophagy at termitaria by bearded sakis (*Chiropotes satanas*) in southeastern Brazilian Amazonia. *American Journal of Primatology*, **69(7)**, 816-820. doi: 10.1002/ajp.20378

Veiga, L. M., & Ferrari, S. F. (2007). Geophagy at termitaria by bearded sakis (*Chiropotes satanas*) in southeastern Brazilian Amazonia. *American Journal of Primatology*, **69(7)**, 816-820. doi: 10.1002/ajp.20378

Vicentini, A. (2004). *A vegetação ao longo de um gradiente edáfico no Parque Nacional do Jaú*. S. H. Borges, S. Iwanaga, C. C. Durigan, M. R. & Pinheiro (Eds) Janelas para a biodiversidade no Parque Nacional do Jaú: uma estratégia par ao estudo da biodiversidade na Amazônia. Fundação Vitória Amazônica/WWF/IBAMA, Manaus, Brazil.

Wasserman, M. D., & Chapman, C. A. (2003). Determinants of colobine monkey abundance: The importance of food energy, protein and fibre content. *Journal of Animal Ecology*, **72(4)**, 650–659. doi: 10.2307/3505642

Welles, J. (1976). A comparative study of manual prehension in Anthropoids. *Saugetierlaundliche Mitteilungen,* **24(1)**, 26–37

Wheelwright, N. T. (1985). Fruit size, gape width, and the diets of fruit-eating birds. *Ecology*, **66(3)**, 808-818. doi: 10.2307/1940542

Wheelwright, N.T. (1993). Fruit size in a tropical tree species: variation, preference by birds, and heritability. *Plant Ecology Vegetatio* **107(1)**, 163-174. doi: 10.1007/BF00052219

Wich, S. A., Fredriksson, G., & Sterck, E. H. M (2002). Measuring fruit patch size for three sympatric Indonesian primate species. *Primates*, **43(1)**, 19-27. doi:10.1007/BF02629 5737.

Wittmann, F., Schongart, J., De Brito, J. M., Wittmann, A. De O., Piedade, M. T. F., Parolin, P., Junk, W. J., & Guillaumet, J. L. (2010). *Annual growth of tree s in central Amazonians varzea floodplains: taxonomy, ecology, and use*. Editora INPA, Manaus, Brazil.

Wrangham, R. W. (1977). *Feeding behaviour of chimpanzees in Gombe National Park, Tanzania*. T.H. Clutton-Brock (Eds.) Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes, London: Academic Press.

Yakou, T., Yamamoto, K., Koyama, M., & Hyodo, K. (1997). Sensory evaluation of grip using cylindrical objects. *Japan Society of Mechanical Engineers (JSME) International Journal Series C Mechanical Systems*, *Machine Elements and Manufacturing*, **40(4)**, 730–735. doi: 10.1299/jsmec.40.730

Youlatos, D. (1999). The schizodactylous grasp of the howling monkey. *Zeitschrift für Morphologie und Anthropologie,* **82(2-3)**, 187-198. doi: 10.2307/25757550

FIGURE 1 Pearson's correlation analysis of the different gape measurement methods.

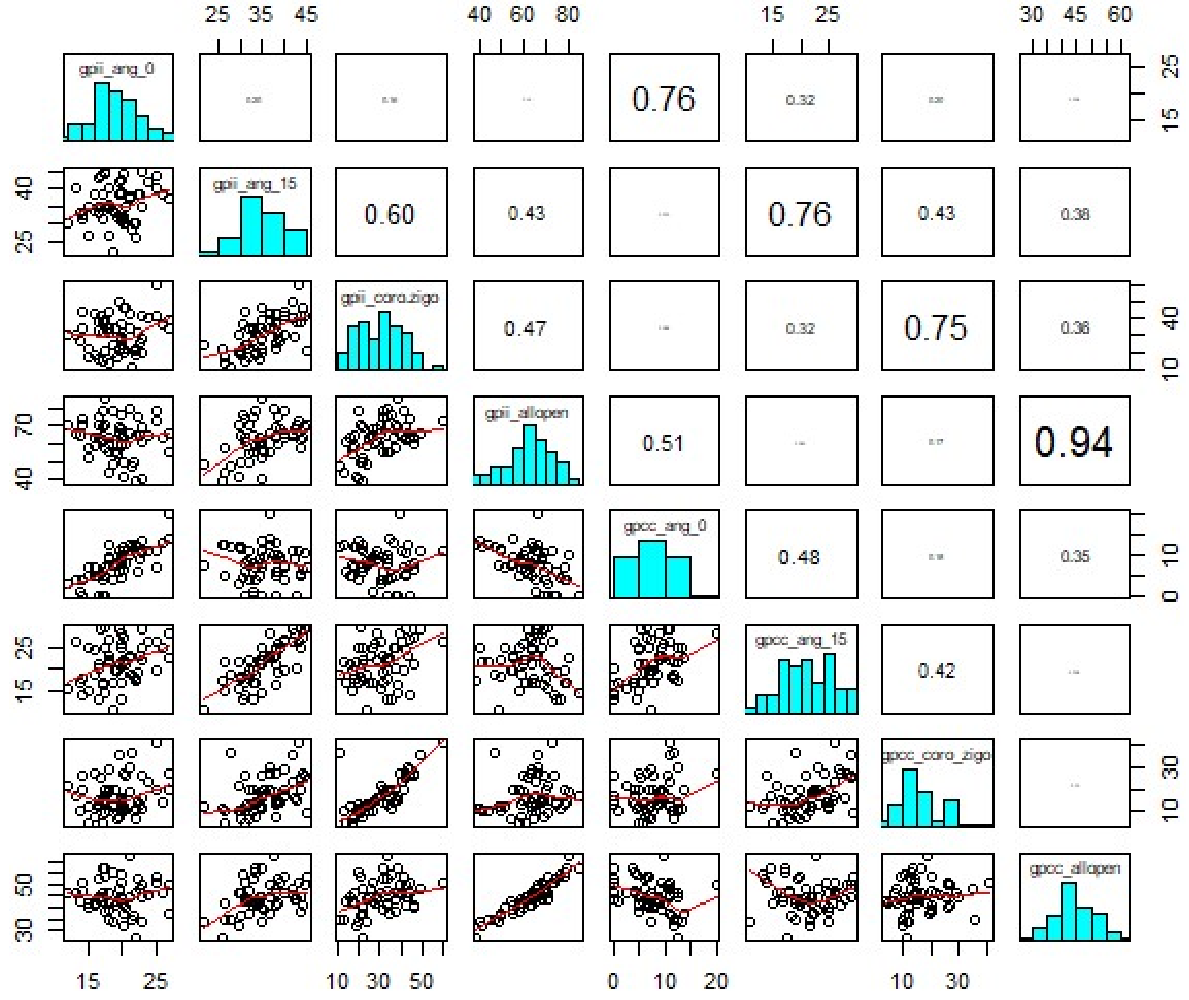
FIGURE 2 Boxplot of the distance between the upper and lower canines of the four species of *Cacajao*.

FIGURE 3 Boxplot of the distance between the upper and lower canines of in members of the genus *Cacajao*.

FIGURE 1 Boxplot of maximum palm width and length (A) and hand size (B) for members of the genus *Cacajao.*

FIGURE 5 Size of eaten and uneaten fruits from plant species in the uacari diet and present in the study group home ranges.

FIGURE 6 Seed size of plant species eaten and uneaten by members of the genus *Cacajao*.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0.76
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0.60
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10 30 50
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FIGURE 1

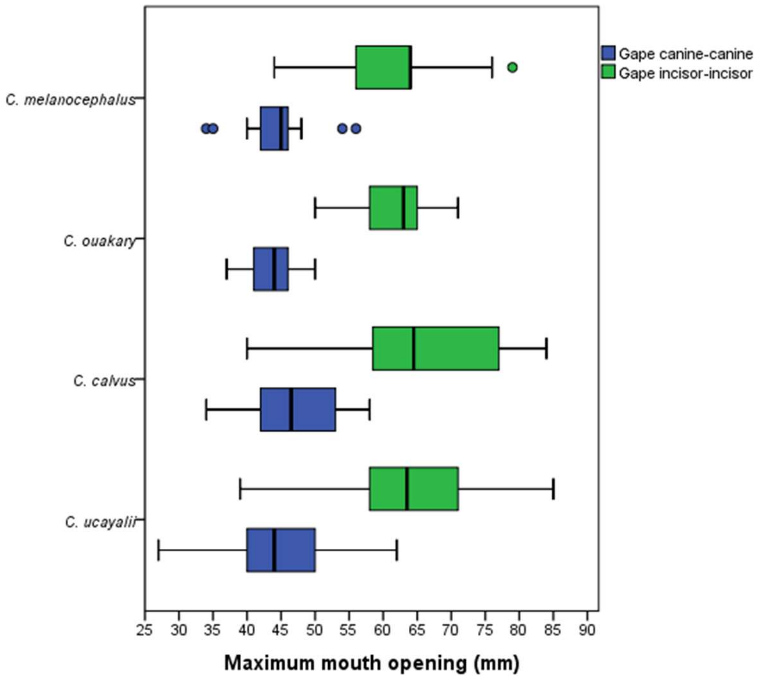

FIGURE 2

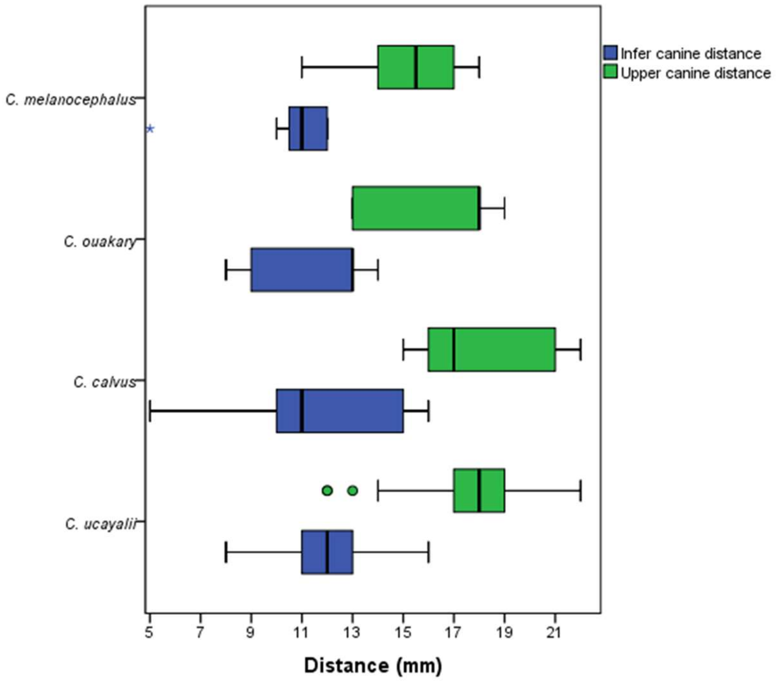

FIGURE 3

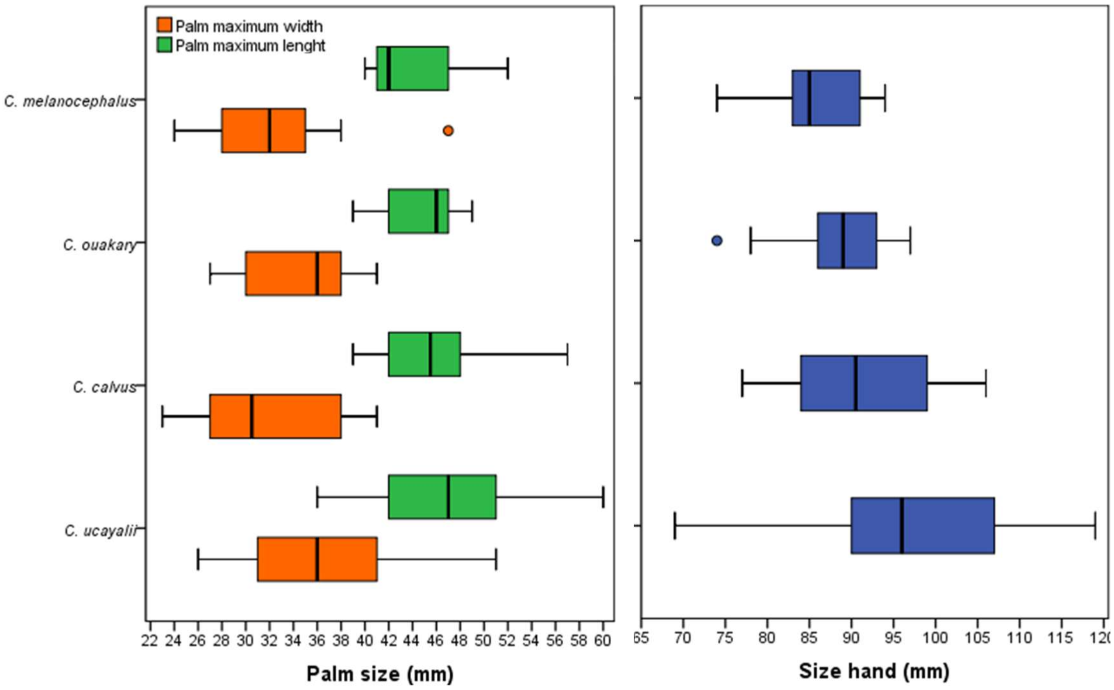

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FIGURE 4

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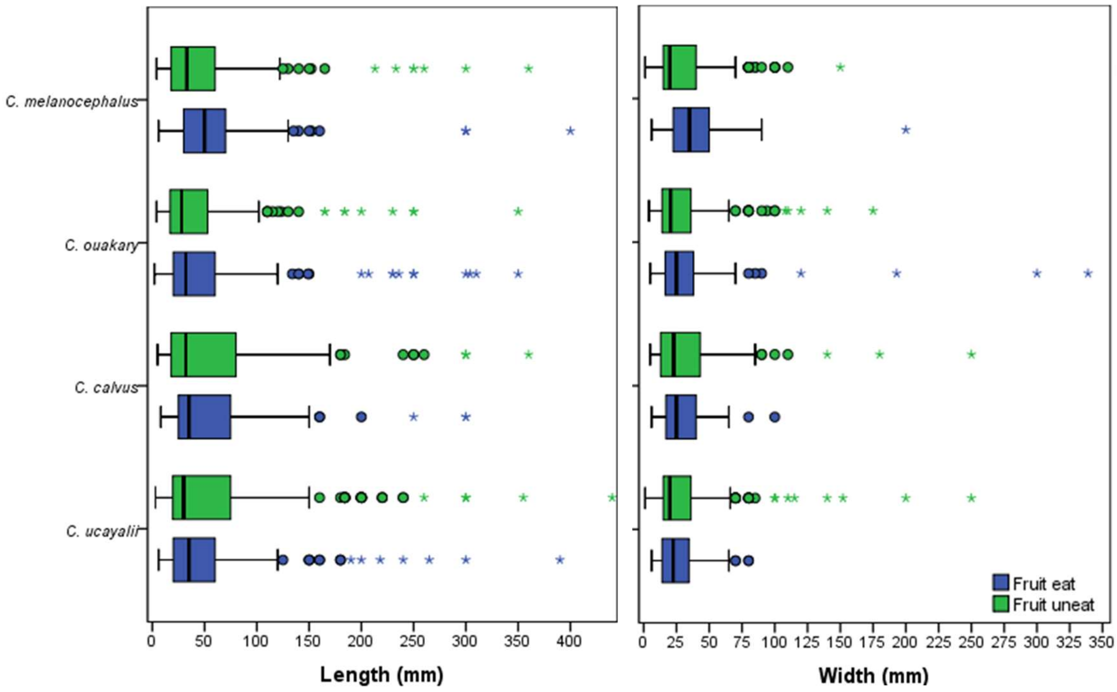

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FIGURE 5

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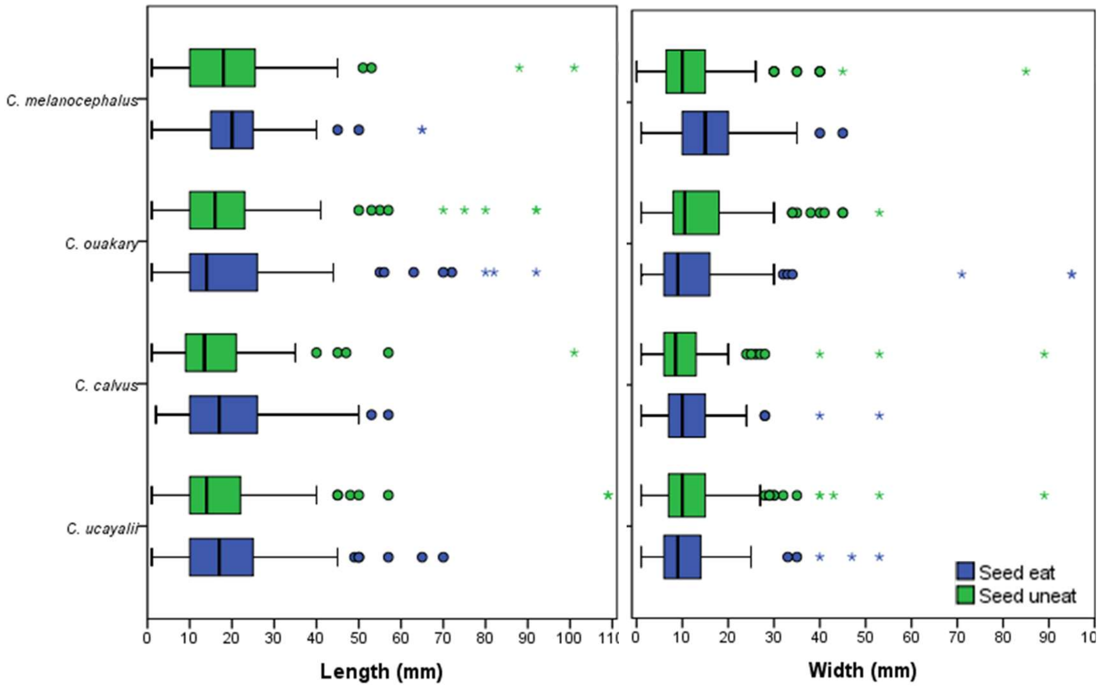

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FIGURE 6

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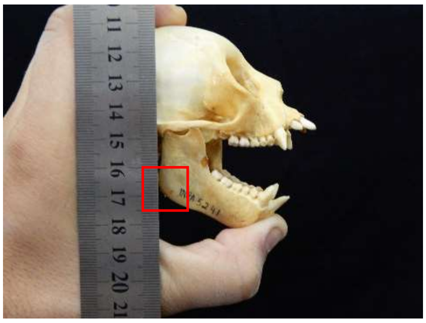
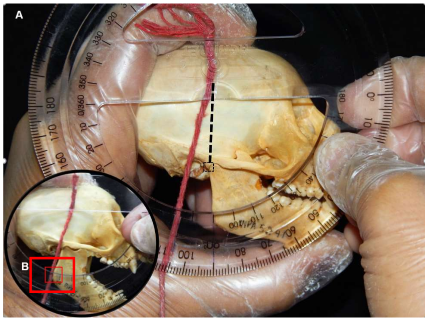
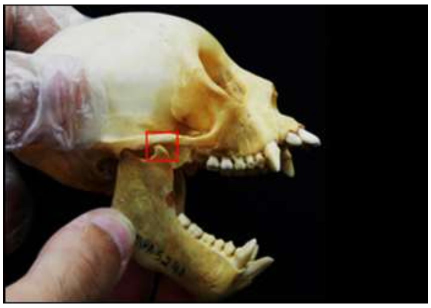
TABLE 1 Different methods used for *Cacajao* gape measurements.

Methods†	**Descriptions**	**Illustrations**
Gape anlge 0°	Measurement was made with a right-angled ruler resting upright on the temporal region of the skull at the back of the zygomatic arch, adjacent to the postglenoid process, moving the jaw back until the mandibular gonion (red square) touched the ruler	
‡Gape angle 15°	The maximum mouth opening angle of *Cacajao's* at 15 ° was standardized, used as a vertex, the post-glenoid process. To ensure standardization of the angle, a 360 ° protractor (Acrimet) was used. Thus, the center of the protractor was placed in the post glenoid process (dashed line). and the values were read from the internal limbus of the protractor, when the jonus of the mandible branch touched the line of faith (the red string in the image on the side).	
Gape coronoid zygomatic	Measuring the mandible opening until the coronoid process lies below the zygomatic arch (red square). This method was chosen because both structures are related to the muscles responsible for opening and closing the mouth, such as the masseter muscle (mandible occlusion) that originates from the zygomatic arch and the temporal muscle (mandible elevation and retraction) which has its insertion in the coronoid process §	
Gape all open	Maximum opening measure was based on the abnormal temporomandibular joint (TMJ) § and is estimated by conduction from the opening of the mouth to the central position to the point where the condylar movement changes from pure hinge rotation to anterior sliding motion known as translation §. The maximum opening is obtained by moving the jaws as far as possible apart without the articular end of the condyle leaving the auricular fossa §	

† In all the methods, the skull was arranged in a Frankfurt horizontal plane of view of Renann H. P. Dias da Silva, and only specimens with condyles present in the mandible and both undamaged skull mandibular fossae were used for data collection.

‡This measurement is based on the maximum opening degree of an adult human's mouth.

§Netter (2011)

TABLE 2 Mean values and standard deviation ($\bar{x}$ ±SD) of all metrics of hand and gape for studied *Cacajao* taxa.

Metrics (mm)	**Primates *Cacajao***			
	C. c. calvus	***C. c. ucayalii***	***C. melanocephalus***	***C. ouakary***
Gape all open incisor-incisor	66.52 ± 11.31	63.87 ± 10.31	61.76 ± 9.83	61.54 ± 6.38
Gape all open canine-canine	47.20 ± 7.00	44.53 ± 7.22	44.38 ± 6.21	43.64 ± 3.70
Distance between upper canines	17.90 ± 2.54	17.62 ± 2.20	15.10 ± 2.04	16.33 ± 2.85
Distance between infer canines	11.70 ± 3.05	12.18 ± 1.81	10.55 ± 2.02	11.51 ± 2.66
Palm width	31.56 ± 5.65	36.21 ± 6.25	32.68 ± 7.03	34.51 ± 4.79
Palm length	46.21 ± 4.67	46.63 ± 5.61	44.06 ± 4.41	44.93 ± 3.28
Size hand	91.47 ± 8.67	95.56 ± 11.89	85.47 ± 6.19	88.26 ± 6.61

TABLE 3 Allometric differences in hand size between male and female for each studied *Cacajao* taxon. Mean values and standard deviation for females is the upper line (♀) and for males the lower line (♂).

Primate	**Dimension**	**Mean**	**SE**	**Median**	**SD**	**Min.**	**Max.**
C. c. calvus	Palm width	33.28	2.04	30.50	5.40	22.70	38.00
		32.57	2.12	28.50	4.24	27.00	36.00
	Palm length	45.59	1.19	44.83	3.15	42.00	51.00
		48.46	3.18	46.00	6.36	42.30	57.00
	Length fourth finger	45.00	2.53	51.00	6.70	39.00	58.00
		46.24	1.04	42.85	2.07	41.70	46.00
	Hand length	90.59	2.98	97.83	7.87	83.00	100.67
		94.71	3.96	87.70	7.91	86.30	103.00
C. c. ucayalii	Palm width	35.38	1.65	33.95	6.18	28.00	51.40
		35.38	1.39	36.00	5.72	25.50	43.50
	Palm length	44.27	1.47	43.95	5.48	36.00	59.50
		47.65	1.25	49.40	5.15	35.50	53.20
	Length fourth finger	53.17	2.31	52.00	8.64	38.00	67.00
		46.41	2.59	42.40	10.70	26.30	66.70
	Hand length	97.44	2.77	97.20	10.38	78.00	110.00
		94.06	3.42	92.00	14.09	68.70	118.90
C. melanocephalus	Palm width	33.88	1.54	34.00	5.10	27.90	46.90
		30.27	2.81	35.10	7.42	23.90	40.70
	Palm length	43.33	0.97	45.90	3.20	40.50	49.00
		45.50	1.77	46.70	4.68	39.50	52.00
	Length fourth finger	42.12	0.66	43.70	2.17	41.00	48.10
		40.00	1.88	42.50	4.98	34.60	48.00
	Hand length	85.45	1.29	90.60	4.27	82.90	94.40
		85.50	3.48	89.20	9.20	74.10	97.10
C. ouakary	Palm width	34.06	3.5	33.50	4.95	30.00	37.00
		35.23	3.56	28.10	6.17	27.00	38.20
	Palm length	44.94	0.5	41.50	0.71	41.00	42.00
		44.92	4.79	42.80	8.30	39.00	54.90
	Length fourth finger	43.93	3.65	40.15	5.16	36.50	43.80
		42.38	3.7	42.00	6.40	35.30	48.10
	Hand length	88.86	4.15	81.65	5.87	77.50	85.80
		87.30	8.38	84.80	14.52	74.30	103.00

TABLE 4 Level of difficulty in handling, fitting fruit between incisor-incisor and canine-canine, and passage of seed between upper canines, according to the length and width of the fruit/seed consumed and not consumed by ***Cacajao c. calvus.***

	Difficulty level							**Chi-square Test (χ^2)**
Handling	**Easy**	**(%)**	**Manageable**	**(%)**	**Difficult**	**(%)**	**Total**	
Length-eaten fruit	46	63.89	14	19.44	12	16.67	72	χ^2= 0.7558, *df*= 2, *p* = 0.6853
Length-uneaten fruit	75	63.03	19	15.97	25	21.01	119	
Total	121		33	-	37	-	191	
Width-eaten fruit	46	82.14	8	14.29	2	3.57	56	χ^2= 1.336, *df* = 2, *p*= 0.5126
Width-uneaten fruit	62	73.81	18	21.43	4	4.76	84	
Total	108	-	26	-	6	-	140	
Fitting fruit between canine-canine								
Length-eaten fruit	46	63.89	-	-	26	36.11	72	χ^2= 0, *df*= 1, *p*= 1
Length-uneaten fruit	75	63.03	-	-	44	36.97	119	
Total	121	-			70	-	191	
Width-eaten fruit	46	82.14	-	-	10	17.86	56	χ^2= 0.8929, *df*= 1, *p*= 0.3447
Width-uneaten fruit	62	73.81	-	-	22	26.19	84	
Total	108	-	-	-	32	-	140	
Fitting fruit between incisor-incisor								
Length-eaten fruit	53	73.61	-	-	19	26.39	72	χ^2= 0.2788, df= 1, *p*= 0.5975
Length-uneaten fruit	82	68.91	-	-	37	31.09	119	
Total	135	-			56	-	191	
Width-eaten fruit	49	87.50	-	-	7	12.50	56	χ^2= 0.0608, *df*= 1, *p*= 0.8053
Width-uneaten fruit	71	84.52	-	-	13	15.48	84	
Total	120	-	-	-	20	-	140	
Passage between the upper canines								
Length-eaten seed	29	50.00	-	-	29	50.00	58	χ^2= 2.3041, *df* = 1, *p*= 0.129
Length-uneaten seed	57	64.04	-	-	32	35.96	89	
Total	86	-	-	-	61	-	147	
Width-eaten seed	39	79.59	-	-	10	20.41	49	χ^2= 0.3398, *df* = 1, *p*= 0.5599
Width-uneaten seed	69	85.19	-	-	12	14.81	81	
Total	108	-	-	-	22	-	130	

TABLE 5 Level of difficulty in handling fruit, fitting fruit between incisor-incisor and canine-canine, and passage of seed between upper canines, according to the length and width of the fruit/seed consumed and not consumed by ***Cacajao c. ucayalii.***

	Difficulty level							**Chi-square Test (χ^2)**
Handling	Easy	(%)	Manageable	(%)	Difficult	(%)	Total	
Length-eaten fruit	94	67.63	23	16.55	22	15.83	139	χ^{22}= 5.6812, *df*= 2, *p*= 0.05839*
Length-uneaten fruit	175	69.44	23	9.13	54	21.43	252	
Total	269	-	46	-	76	-	391	
Width-eaten fruit	71	84.52	13	15.48	0	0.00	84	χ^2= 4.3679, *df*= 2, *p*= 0.1126
Width-uneaten fruit	175	84.13	24	11.54	9	4.33	208	
Total	246	-	37	-	9	-	292	
Fitting fruit between canine-canine								
Length-eaten fruit	89	64.03	-	-	50	35.97	139	χ^2= 0.17202, *df*= 1, *p*= 0.6783
Length-uneaten fruit	168	66.67	-	-	84	33.33	252	
Total	257	-			134	-	391	
Width-eaten fruit	68	80.95	-	-	16	19.05	84	χ^2= 0.0072249, *df* = 1, *p*= 0.9323
Width-uneaten fruit	171	82.21	-	-	37	17.79	208	
Total	239	-	-	-	53	-	292	
Fitting fruit between incisor-incisor								
Length-eaten fruit	109	78.42	-	-	30	21.58	139	χ^2= 1.1189, *df*= 1, *p*= 0.2902
Length-uneaten fruit	184	73.02	-	-	68	26.98	252	
Total	293	-			98	-	391	
Width-eaten fruit	78	92.86	-	-	6	7.14	84	χ^2= 1.2536, *df* = 1, *p*= 0.2629
Width-uneaten fruit	182	87.50	-	-	26	12.50	208	
Total	260	-	-	-	32	-	292	
Passage between the upper canines								
Length-eaten seed	56	50.45	-	-	55	49.55	111	χ^2= 2.1443, *df*= 1, *p*= 0.1431
Length-uneaten seed	105	60.00	-	-	70	40.00	175	
Total	161	-	-	-	125	-	286	
Width-eaten seed	71	81.61	-	-	16	18.39	87	χ^2= 1.1201e-30, *df*= 1, *p*= 1
Width-uneaten seed	123	82.00	-	-	27	18.00	150	
Total	194	-	-	-	43	-	237	

TABLE 6 Level of difficulty in handling fruit, fitting fruit between incisor-incisor and canine-canine, and passage of seed between upper canines, according to the length and width of the fruit/seed consumed and not consumed by ***Cacajao ouakary***.

	Difficulty level							**Chi-square Test (χ^2)**
Handling	**Easy**	**(%)**	**Manageable**	**(%)**	**Difficult**	**(%)**	**Total**	
Length-eaten fruit	86	62.77	22	16.06	29	21.17	137	χ^2= 4.3682, *df*= 2, *p*= 0.1126
Length-uneaten fruit	149	70.95	34	16.19	27	12.86	210	
Total	235	-	56	-	56	-	347	
Width-eaten fruit	70	79.55	13	14.77	5	5.68	88	χ^2= 0.29443, *df*= 2, *p*= 0.8631
Width-uneaten fruit	147	78.19	32	17.02	9	4.79	188	
Total	217	-	45	-	14	-	276	
Fitting fruit between canine-canine								
Length-eaten fruit	86	62.77	-	-	51	37.23	137	χ^2= 2.1768, *df*= 1, *p*= 0.1401
Length-uneaten fruit	149	70.95	-	-	61	29.05	210	
Total	235	-			112	-	347	
Width-eaten fruit	70	79.55	-	-	18	20.45	88	χ^2= 0.00964, *df*= 1, *p*= 0.9218
Width-uneaten fruit	147	78.19	-	-	41	21.81	188	
Total	217	-	-	-	59	-	276	
Fitting fruit between incisor-incisor								
Length-eaten fruit	104	75.91	-	-	33	24.09	137	χ^2= 0.77522, *df*= 1, *p*= 0.3786
Length-uneaten fruit	169	80.48	-	-	41	19.52	210	
Total	273	-			74	-	347	
Width-eaten fruit	79	89.77	-	-	9	10.23	88	χ^2 = 0.0007, *df* = 1, *p*= 0.9784
Width-uneaten fruit	167	88.83	-	-	21	11.17	188	
Total	246	-	-	-	30	-	276	
Passage between the upper canines								
Length-eaten seed	62	56.36	-	-	48	43.64	110	χ^2= 0.9158, *df*= 1, *p*= 0.3386
Length-uneaten seed	58	49.15	-	-	60	50.85	118	
Total	120	-	-	-	108	-	228	
Width-eaten seed	62	73.81	-	-	22	26.19	84	χ^2= 0.011561, *df*= 1, *p*= 0.914
Width-uneaten seed	80	72.07	-	-	31	27.93	111	
Total	142	-	-	-	53	-	195	

TABLE 7 Level of difficulty in handling fruit, fitting fruit between incisor-incisor and canine-canine, and passage of seed between upper canines, according to the length and width of the fruit/seed consumed and not consumed by ***Cacajao melanocephalus***.

	Difficulty level							**Chi-square Test (χ^2)**
Handling	**Easy**	**(%)**	**Manageable**	**(%)**	**Difficult**	**(%)**	**Total**	
Length-eaten fruit	47	41.59	48	42.48	18	15.93	113	χ^2= 15.058, *df*= 2, *p*= 0.00054*
Length-uneaten fruit	108	62.07	38	21.84	28	16.09	174	
Total	155	-	86	-	46	-	287	
Width-eaten fruit	68	63.55	37	34.58	2	1.87	107	χ^2= 11.469, *df*= 2, *p*= 0.00323*
Width-uneaten fruit	121	78.57	26	16.88	7	4.55	154	
Total	189	-	63	-	9	-	261	
Fitting fruit between canine-canine								
Length-eaten fruit	47	41.59	-	-	66	58.41	113	χ^2= 10.754, *df*= 1, *p*= 0.00104*
Length-uneaten fruit	108	62.07	-	-	66	37.93	174	
Total	155	-			132	-	287	
Width-eaten fruit	68	63.55	-	-	39	36.45	107	χ^2 = 6.398, *df* = 1, *p*= 0.01143*
Width-uneaten fruit	121	78.57	-	-	33	21.43	154	
Total	189	-	-	-	72	-	261	
Fitting fruit between incisor-incisor								
Length-eaten fruit	77	68.14	-	-	36	31.86	113	χ^2= 1.4136, *df* = 1, *p*= 0.2345*
Length-uneaten fruit	131	75.29	-	-	43	24.71	174	
Total	208	-			79	-	287	
Width-eaten fruit	97	90.65	-	-	10	9.35	107	χ^2= 0.73832, *df* = 1, *p*= 0.3902*
Width-uneaten fruit	133	86.36	-	-	21	13.64	154	
Total	230	-	-	-	31	-	261	
Passage between the upper canines								
Length-eaten seed	17	16.35	-	-	87	83.65	104	χ^2= 13.582, *df*= 1, *p*= 0.00023*
Length-uneaten seed	43	40.19	-	-	64	59.81	107	
Total	60	-	-	-	151	-	211	
Width-eaten seed	41	45.05	-	-	50	54.95	91	χ^2= 11.81, *df*= 1, *p*= 0.000589*
Width-uneaten seed	70	70.71	-	-	29	29.29	99	
Total	111	-	-	-	79	-	190	

TABLE 8 Mean size in "mm" and standard deviation ($\bar{x}$ ± SD) of the eaten and uneaten fruits by handling classes of the four primate taxa: *Cacajao c. calvus*, *C. c. ucayalii*, *C. melanocephalus* and *C. ouakary*.

Handling	***C. c. calvus***		***C. c. ucayalii***		***C. melanocephalus***		***C. ouakary***	
	Eaten	**Uneaten**	**Eaten**	**Uneaten**	**Eaten**	**Uneaten**	**Eaten**	**Uneaten**
Easy	24.71 (±9.35)	22.24 (± 10.82)	24.34 (±9.84)	23.15 (±10.11)	28.04 (±8.20)	22.42 (±10.20)	22.85 (±10.70)	21.73 (±9.90)
Manageable	58.57 (±13.51)	65 (± 12.12)	58.19 (±10.82)	63.54 (±13.72)	58.60 (±11.67)	61.84 (±14.10)	58.09 (±10.68)	61.95 (±12.13)
Difficult	155.33 (±74.44)	184.64 (± 99.80)	171.85 (±73.59)	177.04 (±73.46)	180.97 (±92.84)	154.44 (±74)	175.01 (±79.53)	151.03 (±66)
N	71	119	139	251	113	174	137	210

TABLE 9 Mean size of **eaten seeds** in total uacaris diets by size classes. Seed size classification followed Cornejo & Janovec (2010).

Class	***C. c. calvus***		***C. c. ucayalii***		***C. melanocephalus***		***C. ouakary***	
size seed	**$\bar{x}$± SD**	**Freq. (%)**	**$\bar{x}$± SD**	**Freq. (%)**	**$\bar{x}$± SD**	**Freq. (%)**	**$\bar{x}$± SD**	**Freq. (%)**
Large	31.12 (±11.22)	25 (43.86)	30.67 (±12.05)	46 (41.44)	27.47 (±9.63)	70 (67.31)	38.26 (±18.95)	39 (35.45)
Medium	14.31 (±2.58)	19 (33.33)	14.51 (±2.99)	42 (37.84)	13.7 (±2.56)	27 (25.96)	13.62 (±2.68)	44 (40)
Small	6.5 (±1.4)	9 (15.79)	6.66 (±1.12)	14 (12.61)	6.8 (±1.56)	4 (3.85)	7.76 (±1.28)	15 (13.64)
Tiny	2.77 (±0.73)	4 (7.02)	2.14 (±0.97)	9 (8.11)	1.86 (±0.77)	3 (2.88)	2.73 (±1.24)	12 (10.91)
N	57		111		104		110	

TABLE 10 Mean size of **uneaten seeds** in total uacaris diets by size classes. Seed size classification followed Cornejo & Janovec (2010).

Class	***C. c. calvus***		***C. c. ucayalii***		***C. melanocephalus***		***C. ouakary***	
size seed	**$\bar{x}$± SD**	**Freq. (%)**	**$\bar{x}$± SD**	**Freq. (%)**	**$\bar{x}$± SD**	**Freq. (%)**	**$\bar{x}$± SD**	**Freq. (%)**
Large	34.56 (± 17.57)	23 (25.84)	65.25 (± 30.44)	10 (5.71)	34.21 (± 15.88)	43 (40.19)	58.56 (±130.9)	39 (33.05)
Medium	14.33 (± 3.02)	40 (44.94)	18.41 (± 6.32)	121 (69.14)	15.34 (± 3.04)	37 (34.58)	16.03 (± 2.93)	49 (41.53)
Small	8.23 (±1.27)	15 (16.85)	8.04 (± 1.54)	24 (13.71)	7.94 (± 1.45)	21 (19.63)	8 (± 1.66)	24 (20.34)
Tiny	3.01 (± 1.36)	11 (12.36)	2.38 (± 1.30)	20 (11.43)	2.15 (± 1.10)	6 (5.61)	2.49 (± 1.15)	6 (5.08)
N	89		175		107		118	

SUPPLEMENTARY INFORMATION

TABLE S1 Overall comparison of *Cacajao* taxa ecology. Table adapted from Boubli (1997).

General ecological characteristics	***Cacajao calvus calvus***	***Cacajao calvus ucayalii***	***Cacajao melanocephalus***	***Cacajao ouakary***
Number of feeding records	637 (2345)	2583	596	11902
Items in diet	-	122	-	189
Mean density per km²	20	0,08 -6,4	14	1.44 - 12
Mean head and body length (Kg)	45.6 cm (3.16)	5.72 cm (4.33*)	41.4 cm (2.93)	44.33 cm (1)*
Group size	30 - 48	20-200 (x̄= 43)	~70	4 - 200
Association pattern	Fission-fusion	Fission-fusion	Single group	Fission-fusion
Social structure	Multiple males and females	Multiple males and females	Multiple males and females	Multiple males and females
Habitat preference	Várzea (baixa and alta restinga)	Várzea, terra firme, chavascal	Caatinga, chavascal, terra firme	Igapó, terra firme, borokotó
Habitat type	Continuous forest	Continuous forest	Continuous forest	Continuous forest
Forest stratum	Upper	Upper	Upper	Upper
Mean daily distance travelled (km)	1.2 – 6.2	6 – 7.3 or more	1.2 – 4.4	100m-5km*
Daily home range (ha)	500 - 550	1200	1053	-
Rest % (dry season)	29 (48- 23)	25	22 (21 - 50)	51
Foraging %	36	35	31	10**
Feeding %	36 (29 -35.5)	28.2	35 (37 - 25)	36
Moving %	35 (23 -41.5)	39	41 (42 - 25)	42.7
Number of species in diet	85	164	120	137
Fruit, ripe (% of diet)	18.4	37.4	29.4	11.6
Fruit, unripe (unripe seeds)	66.9	50.6	63.8	68.3
Leaves	3	1.69	3	10.8
Arthropods	5.2	2.82	2	2.4
Flowers	6.2	3.72	4	7.2
Fruits and seeds (%)	85.3	91.22	91	78.8
Germinating and ripe seeds	-	-	-	4.8

Other parts	-	0.56	-	0.8
Main fruit species %	*Eschweilera turbinata* 13.2%	*Mauritia flexuosa* 20%	*Micrandra spruceana* 14%	*Micropholis venulatus* 18%
Tree species (%)	35	29.13	30	
Volume of vocalizations	-	-	0.77 – 4.14 kHz	-
Vision type	dichromatic (M), trichormatic (F)**	-	-	-
Breeding season	Dry season	Dry season	Dry season	Dry season
Sexual dimorphism in color and size	Yes	Yes	Yes	Yes
Principle plant families in diet (ranked)	Lecythidaceae,Moraceae, Celastraceae (Hippocrateceae), Sapotaceae and Annonaceae	Arecaceae, Sapotaceae, Fabaceae, Lecythidacea, Chrysobalanaceae* Sapotaceae, Apocynaceae, Humiriaceae, Lecithidaceae and Areceae**	Euphorbiaceae, Leguminosae, Sapotaceae, Lecythidaceae and Arecaceae	Sapotaceae, Lecythidaceae, Fabaceae, Combretaceae and Euphorbiaceae
Diversity of insects eaten	Caterpillars, orthopterans, beetles, spiders, butterflies, flies, cicadas and nymphs of homopteran.	Ants, caterpillars, termites, praying mantises, Tettigoniidae	ants, spiders, grasshoppers, Tettigoniidae, cockroaches	Caterpillars, Hymenoptera, beetles, cicadas, orthoptera
Interactions with other primates	*Alouatta senlculus, Sapajus apella, Saimiri vanzolini*	*Ateles chamek, Alouatta seniculus, Callicebus moloch, Cebuella pygmaea, Cebus albifrons, Lagothrix lagothricha, Pithecia monarchus, Saimiri sciureus, Saguinus fusicollis, Saguinus mystax, Sapajus apella*	*Ateles belzebuth, Aotus* sp., *Alouatta seniculus Callicebus torquatus, Cebus albifrons, Chiropotes* sp., *Saimiri* sp., *Chiropotes chiropotes* (terra firme)	*Alouatta seniculus, Aotus* sp., *Lagothrix lagotricha, Callicebus torquatus, Cebus albifrons, Sapajus apella, Saimiri sciureus, Pithecia pithecia*
Conservation status	VU	VU	LC	LC
Study regions	Central Amazon	Western Amazon	Central Amazon	Central Amazon
Distribution (Countries)	Brazil	Brasil and Peru	Brazil and Venezuela	Braszil and Colombia
References	Ayres 1986, Lehman 2013 (weight), Hershkovitz 1987 (size), Corso et al. 2016**	Bowler 2007, Aquino 1988, 1995, Salovaara et al. 2003, Leonard & Bennett 1995, Bartecki & Heymann 1987, Bowler & Bodmer 2011, Aquino & Encarnacion 1999**. Body sizes are from musuem specimens (Appendix.)	Boubli 1997, 2000, Lehman 2013 (weight), Hershkovitz 1987 (size), Defler 2005, Bezerra et al. 2007.	Boubli 2002, Palacios & Peres 2005, Barnett et al. 2005, Barnett 2010, Defler 2004*, Da Cunha & Barnett 1989, Bezerra et al. 2010, Coleta Roosmalen-INPA (n=3, f=2 e m=1) for size and weight*. Ayres 1986 e 1989 (stomach contents). **insects

TABLE S2. Specimens used in the current study. † Specimens damaged, incomplete. ‡Specimens classified as juveniles. Species names are as given on museum labels and do not follow Ferrari et al. (2014).

Taxon	**Collection Number**	**Collector**	**Location**	**Collection Date**	**Museum**
C. c. calvus	212	Coronel Eduardo	CIGS Manaus, Am	01/02/1980	INPA
	576	Jardim Zoológico	River Juruá	01/08/1934	MPEG
	3734	Cezar Pinto Vieira	Pará-Amazonas	20/10/1927	MZUSP
	5241	Tenente Augusto	Sacado do Tarauacá	20/02/1998	INPA
	6911	(Sem dados)	Jardim zoológico		MPEG
	6912	(Sem dados)	Jardim zoológico		MPEG
	8990	INPA 08990	River Solimões, margem esquerd- Fonte Boa, São José, Paracea do Mararei, AM.	19/06/1980	MPEG
	17535	J.M. Ayres & Barroso	Lago do Tracajá, foz do Japura, Am	02/12/1983	MZUSP
	17536	J.M. Ayres & D.J. Chivers	Mamirauá, foz do Japurá, Am	06/09/1983	MZUSP
	17537	J.M. Ayres & D.J. Chivers	Mamirauá, foz do Japurá, Am, Municipio de Alvaraes	06/09/1983	MZUSP
	17539	J.M. Ayres & Barroso	Lago do Taracajá. foz do Japurá	02/12/1983	MZUSP
	17542	J.M. Ayres & D.J. Chivers	Ressaca de Vila Alencar, foz do Japurá	-	MZUSP
	284273	K. Lako	Parana de Manhama, upper Solimoes	04/07/1927	NHML
	284274	K. Lako	Parana de Manhama, upper Solimoes	08/07/1927	NHML
	284275	K. Lako	Parana de Manhama, upper Solimoes	04/07/1927	NHML

	284276	K. Lako	Parana de Manhama, upper Solimoes	04/07/1927	NHML
	497201	Bartlett	-	-	NHML
	604164	Purchsed Stevens, Coll. Bates	Upper Amazon	-	NHML
	604166	H.W. Bates (via Stephens)	Upper Amazonas	-	NHML
	4810281	Bourcier	Upper Amazon	-	NHML
	184811103	Bourcier	Nr. R. Amazon	-	NHML
C. c. ucayalli	49	Jardim Zoológico	River Napo	18/09/1932	MPEG
	461	Jardim Zoológico	Chimboté, Solimões, Scoffer	09/07/1932	MPEG
	462	Jardim Zoológico	River Napo	03/02/1933	MPEG
	468	Jardim Zoológico	Chimboté, Solimões, Peru	31/08/1933	MPEG
	499	Jardim Zoológico	River Napo	06/02/1933	MPEG
	505	Jardim Zoológico	Chimboté, Solimões, Peru	18/07/1932	MPEG
	506	Jardim Zoológico	River Napo	11/02/1933	MPEG
	511	Jardim Zoológico	River Napo	21/09/1932	MPEG
	512	Jardim Zoológico	River Napo	07/02/1933	MPEG
	285239	RW Hendee	Cerro Azul, Contamana Loreto, Peru.	-	NHML
	285240	RW Hendee	Cerro Azul, Contamana Loreto, Peru	-	NHML
C. c. rubincundus	1848	José Hidasi	Estirão do Equador, Amazonas, River Javari	01/10/1960	MPEG
	1849	José Hidasi	Estirão do Equador, Amazonas, River Javari	01/11/1960	MPEG
	1850	José Hidasi	Estirão do Equador, Amazonas, River Javari	01/10/1960	MPEG
	1851[†]	José Hidasi	Estirão do Equador, Amazonas, River Javari	01/11/1960	MPEG
	1852[‡]	José Hidasi	Estirão do Equador, Amazonas, River Javari	01/11/1960	MPEG

1853[†]	José Hidasi	Estirão do Equador, Amazonas, River Javari	01/11/1960	MPEG
1854	José Hidasi	Estirão do Equador, Amazonas, River Javari	01/10/1901	MPEG
4079	(Sem dados)	Meschede V. 36		MPEG
4080	(Sem dados)	Jardim Zoológico, Minas Gerais	19/2/194	MPEG
4088	(Sem dados)	Jardim Zoológico, Minas Gerais	18/03/1934	MPEG
4090	(Sem dados)	Jardim Zoológico	24/11/1940	MPEG
4091	(Sem dados)	Jardim Zoológico	20/03/1934	MPEG
4096	(Sem dados)	Jardim Zoológico	24/03/1934	MPEG
4098	(Sem dados)	Jardim Zoológico	05/10/1933	MPEG
4149	Vieira (Col: A.M. Olalla 1332)	Santa Cruz, River Eiru, AM	01/11/1936	MZUSP
4150	Vieira (Col: A.M. Olalla 1331)	Santa Cruz, River Eiru, AM	01/11/1936	MZUSP
4151	Vieira (Col: A.M. Olalla 1333)	Santa Cruz, River Eiru, AM	16/10/1936	MZUSP
4330	Vieira (Col: A.M. Olalla 1832)	Santa Cruz, River Eiru, AM	05/11/1936	MZUSP
4331	Vieira (Col: A.M. Olalla 1766)	Santa Cruz, River Eiru, AM	24/10/1936	MZUSP
4332	Vieira (Col: A.M. Olalla 1900)	Santa Cruz, River Eiru, AM	19/11/1936	MZUSP
4333	Vieira (Col: A.M. Olalla 1897)	Santa Cruz, River Eiru, AM	19/11/1936	MZUSP
4334	Vieira (Col: A.M. Olalla 989)	Santa Cruz, River Eiru, AM	25/11/1936	MZUSP
4335	Vieira (Col: A.M. Olalla 1919)	Santa Cruz, River Eiru, AM	25/11/1936	MZUSP
4336	Vieira (Col: A.M. Olalla 1923)	Santa Cruz, River Eiru, AM	27/11/1936	MZUSP
4337	Vieira (Col: A.M. Olalla 1911)	Santa Cruz, River Eiru, AM	23/11/1936	MZUSP
4338	Vieira (Col: A.M. Olalla 1859)	Santa Cruz, River Eiru, AM	10/11/1936	MZUSP
4339	Vieira (Col: A.M. Olalla 1891)	Santa Cruz, River Eiru, AM	17/11/1936	MZUSP
5141	C. L. L. Horqui	Santarém Gessaufr	01/08/1924	MPEG
5496	Vieira (Col: A.M. Olalla 1925)	Santa Cruz, River Eiru, AM	27/11/1936	MZUSP
6913	C. Grim	(Sem informação)	01/05/1935	MPEG
11245	Sem Dados	Zoológico	-	MZUSP
17552[†]	J.M.Ayres	Buiuçu, Auati-paraná, AM	01/12/1983	MZUSP
17553[†]	J.M.Ayres (Ubessa, ex J.M. Ayres)	Buiuçu, Auati-paraná, AM	01/12/1983	MZUSP
19359	Vieira (Col: A.M. Olalla 1934)	Santa Cruz, River Eiru, AM	17/10/1936	MZUSP
19701	Vanzo (Col: A.M. Olalla 1894)	Santa Cruz. Rio Eiru. AM	18/11/1936	MZUSP

	19923	Vanzo	(Sem informação)	01/10/1985	MZUSP
	27365	W. Ekrhard	Indy Parana, upper Amazonas	14/10/1926	NHML
	27366	W. Ekrhard	Indy Parana, upper Amazonas	15/10/1926	NHML
C. c. novaesi	21861	F. Ramos e E. Martins	River Jurupari, afluente do River Envira, margem direita, AM, Brasil.	08/08/1989	MPEG
	21862	F. Ramos e E. Martins	River Jurupari, afluente do River Envira, lado direito, AM, Brasil.	08/08/1990	MPEG
	21863	E. Martins	River Jurupari, afluente do River Envira, lado direito	08/08/1988	MPEG
	346141	Lako & Salaoke	River Iça, Paraana de Jacare, Amazonas	01/05/1930	NHML
C. ayresi	5246	Jean P. Boubli	Igarapé Madixi, Am	25/03/2005	INPA
	5247	Jean P. Boubli	River Aracá, Barcelos, Am, Brazil 0°32'531"S 62°54'404"W	-	INPA
	5248	Jean P. Boubli	River Aracá, Barcelos, Am, Brazil 0°32'531"S 62°54'404"W	-	INPA
C. melanocephalus	9421	MdVivo	Sem dados, ex Zoo	14/05/1905	MZUSP
	4323	Vieira (Col: A.M. Olalla767)	River Solimões: Codajás, AM	24/08/1935	MZUSP
	4340	Vieira (Col: A. M. Olalla 768)	River Solimões: Codajás, AM	24/08/1935	MZUSP
	5242	Jean P. Boubli	Parque Nacional Pico da Neblina, Maturacá, 0°37'N 66°07W	1994/1995	INPA
	8991	INPA	River Curuoluri, afluente do River Araçá, afluente do River Negro	19/05/1980	MPEG
	9715	C.T. Carvalho	Sem dados, ex Zoo	-	MZUSP
	9948[‡]	Vieira (Of. Di. Della Serra)	Pará	24/05/1938	MZUSP
	12883	MdVivo	Moura, AM EPA72.0177	30/01/1962	MZUSP
	17534	J.M.Ayres & D.J. Chivers	São Pedro, River Japurá, AM, 11.ix.83 (margem esquerda)	11/09/1983	MZUSP
	17538	J.M.Ayres & D.J. Chivers	São Pedro, River Japurá, AM (maraã)	11/09/1983	MZUSP
	17545	J.M.Ayres & D.J. Chivers	São Pedro. Rio Juruá. Am	11/09/1983	MZUSP

	32382	(Sem dados)	ex. Fundação Parque Zoologico de São Paulo	-	MZUSP
	36615	João Valsecchi	Maraã, Amazonas, Comunidade Boa Esperança, Igarapé da Seringa - RDSA	11/06/2004	MPEG
	36630	João Valsecchi	Maraã, Amazonas, Comunidade Boa Esperança, Igarapé Juá Grande - RDSA	14/06/2004	MPEG
	36635	João Valsecchi	Maraã, Amazonas, Comunidade Boa Esperança, Igarapé Juá Grande - RDSA	15/06/2004	MPEG
	36637	João Valsecchi	Maraã, Amazonas, Setor Coraci, River Coracizinho- RDSA	17/06/2004	MPEG
	36638	João Valsecchi	Maraã, Amazonas, Setor Coraci, River Coracizinho- RDSA	17/06/2004	MPEG
	36644	João Valsecchi	Maraã, Amazonas, Setor Coraci, River Coracizinho- RDSA	17/06/2004	MPEG
	36649	João Valsecchi	Maraã, Amazonas, Setor Coraci, River Coracizinho- RDSA	18/06/2004	MPEG
	36650	João Valsecchi	Maraã, Amazonas, Setor Coraci, River Coracizinho- RDSA	18/06/2004	MPEG
	36651	João Valsecchi	Maraã, Amazonas, Setor Coraci, River Coracizinho- RDSA	18/06/2004	MPEG
C. ouakary	5238	Marc Van Roosmalen	River Solimões, Lago Amanã, ca.100km acima de Manacapuru, Am, Brasil	18/06/1996	INPA
	5239	Marc Van Roosmalen	River Solimões, Lago Amanã, ca.100km acima de Manacapuru, Am, Brasil	18/06/1995	INPA
	5240	Marc Van Roosmalen	River Solimões, margem esquerda, Manacapuru	26/06/1998	INPA
	265518	W. Ekrhard	Castaneiro Miri, Solimoes	19/08/1925	NHML
	3310112	R. Ward	Manaca-quiru	-	NHML

TABLE S3 Size and body weight for black and red-headed uacaris used in the current study (classified according to museum label), plus additional material in Hershovitz (1987).

Species	**Sex**	**Age**	**Weight kg**	**Size body cm**	**Collection number**	**Museum/ Ref.**
Cacajao c. calvus	♂	ad	3.45	40,0	17535	MZUSP
	♂	juv	1.72	34.6	17536	MZUSP
	♀	ad	2.98	40.0	17537	MZUSP
	♀	-	2.34	37.6	17542	MZUSP
	♀	-	2.75	38.8	-	Hershovitz 1987
	♀	-	3	40.0	-	Hershovitz 1987
	♂	-	3.45	40.0	-	Hershovitz 1987
	♀			44,0	N=21	Hershovitz 1987
	♂			45.6	N=19	Hershovitz 1987
Cacajao c. rubicundus	♂	-	-	58.0	4151	MZUSP
	♀	-	-	62.0	4330	MZUSP
	♀	-	-	60.5	4331	MZUSP
	♀	ad	-	58.5	4331	MZUSP
	♂	-	-	61.5	4333	MZUSP
	♀	-	4.33	65.2	4334	MZUSP
	♂	-	-	58.5	4335	MZUSP
	♂	-	-	62.0	4336	MZUSP
	♀	-	-	53.5	4337	MZUSP
	♀	juv	-	54.0	4338	MZUSP
	♂	-	-	66.0	4339	MZUSP
	♂	-	-	60.5	5496	MZUSP
	♀	ad	-	46.0	11245	MZUSP
	♀	ad	-	56.0	19701	MZUSP
Cacajao melanocephalus	♂	ad	-	54.5[†]	4323	MZUSP*
	♀	-	-	54.0[†]	4340	MZUSP*
	♀	-	-	32.0	12883	MZUSP
	♀	-	1.59	31.0	17534	MZUSP
	♀	ad	2.82	38.8	17538	MZUSP
	♀	-	2.66	35.2	17545	MZUSP
	♂			41.4	N=17	Hershovitz 1987
	♀			38.9	N=21	Hershovitz 1987
Cacajao ouakary	♀	-	2.66	35.2	-	Hershovitz 1987
	♀	-	2.79	37.0	-	Hershovitz 1987
	♀	-	2.82	38.8	-	Hershovitz 1987

[†] Collected on the Solimões River, Vieira (Col: A.M. Olalla 767)

TABLE S4 Dimensions of hands of members of the genus *Cacajao*, classified as given on museum labels.

Taxon	**N**	**Dimension of Hand**			
		Hand, length $\bar{x}$ ± SD	**Palm, width** $\bar{x}$ ± SD	**Palm, length** $\bar{x}$ ± SD	**Longest finger length** $\bar{x}$ ± SD
Cacajao c. calvus	14	91.78 (± 8.42)	29.62 (± 5.03)	45.28 (± 6.37)	47.09 (±6.82)
Cacajao c. novaesi	4	89.5 (± 8.96)	36.92 (± 3.79)	45.75 (± 4.17)	41.75 (±6.36)
Cacajao c. rubicundus	22	99.97 (± 13.47)	36.47 (± 8.03)	47.15 (± 7.75)	53.19 (±9.23)
Cacajao c. ucayalli	11	83.44 (±9.52)	34.66 (±6.63)	44.75 (±6.12)	38.58 (±6.61)
Cacajao ayresi	3	85.41 (± 3.22)	32.45 (± 3.44)	43.89 (± 2.99)	41.58 (±0.36)
Cacajao melanocephalus	16	88.84 (± 7.95)	35.22 (± 7.45)	40.03 (±4.18)	43.07 (±4.52)
Cacajao ouakary	4	80.6 (± 4.51)	30.52 (± 3.61)	41.2 (± 1.34)	39.4 (±3.33)
Overall	74	91.65 (±10.13)	33.87 (±5.77)	45.57 (±4.75)	46.08 (±7.89)

TABLE S5 Hand dimensions for members of the genus *Cacajao* after combining specimens, following nomenclature of Ferrari et al. (2014).

Taxon		**Dimension of Palm**				**Dimension of Hand**		
	N	**Width**	**Length**	**Width two palms**	**Length two palms**	**Length**	**Length dual Hands**	**Length finger**
Cacajao c. calvus	18	31.3 (±5.63)	45.3 (±4.99)	62.7 (±11.26)	90.7 (±9.99)	91.2 (±8.30)	182.5 (±16.61)	45.9 (±6.82)
Cacajao c. ucayalli	33	35.3 (±5.65)	46.2 (±5.25)	70.9 (±16.66)	92.4 (±10.52)	94.8 (±12.06)	189.6 (±24.12)	48.5 (±9.71)
Cacajao melanocephalus	10	32.8 (±7.28)	44.5 (±4.64)	65.6 (±14.57)	89.1 (±9.28)	86.32 (±6.95)	172.6 (±13.91)	41.7 (±3.33)
Cacajao ouakary	13	34.5 (±4.79)	44.9 (±3.27)	69.0 (±9.58)	89.8 (±6.55)	88.6 (±6.61)	176.5 (±13.22)	43.3 (±3.84)

FIGURE S1 Measurements of *Cacajao calvus calvus* hand length from the wrist crease to the interphalangeal region toward the middle finger (A) and palm width from the widest part of the palm (B); measurements of the length of the largest finger from the interphalangeal base to the apex of the finger using callipers on a well taxidermized *C. c. calvus* with a fully-extended hand (C); the longest finger of a *C. melanocephalus* being measured with the help of a cord from the interphalangeal base to the apex of the finger (D); examples of (E) complete and measurable hand (*C. melanocephalus*) and a damaged, not measurable, hand (F) of *C. c. rubicundus*.

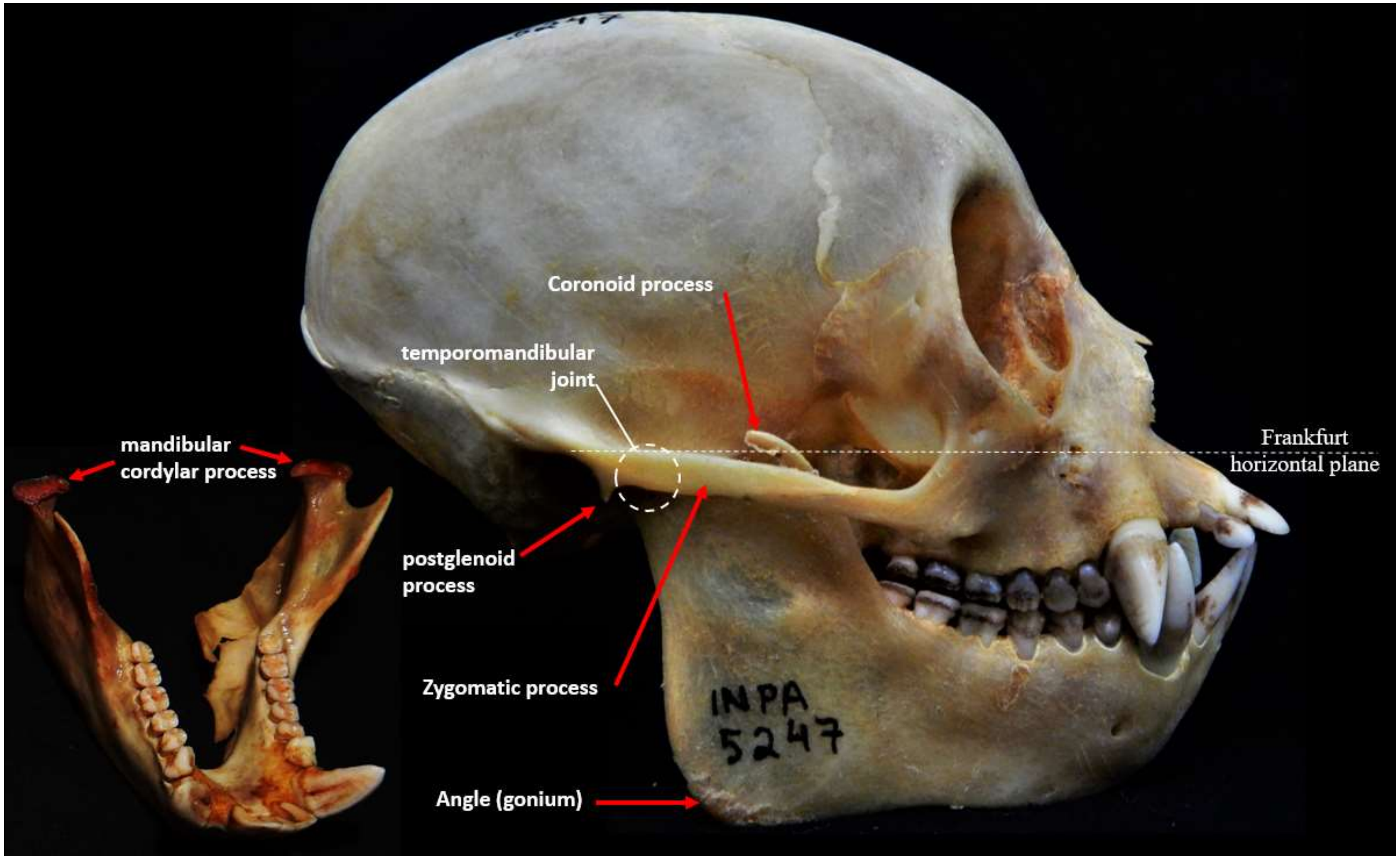


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FIGURE S2 Image of location and nature of features mentioned in Table 1. Photo and art: Renann H. Paiva Dias da Silva.

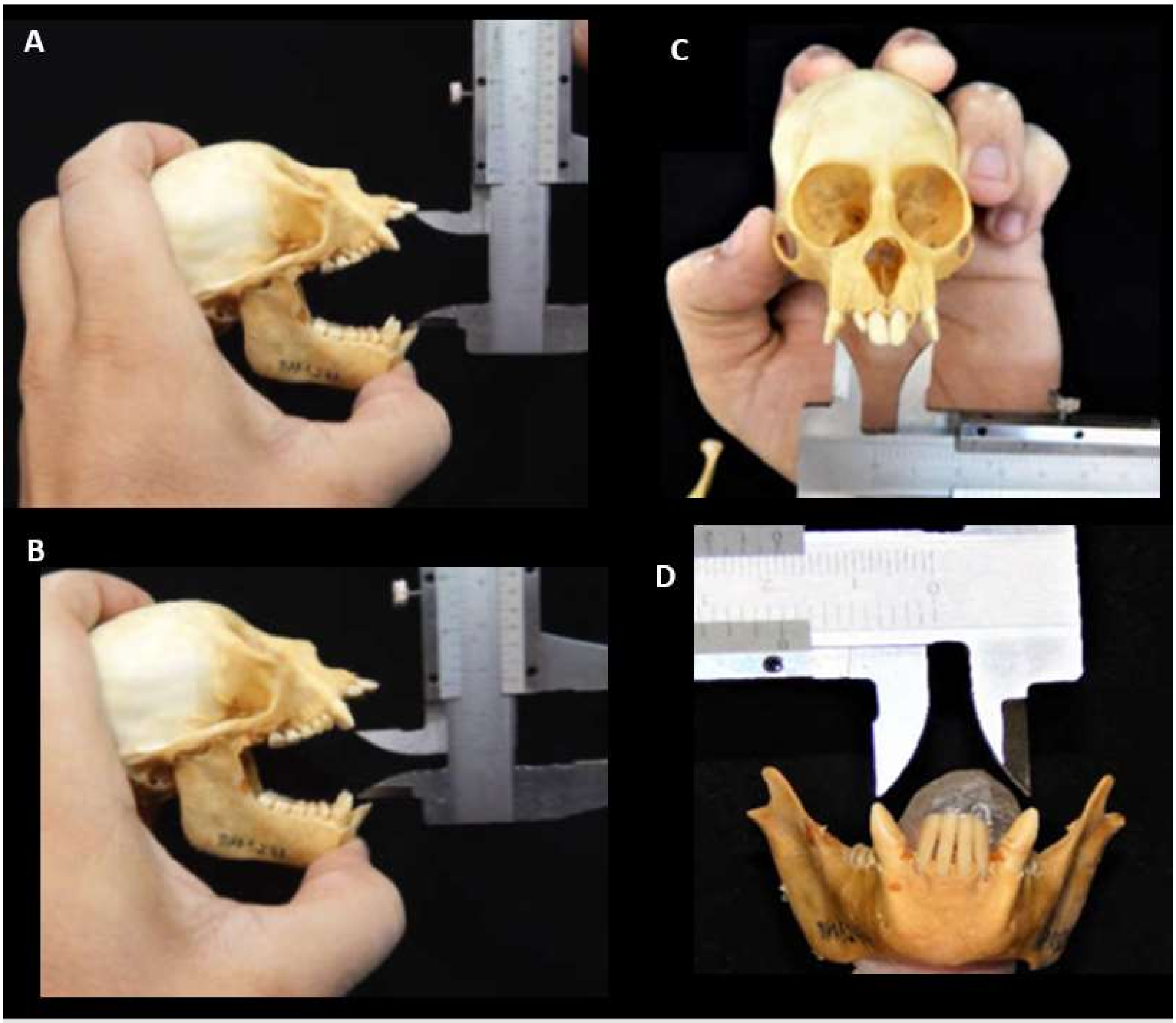

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FIGURE S3 Image A and B show the measurement of the maximum distance between upper and lower incisors at different angles, and the maximum distance between the upper and lower canine tips; C and D the distance between the upper (A) and lower (B) canines at the extremity.

CONCLUSÃO GERAL

No primeiro capítulo*,* *Cacajao ouakary* seguiu as predições da teoria do forrageamento ótimo, quando selecinou frutos de *Aldina latifolia* com tamanho médio e peso desproporcional a sua abundância, minimizando o tempo despendido no processamento do alimento e simultaneamente, maximizando o ganho energético. Em termos de energia gasta por unidade de tempo, a escolha de frutos drupóides de tamanho médio foi ótimo. O maior tempo gasto no processamento de drupóides grandes de *A. latifolia* para *C. ouakary* também podem ser atribuídos a dificuldades em manipular objetos de cinco a sete vezes o tamanho da palma da mão do animal e um sexto do seu próprio peso corporal. Este resultado nos levou ao segundo capítulo desta dissertação.

Diante desse fato, para o segundo capítulo levantamos a hipótese de que o tamanho anatômico do primata poderia ser um limitante na escolha das espécies para sua dieta, considerando o nível de dificuldade de manuseio do fruto para obter acesso a semente. Entretanto, salvo *C. melanocephalus*, os uacaris, no processo de escolha das espécies que irão compor sua dieta, não consideram o nível de dificuldade de manuseio com base no tamanho do fruto, frutos de "fácil" manuseio foram predominantes na dieta e no ambiente. As diferenças encontradas na seleção de frutos da dieta de *C. melanocephalus* em relação aos demais primatas foram atribuídas ao seu tamanho corpóreo e habitat.

No processo de escolha da espécie vegetal em meio as outras, o tamanho do fruto e o grau de dificuldade de manuseio não mostrou ser tão relevante para três dos quatro táxons de uacaris, etretanto, a nivel de espécie o tamanho do fruto dentro de um mesmo individuo é considerado conforme foi observado em *C. ouakary*.