AGE-RELATED DIFFERENCES IN PALM-FRUIT HANDLING AND FEEDING DURATIONS IN *CEBUS CAPUCINUS* ON THE OSA PENINSULA, COSTA RICA

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Abstract

Capuchin monkeys are well known for their large brains and a protracted juvenile period. According with one formulation of the needing-to-learn hypothesis for the evolution of extended juvenile periods, longer juvenility may be necessary for acquiring behaviors needed to exploit hidden or well-protected foods. I tested predictions of this hypothesis against observational data on the behavior of free-ranging *Cebus capucinus* at Piro Biological Station on the Osa Peninsula, Costa Rica. Small juveniles (ca. 1-3 years) appeared unable to follow the adult technique for processing the palm fruits of *Attalea butyracea* (Arecaceae), and large juveniles (ca. 3-5 years) spent significantly more time processing each fruit than did adult males and females. Furthermore, according to a ratio of feeding time to processing time, large juveniles were significantly less efficient than monkeys of both adult sexes in their foraging technique on this substrate. These findings show limited support for a foraging-focused formulation of the needing-to-learn hypothesis because they do not rule out alternative hypotheses, both ultimate and proximate, that would predict the same result.

Key words: Needing to learn, *Cebus capucinus*, juvenile, *Attalea*, capuchin monkeys.

Resumen

Los monos capuchinos son bien conocidos por sus grandes cerebros y por tener un período juvenil prolongado. Según una formulación de la hipótesis de la necesidad de aprender para la evolución de los períodos juveniles extendidos, puede ser necesaria una juventud más larga para adquirir comportamientos necesarios para explotar alimentos ocultos o bien protegidos. Probé las predicciones de esta hipótesis frente a datos de observaciones del comportamiento de *Cebus capucinus* libres habitando en la Estación Biológica Piro de la Península de Osa, Costa Rica. Los juveniles pequeños (aproximadamente 1-3 años) parecieron incapaces de seguir la técnica de los adultos para procesar los frutos de la palma *Attalea butyracea* (Arecaceae), y los juveniles grandes (aproximadamente 3-5 años) pasaron significativamente mucho más tiempo procesando cada fruto que los adultos machos y hembras. Además, según una proporción de tiempo de alimentación y tiempo de procesamiento, los juveniles grandes fueron significativamente menos eficientes que los individuos adultos de ambos sexos en su técnica de forrajeo sobre este sustrato. Estos hallazgos indican un soporte limitado de una formulación enfocada en el forrajeo de la hipótesis de la necesidad de aprendizaje porque no descartan hipótesis alternativas, tanto finales como inmediatas, que predecirían el mismo resultado.

Palabras clave: Necesidad de aprendizaje, *Cebus capucinus*, juvenil, *Attalea*, monos capuchinos.

Introduction

Juvenility begins at weaning (Leigh and Blomquist, 2011; Sherrow and MacKinnon, 2011), and the extension of this phase of life presents an interesting evolutionary problem: any prolongation of immaturity translates to an offset of reproduction. In addition, as species evolve larger brains, they also lengthen their time spent in sexual immaturity (Barrickman et al., 2008; van Schaik & Isler, 2012), effectively incurring reproductive opportunity-costs for every unit of time spent in this prereproductive state. An important related avenue of inquiry is how large-brained species compensate for such a delay. Several hypotheses have been crafted to explain the ways in which a lengthened period of juvenility might evolve within Primates, and two have received at least partial support from the literature (Deaner et al., 2003; Ross, 2003; van Schaik and Isler, 2012).

The first of these hypotheses is an extension of Janson and van Schaik's (1993) ecological risk aversion hypothesis. Deaner et al. (2003) posited a model that would focus not on a problem as general as starvation avoidance, but on the more specific problem of avoiding neural damage due to malnutrition. Because of the nutritional sensitivity of the brain during critical periods of neural growth and development, the brain-malnutrition (BM) hypothesis (Deaner et al., 2003) states that selection will favor a lengthening of immaturity in order to dilute the risk of incurring brain damage due to the excessive nutritional requirements of growing large brains. The second hypothesis to explain extended juvenility is the needing-to-learn hypothesis (Ross and Jones, 1999). According to this model, it may be adaptive to lengthen juvenility to accommodate the learning necessary to acquire the behaviors that animals will need as adults (Ross and Jones, 1999). In response to criticisms that the needing-to-learn hypothesis may be simplistic or theoretically undeveloped, Deaner et al. (2003) introduced a revised model that would connect large brains more directly to extended juvenility: the maturational constraints (MC) hypothesis. This model holds that evolutionary increases in brain size should be accompanied by extended developmental periods during which the proper neural circuitry for adult-like behaviors is laid down (Deaner et al., 2003).

Overall, a version of the MC hypothesis focused on foraging behaviors has shown mixed success in explaining the length of juvenility in capuchin monkeys, regardless of genus. On one hand, robust capuchins (*Sapajus* spp.) show a pattern that aligns well with this hypothesis when foraging on some foods (Mannu, 2002; Gunst et al., 2010a) but not with others (de Resende et al., 2008; Gunst et al., 2010b). Evidence for the MC hypothesis from gracile capuchins (*Cebus* spp.) is mixed as well. For examples, Bezanson (2009) found nearly identical foraging efficiencies across three age groups of *C. capucinus*, but Eadie (2015) showed that all immature age classes showed significantly lower fruit return-rates than both adult sexes when animals were feeding on fruits that required great strength or manipulative capacity. In this last case, however, Eadie (2015) could not directly exclude either strength or cognitive difficulty as the reason for this effect; thus it was unclear whether juvenile *C. capucinus* need to build strength or whether they need to learn before reaching adulthood.

In order to test the MC hypothesis (see below), I observed free-ranging *Cebus capucinus* foraging on the fruits of the palm tree *Attalea butyracea* (Arecaceae). This particular food item was chosen for three main reasons. First, fruit in general is very abundant at the time of year when this study took place (Lobo et al., 2008), and the capuchins were commensurately frugivorous, eating fruit in up to 78% of the instantaneous scans taken as part of a larger study (Chaney, 2015). Second, the adult foraging sequence for this fruit was very similar between males and females, following a predictable two-step procedure to harvest individual fruits from a larger infructescence. Lastly, this species of palm was chosen because it is from a close relative of another species, *A. maripa*, which was the subject of a similar study involving age-related foraging differences in *Sapajus apella* in Suriname (Gunst et al., 2010).

I generated and tested two predictions from the MC hypothesis. First, this hypothesis predicts that juveniles (i.e., ages between 1-5 years) should require more time to process a given palm fruit as compared to adults because of their relative lack of experience relative to adults. Second, reflected by this lack of foraging experience, juveniles should spend less time feeding on individual fruits as compared to the time required to handle or process that food item.

Methods

The data for this study were collected from two troops of capuchin monkeys with slightly overlapping home-ranges, and data were pooled between the two groups. Both groups were similar in composition and contained approximately 18-19 monkeys each: 3-4 small juveniles, 3-4 large juveniles, 5-6 adult females, 3 subadult males and 2 fully adult males. All data were collected between June 24, 2014 and August 4, 2014 at Piro Biological Station, which is located at 8°23' N, 83°19' W on the Osa Peninsula in southern Costa Rica. This site sits within a wildlife refuge of more than 860 ha, and the forest within the refuge ranges from tropical wet forest to premontane basal forest (Tosi, 1969).

Subjects in the study were classified into age/sex categories, following MacKinnon (2006, 2013). A full explanation and description of my age/sex classification schema can be found in Chaney (2015). Age/sex categories included adult males and females, as well as large and small juveniles. The small-juvenile age category encompassed monkeys within the approximate age-range of 6 months to 3 years, while the large juveniles were estimated to be within the ages of 3-5 years and were characterized by their adult-like limb lengths but slender bodies (MacKinnon, 2006, 2013). Any records for which the age/sex category was uncertain were omitted from this study; as a result subadult males (age: ~5-10 years; Jack et al. 2014) are not considered here because of their intermediate features, which reduced my confidence of categorization during data collection. Because the individual identities of the animals could not be ascertained reliably, all instances of foraging are pooled by age/sex class.

This study focuses solely on palm-fruit foraging bouts, which began whenever a monkey was observed to bring its hands into contact with an infructescence of an *Attalea butyracea* palm tree, and it ended when the monkey had ceased ingesting or handling a particular fruit. Standing approximately 3-5 meters from the base of the palm tree, I recorded durational data on one focal animal at a time. These palm-fruit foraging records (PFRs) were considered usable only if the focal animal was visible for the entirety of the record. All PFRs were dictated into an audio recorder and were transcribed later that day. Any given record included two phases, recorded in seconds: (1) processing and (2) feeding phases. In addition to analyzing these phases separately, I combined them for each PFR to calculate a ratio of feeding time to processing time. In cases where the animal did not open the *A. butyracea* fruit or otherwise failed to feed on it, 0.00 seconds were input for the feeding time in that bout. In other cases, where the animal being observed harvested more than one fruit from the infructescence, the number of fruits that the animal took was noted, and the processing time was divided by the number of fruits that the animal extracted in order to correct for the longer processing time necessary to pick multiple fruits. Following the recording of one PFR event, I shifted to the next visible monkey that began the standard foraging sequence described above. If only one monkey was foraging in an *A. butyracea* tree, that focal animal would be used for multiple consecutive samples.

I used a parametric one-way ANOVA to test for differences in the processing phase, but I used a Kruskal-Wallis ANOVA to test the feeding data because a Bartlett's test of homoscedasticity indicated that variances were significantly different (x^2 = 19.99, P < 0.001). The feeding:processing ratio was tested by a Kruskal-Wallis ANOVA for the same reason (x^2 = 19.62, P < 0.001). Post-hoc tests were corrected for multiple comparisons with a Bonferroni correction. Analysis was carried out in R version 3.1.0 (R Core Team, 2016).

Results

The total amount of time devoted to each foraging bout was not significantly different among age/sex classes (x^2 = 0.30, df = 2, P > 0.8; Table 1). Of the two discrete phases of foraging on these fruits (i.e., processing and feeding phases), the processing phase differed significantly among the three groups (F2,138 = 3.973, P < 0.025). Post-hoc tests of this processing phase revealed that large juveniles spent significantly longer times in the processing phase only when compared to adult males (Padj < 0.025). Adults fed for longer times than did juveniles, although this difference in the feeding phase was not quite significant (x^2 = 5.396, df = 2, P = 0.067). More qualitatively, large juveniles spent a longer average amount of time processing fruits than they did consuming those fruits—a pattern that was inverted compared to the processing and feeding times of the adults (see Table 1).

Table 1. Descriptive statistics of three age/sex classes foraging on *Attalea butyracea* fruits. Numbers in parentheses are standard errors. Multiple comparisons were corrected with a Bonferroni correction. PFR: palm-fruit foraging record; a: Significantly different from adult males (two-sample *t*-test: P < 0.05); b: Significantly different from both adult groups (Wilcoxon rank-sum test: P < 10-6).

	Large Juvenile (n = 47; 6-8 individuals)	**Adult Female (n = 44; 10-12 individuals)**	**Adult Male (n = 50; 3-4 individuals)**
Total Time per PFR	40.21 (2.62)	45.7 (4.47)	40.6 (3.03)
Mean Processing Time (s)	**23.1 (1.65)a**	18.8 (1.48)	17.2 (1.44)
Mean Feeding Time (s)	17.2 (1.66)	27.0 (3.37)	23.3 (2.19)
Mean Feeding: Processing	**0.94 (0.10)b**	1.49 (0.12)	1.60 (0.12)

The feeding: processing ratios showed a stronger pattern. This ratio was significantly different among the three test groups (x^2 = 20.97, df = 2, P < 0.001). Post-hoc testing showed that both adult age/sex classes were each significantly more efficient than large juveniles (Padj < 0.01 for both) while displaying non-significant differences between each other (Padj = 0.95).

As mentioned above, small juveniles were excluded from statistical analysis here because animals in this age class seldom foraged on *A. butyracea* fruits (N = 3) compared to the other age/sex classes (N = 44-50; see Table 1), despite being observed just as often as the other age/sex classes (see Chaney, 2015). The technique of small juveniles was irregular and qualitatively different from that of older groups. For example, instead of removing fruits from the tree's infructescence, small juveniles would attempt to remove the fruit's exocarp while the fruit was still firmly attached to its parent tree.

Discussion

Large juveniles spent significantly more time in the processing phase than adult males, and their feeding times were shorter on average than the adults (although this latter difference was not quite significant). The difference in feeding time may have to do with the fact that juveniles were the only class to drop a fruit while processing it, which led to PFR scores of 0.0 in 3/47 cases. Insofar as the feeding:processing ratio measures efficiency, juveniles were significantly less efficient at foraging on these fruits. These data show limited support the MC hypothesis, especially if the absence of small-juvenile data indicates an inability to forage on *A. butyracea* palm fruits. This support is limited because this pattern would also be predicted by the BM hypothesis.

In line with the MC hypothesis, these animals' longer processing times might be due to a lag in neural development (Deaner et al., 2003). According to the BM model, however, a delay in the acquisition of adult-like foraging behavior may not be due to a need to learn at all; rather, these differences may be ultimately attributed to the avoidance of starvation or malnutrition during critical growth periods, which is the foundation of the ERA hypothesis proper (Janson and van Schaik, 1993; Deaner et al., 2003; Stone, 2006, 2007). Indeed, the BM hypothesis would predict the same differences predicted from the MC hypothesis above. According to BM, juvenile-adult differences in foraging behavior would be caused directly by a protracted period of growth or development (Deaner et al., 2003; Janson and van Schaik, 1993)Juvenile Primates, Oxford Univ. Press, New York (1993. Prolonging somatic growth may mean that the large juveniles examined in this study lacked the physical strength of their adult counterparts, and this lack could be attributed to their delayed somatic maturation (Janson and van Schaik, 1993). For example, age-related differences in foraging on *Attalea maripa* palm fruits among the same populations were attributed to biomechanical constraints of development, such as dental development or somatic growth (Gunst et al., 2008). Additionally, MacKinnon (2006) found statistically similar diets among small juveniles, large juveniles, and adults during a twelve-month study of *C. capucinus* in Sector Santa Rosa, Costa Rica. From this, she argues that the length of juvenility in *C. capucinus* is likely not due to learning because an inability to successfully forage on different substrates will lead to dietary variation (MacKinnon, 2006). If ERA provides the ultimate underpinning for the differences reported in the present study, then this may suggest that the extended juvenility of capuchin monkeys, and *C. capucinus* in particular, is not a response to learning any more than it is a response to energetic constraints of growing or developing a large brain (Deaner et al., 2003; van Schaik and Isler, 2012).

It does bear mention that the foraging differences reported here may not be caused by any evolutionary pressure; rather, such differences may be variable among different populations or species. This may explain why some studies of capuchins report differences in foraging behavior between juveniles and adults (e.g., Agostini and Visalberghi, 2005; Eadie, 2015; Gunst et al., 2010a)either due to competition (part of the ecological risk avoidance hypothesis, while other studies find no such differences (e.g., Bezanson, 2009; de Resende, et al., 2008; Gunst et al., 2010b; Mannu, 2002; but see Chalk et al., 2016)many factors may influence the positional repertoire. The biological and behavioral changes that accompany a growing individual are expected to influence foraging strategy, social status and interaction, diet, predator avoidance strategies, and ultimately positional behavior as a behavioral link between anatomy and the environment. In this work, positional behavior is considered as an important feature of life history in juvenile and adult white-faced capuchins (Cebus capucinus. Inter-population differences also may also explain why the results reported in the present study are different from those reported by Gunst et al. (2008, 2010). Rather than adult-like foraging competence being present midway through juvenility, as reported by Gunst et al. (2008, 2010), the large juveniles in the present study showed a lower efficiency, longer handling durations, and briefer ingestion durations than their adult counterparts. This difference may theoretically be due to structural differences in the fruits of *A. maripa* and *A. butyracea*, but this seems an unlikely explanation because of the anatomical similarity of the two fruits (van Roosmalen, 1985; personal observation).

A limitation of the findings here is certainly the inability to partition variance among individual animals, as well as variance between the two capuchin populations. No other published reports of this population exist, and this is the first systematic study of this population of *Cebus capucinus* at this site; as such, the individual identities could not be dependably called for the entire duration of this study. This to also led to my pooling the data of the two groups together during data collection.

In summary, large juvenile capuchins processed *A. butyracea* fruits for longer periods than did adult males and females, and they showed lower feeding:processing ratios per fruit as compared to adults. These differences are predicted by the MC hypothesis (Deaner et al., 2003), but they are not incompatible with the BM hypothesis (Deaner et al., 2003)—both of which are subsumed into the broader expensive-brain framework, which seeks to explain various life-history correlates among encephalized species (Isler and van Schaik, 2009). Finally, it is entirely possible that these results are particular to this population of capuchins rather than connected with the deeper life-history evolution of these monkeys.

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