LEARNING TO LIVE, OR LIVING TO LEARN?
AGE-RELATED DIFFERENCES IN FORAGING BEHAVIOR, AND
THE EXTENDED JUVENILITY OF *CEBUS CAPUCINUS*

A thesis submitted
To Kent State University in partial
Fulfillment of the requirements for the
Degree of Master of Arts in Anthropology

by

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CHAPTER 1: LIFE HISTORY THEORY

The study of life history is central to understanding the evolution of any species, for this field of study encapsulates many generalities that articulate directly or indirectly with fitness (Stearns, 1992). By comparing the timing of developmental events, we can gain a deeper understanding of large-scale selective pressures in the evolution of those species’ lineages. Anatomical, demographic, and allometric measurements can be correlated to these analyses to refine the understanding of these processes, and these variables may be further investigated through the use of mathematical models. The end-product is the development of plausible hypotheses about how lineages evolve. Such analyses are often undertaken in the study of life-history theory, and this field’s purview is therefore quite broad. Acknowledging this wide domain, I follow Leigh and Blomquist (2011: p. 418) in my definition of life-history theory as a framework that “explains the evolution of life-course changes by analyzing demography, genetics, behavior, and morphology developmentally and mathematically.”

In this section, I review aspects of general life-history theory and recent findings that are relevant to the evolution of extended juvenility. I begin by outlining some of the correlations that have been found among the life-history variables that are relevant to this thesis (i.e., length of the juvenile period). Then, I recount hypotheses for the evolution of extended life-histories. These hypotheses have matured over the last few decades; thus, some background on related forerunning hypotheses is included. I include tests of the various predictions that have been made from them.
The study of primate life-histories began with the examination of very general trends. In the mid-twentieth century, for instance, A. H. Schultz very effectively popularized the notion that, as primates evolve longer lifespans, all life stages are lengthened in a manner that is proportional to the amount by which their entire lifespans are lengthened (Schultz, 1969; Leigh and Blomquist, 2011). A glance at an often-reproduced figure from Schultz (1969: p. 149) gives the impression of the uniform extension of, say, infancy as overall lifespan increases. From this classical perspective, animal life-histories should follow a particular pattern in which infancy, juvenility, adolescence, and adulthood compose a portion of an animal’s life that may be essentially predetermined before even observing the animal; all that is required in order to deduce the length of a species’ juvenile period, for example, is its maximum lifespan. Built upon this foundation is the outdated paradigm of \( r-K \) selection, an idea that was introduced in the context of island biogeography (MacArthur and Wilson, 1967) but has roots further in the past (Pianka, 1970).

In an early attempt to explain the variation in biodiversity that is evident among habitats at different latitudes, Dobzhansky (1950) laid some of the early groundwork for the \( r-K \) selection theory that MacArthur and Wilson (1967) would canonize years later. Because tropical environments are more seasonally stable and therefore offer subtler “challenges” to the species that inhabit them, the adaptive responses of these species would therefore be relatively more suited to outcompete other species that are all vying for the same limited space or resources (Dobzhansky, 1950). This tropical process is presented in stark opposition to its higher-latitude counterpart:

The struggle for existence in habitats in which harsh physical conditions are the limiting factors is likely to have a rather passive character as far as the organism is concerned. . . .
[Such environments as] arctic tundras or high alpine zones of mountain ranges are inhabited by few species of organisms. The success of these species in colonizing such environments is due simply to the ability to withstand low temperatures or to develop and reproduce during the short growing season. (Dobzhansky, 1950: p. 220, emphasis mine)

This passage illustrates how Dobzhansky was discussing some of the same processes that would be developed by others (MacArthur and Wilson, 1967; Pianka, 1970) into the $r$-$K$ theory, though the text itself mentions neither the intrinsic rate of increase ($r_{max}$) nor carrying capacity ($K$).

A formalized theory may be envisioned as that of $r$-$K$ selection as an idealized continuum, on which the most extremely $r$-selected species invest minimal energy to produce the greatest number of offspring in the shortest amount of time. On the other end of this spectrum, individuals $K$-selected species are perpetually at odds with each other, competing in ways that decrease the extrinsic mortality of individuals in environments with high population density (MacArthur and Wilson, 1967; Pianka, 1970). In a landmark paper, Stearns (1983) used principal components analysis to describe life-history variation of mammalian taxa along two factors that would seem to correspond to the $r$-$K$ continuum: the first was associated with neonatal mass and maternal fecundity, and the second principal component described the relative precocity or altricity of neonates. Nested ANOVAs revealed that these factors lost much of their power when order- or family-level effects were removed, supporting the notion that “[taxa below the family level] are mosaics of relatively recent adaptations contained within a framework defined by relatively old constraints” (Stearns, 1983: p. 186). Subsequent large-scale comparative studies have produced similar results as Stearns’s (1983) analysis (Gaillard et al., 1989; Bielby et al., 2007).
Regardless of the heuristic value of $r$-$K$ selection at higher taxonomic levels, it is evident that life-history evolution is more complex than this model would suggest (Stearns, 1992). Still, notions of primate life-histories as existing along a fast-slow continuum have been repeatedly put forth even in recent times (Leigh and Blomquist, 2011). An alternative paradigm presumes that various aspects of primate development may be at least somewhat dissociated. For example, Pereira and Leigh (2003) suggest that life histories cannot be reduced to such a simple continuum. While some life-history characters may be linked or integrated, others may also be dissociated. Garber and Leigh (1997) showed that brain growth in several platyrrhine taxa proceeds according to different schedules that do not evenly correspond to their ages at adult body mass. To shift the lens to cercopithecoids, baboons display a mode of immaturity in which they reach adult brain size at least one year before other papionins, despite having a larger adult body-mass (Pereira and Leigh, 2003). Nor do dental characteristics necessarily correlate with the speed at which various primate taxa mature (Godfrey et al., 2003, 2004). Adopting a comparative approach, Godfrey and coauthors (2003) found that primate families display significant differences in dental precocity at different absolute and relative life stages. They related the life-history differences to diet, with folivores developing their adult dentitions before frugivores (Godfrey et al., 2004). Thus, among primates, there are many different ways to be juvenile, many different paths to take along the road to adulthood.

Even so, it would be a fallacy to propose that primates do not, in some way, display a slower schedule of processing through their life stages when compared to other mammals (see Charnov and Berrigan, 1993). As noted above, principal-components studies have shown that taxa may indeed be viewed as fast- versus slow-living (Stearns, 1983; Gaillard et al., 1989; Bielby et al., 2007), and thus, energy expenditure may also provide insight into life-history
variation. Recently, Pontzer and colleagues (2014) investigated the total energy expenditure (TEE) in a diverse array of taxa; these authors contend that TEE is a more robust measure of energy throughput than is basal metabolic rate (BMR) because it encompasses more metabolic processes than does BMR. When TEE is plotted against body mass, primates seem to have undergone a grade shift such that they use significantly less energy per unit body-mass than would be expected by the nonprimate reduced major-axis (OLS regression: Pontzer et al., 2014). Thus, primates do seem to live more slowly than other mammals when studied in a broad sense (i.e., in comparison to other taxonomic orders). At lower taxonomic levels, however, there appears to be considerable variation in life-history schedules among primates.

**The Importance of Body Mass and Brain Size**

Interspecific data must be normalized by a variable that scales similarly among all taxa involved. Body mass at adulthood is very widely used for this purpose, though it may be problematic if captive and wild datasets are used in the same analyses (Deaner et al., 2003; Barrickman et al., 2008). Nonetheless, body mass does show a significant relationship to both weaning age and age at first reproduction (AFR; (Lee and Kappeler, 2003; van Schaik and Isler, 2012), which are the events in ontogeny that respectively define the beginning and end of juvenility (Sherrow and MacKinnon, 2011). For instance, Lee and Kappeler (2003) investigated correlations between body mass and many life-history traits and found that body mass, among anthropoids, accounted for 70.3% of the observed variance in AFR ($N = 27$ taxa; $P < 0.05$). Additionally, body mass explained 65.6% of the variance in age at weaning ($N = 53$ taxa; $P < 0.05$) (Lee and Kappeler, 2003). Thus, the two points that form the definition of juvenility are strongly tied to the body size of the animal.
As noted above, body mass may be unreliable in some circumstances because of its wide variability, especially between captive and free-ranging animals (Economos, 1980; Ross and Jones, 1999; van Schaik and Isler, 2012). As a possible solution to this problem, Economos (1980) suggested using the weight of visceral organs instead of the an animal’s overall body mass. This conclusion was reached because of the finding that more variance in lifespan is explained by the weights of the liver ($r = 0.78$) or kidneys ($r = 0.81$) than by body mass ($r = 0.65$). Deaner and coauthors (2003) acknowledged this problem but pointed out that visceral weights are not as widely available as body-mass data. They advocated using body-mass data exclusively from free-ranging animals or at least identifying the sources of mixed (i.e., captive and free-ranging) datasets. This stringent approach reduces variance in those data, and it provides a more accurate result because “conditions in the wild are most similar to those conditions in which a species’ life history traits evolved” (Barrickman et al., 2008: p. 573). The so-called “Economos problem” (see Barton, 1999: p. 173) is now a mainstay of many life-history analyses.

An additional effect of Economos’s (1980) argument on the field of life-history theory was a shift away from morphometric correlations (e.g., brain size) and toward demographic parameters such as mortality (van Schaik and Isler, 2012), but this paradigm has changed. More recent analyses have returned to the brain as a correlate of many life-history phenomena through the introduction and development of the expensive brain framework (Isler and van Schaik, 2009). This framework is really an open-ended network of complementary hypotheses that interweaves brain-related measures with various causes and effects of life-history evolution.

Brain size correlates positively with weaning age and AFR (Barton, 1999; Ross, 2003; Isler and van Schaik, 2009). Utilizing residual analysis to control for body size, van Schaik and
Isler (2012) found that residual brain-mass correlates with both residual weaning-age and residual AFR. Furthermore, the slopes of these two plots are divergent in such a way that, as residual brain-mass increases, residual weaning-age increases at a rate less than that of residual AFR (see van Schaik and Isler, 2012: Fig. 10.11). This differential increase of AFR over weaning age would seem to indicate that length of the juvenile life-stage (i.e., weaning age subtracted from AFR) increases with in species with larger brains. Indeed, a very rigorous analysis by Barrickman and colleagues (2008) showed that, after accounting for body size through the use of multiple regressions and residual analysis, adult brain size positively affects the length of juvenility ($r^2 = 0.69, P = 0.0001$). In other words, as primate species evolve along trajectories toward larger brains, the relative time spent in juvenility increases (Barrickman et al., 2008). As with any correlational argument, the question shifts to causality: are large brains driving the length of juvenility, or vice versa?

Juvenility begins at weaning (Leigh and Blomquist, 2011; Sherrow and MacKinnon, 2011). It is in the interest of the mother to wean her offspring as soon as they are able to sustain themselves, yet it is in the interest of the offspring to nurse as long as possible; thus, a conflict of interests arises between mother and offspring (Trivers, 1974; Altmann, 1980; Maestripieri, 2002). Since this tumultuous weaning-period occurs well before offspring reach adult weight (Charnov, 1993), juvenility is a time of many forms of growth, beginning with weaning and ceasing at sexual maturity. The evolution of a juvenile period in mammals results from this parent-offspring conflict insofar as weanlings still need to grow, and this growth requires time and energy (Pagel and Harvey, 1993).

In addition, a very stark evolutionary problem presents itself in discussions of extended juvenility: any longer period of immaturity translates to a delay in the onset of reproduction. As
species evolve larger brains, they also lengthen their time spent in sexual immaturity (Barrickman et al., 2008; van Schaik and Isler, 2012), effectively incurring reproductive opportunity-costs for every unit of time spent in this prereproductive state. Under what conditions could such an expensive organ – and thus such a long time in a prereproductive state – evolve? An important secondary avenue of inquiry is how large-brained species compensate for such a delay. Several hypotheses have been proposed 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 (Table 1.1; Deaner et al., 2003; Ross, 2003; van Schaik and Isler, 2012). It is important to note that these two hypotheses do not wholly exclude each other and may therefore be adequate partial explanations in a single case-study.

**Juvenility as a Time of Growth or Development**

Framing juvenility as a time of “phenotypic limbo”, Pagel and Harvey (1993) proposed that young mammals should use these inescapable life stages to increase fitness later in life; this may take the form of learning valuable skills or, in social species, building relationships. If a species’ ecological or social environment is sufficiently complex, it may be adaptive to lengthen juvenility to accommodate the learning necessary to acquire the behaviors that animals will need as adults (Pagel and Harvey, 1993; Ross and Jones, 1999). This general notion – that extended juvenility is an adaptation to learn skills that will be required in adulthood – may be called the “needing-to-learn” (NTL) hypothesis (Ross and Jones, 1999). Since its initial application to birds, this idea has been applied to various mammalian taxa with mixed results (Schuppli et al., 2012).
Table 1.1: Two Hypotheses to Explain Extended Juvenility in Primates. Both of these hypotheses were refined by Deaner and coauthors (2003) from less-precise precursors, which are listed in the table. These two newer hypotheses fit within the paradigm known as the expensive brain framework (Isler and van Schaik, 2009).

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Adaptive?</th>
<th>Precursor</th>
<th>Predictions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maturational constraints (MC)</td>
<td>No; this model would claim that extended juvenility is a developmental byproduct of selection for increased encephalization.</td>
<td>Needing to learn (NTL) hypothesis (Ross and Jones, 1999)</td>
<td>The complexity of learned behaviors will covary with both brain size and the length of juvenility</td>
</tr>
<tr>
<td>Brain malnutrition (BM) hypothesis</td>
<td>Yes; an extension of the period in which brains are growing is a risk-averse strategy for avoiding damage during critical periods of brain growth or development.</td>
<td>Ecological risk-aversion (ERA) hypothesis (Janson and van Schaik, 1993)</td>
<td>Brain growth will be prioritized over somatic growth under nutritional stress.</td>
</tr>
</tbody>
</table>
With many social and ecological challenges ahead of them, young primates have much to learn before reaching adulthood (Pereira and Fairbanks, 1993; Sherrow and MacKinnon, 2011; MacKinnon, 2013a), but has natural selection favored an increased time in juvenility in order to acquire various skills, as NTL would posit? Joffe (1997) found a positive correlation between group size and length of the juvenile period \( r^2 = 0.329, P = 0.007; N = 11 \) taxa and another positive relationship between the proportionate length of juvenility compared to maximum lifespan and the ratio of nonvisual cortex \( r^2 = 0.380, P = 0.037; N = 13 \) taxa. Since nonvisual neocortex deals in part with social problem-solving, these findings are taken as evidence that the pressures provided by learning social skills have selected for a lengthened period of juvenility across Primates (Joffe, 1997).

The key to the evolution of lengthened immaturity need not be utterly social in nature; some learning-centered hypotheses focus at least to some degree on foraging ability. For instance, the embodied-capital (EC) model, which aims to explain lengthened juvenility specifically in humans, hypothesizes that the losses in reproductive value incurred by prolonging immaturity can be offset by the gains of high-quality food hunted and gathered as an adult (Kaplan et al., 2000; Crittenden et al., 2013). Differentiating the EC model from the more general NTL hypothesis, Schuppli and colleagues (2012) predict that, under the general NTL hypothesis, the age at skill competence should equal age at first reproduction (AFR); the EC model, on the other hand, depends on food-sharing among individuals so that age at skill competence is no longer limited by AFR. Thus, in the absence of the complex system of food-sharing observed in human societies, animals with complex foraging niches may be expected to reduce the interval between age at skill competence and AFR, but the relationship between these
two ages can never be inverted. In other words, humans are exceptional in the evolution of an age at skill competence that is later than the human AFR.

In response to criticisms that the NTL hypothesis may be simplistic or theoretically undeveloped, Deaner and coauthors (2003) introduced a revised model that would connect large brains more directly to extended juvenility: the maturational constraints hypothesis. This specific hypothesis has been incorporated into the expensive brain framework because of its emphasis on brain tissue (van Schaik and Isler, 2012). Insofar as complex behavior requires a commensurately complex neural underpinning, 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). Moreover, this hypothesis explicitly assumes that learning is so important in terms of fitness that extended periods of learning have acted to limit the age at which animals reach sexual maturity over evolutionary time (Deaner et al., 2003). The first prediction of the maturational constraints hypothesis – that brain size and extended immaturity should be correlated – does not appear to be true for mammals in general (Isler and van Schaik, 2009). However, there is indeed a correlation between brain size and AFR for precocial, single-birth mammals (Isler and van Schaik, 2009) and primates in particular (Barrickman et al., 2008; van Schaik and Isler, 2012). Thus, this hypothesis may not be applicable to all mammalian taxa, but its use for primates does seem to be warranted.

**Juvenility as a Time of Risk**

Viewing the juvenile life-stage as a time of multifaceted risk, Janson and van Schaik (1993) proposed the ecological risk aversion (ERA) hypothesis, that juvenility is lengthened within Primates as an evolutionary strategy of avoiding starvation or predation during
development. No longer allowed the easy and nutritive diet offered by nursing, juveniles must still reach nutritional requirements in order to grow and develop properly. Furthermore, juvenile primates are often inefficient foragers, or they may be excluded from high-quality foods by dominant members of their social group (Janson and van Schaik, 1993; Johnson and Bock, 2004; Gunst et al., 2010b). Another risk incurred by juveniles is due to their smaller size relative to adults: this size difference puts them at greater risk for predation (Janson and van Schaik, 1993). If juveniles are more susceptible to predation, then this risk-aversion model predicts that they should position themselves in closer to the center of their social group, a position that puts them at odds with others in terms of feeding competition (Janson and van Schaik, 1993; Stone, 2007). Thus, an extended time in juvenility would be an adaptive slowing of somatic growth rates to accommodate the pressures of inefficient foraging and increased feeding competition (Janson and van Schaik, 1993).

Since the debut of the ERA model, it has been met with mixed results (Garber and Leigh, 1997; Stone, 2006, 2007; Leigh and Blomquist, 2011). Leigh (1994) found support for ERA among folivorous anthropoids: faster growth rates and earlier ages at growth cessation were observed for folivores than for nonfolivores of similar body weights. Because foliage is assumed to be more ubiquitous, and therefore a less-risky food resource, this finding is a confirmation of one of the model’s predictions. Different growth rates between Pan and Gorilla have been explained similarly (Leigh and Shea, 1996; McFarlin et al., 2013). Moreover, the differing growth rates of mountain and lowland gorillas seem to vary in accordance with the ERA hypothesis: the more-folivorous mountain gorillas show a faster growth rate than lowland gorillas (Stoinski et al., 2013). On the other hand, Godfrey and coauthors (2004) find minimal support for the ERA hypothesis among the somatic growth rates of lemurs: lemurids displayed
substantially faster somatic-growth rates than the folivorous indriids, though dental development showed the opposite pattern. Also investigating dental development, Dirks (2003) compared two pairs of closely related catarrhines (i.e., Papio hamadryas versus Semnopithecus entellus, and Hylobates lar versus Symphalangus syndactylus) and found a similar acceleration of dental development for the more-folivorous of each pair. Because dental development may not be the primary target of selection under the ERA hypothesis, other hypotheses that focused on the importance of food processing would be more informative in explaining this variation in dental development among lemuroids (see Godfrey et al., 2004).

Evaluating growth rates among 11 small-bodied platyrrhine taxa, Garber and Leigh (1997) found more variation in growth rates than would be expected under Janson and van Schaik's (1993) model. In particular, Aotus, Callicebus, and 8 callitrichine species did not conform to the expectations of slowed growth curves after weaning. They explained exceptions by noting that these species have specialized infant-care strategies such as provisioning and cooperative infant-care (Garber and Leigh, 1997). Some support for ecological risk aversion was found for Saimiri sciureus in that growth rates declined at the time of weaning (Garber and Leigh, 1997). However, Stone (2006, 2007) investigated numerous predictions of the risk-aversion model in S. sciureus and found no support for any of the predictions generated from Janson and van Schaik's (1993) model. S. sciureus infant age-classes were significantly different from juveniles in terms of foraging efficiency and their ingestion rates of food types (Stone, 2006). However, juvenile age-classes were not significantly different from adults with regard to these variables, and there was no evidence for feeding competition among age groups (Stone, 2006, 2007). It would seem that, at least for small-bodied platyrrhines (e.g., Saimiri, callitrichines), the ERA hypothesis (Janson and van Schaik, 1993) has hitherto failed to support
empirical predictions, while it has performed quite well with other groups of primates (e.g., Leigh and Shea, 1996; see above).

Extending the ERA hypothesis, Deaner and coauthors (2003) revised the hypothesis so that it would focus not on a problem as general as starvation avoidance, but on the more specific problem of avoiding brain damage due to malnutrition. In humans, if children are severely undernourished during the first few years of life (e.g., in cases of marasmus), irreparable cranial and intellectual abnormalities result (Ivanovic, 1996). Because of the nutritional sensitivity of the brain during critical periods of neural growth and development, the brain-malnutrition (BM) hypothesis for the extension of immaturity (Deaner et al., 2003) states that selection will favor a lengthening of immaturity in order to dilute the risk of incurring brain damage if the child is exposed to limited or low-quality resources. Predicting that an evolutionary increase in brain size should be accompanied by an extension in the brain-growth period, and not the growth rate, Deaner and colleagues (2003) point out that humans achieve their much larger brain size relative to chimpanzees by doing just this (McKinney and McNamara, 1991). The second prediction of this model is that a somatic growth spurt should accompany the completion of brain growth in primate species. This prediction was supported in species for which data were available (Deaner et al., 2003).

Other findings published since the formalization of the BM hypothesis also support it. For instance, the finding that primates as an order display a lowered TEE (Pontzer et al., 2014) accords well with the long-observed, and order-wide, increase in brain size that primates have undergone relative to other mammals (Economos, 1980; Allman et al., 1993; Barton, 1999). If growing a large brain is seen as a nutritionally risky strategy, as the BM hypothesis holds, then this lowered TEE would be beneficial to an evolutionary increase in brain size insofar as it would
result in a lowered brain-growth rate. Adding additional support to the BM hypothesis, Kuzawa and coworkers (2014) have recently shown that the brain’s glucose uptake peaks at the age of 5.2 years and coincides with the lowest somatic growth rate. Thus, brain and body growth are not linked; rather, the growth of the very large human brain relates inversely to body growth and acts to extend the period of body growth during childhood.
CHAPTER 2: THE LIFE HISTORY AND BIOMETRY OF CAPUCHIN MONKEYS

Brown capuchins (Sapajus apella) and the closely related squirrel monkeys are widely used as model animals in many research laboratories (Fragaszy et al., 2004). As a result of captive studies and several long-term research stations devoted to the study of these monkeys in the wild (S. nigrirus: see Janson et al., 2012; Cebus capucinus: see Fedigan and Jack, 2012 and Perry et al., 2012), the literature contains a relative surfeit of knowledge about capuchin biology and life histories compared to those of other platyrrhines. The purpose of this section is to summarize some of the aspects of these topics as they pertain to this thesis.

Brain Size

Known sometimes as “the apes of the New World” (Perry and Manson, 2008: p. 5), capuchins are widely recognized for their high degree of encephalization (Stephan et al., 1981; Fragaszy et al., 2004) and behavioral complexity (see below). Rilling and Insel (1999) used magnetic-resonance imaging (MRI) scans from 11 anthropoid species and showed that capuchin monkeys (represented by S. apella) are just as encephalized as Pan troglodytes or P. paniscus; this discovery holds just as well if relative neocortical volume is examined in isolation. Especially when considered among other platyrrhine genera, Cebus and Sapajus stand out very starkly for their large brains (Fig. 2.1).
The large brains of capuchins follow a very fast postnatal growth trajectory, increasing in total volume by 125% between parturition and the age of 2.5 years (S. apella: Phillips and Sherwood, 2008), and the overall growth velocity of the brain decreases drastically around the

Figure 2.1: \( \log_{10} \) Body Weight versus \( \log_{10} \) Brain Weight among 14 Platyrrhine Genera.

Data for these genera are mean values from 27 total different species. If a source provided cranial capacity (CC) but not brain weight (BW), then I used Martin's (1990) formula \( CC = 0.94 \times BW^{1.02} \) to provide a projected value for BW.

References for figure: Stephan et al., (1981); Barton, (1999); Kappeler and Pereira (2003); van Schaik and Isler (2012)
These massive brains follow a very fast postnatal growth trajectory, increasing in total volume by 125% between parturition and the age of 2.5 years (*S. apella*: Phillips and Sherwood, 2008), and the overall growth velocity of the brain decreases drastically around the age of 6 months (*C. albifrons*: Wood, 2001). A differential increase of white matter in the frontal lobe occurs within the first 2 years of life; because white matter is composed primarily of glial cells and myelinated axonal projections, Phillips and Sherwood (2008) argue that this developmental burst may be beneficial for young monkeys as they learn the complicated foraging skills they will require as adults.

**Life History**

Transitions among life stages in capuchin monkeys are not sharply-defined events; they are often gradual processes. Nonetheless, many tables and spreadsheets treat these variables as distinct, and the rationale for this form of data presentation is likely rooted in statistical analysis. For instance, weaning is a process of decline in suckling rates that may continue for many months among *C. capucinus* (Perry, 2012: Fig. 2.3), yet many spreadsheets display these variables as point estimates without measures of variation (e.g., Kappeler and Pereira, 2003). Thus, along with other life-history traits, I have presented the limits of capuchin life-stages as ranges in Table 2.1.

In comparison to other platyrhines, capuchins reach sexual maturity later than expected based on body size (Fig. 2.2). Ultimate hypotheses of this particular feature of capuchin life history focus on either their large brains or the manifold skills they will need as adults.
Table 2.1: Life History Traits of *Cebus capucinus* and *Sapajus nigrurus*. Aside from *Maximum Lifespan*, all values are from free-ranging populations. References and notes are denoted by superscript and listed below the table.

<table>
<thead>
<tr>
<th></th>
<th><em>Cebus capucinus</em></th>
<th><em>Sapajus nigrurus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Weaning Age</strong></td>
<td>12-24 months&lt;sup&gt;1&lt;/sup&gt;</td>
<td>8-18 months&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Juvenility</strong></td>
<td>1-6 years&lt;sup&gt;3&lt;/sup&gt;</td>
<td>1.5-6 years&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Subadulthood</strong>&lt;sup&gt;*&lt;/sup&gt;</td>
<td>6-10 years&lt;sup&gt;3&lt;/sup&gt;</td>
<td>6-8 years&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Maximum Lifespan</strong></td>
<td>55 years&lt;sup&gt;4&lt;/sup&gt;</td>
<td>45 years&lt;sup&gt;5&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>First Reproduction&lt;sup&gt;†&lt;/sup&gt;</strong></td>
<td>6 years&lt;sup&gt;1&lt;/sup&gt;</td>
<td>6 years&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Interbirth Interval</strong></td>
<td>25.6 months&lt;sup&gt;1&lt;/sup&gt;</td>
<td>19.4 months&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Age at First Dispersal</strong>&lt;sup&gt;*&lt;/sup&gt;</td>
<td>4.5 years&lt;sup&gt;6&lt;/sup&gt;</td>
<td>6.5 years&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>7 years&lt;sup&gt;1&lt;/sup&gt;</td>
<td></td>
</tr>
</tbody>
</table>

1: Perry (2012); 2: Janson et al. (2012); 3: Jack et al. (2014); 4: Hakeem et al. (1996); 5: Fragaszy et al. (2004); 6: Jack et al. (2012)

* These values are reported only for males because they do not apply to females (see text).

† Reproductive success is highly variable in males and is dependent on securing dominance in the group (Jack and Fedigan, 2006; Muniz et al., 2010). Because this is a highly contingent parameter for males, only female values are reported.
(Table 2.1); nearly every hypothesis that has been put forth to explain extended juvenility in general has been tested with some data measured from capuchin monkeys. Indeed, the highly influential ERA hypothesis (Janson and van Schaik, 1993) was originally formulated at least partially from data on several species of capuchins.

A conservative point estimate for capuchin weaning age (359 days, derived from van Schaik and Isler [2012]) is higher than that expected based on body size (Fig. 2.3). This extended period of nursing may be due to several factors, principal among which are allonursing behavior and brain growth; the former may allow nursing to continue for longer than a default period that would be expected, while the latter provides a strong pressure for youngsters to continue nursing in order to have sufficient nutrition. Allonursing is observed across many capuchin species (Fragaszy et al., 2004), and though the behavior is usually present at low levels, infants increase the frequency of these behaviors as their mothers resist their attempts to nurse (O’Brien, 1988; Perry, 2012). The presence of allomothers, from which infants can derive milk, must act to increase the time to weaning. Allonursing may also benefit young females, possibly providing an avenue for their social development (Hrdy, 1976; Perry, 1996; Baldovino and di Bitetti, 2008; but see O’Brien, 1988). Brain growth, on the other hand, is thought to cease at around the age of 2.5 years (Phillips and Sherwood, 2008), though the velocity of brain growth slows drastically sometime around 7-8 months of age (Wood, 2001; see Chapter 1). In conjunction with weaning ages, this brain-growth trajectory places a large majority of infant development on the mother. Insofar as malnutrition could result in permanent neurological damage, this long nursing period could function as a buffer against such risks as long as the mean payoff from these allonursing bouts is above some threshold that would be required by a growing capuchin (see Stephens, 1981).
Figure 2.2: Log_{10} Body Weight versus Log_{10} Age at First Reproduction (AFR, in days) among 14 Platyrhine Genera. The technique for generating these genus values was the same as that described for Figure 1.1. No projected values were used. References for this figure are the same as Figure 1.1, but Stephan et al. (1981) do not provide AFR in their dataset.
Upon being weaned young capuchins spend at least 4-5 years as juveniles (Fragaszy et al., 2004; Janson et al., 2012). At the end of juvenility, females are fully adult and able to reproduce (Table 2.2). Males, however, enter a subadult period during which they are capable of ejaculation and may sire offspring (Hakeem et al., 1996).

Figure 2.4: $\log_{10}$ Body Weight versus $\log_{10}$ Weaning Age (in days) among 14 Platyrrhine Genera. The technique for generating these genus values was the same as that described for Figure 1.1. No projected values were used.

References for body-weight are the same as Figure 1.1, but I used weaning-age values only from van Schaik and Isler (2012).
Upon weaning, young capuchins spend at least 4-5 additional years as juveniles (Fragaszy et al., 2004; Janson et al., 2012). At the end of the juvenile period, females are fully adult and able to reproduce (Table 2.2). Males, however, enter a subadult period during which they are capable of ejaculation and may sire offspring (Hakeem et al., 1996), but they do not begin to display fully adult male behavior patterns (e.g., rare social behaviors, dominance displays) until around the age of 8-10 years (Janson et al., 2012; Jack et al., 2014). The subadult life stage through which male C. capucinus pass is associated with an inferred increase in the metabolism of the androgen dihydrotestosterone (DHT), which has been measured as a sharp and significant decrease in the ratio of DHT to testosterone in fecal samples (Jack et al., 2014). This coincides with an increase in nonconceptive sexual behaviors (e.g., pelvic thrusts) observed in the same monkeys (Jack et al., 2014).

As juvenility ends around the age of 5-6 years, young male capuchins disperse from their natal groups, and they may disperse again multiple times throughout their lifetimes (Jack and Fedigan, 2004a,b; Janson et al., 2012). In S. nigritus, dispersal is often a solitary event. For example, males rarely disperse together following a takeover of the alpha-male position from their resident alpha (Janson et al., 2012). In C. capucinus, however, related males often disperse together, a phenomenon known as parallel dispersal (Perry, 2012; Wikberg et al., 2014). Immigration into new groups usually evokes aggressive behavior, fighting with the current resident males (Fragaszy et al., 2004; Perry and Manson, 2008), and C. capucinus males usually do this with co-migrants, which are significantly more closely related than expected using randomized computer simulations (Wikberg et al., 2014). Between migration events, males are thought to live in all-male groups, which have been directly observed and studied at only one site, Lomas Barbudal (Perry et al., 2012). Males in all-male groups display a different activity
budget than males in the more widely-studied bisexual groups; they seldom vocalize and attempt to invade groups with resident females opportunistically (Perry, 2012). When a male *C. capucinus* eventually succeeds in seizing his position as alpha, he will have preferential access to ovulating females (Carnegie et al., 2005), which results in a very high reproductive skew in his favor for as long he remains at the top of the hierarchy (Muniz et al., 2010).

**Behavioral Development**

At least with regard to primates, maturity means more than simply learning the proper knowledge about one’s foraging niche; there are social and ecological skills and knowledge that must be gained as well (Sherrow and MacKinnon, 2011). As already noted, capuchin monkeys have longer life expectancies and remain as juveniles for longer than would be expected based on a monkey of their size (Fragaszy et al., 2004; Perry et al., 2012; Perry & Manson, 2008; see van Schaik & Isler, 2012). Researchers have studied many aspects of behavioral development; the purpose of this subsection is to summarize current knowledge about some of these topics.

**Social Behavior**

Social-skill complexity is very often associated with extended juvenility (Joffe, 1997; Sherrow and MacKinnon, 2011; MacKinnon, 2013a). In early infancy, infant capuchins are a focal point of their social groups. Throughout infancy, young capuchins are observed and carried, sometimes for extended periods, by many different monkeys (Perry, 1996; Manson, 1999; MacKinnon, 2013a). While infant handling in other primate species is sometimes anything but benign (see Altmann, 1980), this does not seem to be the case with *C. capucinus*. Manson (1999) observed very low frequencies of abusive bouts of infant handling among infant-handler dyads (<1% of handling time), and mothers very rarely showed agonistic behaviors
toward others seeking to handle their dependent infants. Allonursing is also common among many capuchin species (O’Brien, 1988; Perry, 1996; Fragaszy et al., 2004), providing infants with opportunities to interact with other females in its social group. In the closely related species *C. olivaceous*, allonursing appears to follow an inverse relationship between the relative rank of an infant’s mother and the frequency of allonursing (O’Brien, 1988). This led O’Brien (1988) to conclude that allonursing is a form of parasitism of allomothers by infants of high-ranking mothers. In *C. capucinus*, however, maternal rank has no statistical effect on allonursing frequencies (Perry, 1996). During the first three months of life, when infants are nearly completely dependent on others (MacKinnon, 2013a), infants are already interacting with many individuals and likely learning from these interactions as well.

Beginning at about the eleventh week of life, social play is a very noticeable feature of infancy and juvenility; for instance, MacKinnon (2002) observed some small juveniles (i.e., 1-3 years old) spending between 5-20% of their overall daytime activity budgets in social play over a one-year field study. Play behavior is very commonly thought to be advantageous to individuals as a form of practice for many different things (e.g., motor skills, social skills), though there is no shortage of hypotheses concerning the possible functions of this behavioral category (see Graham and Burghardt, 2010 for a review). Regardless, if social play is in any way an avenue for learning, then young capuchins have ample opportunity to acquire skills associated therewith.

Studying *C. capucinus*, MacKinnon (2002) found very high affiliative associations between juveniles and alpha males (e.g., grooming frequencies), and Sherrow and MacKinnon (2011) discuss this phenomenon as a strategy by which immatures may be using adults as role models in order to learn proper social skills (i.e., Sherrow’s [2008] behavioral role-modeling hypothesis). This may not be the only interpretation of these data, at least for young males.
Adult males of this species are known to disperse multiple times from one group to another, often accompanied by related males, in a phenomenon known as “parallel dispersal” (Jack and Fedigan, 2004; Jack, 2011; Wikberg et al., 2014). Given this background, perhaps at least young males are building relationships with alphas in order to benefit themselves later in life after dispersing. With the exception of a few likely anomalous instances of female dispersal (see Jack and Fedigan, 2009), males are the sex to leave their natal groups upon reaching maturity; thus, this alternative would only apply to males. Juvenile females may be affiliating with adult males in order to acquire some benefit that would not be afforded by affiliating with adult females, as MacKinnon (2002) suggests. Regardless of the explanation, this tendency of juveniles to be in close proximity to alpha males is not confined to *C. capucinus*; it appears to be a general characteristic of capuchin juvenility, spanning both *Cebus* and *Sapajus* (Fragaszy et al., 2004).

**Positional Behavior**

As any animal grows, the ways in which that animal uses its own body in a variety of settings must adjust to its own changing body, and this age-dependent positional behavior involves the study of an animal’s behavior, physiology, and life history (Bezanson and Morbeck, 2013). Studying the positional behavior of *C. capucinus* and *Alouatta palliata* in Costa Rica, Bezanson (2006, 2009) found that capuchins attained an adult-like positional repertoire more quickly than howlers. Whereas howler monkeys required a full 24 months to begin displaying a profile of positional behavior, capuchins reach this same milestone in only about 12 months, around the time of weaning (Bezanson, 2009). These positional-behavior profiles also coincide with rough measures of the two species’ foraging efficiency, measured as a ratio of feeding scan-samples to foraging scan-samples: *C. capucinus* showed no differences of foraging efficiency based on age-class, while *A. palliata* displayed a trend in increasing efficiency as they
approached adulthood (Bezanson, 2009). In terms of how juvenile capuchins use their body in various positional modes, capuchins are quite precocious.

**Vocal Communication**

Immatures also show less aptitude in making appropriate alarm calls, an ability that improves as animals approach adulthood (Perry et al., 2003a). *C. capucinus* give different alarm calls based on the location of predators (e.g., terrestrial or airborne), and some predators, especially large snakes, are even mobbed by the group following the calls (Rose et al., 2003; Perry and Manson, 2008). Capuchins seem to have a more subtle understanding of the snakes which are a threat to them and which species are harmless; for instance, Rose and coauthors (2003) describe an instance when an adult female visited a water hole and hydrated herself directly next to an indigo snake (*Drymarchon corais*), which is a relatively large, nonvenomous, and harmless snake. This bespeaks a nuanced system of predator detection – one that requires time to master.

Investigating the development of these snake-detection abilities, Meno and coworkers (2013) performed a field experiment that involved several snake models and an inflatable airplane. In this experiment, infant *C. capucinus* alarm-called significantly more often at an inflatable airplane, which was used as a novel and harmless object, than juveniles and adults (Meno et al., 2013). Furthermore, regressions showed that age was a very significant predictor of the amount of time spent looking at the snake and plane models: adult monkeys ostensibly require less time to recognize an object as either dangerous or innocuous (Meno et al., 2013). These findings accord well with data reported by Perry and colleagues (2003) in which infants and juveniles alarm-called to harmless stimuli in 19.4% and 10.6% of their calls, respectively;
adults, on the other hand, had a false-alarm rate of only 5.2% for males and 4.5% for females. In contrast to their rapid development of positional behavior, it would seem that alarm-calling is a behavior that is being honed by young capuchins over their extended period of juvenile development.

**Sensorimotor Abilities**

Capuchins have long been known as very dexterous, extractive foragers (Parker and Gibson, 1977), and some researchers have therefore investigated the development of these manipulative faculties that are so important to these monkeys. For instance, adult brown capuchins (*Sapajus* sp.) display lateralized manipulation (Phillips et al., 2007), which is sometimes a population-level preference (Westegaard and Suomi, 1993), and this hand preference becomes more pronounced as individuals age such that at least infants (median age = 0.5 years) do not show a strong hand preference (Westegaard and Suomi, 1993). Additionally, infant capuchins also show an increase in manual prehensile activities at about 9-10 weeks of age (Adams-Curtis et al., 2000), and their prehensions become more destructive in their second 6 months of life as they begin to display a more adult-like repertoire of manipulations (Byrne and Suomi, 1996; Fragaszy and Adams-Curtis, 1997). Further, by about 2-4 years of age, juvenile *S. apella* show no difference in their ability to plan a grasping-based foraging task (Zander and Judge, 2015). Indeed, infancy is certainly the most dramatic time in the timetable of capuchin motor development: many adult motor behaviors are present by the time of weaning, and motor development seems to shift toward refinement of skills rather than completely learning new manual actions (Fragaszy et al., 2004).
Foraging Behavior

Building from studies of the ontogeny of manipulative behaviors (e.g., Fragaszy and Adams-Curtis, 1997), de Resende and coauthors (2008) observed the ontogeny of nut-cracking tool use in *S. apella (sensu lato)* over 29 months. Interpreted through a perception-action paradigm, they report that the sequence of developmental milestones that precede efficient nut-cracking are very similar to those of *Pan troglodytes* and *Homo sapiens* (see de Resende et al., 2008: Table 4). Furthermore, young capuchins of this semifree-ranging population were not able to proficiently perform this foraging task until 25-29 months of age (de Resende et al., 2008). Studying the same population in an earlier study, Mannu (2002) observed that no monkeys younger than 36 months were able to open the palm nuts used in this foraging task. Thus, at least until midway through their juvenile period (i.e., ~1-5 years), young brown capuchins are not able to capably crack open palm nuts, a task that involves the employment of two different objects to access protected resources within a third (de Resende et al., 2008).

In a separate population of brown capuchins (*S. apella, sensu stricto*), age-related differences in foraging ability on two challenging substrates were detected (Gunst et al., 2008, 2010a,b). Until about 3 years of age, young capuchins devoted significantly more time to browsing fruit bunches of the palm *Attalea maripa* (Arecaceae), and a time-based value of their foraging efficiency on these fruits was significantly higher after the same age of about 3 years (*P* < 0.05 for both; Gunst et al., 2010b). The same population of monkeys showed more-drastic age differences in their abilities to forage on bamboo stalks for larvae; statistical differences (*P* < 0.05) in the number of larvae per foraging bout up until about 5 years of age (Gunst et al., 2008).

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1 This population of monkeys is descended from some released capuchins of various species of *Sapajus*. Because of this hybrid origin of these monkeys in São Paolo’s Tieté Ecological Park, the authors elect to use the species name *Cebus [Sapajus] apella*. (de Resende et al., 2008)
Utilizing known data on the dental eruption of gracile capuchins (C. albifrons: Fleagle and Schaffler, 1982), Gunst and colleagues (2008) argued that the larvae-foraging differences are likely caused by differences in detection and perception, rather than abilities related to muscular or dental strength. Conversely, the age-related differences observed with the A. maripa palm fruits may be more readily attributed to biomechanical constraints such as dental development or somatic growth (Gunst et al., 2008, 2010a).

Studying S. nigritus in Argentina, Agostini and Visalberghi (2005) detected sex differences in diet alongside age differences in foraging efficiency. While males’ diets contained significantly more invertebrate prey and females’ contained more fruit ($P < 0.01$ for both), there were no evident age differences in diet (Agostini and Visalberghi, 2005). On the other hand, juvenile monkeys did show a progressive increase in foraging efficiency from younger to older age groups (Agostini and Visalberghi, 2005).

In a 7-year longitudinal study of C. capucinus, Perry (2009) found that 1 year-old infants used many, often very inefficient, methods of opening particular food item (Luehea candida), but individual monkeys’ techniques had been reduced down to one of two different methods by the time they reached the age of 5 years. Furthermore, the technique most often observed by females covaried significantly with the processing technique that was eventually adopted by those monkeys when they reached adulthood (Perry, 2009). Thus, at least for one particular food item, C. capucinus show developmental trends in foraging ability, and despite controversy over whether capuchin monkeys are capable of true imitation (Visalberghi and Addessi, 2000; Fragaszy and Visalberghi, 2004), these monkeys seem capable of some form of observational learning.
**Aims of this Study**

This study was undertaken because, though some researchers have noted age-related differences in foraging abilities in *Sapajus* (e.g., Gunst et al., 2008; see above), such results have not been replicated for *Cebus* (but see Perry, 2009). Quite the contrary: as part of a doctoral study of positional behavior in *C. capucinus*, Bezanson (2006, 2009) found no differences in foraging efficiency among age classes *C. capucinus*. In addition, MacKinnon (2006) described young *C. capucinus* as “very capable foragers” (p. 358) from about the age of 1-2 years because small and large juveniles in her study consumed all of the same foods that were eaten by adults. In a previous study, however, MacKinnon (1995) found higher failure rates in the foraging of younger capuchins, and these same monkeys also displayed a decreased rate of ingestion.

Because of this discrepancy, it is unclear whether the ontogeny of foraging behavior in *Cebus* is truly different from that of *Sapajus*. Evaluation of this hypothesis would have implications for the life-history evolution of these phylogenetically distinct groups because it may reflect different selective pressures acting on the length of juvenility in these two clades of capuchins. It may be hypothesized that the equivalently extended periods of *Sapajus* and *Cebus* (Table 1.2) are being maintained by the different kinds of behavioral complexity and youngsters’ needs to acquire these important skills before they become full adults. This hypothesis is not unprecedented. For instance, Sherrow and MacKinnon (2011) argued that, while many developmental studies of primates focus on the acquisition of foraging skills, the acquisition of foraging skills is also of prime importance “depending upon the species considered, the ecological niche it occupies, and the local demographic and ecological contexts” (p. 461). These reasons align well with the differences between *Cebus* and *Sapajus* as they have been discussed
recently (see Lynch Alfaro et al., 2012c) and therefore provide good reason to at least entertain the hypothesis that *Cebus* may be more precocious foragers as compared to *Sapajus*.

This study tests behavioral predictions about the *foraging* skills of juveniles. The following predictions were formulated primarily from the maturational-constraints (MC) and brain-malnutrition (BM) hypotheses (Deaner et al., 2003; see Table 1.1):

1. As indices of foraging efficiency, ratios of feeding-to-foraging behavior will be highest in adult age classes and lowest in the youngest age class. I make this prediction because of the hypothesis that juveniles are relatively inefficient foragers until reaching adulthood; this is predicted by both MC and BM hypotheses. This prediction can be disaggregated into two secondary predictions:
   a. Capuchins in the youngest age class will be the least efficient when general activity-budget data are used to calculate efficiency.
   b. Capuchins in the youngest age class will be the least efficient when considering one specific, high-value food, the fruit of the tree *Attalea butyracea* (Arecaceae).
2. Immature monkeys will forage more often in proximity to others than will older age-classes because of the benefits provided to them by social foraging (e.g., learning opportunities, nutrition [Rapaport and Brown, 2008]).
3. The proportions of consumed food types will differ between immatures and adults. Both hypotheses would predict that immatures will prefer foods that are easier to access (e.g., soft fruits). However, if youngsters are attempting to avoid malnutrition, as stated by the BM hypothesis, they will focus on fallback foods, such as embedded invertebrates (Melin et al., 2014).
CHAPTER 3: METHODS

Study Subjects and Site

Data for this study were collected between June 24, 2014 and August 4, 2014 at Estación Biológica Piro (EBP), which is located at 8°23′ N, 83°19′ W on the Osa Peninsula in southern Costa Rica. EBP 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). Annual precipitation ranges between 3,500 mm and 5,000 mm of rain, while monthly precipitation during the wet season (early April until late December) fluctuates between 200 and 900 mm of rain. In addition to Cebus capucinus, other primate species that live in this forest are Alouatta palliata, Ateles geoffroyi, and Saimiri oerstedii. (Hidalgo-Chaverri and Cruz Lizano, 2009)

The data for this study were collected from two troops of capuchin monkeys with overlapping home-ranges: the Playa Piro (PP) and Casa Sánchez (CS) groups. PP group was the source for the majority of this study’s data and contained approximately 18 monkeys: 3-4 small juveniles, 3-4 large juveniles, 5-6 adult females, 3 subadult males and 2 fully adult males. The CS capuchins were a similarly sized group with about 19 monkeys, and the age/sex distribution was also very similar to that of the PP capuchins.

Subjects in the study included adults who were classified by sex (i.e., adult male and adult female), while immature individuals were placed into one of two categories: small juvenile and large juvenile (Fig. 2.1). A higher-resolution classification schema would have been
preferable, but since this study is the first to follow these particular groups of *C. capucinus*, the knowledge necessary for making these categories more specific (e.g., absolute ages and individual identification) was unavailable. Additionally, differentiating between males and females can be problematic in younger individuals because of the visual similarity of the two sexes’ genitals early in life (but see Fedigan et al., 2008 for description of how such sexing may be accomplished); for this reason, immatures were not classified according to sex.

The category of *small juvenile* encompasses monkeys within the approximate age-range of 6 months to 3 years (following MacKinnon, 2002, 2006, 2013). Visual characteristics used to classify individuals into this category were a small body size compared to adults, infrequent contact with other individuals (e.g., riding on their backs), and rare bouts of nursing. Because capuchins of this age may still be infants, and therefore still nursing (see van Schaik and Isler, 2012), any instances of suckling were also used for classification. Very small capuchins that spent large amounts of time on the backs of females were considered dependent infants (age: birth – 6 months) and were not considered in this study.

*Large juveniles* were assumed to be within the age-range of 3-5 years and were characterized by their adult-like limb lengths but slender bodies, following from MacKinnon (2002, 2013). Capuchins’ limbs grow with strong positive allometry to their body mass (Young et al., 2010). At this stage of life, individuals are approaching full adulthood and may simply be adding mass to a comparatively lanky frame. Both immature age-classes had comparatively young faces, free of the scars that, especially for males, accompany adulthood in this species.

**Data Collection**

An ethogram was compiled using multiple sources, primarily MacKinnon (2013b).
Figure 3.1: Four Age/sex Classes of *Cebus capucinus*. Clockwise from the upper left: small juvenile, large juvenile, adult male, adult female. Small juveniles (approx. 1-3 years) were identified through their absolutely smaller bodies and relatively large heads. Large juveniles (approx. 3-5 years) had adult-sized bodies with a lanky appearance to their limbs due to positively allometric limb growth (see Young et al., 2010).

Photographs courtesy of Christopher Penning (upper left), Manuel Sánchez Mendoza (upper right), and Alex Kiser (lower right and left)
borrowed my definitions from multiple sources in hopes of allowing for the greatest amount of
comparison between my study and other sources (see Table 3.1). Two kinds of data were
collected on the four age/sex classes: individual activity records (IARs) in the form of
instantaneous scan samples, palm-fruit feeding records in the form of durations.

For behavioral data concerning behavioral states (*sensu* Altmann, 1974), a focal animal
was observed continuously for five minutes during which behaviors relating to traveling, resting,
feeding/foraging and social behavior were recorded (see Table 3.1). These records are referred to
as individual activity records (IARs). In addition to information on an animal’s state, each of the
five lines within one IAR included the number of monkeys within approximately one meter of
the focal animal, and any foraging events that occurred within the previous one-minute interval
(see Table 3.1). Every 60 seconds, I would take an instantaneous sample (Martin and Bateson,
2007), which is essentially a snapshot of the animal’s state at the moment of sampling.

A focal animal was selected initially as the juvenile closest to me at the point when I
began collecting data on a given day. After the first complete IAR, data were collected on the
nearest visible individual. If the focal animal was out of sight for more than two of the one-
minute scans in any IAR, that record was aborted at the time, and a new IAR was begun with a
new focal animal. Sampling preference was given to immature monkeys so that, in cases where I
had to choose between adult and juvenile focal animals, I chose the juvenile as a default.
Throughout the data-collection period of this study, however, I monitored the distribution of my
data nearly daily so that I could prioritize or deemphasize collection on individuals of a
particular age/sex category in order to balance the sample sizes as much as possible. For this
reason, the aforementioned rule was indeed a default, but it was not followed on days on which I
emphasized adult data-collection.
Table 3.2: Ethogram Designed for this Study. All italicized behaviors are behavioral events, and behaviors written in standard typeface are states (*sensu* Altmann, 1974).

<table>
<thead>
<tr>
<th>Category</th>
<th>Behavior</th>
<th>Description</th>
<th>Refs.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rest</td>
<td>Rest</td>
<td>Immobile and inactive; includes sleeping</td>
<td>--</td>
</tr>
<tr>
<td>Social</td>
<td>Groom</td>
<td>Picks through an animal’s hair using its own hands or mouth; or is groomed</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>Watch</td>
<td>Observes the actions of another monkey except if the observed monkey is handling a food item in any way (see <em>Food Interest</em>)</td>
<td>1</td>
</tr>
<tr>
<td>Food Interest</td>
<td>Any Watch state in which the observed monkey is manipulating a food item in some way</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Anoint</td>
<td>Along with other monkeys, rubs berries all over its own fur in a frenzied state</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Aggression</td>
<td>Any prolonged state of aggression or chain of aggressive events</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Beg</td>
<td>Any <em>Food Interest</em> bout in which “begging with outstretched hand,” threatening the prey item, or attempting to gnaw on the prey is observed</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Category</td>
<td>Behavior</td>
<td>Description</td>
<td>Refs.</td>
</tr>
<tr>
<td>----------------</td>
<td>----------</td>
<td>------------------------------------------------------------------------------</td>
<td>-------</td>
</tr>
<tr>
<td>Social (cont.)</td>
<td>Displace</td>
<td>“Approaching within proximity and taking the exact place of another individual at a food or social resources; individuals need not come into contact”</td>
<td>4</td>
</tr>
<tr>
<td>Forage</td>
<td>Forage</td>
<td>Rummaging through or manipulating a substrate nondestructively in search of a food item; or holding a food item while breaking, rubbing, peeling, or otherwise altering it</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>Heavy Forage</td>
<td>Any state in which the focal monkey is tearing, breaking, or in any way destructing a food item or potentially food-holding substrate</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Insert</td>
<td>“Insert [a part of the forelimb] into or through a substrate”</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Rub</td>
<td>“Rub [a food] item or the hand along a surface in continuous contact”</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Strip</td>
<td>Pulling apart a food item using the animal’s own teeth</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>Pound</td>
<td>“Hits an object against a fixed substrate”</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Tap</td>
<td>“Uses fingertips to tap against an object. . . usually involves a rhythmic series of rapid taps on one object with one hand”</td>
<td>7</td>
</tr>
<tr>
<td>Category</td>
<td>Behavior</td>
<td>Description</td>
<td>Refs.</td>
</tr>
<tr>
<td>---------------------</td>
<td>-------------</td>
<td>-----------------------------------------------------------------------------</td>
<td>-------</td>
</tr>
<tr>
<td>Foraging (cont.)</td>
<td><em>Foraging Bite</em></td>
<td>Biting a food item with the apparent goal being <em>to break down the item</em></td>
<td>6</td>
</tr>
<tr>
<td>Travel</td>
<td>Travel</td>
<td>“Climb, walk, run, or otherwise move above or on ground from one location to another” while the group is generally traveling</td>
<td>1</td>
</tr>
<tr>
<td>Feed</td>
<td>Nurse</td>
<td>Nursing from an adult female</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>Eat</td>
<td>Inserting food item into mouth</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Scrounge</td>
<td>Any Eat event where a food item is scavenged from the remains of another monkey’s food</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Drink</td>
<td>Ingests water in some way (e.g., off of a wet surface, directly from ground, etc.)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Receive food</em></td>
<td>Receives food transferred from another monkey</td>
<td>8</td>
</tr>
<tr>
<td>Play</td>
<td>Play</td>
<td>Any state of solitary or social play behavior; such states may or may not be accompanied by play signals</td>
<td>9</td>
</tr>
</tbody>
</table>

1: MacKinnon (2013b); 2: O’Malley and Fedigan (2005); 3: Rose (1997); 4: Bergstrom and Fedigan (2010); 5: Rose (1994);
6: Fragaszy et al. (2004); 7: Panger et al. (2002); 8: Rapaport and Brown (2008); 9: Lewis (2003)
A palm-fruit feeding bout began, and the stopwatch was started, when a monkey brought 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. Data recorded in palm-fruit foraging records (PFRs) included two durations, recorded in seconds: (1) searching/handling and (2) feeding. 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 took more than one fruit from the infructescence, the number of fruits that the animal took was noted, and the searching/handling time portion was divided by the number of fruits that the animal extracted. I used these values to calculate an index of foraging efficiency ($E$) as follows:

$$E = \frac{P/N_f}{F}$$  \hspace{1cm} (1)

where the length of the processing phase ($P$) of the $i$th PFR is devalued by the number of fruits harvested in that interval ($N_f$); and this quotient is divided by the length of the feeding phase in seconds ($F$). Following the recording of one PFR into my audio recorder, I would record my next sample from the next visible monkey that began the standard foraging sequence described above. If only one monkey was foraging in an *A. butyracea* tree, that monkey would be used for multiple samples. However, multiple capuchins fed in a single *A. butyracea* palm tree very often, and in these cases, subsequent samples were taken from the next monkey I observed to initiate the foraging sequence after collecting a given PFR.

If possible, all plant foods were classified to at least the genus level, and these classifications were used to compile a food list (Appendix B). I utilized on-site field manuals, the staff of EBP, and the expertise of others staying at EBP in order to aid in the identification of
these foods. I dictated all data for this project into a voice-activated audio recorder\textsuperscript{2}. I transcribed and coded all PFR and IAR data into a spreadsheet within 24 hours of collection.

**Data Analysis**

Food items were grouped into four different categories: animal food, fruit, flowers, and other plant foods. These categories were further parsed into six total subcategories (Table 3.2). All statistical analyses were carried out using IBM SPSS 22.0, and alpha was set at 0.05. Nonparametric analyses were chosen because, in some cases (e.g., food preference), the data being tested were categorical, while in other cases (e.g., sample frequencies), though continuous data were being tested, the data did not agree with the assumption of homoscedasticity that is inherent in parametric analyses. In testing Prediction 1b, however, I used parametric analysis because, in this case, the data are continuous and they meet the assumptions of parametric analysis.

All scans were input as individual lines of data, and I used counts of different behavioral states to create activity budgets, first, for all samples pooled together and, second, for each of the four age/sex classes. Aside from the proportions in the activity budgets, these counts were used to evaluate Prediction 1a. Focusing only on foraging or feeding IARs, I tested for differences among the four groups using a $4 \times 2$ chi-square contingency table. I then compared groups pairwise with five separate $2 \times 2$ contingency tables. Thus, all of the $P$-values from these tests were increased with Bonferroni correction-factor of 5; however, because Prediction 1a is a directional prediction, I divided my Bonferroni-corrected $P$-values by a divisor of 2 to arrive at the significance values reported in the next section.

---

\textsuperscript{2} VN-701 PC2 (Olympus Corporation, Tokyo, Japan)
Table 3.2: Food Types Used in Analysis (adapted from Rose, 1994 and MacKinnon, 2006)

<table>
<thead>
<tr>
<th>Categories</th>
<th>Subcategories</th>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Animal Food</td>
<td>Embedded</td>
<td>Larvae or other invertebrate prey gathered from within a substrate</td>
</tr>
<tr>
<td></td>
<td>Invertebrates</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Other Invertebrates</td>
<td>Arthropods (e.g., scorpions, orthopterans, hemipterans, blattarians, etc.)</td>
</tr>
<tr>
<td>Fruit</td>
<td>Hard fruits</td>
<td>Fruits with dense and difficult-to-process mesocarp layers (e.g., <em>Inga</em> pods)</td>
</tr>
<tr>
<td></td>
<td>Soft fruits</td>
<td>Fleshy fruits that require little or no processing (e.g., <em>Ficus</em> inflorescences, <em>Guettarda</em> berries)</td>
</tr>
<tr>
<td>Flowers</td>
<td>. . .</td>
<td>Reproductive organs of angiosperm plants (e.g., <em>Symphonia globulifera</em> flowers)</td>
</tr>
<tr>
<td>Other Plant Material</td>
<td>. . .</td>
<td>Petioles, buds, shoots, etc.</td>
</tr>
</tbody>
</table>
I evaluated Prediction 1b in three different ways for three of the four age classes\(^3\): (1) comparing the absolute times of the searching/processing phase, (2) comparing the absolute times of the feeding phase, and (3) comparing the mean efficiency of each PFR (see Equation 1). I used a parametric one-way ANOVA to test for differences in the searching/processing phase, but I used a Kruskal-Wallis ANOVA to test the feeding data because a Levene’s test of homoscedasticity indicated that variances were significantly different \((F = 4.010; P < 0.025)\). Prior to running the ANOVA on the PFR-efficiency data, a Levene’s test returned trending differences among my groups \((P = 0.072)\), but one particular adult-male record was extremely higher than all others (Fig. 3.2). A one-sample \(t\)-test revealed that this case was a significant outlier from the rest of the adult-male data \((t = 4.345; df = 49; P < 0.001)\); for this reason, I excluded this particular record from my final analysis.

In order to calculate data to test Prediction 2, all data from instantaneous scan samples were used to evaluate whether individuals spent less time foraging in proximity \((\leq 1 \text{ m})\) with others. My social-foraging index (SFI) was calculated as follows:

\[
\text{SFI}_i = \frac{\sum_{j=1}^{n} S_{ij}}{n} \tag{2}
\]

where \(n\) is the total number of scan samples in a given IAR wherein the focal animal was foraging (range: 1-5), and \(S_{ij}\) is the number of monkeys in proximity \((\leq 1 \text{ meter})\) of the \(j\)th scan for IAR \(i\). I calculated these values separately for individual IARs, these individual scores were used as samples for different age groups, according to the age/sex classification of the monkey in the particular IAR. Using Equation 2, I calculated 305 total SFIs. A Levene’s test indicated that

\(^3\) Small juveniles were excluded from this analysis (see Chapter 4 for a justification).
Figure 3.2: Box-plot of the Foraging-Efficiency Records for Three Age/sex Classes.

The case indicated by an asterisk was identified as a significant outlier ($t = 4.345; P < 0.001$) and removed from further parametric analysis.
the variances the different age/sex categories were significantly dissimilar ($F = 5.71; P < 0.001$); therefore, I used a Kruskal-Wallis ANOVA to compare SFIs.

I recorded food type (see Table 3.2) whenever a focal animal was feeding during an instantaneous scan, and I used these data to estimate the diets of the four age/sex classes. Similar to my calculation of the activity budgets, the estimations were counts of individual instances in which focal animals of a given age/sex class were feeding on a particular food type. These counts were divided by the total number of feeding IARs per each age/sex class in order to generate proportions, which I used to describe the diets of the four age/sex classes. Prediction 3 was tested using the raw counts of the different food-types that were eaten by monkeys in these classes. Because of (1) the relatively high degree of frugivory and (2) the limited size of this dataset, I divided foods into two categories for statistical analysis: fruit and non-fruit. Using this arrangement of the dietary data, I compared all age/sex groups using chi-square contingency tables. I used the food-type classification described in Table 3.2 to compare the proportion of scans in which individuals were observed eating soft fruits or hard fruits. Similar to the preceding test, I tested for differences among the groups using $\chi^2$ contingency tables.
CHAPTER 4: RESULTS

Activity Budgets

The pooled activity budget suggests two trends. First, these capuchins spent nearly 80% of their activity in a state of locomotion, feeding, or foraging. Second, these animals were rarely observed in affiliative behavior (Fig. 4.1), but some of the 15% resting time was spent in close proximity, or in direct contact, with other group members. Thus, these results suggest that the monkeys were very active during the study period, but affiliative behavior may be underestimated because of my general definition of the behavioral state Rest (see Table 3.1).

The activity budget for small juveniles (estimated age = 1-3 years; Fig. 4.2a) suggests that they foraged\(^4\) about as often as large juveniles (32.9% versus 34.4% of scans, respectively; Figs. 4.2a and 4.2b) but more often than both adult age/sex classes (adult females: 19.2%; adult males: 23.8%; Figs. 4.2c and 4.2d). In contrast, small juveniles rested\(^5\) much less often (12.9% of scans) than did either adult females or adult males (33.3% and 34.4%, respectively), and they played more often than large juveniles. The two adult age-classes were never observed to play. The activity budget of large juveniles (see Fig. 4.2b; estimated age = 3-5 years) deviated less from the pooled activity budget (see Fig. 4.1).

\(^4\) Foraging was differentiated from feeding by the action of chewing on a food item: if the focal animal was masticating at the time of the scan, that scan was scored as feeding (see Table 3.1).
\(^5\) Resting was simply defined as a lack of physical activity, and social resting was aggregated with solitary resting under my definition (see Table 3.1)
Figure 4.5: Pooled Activity Budget of All Age/sex Classes. Only IAR data were used for activity budgets ($N = 1873$ scans). Out-of-sight scans were excluded from this analysis.
Though higher than the pooled average (see Fig. 4.1), social behavior was scored during scans of small juveniles about as often as they were observed for adult females (9.9% and 10.1%, respectively). The *social behavior* category comprised, but was not limited to, grooming as well as anointing behavior, but anointing was rarely observed (3% of all scan samples). Anointing was recorded only for small juveniles or adult females. When the focal animal was a small juvenile, they were observed to receive grooming about as often they provided grooming to others (43% and 57% of small-juvenile grooming scans, respectively). Of these grooming scans, 43% were of small juveniles grooming the alpha male.

Because I did not systematically record the age/sex class of grooming partners, grooming directionality cannot be rigorously tested with these data; nonetheless, this grooming trend does appear to differ significantly from chance ($\chi^2 = 6.00; df = 1; P < 0.025$). Thus, grooming was slightly more common with small juveniles than with the group in general, and their grooming preference does appear to differ from chance. The proportion of scans in which large juveniles were observed in social behavior (2.2%) was similar to that of adult males (1.8%). Thus, the social behavior of large juveniles resembles that of adult males, while the same behavioral category for small juveniles resembles that of adult females.

Scans that captured resting behavior followed a graded pattern with small juveniles having the lowest incidence of this behavior. Both adult age/sex-classes were similar to each other, and large juveniles were intermediate between small juveniles and adults. In an inversely graded pattern, large juveniles played less often than small juveniles but more often than both adult age/sex-classes. Thus, the activity budget of large juveniles was intermediate between some behavioral categories (i.e., resting and play). However, large juveniles emphasized foraging in a way that was similar to that of small juveniles.
Figure 4.6: Activity Budgets of the Four Age/sex Classes. a: small juveniles ($N = 402$ scans); b: large juveniles ($N = 690$); c: adult females ($N = 436$); d: adult males ($N = 336$). Out-of-sight scans were excluded from this figure.
In summary, the small-juvenile activity budget emphasized foraging and play, which is similar to the budget for large juveniles. Small juveniles displayed relatively frequent social interactions, which is similar to adult females. Conversely, small juveniles were observed resting less often than all other age/sex classes.

**Prediction 1: General and Specific Foraging Behavior**

In Chapter 3, I defined *foraging efficiency* as a ratio of feeding time to foraging time. In the section immediately below (i.e., Prediction 1a), this measure was derived from instantaneous scans, while foraging efficiency was calculated from durational data.

**Prediction 1a: Foraging Efficiency Based on Activity-Budget Data**

A $4 \times 2 \chi^2$ contingency table revealed highly significant differences among the four groups when the test variables were foraging and feeding on any food item ($\chi^2 = 28.698; df = 3; P < 0.001$; see Table 3.1 for ethogram). Odds ratios (Table 4.1) estimate the likelihood that monkeys of any age/sex class would be observed to feed *given how often these monkeys were observed to forage*.

Therefore, these odds ratios may be taken as indices of relative foraging efficiencies. Adult females were clearly the most efficient age/sex class by this index: they were between 2.26 and 2.52 times more likely than were either of the juvenile age-classes to be observed ingesting food when in a feeding/foraging state. The odds-ratio trend was less strong with adult males, who were 1.7 times more likely to be ingesting food when in a feeding tree than small juveniles. After correction for multiple comparisons, large juveniles and adult males were not significantly different.
Table 4.3: Results from Pairwise Chi-square Tests on Feeding and Foraging Data. See Chapter 3.3 for the procedure used to adjust the significance values below. Odds ratios are not reported for nonsignificant tests.

<table>
<thead>
<tr>
<th>Groups Compared</th>
<th>$\chi^2$-value</th>
<th>Adj. Sig.</th>
<th>Odds Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small Juvenile – Adult Female</td>
<td>16.580</td>
<td>$&lt; 0.001$</td>
<td>2.520</td>
</tr>
<tr>
<td>Small Juvenile – Adult Male</td>
<td>5.229</td>
<td>0.05</td>
<td>1.743</td>
</tr>
<tr>
<td>Large Juvenile – Adult Female</td>
<td>17.234</td>
<td>$&lt; 0.001$</td>
<td>2.255</td>
</tr>
<tr>
<td>Large Juvenile – Adult Male</td>
<td>4.320</td>
<td>0.094*</td>
<td>--</td>
</tr>
<tr>
<td>Small Juvenile – Large Juvenile</td>
<td>0.293</td>
<td>1.00</td>
<td>--</td>
</tr>
</tbody>
</table>

a: This value was initially significant ($P = 0.038$), but significance diminished upon correction for multiple comparisons.
Thus, Prediction 1a was partially supported. Females were significantly more likely to be observed feeding when they were in a feeding/foraging state compared to large or small juveniles, and males were more likely to be so observed in comparison only with small juveniles. After correction for multiple comparisons, relative foraging efficiency trended to be lower for large juveniles than for adult males, although it was not statistically significant.

**Prediction 1b: Feeding on *Attalea butyracea* (Arecales) Fruits**

Small juveniles were well represented in the instantaneous-scan data, but these monkeys rarely fed on the fruits of *Attalea butyracea* palms (Fig. 4.4). While I recorded 44-50 samples of *A. butyracea* foraging for the other three age/sex classes, I observed only two instances in which small juveniles attempted to process fruit that was embedded in the infructescence. Their technique was also 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. Very often, small juveniles would sit nearby or watch older monkeys feed on these fruits (pers. obs.). Because of the very low sample size for small juveniles, they were excluded from the statistical analysis in this subsection. Adult males were recorded feeding on *A. butyracea* palms most often (*N* = 50 foraging records), followed by adult females (*N* = 47) and large juveniles (*N* = 44).

Of the two discrete phases of foraging on these fruits (i.e., searching/handling and feeding phases), the searching/handling phase differed significantly among the three groups (*F* = 3.973; *df* = 2; *P* < 0.025; see Fig. 4.3). Differences in the feeding phase approached significance (*H* = 5.396; *P* = 0.067). Post-hoc tests of the searching/handling phase revealed significantly longer foraging times between only large juveniles and adult males (*P* < 0.025; Table 4.2).
Figure 4.7: Two Phases of Palm-fruit Foraging, comparing three classes of subjects.

Significant differences were only evident in the foraging phase ($F = 3.973; P = 0.021$); the asterisk denotes the significant pairwise difference ($P < 0.05$). Observations of small juveniles foraging on these fruits were rare.
Table 4.2: Post-hoc Tests of Palm-fruit Foraging Data (Foraging Phase Only). The post-hoc testing method was to use two-sample *t*-tests with Bonferroni corrections. There were no differences among adult males and females and large juveniles and adult females, but large juveniles were significantly slower at locating and processing fruit to ingest.

<table>
<thead>
<tr>
<th>Age/sex Class (I)</th>
<th>Age/sex Class (J)</th>
<th>Mean Difference (I-J; in seconds)</th>
<th>Std. Error</th>
<th>Sig.</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Lower Bound</td>
</tr>
<tr>
<td>Large Juveniles</td>
<td>Adult Females</td>
<td>4.303</td>
<td>2.198</td>
<td>.157</td>
<td>-1.023</td>
</tr>
<tr>
<td></td>
<td>Adult Males</td>
<td>5.820*</td>
<td>2.129</td>
<td>.021</td>
<td>.662</td>
</tr>
<tr>
<td>Adult Females</td>
<td>Adult Males</td>
<td>1.517</td>
<td>2.166</td>
<td>1.000</td>
<td>-3.731</td>
</tr>
<tr>
<td>Adult Males</td>
<td>Adult Females</td>
<td>-1.517</td>
<td>2.166</td>
<td>1.000</td>
<td>-6.765</td>
</tr>
</tbody>
</table>
**Figure 4.4:** *Attalea butyracea* (Arecaceae) Palm and Infructescence. To the left, a ripe infructescence can be seen just below the palm tree’s canopy. To the right, an adult female *Cebus capucinus* bites off the perianth of a palm fruit while holding a second fruit.

Photographs courtesy of Katherine Markham (left) and Christopher Penning (right).
Figure 4.5: Mean Foraging Efficiencies of Three Age/sex Classes on Palm Fruits (*Attalea butyracea*). In order to calculate efficiency, I divided each foraging record’s feeding-phase duration by the foraging/processing phase for the same record. Error bars denote 95% confidence intervals. Differences were very significant among the three groups with a medium-high effect size (*F* = 9.853; *P* < 0.001; η² = 0.13). A single asterisk denotes *P* < 0.01; a double-asterisk denotes *P* < 0.001.
Table 4.3: Post-hoc Tests of Palm-fruit Foraging Efficiencies. The test statistic for these comparisons was a unitless ratio of feeding durations to foraging/processing durations, both in seconds. This ratio may be conceptualized as a time-based index of foraging efficiency inasmuch as it represents how much time animals devoted to ingesting a particular palm fruit, relative to how much time they spent locating and processing the same fruits. The significance values below were calculated from two-sample *t*-tests with Bonferroni corrections, as in Table 4.2. Asterisks refer to differences for which $P < 0.01$.

<table>
<thead>
<tr>
<th>Age/sex Class (I)</th>
<th>Age/sex Class (J)</th>
<th>Mean Difference (I-J; unitless ratio)</th>
<th>Std. Error</th>
<th>Sig.</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Lower Bound</td>
</tr>
<tr>
<td>Large Juveniles</td>
<td>Adult Females</td>
<td>-.547*</td>
<td>.173</td>
<td>.006</td>
<td>-.965</td>
</tr>
<tr>
<td></td>
<td>Adult Males</td>
<td>-.718*</td>
<td>.168</td>
<td>&lt;.001</td>
<td>-1.126</td>
</tr>
<tr>
<td>Adult Females</td>
<td>Adult Males</td>
<td>-.171</td>
<td>.171</td>
<td>.953</td>
<td>-.586</td>
</tr>
</tbody>
</table>
The efficiencies of each age class showed a stronger pattern (Fig. 4.5). The 95% confidence interval for large-juvenile foraging efficiency is completely below those of both adult classes, which overlap each other (see Fig. 4.5). Efficiency was very significantly different among the three test groups ($F = 9.853; df = 2; P < 0.001$) and showed a medium-high effect size ($\eta^2 = 0.13$; see Cohen, 1988). Post-hoc testing showed that both adult age/sex classes were each significantly more efficient than large juveniles while displaying non-significant differences between each other (Table 4.3).

Therefore, the observed data support Prediction 1b, especially if the absence of small-juvenile data indicate an inability to forage on A. butyracea palm fruits. Large juveniles spent significantly more time in the searching/handling phase for these palm fruits, and they were significantly less efficient at foraging on these fruits.

**Prediction 2: Social Foraging, or Foraging within Proximity of Others**

Social foraging was tested using a social foraging index that estimated the frequency with which individuals foraged within proximity of others (Chapter 3: Equation 2). I found significant differences among the four groups ($H = 8.587; df = 3; P < 0.05$), but Mann-Whitney U-tests revealed that, after correcting for multiple comparisons, the only significant pairwise difference was between that between adult males and female ($Z = 2.750; P_{adj} < 0.05$; Table 4.4). Thus, adult males and females were less likely to foraging in proximity to each other than either was to forage near juveniles.

In all, these data do not support Prediction 2. The social foraging indices of both juvenile classes did not differ from each other or from that of the adult males. According to these data, only the two adult age classes differed significantly from each other; adult females were observed to forage in proximity significantly more often than were adult males.
Table 4.4: Results of Post-hoc Mann-Whitney U-tests on the Social-Foraging Indices of Four Age/sex Classes. Only adults differed in the degrees to which they foraged in proximity (≤ 1 m) of others. All $P$-values are displayed with a Bonferroni correction; any comparisons that are not displayed returned a $P$-value ≥ 1.00.

<table>
<thead>
<tr>
<th>Age/sex Classes</th>
<th>Z-score</th>
<th>Adj. Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult Males – Adult Females</td>
<td>2.750</td>
<td>0.036</td>
</tr>
<tr>
<td>Adult Males – Small Juveniles</td>
<td>2.270</td>
<td>0.139</td>
</tr>
<tr>
<td>Adult Males – Large Juveniles</td>
<td>1.667</td>
<td>0.574</td>
</tr>
<tr>
<td>Large Juveniles – Adult Females</td>
<td>1.527</td>
<td>0.760</td>
</tr>
</tbody>
</table>
**Prediction 3: Dietary Differences between Adults and Juveniles**

These capuchins were highly frugivorous during the study period, consuming fruit in at least 78% of the instantaneous scans (Fig 4.6). The next-highest feeding category was that of unknown foods (8.5%), which were often instances of monkeys chewing on sticks, or pieces of dead wood. Such feeding may have been aimed at ingesting the woody substrate itself or perhaps eating embedded invertebrates therein. Neither of these options could be ruled out, given that I was often several meters from my focal animal and viewed them through binoculars. A sizeable proportion of the instances of flower feeding were on flowers of the tree *Symphonia globulifera* (Clusiaceae; see Appendix B), a food that attracts *Cebus capucinus* as well as *Ateles geoffroyi* (Riba-Hernández & Stoner, 2005; pers. obs.). The insects category (Figs. 4.6 and 4.7) includes insects that were not embedded within a woody substrate (e.g., larvae or termites). Rather, this category consisted of insects that were discernable from my perspective (e.g., scorpions, orthopterans, blattarians).

All members of the group were strongly frugivorous during the sample period (range: 75%-84% of identified feeding scans), although three differences were identified. First, females were observed to eat flowers much more often (11.7% of feeding scans) than other age/sex classes (range: 2.1-3.9%; Fig. 4.7). Second, both younger and older juveniles and adult females were similar in their ingestion of non-embedded insects (4.6-6.5%), while adult males appeared to feed on this type of food much more often (11.5%). Lastly, the proportion of unknown feeding scans was high for adult males (9.6%) and particularly high for large juveniles (13.4%). In the majority of these *unknown* scans, the focal animal manipulated broken pieces of wood.
Figure 4.6: Pooled Diet of All Age/sex Classes. Nursing is not included in this figure because it was restricted only to small juveniles and it would have composed <1% of all feeding scans here. \((N = 276\) scans)
The capuchins did not differ in frugivory by age or sex \( \chi^2 = 0.252; df = 3; P > 0.50 \). In addition, there were no group-wide differences in their preference for hard or soft fruits \( \chi^2 = 5.611; df = 3; P > 0.10 \); see Table 3.2).

In summary, the age/sex classes of this group essentially had the same diet. Fruit was ingested in at least 75% of the feeding bouts. Small juveniles had the highest intake of fruit and adult males, the lowest. Adult females had the highest intake of insects of the four classes. There was minor, but non-significant, variation among age/sex classes in the amount of fruit, flowers, and insects in the diet. Thus, Prediction 3 is not supported by these data.
Figure 4.7: Diets of Each Age/sex Class. 

a: small juveniles ($N = 49$ scans); b: large juveniles ($N = 98$); c: adult females ($N = 77$); d: adult males ($N = 52$).
CHAPTER 5: DISCUSSION

The maturational constraints and brain malnutrition hypotheses (Deaner et al., 2003) were of limited use in predicting the observed data for this study. Nonetheless, these results are not incoherent when this study is considered alongside explanations of other findings in the literature and the phenological context in which data were collected.

Interpreting Differences in Foraging Behavior among Capuchins of Different Age and Sex

Foraging success is important for a growing monkey because growth is an energetically demanding process. For instance, Janson and van Schaik (1993) demonstrate that the risk of starvation is especially high for growing animals by showing that metabolic rate and starvation risk correlate positively and exponentially. Assuming that starvation is not the prime risk of a growing animal, one could still cogently argue for the importance of foraging success or efficiency for juvenile animals. In particular, S. Altmann's (1991, 1998) long-term study of juvenile yellow baboons (Papio cynocephalus) showed that an animal’s foraging success around the time of weaning correlated positively with its fitness later in life. This study and others from diverse primate taxa present evidence of the importance of foraging success for weanlings, and not necessarily juveniles. In addition, such studies tend to show that many primate taxa are very precocious in their foraging abilities after they are weaned, and these findings contradict some formulations of learning-based hypotheses for the extension of the primate juvenile-period (see Table 1.1)
I estimated foraging efficiency in wild capuchins by calculating the proportion of time, as either scan samples (i.e., for Prediction 1a) or actual durations (i.e., for Prediction 1b). My method makes use of time, which assumes that nutrition correlates strongly with time. Making such an assumption is not without controversy. For instance, P. A. Garber (pers. comm., February, 2014) cautions that such a measure may obfuscate important nutritional information. For example, processing a hypothetical food item for 60 seconds in order to obtain 5 g of digestible carbohydrates may be more beneficial for a young monkey than processing another item for 30 seconds for the reward of 500 mg of carbohydrates. If these two food items were ingested for similar periods of time, then a truly false conclusion would be drawn, i.e., the animal was just as efficient in the former foraging bout as it had been in the latter. I have considered this throughout this study, and my findings regarding Prediction 1 should be interpreted in light of this caveat.

**Prediction 1: Increases in foraging efficiency over the juvenile period**

Significant differences of general foraging efficiency were evident between small juveniles and both adult age-sex groups, and between large juveniles and adult females (Table 4.1). The difference between large juveniles and adult males would have been significant if the raw significance value of this comparison were considered without correction for multiple comparisons ($P_{\text{raw}} = 0.03$), but after I made corrections for multiple comparisons, this difference disappeared. Bezanson (2009), using a methodology very similar to mine, found nearly identical foraging efficiencies across similar *Cebus capucinus* age/sex groups. Given her result, it is not overly conservative to accept the null hypothesis that large juveniles and adult males are similar in their foraging efficiency. Assuming the ontogenetic trajectory of capuchin foraging behavior reaches a plateau at a particular age, my findings would indicate that *C. capucinus* is relatively
precocious in terms of overall foraging efficiency: juveniles attain adult-like feeding-to-foraging ratios well before reaching sexual maturity. In this respect, my findings for Prediction 1a accord with MacKinnon’s (2006) argument that the extended life histories of capuchins are not necessary to learn foraging skills. Young capuchin monkeys show an adult-like repertoire of manipulation and foraging behavior by three years of age, and these behaviors are refined as the juvenile approaches adulthood (MacKinnon, 2006). This pattern is not as consistent with a learning model as it is with a model having to do with motor skills because entirely new behaviors are not being acquired after two years of age. MacKinnon (2006) concludes that deficits in foraging behavior are caused by age-based differences in strength or dexterity, and my results for Prediction 1 cannot rule out this hypothesis.

The pattern of age-based differences in foraging proficiency is not unprecedented in the literature on capuchin behavior. For instance, Fragaszy and Boinski (1995) found that juvenile C. olivaceous devoted proportionally more instantaneous samples to heavy or extractive foraging than did adults. Insofar as this high proportion of scans means that juveniles devoted more energy to foraging, these young capuchins were less efficient than adults. In this study, age explained 13% of the variance in the data, but sex explained 40% (Fragaszy and Boinski, 1995: Table 3). Further, differences in efficiency, calculated as feeding scans divided by foraging scans, showed a similar pattern: classes were ranked in efficiency first by sex, and then ranked secondarily by age (Fragaszy and Boinski, 1995). Fragaszy and Boinski (1995) could not suggest a specific ontogenetic course of foraging ability because they used a single juvenile age-group. Thus, while they found that juveniles were less efficient than adults, these findings are equivocal in answering the question, “Do juveniles require nearly all of their juvenile lives to acquire adult-like foraging proficiency?”
A recent study of *Sapajus apella* in Suriname found a different pattern that would imply that the pattern of early sex differences is variable among capuchin species and that all foraging skills are not learned equally fast. Gunst and coauthors (2008: p. 210) found that age had a strong effect on the time spent extracting embedded larvae from bamboo stalks (GLM: adj. $r^2 = 0.77$, $P < 0.001$), but sex had a nonsignificant effect on this measure ($P > 0.20$; $N = 19$ males and 14 females). Pairwise comparisons of the time-based efficiencies at the 5 different age groups foraged for embedded larvae revealed significant differences between nearly all groups up until adulthood (ca. 6 years [see Table 2.1, this thesis]), leading to the conclusion that skilled extraction of embedded larvae is a task that improves throughout juvenility and levels off at adulthood (Gunst et al., 2008, 2010a). As further work by this group shows, however, the trajectories of foraging skills for all foods are not equally prolonged.

Extracting embedded invertebrates appears to be a greater cognitive challenge for a young foraging capuchin—more so than eating other foods such as fruits (Gunst et al., 2008). Such embedded prey (e.g., grubs, termites) must be located using indirect cues, which require a specialized skillset (e.g., tap-scanning [see Phillips et al., 2003]). Unlike Fragaszy and Boinski (1995), Gunst and coauthors (2008) divided immature monkeys into four separate age classes: infants, small and large juveniles, and subadults. Although they did not separate these groups by sex, this higher-resolution classification of age groups allowed them to estimate ontogenetic trends for different foraging behaviors. As compared to adults, large juveniles and subadults (i.e., ≥3 years old) were able to harvest a statistically similar number of *Attalea maripa* fruits per unit of foraging time, but the younger age-classes harvested fewer fruits (Gunst et al., 2010b). Therefore, some tasks (e.g., embedded-invertebrate foraging) may require the entire juvenile period to learn, while others (e.g., *A. maripa* foraging) are learned earlier in life.
A generalized version of the findings of Gunst and coauthors (2008, 2010a,b) could be stated as follows: capuchin resources are diverse and require different skills to extract them or feed on them, preventing all foraging behaviors from reaching adult-level proficiency en masse. Such a model would explain my findings for Prediction 1a because I collapsed all types of foraging behavior into one category. Juvenile foraging efficiencies may have been slightly decreased by foraging techniques that are developed according to more-prolonged developmental schedules. Such a pattern of efficiency would still be graded by age, but the increased efficiency of easier foraging tasks may have caused the faster trajectory found for Prediction 1a. This explanation is supported by the fact that the efficiency trend was not the same between general foraging-efficiency (Prediction 1a) and that for *Attalea butyracea* (Prediction 1b).

Feeding on *A. butyracea* palm fruits, large juveniles were significantly less efficient than adults, while small juveniles very seldom attempted to extract these fruits. When small juveniles did forage on these fruits, they would require > 60 seconds to detach the fruit from the tree, if they could accomplish this task at all. Alternatively, small juveniles would adopt a processing sequence very different from that of older individuals. These observations suggest an inability to exploit these foods, and in this way, these qualitative data fit into the schema of Prediction 1b (i.e., foraging ability improves throughout immaturity). Therefore, maximizing the efficiency of this foraging task may require the entire juvenile period of *C. capucinus*.

Some other foods also require similar training or experience before the adult technique is mastered. In a longitudinal seven-year study of *C. capucinus*, Perry (2009) found that individuals required about five years to process the well-protected fruits of *Luehea candida* trees and access the seeds therein. Early in life, young monkeys used many techniques that did not resemble those used by adults; by the age five, however, individuals had eliminated all
techniques but the one that was most frequently observed over the previous years of life (Perry, 2009). These results support the conclusion that some foraging tasks require more time to acquire than did others.

My results and conclusions for Prediction 1 are similar to Stone’s (2006) findings about the development of foraging behavior in squirrel monkeys (Saimiri sciureus). Testing some predictions of the needing-to-learn (NTL) hypothesis (see Ross and Jones, 1999), Stone (2006) found that, by about 1 year of age, juvenile foraging behavior was highly similar to that of adults for several fruits and with insect prey. For instance, juvenile S. sciureus resembled adults in their intake rates of legumes and berries; however, these age classes did display significant, and age-graded, differences in their intake rates of A. maripa fruits (Stone, 2006). Thus, these close relatives of capuchins seem to acquire many adult foraging skills early, with the exception of some foods, notably a palm fruit within the same genus as the A. butyracea, the fruit studied for Prediction 1b of this thesis. However, because most skills did not require all of juvenility—notably, the catching of highly nutritious insect-prey—Stone (2006) concludes that the needing-to-learn hypothesis (Ross and Jones, 1999; see Chapter 1) does not adequately explain the length of juvenility in S. sciureus.

Outside of the platyrrhine infraorder, multiple studies have investigated developmental differences in foraging ability among baboons (Papio spp.), and these studies often have exact ages for their subjects. Studying foraging efficiency in P. ursinus in Botswana, Johnson and Bock (2004) found that age had a positive and significant effect on the feeding efficiencies of several food items (e.g., mixed grasses, roots, grass stems; ordinary least-squares regression: $P \leq 0.005$ for all). Furthermore, these efficiency scores were related to feeding durations on the same foods ($P < 0.05$); Johnson and Bock (2004) conclude from this result that juvenile baboons are
compensating for their lack of efficiency by eating foods on which they feed more efficiently. Importantly, these efficiency trends extend past the age at first reproduction (AFR) for *P. ursinus*, which is 6.75 years (Swedell, 2011). Indeed, lowess curves made from cross-sectional data of this population show efficiency increasing over the first 18 years of life (Johnson and Bock, 2004: Fig. 1)! If foraging efficiency is found to increase continually over an animal’s lifetime, then this may lead one to question the importance of *adult-level proficiency* as I have emphasized repeatedly. Among baboons, are there any stages of life during which efficiency is most important?

This inquiry has been addressed by a landmark study of *P. cynocephalus* by S. A. Altmann (1991, 1998) in Amboseli National Park, Kenya. In this longitudinal study, Altmann (1991, 1998) estimated yearling baboons’ optimal diets based on their nutritional requirements and the foods in their feeding inventory; from the observed diets of these monkeys, he calculated the nutritional shortfalls that individuals incurred during development. Because the study included longitudinal data on the same monkeys, Altmann was further able to compare each monkey’s nutritional shortfalls with fitness variables (e.g., reproductive lifespan, infants/yearlings produced). Importantly, these nutritional data were all collected when the study subjects were being weaned by their mothers, and the baboons with greater protein surpluses and less energetic shortfall produced more infants (0.86 ≤ adj. $r^2$ ≤ 0.89) and yearlings (0.76 ≤ adj. $r^2$ ≤ 0.94; Altmann, 1998: p. 531). This work shows that the age of one year, a time at which weaning occurs in these animals (see Swedell, 2011), is a critical time at which foraging efficiency, in terms of nutrition, is very important for an animal’s fitness (Altmann, 1998). Thus, perhaps weaning is a time of life during which foraging efficiency takes on extra importance.
Weaning is critical point in the foraging ontogenies of apes. The diets of mountain gorillas (*Gorilla gorilla beringei*) reach adult compositions around this relative age\(^6\) (Watts, 1985). The adult techniques used to process problematic food items are also present by weaning as well, though particular details such as handedness take longer to become a fixed pattern (Byrne and Byrne, 1991, 1993). Among the Gombe chimpanzees (*Pan troglodytes schweinfurthii*), all of the adult techniques for termite-fishing are present within months of being weaned (Lonsdorf, 2005, 2013), and infant chimpanzees at Mahale show all of the techniques for processing *Saba florida* fruits approximately one year before they are weaned (Corp and Byrne, 2002). These apes process such foods in multiple, nested phases (e.g., Corp and Byrne, 2002: Fig. 1), and despite this complexity relatively young animals are able to learn the abilities they will need to exploit these foods.

In terms of foraging success, weaning appears to be a critical point at which foraging abilities undergo the biggest developmental change. If the maximization of efficiency is the goal of young primates, then some techniques require longer periods of learning than others (Gunst et al., 2008; Perry, 2009), but Johnson and Bock’s (2004) results from *P. ursinus* imply that these gains in efficiency need not be limited to the juvenile period. Instead, foraging efficiency may continue to increase well into adulthood (Johnson and Bock, 2004). Weaning, on the other hand, is accompanied by many milestones related to foraging ability (Watts, 1985; Altmann, 1998; Lonsdorf, 2013).

These comparative results contrast with the predictions that I have generated from a foraging-centered formulation of the maturational-constraints (MC) hypothesis (Deaner et al.,

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\(^6\) The weaning ages for free-ranging *G. g. beringei* and *P. troglodytes* are 3.5 years (Byrne and Byrne, 1993) and 5 years (Stumpf, 2011).
2003; see Chapter 2), as do some of my own results. Linking large brains with extended life-histories, the MC hypothesis predicts that complex behaviors limit the age at sexual maturity because the complex neural underpinnings of those behaviors require such long periods of time to establish (Deaner et al., 2003). Essentially, the learning of foraging skills would constrain sexual maturity, and such evolutionary pressure should show a close correspondence between foraging-based ages at skill competence and age at first reproduction. The anthropoid examples above, including my own results, do not appear to conform to this prediction. A coherent model for these findings does exist, however, and this model was originally developed to explain the particularly late development of humans (i.e., fully competent foraging and hunting behavior).

**Explaining Extended Juvenility and Late Ages at First Reproduction**

With a very late age at skill competence (ASC), humans have been widely mentioned in discussions of the evolution of extended juvenility (Kaplan et al., 2000; Kaplan and Robson, 2002; Schuppli et al., 2012; Crittenden et al., 2013). Modern hunter-gatherers tend to reach their maximum foraging/hunting yields well after sexual maturity (Gurven, 2012; Crittenden et al., 2013). Humans, along with other mammals inhabiting complex foraging-niches, may show later ASCs in order to learn such skills (Kaplan et al., 2000; Crittenden et al., 2013). In order to test this hypothesis, Schuppli and coauthors (2012) assigned niche-complexity scores to 34 mammalian species and found a significant, positive relationship between niche complexity and ASC (PGLS regression: \( P < 0.001 \)). However, most mammalian species (i.e., 24/34) still had ASC/age-at-first-reproduction (AFR) ratios that did not approach 1.00 (Schuppli et al., 2012). Humans showed an ASC/AFR ratio that was greater than 1.00—an interesting life-history trait has evolved ostensibly through cooperative breeding and pre-weaning provisioning (Schuppli et al., 2012; Crittenden et al., 2013). Indeed, the only other animals showing an ASC/AFR > 1.00,
which were mostly birds, were cooperative breeders for which provisioning was part of their reproductive strategies. Among mammals, humans may be unique in having such a late ASC, but they do follow a mammalian pattern insofar as cooperative breeding has affected human life-history evolution predictably.

The findings of Schuppli and coauthors (2012) indicate that, in reaching adulthood, mammals tend to be limited not by the costs of learning, but rather by the energetic costs of growth. Mammalian ASCs appear to be high due to the complexity of their foraging niches, but this increase is more or less independent of the length of the juvenile period (Schuppli et al., 2012). ASC correlate with AFR among mammals (Schuppli et al., 2012), and AFR also correlates with relative brain size (Barton, 1999; Ross, 2003; Isler and van Schaik, 2009). The brain size-AFR correlation is underpinned by two related primate characteristics: relatively slow growth rates in comparison to other mammals (Charnov and Berrigan, 1993; Pagel and Harvey, 1993; Isler and van Schaik, 2009), and significantly lower energetic throughput (Pontzer et al., 2014). In this context, primates are expected to have very late AFRs (i.e., long periods of juvenility) because of their relatively slow metabolisms; furthermore, those with complex foraging-niches should display the shortest time between sexual maturity and attaining proficiency in foraging ability. Above all, a simple finding emerges from the literature: primates are very seldom limited in reaching sexual maturity by ages at which they reach foraging ability.

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7 On the other hand, birds do seem to be limited by learning: Schuppli and coauthors (2012) find that the 20/23 bird species show an ASC/AFR ratio that approximates 1.00. Since the NTL hypothesis was originally developed for use with birds (see Ross and Jones, 1999), this result is relatively unsurprising, but it does bespeak the behavioral complexity that many birds have to use in adult life.
Capuchin monkeys appear to be relatively late-maturing in terms of their foraging behavior but not so late that they require all of juvenility to become proficient (Gunst et al., 2008; Perry, 2009; Chapter 4). The entirety of juvenility is required for *Sapajus apella* to detect and otherwise forage on embedded vertebrates (Gunst et al., 2010a), while my own results show that efficient *Attalea butyracea* foraging may require all of juvenility to learn for young *Cebus capucinus* (Chapter 4). Nonetheless, several studies of *Sapajus* and *Cebus* species show that, before reaching sexual maturity, youngsters are adult-like in their foraging sequences (de Resende et al., 2008) or foraging efficiencies (Gunst et al., 2008, 2010b; Bezanson, 2009). This is a pattern that goes against a foraging-focused version of the maturational-constraints (MC) hypothesis. Thus, the extension of capuchin juvenility has likely not occurred because of the evolutionary forces posited by a foraging-skills formulation of the MC hypothesis.

A growth-centered explanation for the extension of capuchin juvenility is also unlikely because brain and body growth are completed well before the capuchin AFR of about 6 years (Table 2.1). Body growth in captive female *Sapajus apella* seems to plateau between 3-4 years of age (Fragaszy and Bard, 1997: Fig. 2) while brain growth in captive *C. albifrons* appears to cease by 8 months of age (Wood, 2001: Fig. 2.12). Brains are important for the life history of a capuchin because they are so encephalized, but their large brains indicate an evolutionary history of selection for such a large organ: after all, the brain is very nutritionally expensive (Navarrete et al., 2011; Kuzawa et al., 2014). Experience-dependent learning stands out in this context as a selective force on the juvenile period, and this learning need not only be ecological (e.g., foraging, diet); the learning of social skills (e.g., relationship building, mothering) is likely equally important, if not more so.
In general, the maturational-constraints (MC) hypothesis is about learning, and capuchin social behavior presents a sizeable repertoire for youngsters to learn before they reach adulthood (MacKinnon, 2002, 2013; Perry et al., 2003; see Perry and Manson, 2008: chs. 5-8). Although I did not address any social-skill learning in my study, a social-behavior formulation of MC may hold interesting results for future research. Following from this model, one should expect social competence to accompany sexual maturity. A complication to this perspective may arise if pubertal hormones, which ultimately cause the onset of sexual maturity when puberty is over, also necessitate a new phase of learning (e.g., of sexual behaviors) by stimulating neural reorganization. Human brains are stimulated to develop sexually divergent morphologies by pubertal steroids (Sisk and Foster, 2004; Sisk and Zehr, 2005), and C. capucinus males show an increase in ratio of two of these hormones (dihydrotestosterone : testosterone [DHT:T]) around the age of 1-3 years (Jack et al., 2014). Jack and coauthors (2014) suggest that this increase in DHT:T may be involved in young males’ sexual learning as it coincides with the appearance of sexual exploratory behavior (e.g., mounting, pelvic thrusting). If these pubertal signals are triggering a phase of learning, then this would translate to a later age at the onset for these behaviors, whereas foraging and other ecologically-focused behaviors do not require such a stimulus and therefore are started earlier. As far as I am aware, such a model has not been tested (but see MacKinnon, 2013), but such results would prove valuable in understanding the evolutionary extension in capuchin monkeys and, by inference, other encephalized primates.

Summary

The capuchins in my study groups on the Osa Peninsula showed significant and age-graded differences in their abilities and efficiencies to forage on Attalea butyracea palm-fruits. Small juveniles were unable to perform the adult foraging sequence, and although large juveniles
could execute the adult foraging sequence, they were significantly less efficient than both adult sexes. Scans of behavioral states showed a less cohesive pattern: adult females were the most efficient by far, and notably more efficient than adult males. In addition, the general foraging efficiency of large juveniles was not significantly different from that of adult males. These findings may be generalized to suggest that *C. capucinus* may require the entire juvenile period to master processing some particularly challenging foods, but they are fully able to exploit many other foods early in juvenile life. This generalization of my findings is in accordance with the literature on the foraging ontogeny of other species of capuchin monkeys. For this reason, I conclude that a foraging-skills formulation of the maturational-constraints hypothesis is inadequate in addressing the evolutionary extension of the capuchin juvenile period, but a hypothesis that accommodated the rich social repertoire of capuchin monkeys stands a greater chance at yielding better results.

**Interpreting Two Null Hypotheses (Predictions 2 and 3)**

I predicted that younger monkeys would forage in proximity to other monkeys more than older monkeys (see Chapter 2), and this prediction was made because social foraging should promote social *learning* of foraging tasks (Rapaport and Brown, 2008). The capuchins at Estación Biológica Piro did not behave according to this prediction: only adult females showed a significantly higher social foraging index, and this difference was only significant in comparison to adult males (Chapter 4). Thus, neither small nor large juveniles engaged in significantly more social foraging than the average for the group.

Additionally, I predicted dietary differences between older and younger age classes to emphasize either more accessible foods following from the learning-based maturational
constraints (MC) hypothesis (Deaner et al., 2003) or fallback foods following from the brain-
malnutrition (BM) hypothesis, which is a risk-aversion model. Because my study animals were 
highly frugivorous during the relatively brief study period (see Fig. 4.5), I investigated only 
differences among the age/sex classes’ degrees of frugivory. In this respect, all age/sex classes 
were similarly frugivorous. Nonetheless, I did find some qualitative differences among age/sex 
classes in the ingestion of non-fruits.

The most noticeable difference in the diet of large juveniles is the high incidence of 
unknown/ambiguous foods: about 14% of all scans (Fig. 4.6b). I estimated that this food 
category may have been composed mostly of embedded invertebrates. I was unable to discern 
the actual food consumed by focal animals when they foraged on bark, twigs, or dead wood. 
Because embedded invertebrates have been classified as a fallback resource for capuchins in 
Costa Rican dry forests (Melin et al., 2014), the possibility that large juveniles devoted much 
time to extracting embedded invertebrates may suggest support for a BM formulation of 
Prediction 3. Nonetheless, this suggestion is speculative; more data are needed to resolve this 
ambiguity.

As discussed, the capuchins at Piro consumed fruit very often (78% of scans; Fig. 4.5), 
and this high degree of frugivory in the wet season may be explained by fruit availability. 
Alternatively, the diet of *Cebus capucinus* in tropical wet forests may be stably and highly 
frugivorous, but this hypothesis is unlikely. A peak of fruit availability for the Osa Peninsula 
region coincided with the entire study period of this thesis (i.e., June to August). Diet fluctuates 
according to food availability among *C. capucinus* in the dry forests of Santa Rosa National 
Park, Costa Rica (Carnegie et al., 2011; Mosdossy, 2013; Hogan, 2015), as it does in the wetter 
forests of Barro Colorado Island, Panama (Oppenheimer, 1968). Furthermore, the diet of the
Santa Rosa capuchins can be composed of up to 81% fruit at some times (Chapman, 1988). Indeed, Melin and coauthors (2014) found significant overlap in fruit availability to fruit-patch visits. Therefore, a parsimonious explanation would be that this population’s diet fluctuates seasonally, like those of other C. capucinus populations.

Given that diets fluctuate over time, juveniles may show differences in diet as compared to those of adults if studied when fruit availability is less pronounced. If a preferred food is abundant, then it should be eaten by members of all age classes. Dietary differences may develop between age classes when preferred foods are scarce. For instance, Robl (2008) investigated dietary diversity in a group of *Pithecia pithecia* in two stages: one study period when fruiting species were low and another when they were relatively high. During the plentiful period, juveniles and adults showed no detectable differences in dietary diversity, but juvenile dietary diversity was significantly less than that of adults during the resource-scarce period (Robl, 2008). Because my study only examined diet during one period of fruit abundance, I cannot rule out the possibility that juveniles in this study population may show greater dietary dissimilarity from adults if follow-up data were collected during a separate phenological period.

Though I could not reject null hypotheses about social foraging (Prediction 2) or diet (Prediction 3), I could not consider these questions fully because my study occurred during a time a high fruit-availability (see Lobo et al., 2008). I suspect that dietary differences may have been less pronounced because fruit was an abundant food resource for these capuchins. Testing these hypotheses would require further data on diet as it relates to seasonality and food availability at or around Estación Biológica Piro.

**Limitations of this Study**
The methodology used in this project was not the most powerful of sampling methods; rather, my use of instantaneous scan samples and the classification of individuals in my primary data were optimal choices that were forced by the fact that I could not differentiate individual monkeys reliably from one another. If individual identities had been known and reliable, a more classical focal-animal method (*sensu* J. Altmann, 1974) would have been used. Individual profiles of behavior allow for within-group comparisons (e.g., within large juveniles), and such comparisons would certainly have strengthened my analysis and conclusions. For instance, individual foraging efficiency may be individually variable to such a degree that my decision to pool all samples of each age/sex class may have increased my likelihood of type-II errors in my tests of Prediction 1. Within-group testing is the obvious way to test for this, and such tests are precluded by the methodology of this thesis. Only further data with known individual identities can address this problem.

Another aspect of methodology that warrants discussion is the independent variable of my analyses: age/sex class. Obviously, age is not a ranked categorical variable; it is a continuous variable. My decision to group individuals in the present system was based primarily on MacKinnon (2002, 2006, 2013). At other capuchin study sites, known ages are possible because of long-term research projects that each span over 20 years in duration (Santa Rosa, Costa Rica: Fedigan and Jack, 2012; Iguazú, Argentina: Janson et al., 2012; Lomas Barbudal, Costa Rica: Perry et al., 2012). Another study of the development of capuchin foraging behavior would be best carried out in a context where such known ages were available to the researcher.

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8 A powerful case example of this is Perry's (2009) longitudinal study, in which she utilizes seven years of continuously collected focal-animal data to complete an impressive multivariate analysis of the ontogeny of processing techniques among juvenile *C. capucinus* (see Chapter 2 for a summary).
CHAPTER 6: CONCLUSIONS

1. Age-groups of *Cebus capucinus* varied in the times they devoted to processing and feeding on fruits of *Attalea butyracea* (Arecaceae). Small juveniles did not perform the adult foraging sequence and appeared to lack the strength or dexterity to do so. While large juveniles did forage according to the adult sequence, they spent significantly more time handling these fruits and the mean efficiency (i.e., [feeding time]/[processing time]) with which they foraged on these fruits was lower than those of both adult age-classes. All measures for adult *A. butyracea* were statistically similar. Because of such qualitative and quantitative differences, these data are consistent with the hypothesis that the acquisition of foraging skill competence (in terms of adult foraging efficiency) requires all of juvenility, but such efficiency may be much less important for survival than simple aptitude with the adult technique. If this is true, then this alternative formulation of skill competence may be acquired around the age of 3 years because of small juveniles’ (estimated age: 1-3 years) apparent inability to exploit these foods.

2. Calculated using instantaneous scans of behavioral states, general foraging efficiency did vary among the four age/sex groups, but large juveniles were not significantly less efficient than adult males. Therefore, these data do not support the hypothesis that young capuchins require all of juvenility to attain adult-like general foraging-efficiencies. Further complicating this picture was the inordinately high efficiency of adult females in comparison
to all other age groups. Taken together, these results undermine the hypothesis that adult-like efficiency requires the whole juvenile period.

3. According to my own social foraging index (Chapter 3: Equation 2), both juvenile age-classes did not forage any more socially than any other age/sex class. Indeed, the only significantly different pairwise comparison was between adult males and adult females, with females the more social of these two classes. In addition, the pooled diet greatly emphasized frugivory (78% of all feeding scans), as did the diets of each age/sex class. No differences in frugivory were detected among the four age/sex groups, but this is relatively unsurprising given the preponderance of fruit available between June and August in the Osa Peninsula-Golfo Dulce region. These data (i.e., regarding Predictions 2 and 3) do not support a foraging-based learning model for the evolutionary extension of juvenility; however, these results must be seen against the phenological background for this region. Follow-up data should be collected at times of resource scarcity (see Lobo et al. 2008) in particular in order to most effectively examine any age-related social-foraging or dietary differences.

4. In all, these findings do not support a learning-focused hypothesis for the evolutionary extension of the juvenile period in *C. capucinus* if such a hypothesis excludes social learning. A model that accommodates the learning of the social-behavioral repertoire of *C. capucinus* was not tested here, but developing and testing such a hypothesis is recommended for future research into the life-history evolution of these encephalized monkeys.
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and nut-cracking in young tufted capuchin monkeys (Cebus apella): a perception-action


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APPENDIX A: ON THE USE OF SAPAJUS

Recently, the genus *Cebus* has been bifurcated along the lines of the tufted (*Cebus* spp.) and untufted (*Sapajus* spp.) capuchins (Lynch Alfaro et al., 2012c), a change that is certainly not without controversy (Rosenberger, 2012). Monkeys that are classified into the genus *Sapajus* are distinct from those in *Cebus* for reasons of anatomy, ecology, behavior, and phylogeny (reviewed in Lynch Alfaro et al., 2012c). Given that I employ the controversial terminology of Lynch Alfaro and colleagues (2012c) in this thesis, it is therefore germane to recount the argument for the usage of this increasingly recognized taxonomy within the capuchin-monkey clade. In addition, nearly all laboratory-based studies of capuchin monkeys (e.g., Adams-Curtis et al., 2000; Phillips and Sherwood, 2008), many of which are cited in these pages, are performed on *S. capella*. Before generalizing these findings to the untufted capuchin monkeys, it is fitting to discuss the differences that have been noted between *Cebus* and *Sapajus*.

*Sapajus* is noted for its more robust cranial anatomy as compared with *Cebus* (see Lynch Alfaro et al., 2012c for a more complete description). In particular, the flaring and robust zygomatic arches accompanied by the presence of a sagittal crest distinguish *Sapajus* very clearly from *Cebus* (Lynch Alfaro et al., 2012c). These masticatory differences are possibly of adaptive value to *Sapajus* (Lynch Alfaro et al., 2012c) because of the much tougher foods exploited by the tufted capuchins (Wright et al., 2009). Indeed, ecological differences, as opposed to divergence time, appear to be the major driver of morphological differences within the *Sapajus* clade (Wright et al., 2015). In some areas of Amazonia, tufted and untufted
capuchins are sympatric (e.g. Brownsberg Natuurpark, Suriname [Norconk et al., 2003]), and in these sympatric zones, *Sapajus* and *Cebus* inhabit different microhabitats and utilize resources differently; these ecological differences, taken alongside anatomical differences, may reflect niche partitioning in such areas (Lynch Alfaro et al., 2012c).

With regard to behavior, the tufted capuchins are extremely well known for their use of stone tools in wild settings (Humle and Fragaszy, 2011; Spagnoletti et al., 2011). Untufted capuchins have yet to be observed using such stone tools (Lynch Alfaro et al., 2012c), though all capuchins are known for their use of tools and other objects (Fragaszy et al., 2004; Panger et al. 2002; Perry and Manson 2008; Souto et al., 2011). For example, *S. libidinosus* in the Caatinga of Brazil use hammer-stones to crack open several kinds of nuts, selecting their stones based on their hardness and weight (Spagnoletti et al., 2011). An additional behavioral difference is the use of different substances for anointing, a behavior in which capuchin smear and rub a substance all over their bodies, and often the bodies of other monkeys, in a frenzied and vigorous manner (Lynch Alfaro et al., 2012b). *Sapajus* tends to select soils and arthropods for their anointing bouts, while *Cebus* would seem to prefer plant parts (e.g., *Citrus* fruits; Lynch Alfaro et al., 2012b).

Finally, a recent phylogenetic analysis of cytochrome *b* and ribosomal RNA has shown that the two groups of capuchins are phylogenetically distinct at approximately 6.2 Ma, in the late Miocene (Lynch Alfaro et al., 2012a). Possibly caused by the emergence of the Amazon River at about 7 Ma, the *Cebus* and *Sapajus* lineages were split and restricted to the Guianan Shield and Brazilian Shield, respectively; this split also accords with phylogenetic analyses of other platyrrhine clades, which show speciation events at the same time (Schneider and Sampaio, 2013). Sympatry of the two capuchin lineages would seem to be caused by a recent sudden
reinvasion of the Guianan Shield by *Sapajus* (Lynch Alfaro et al., 2012a). Recently, however, the data used to reach this conclusion were reanalyzed (Nascimento et al., 2015). After a conservative reorganization of the data, Nascimento and coworkers supported late Miocene split proposed by Lynch Alfaro and colleagues (2012a); however, posterior-probability analysis showed that the likely *Cebus-Sapajus* common ancestor ranged in the Atlantic forests and not Amazonian forests (Nascimento et al., 2015). Thus, the presence of *Sapajus* in these more northern zones appears to be the result of an invasion instead of a reinvasion.

For the reasons above, I use *Sapajus* when referring to the tufted capuchins. The two lineages are distinct for several reasons, and the reminder of these differences that accompanies a separate name is a helpful one. Taxonomic consistency is certainly important so that researchers may communicate clearly and efficiently (Simpson, 1963), and in this light, some other recent taxonomic reassignments within the genus *Cebus* (e.g., see Lynch Alfaro et al., 2014) are at least questionable or possibly inappropriate. Nonetheless, the desire for taxonomic consistency should not preclude taxonomic revision when strong arguments are made in its favor.
APPENDIX B: PLANT FOODS CONSUMED BY CEBUS CAPUCINUS AT

ESTACIÓN BIOLÓGICA PIRO

Below, I have composed a list of the fruits that were certainly eaten by C. capucinus during the study period of this thesis. The majority of these foods were fruits, but one identified case was the consumption of the flowers of Symphonia globulifera, which is consumed by Ateles geoffroyi as well (pers. obs.; Riba-Hernández and Stoner 2005). The list below was composed primarily from the invaluable botanical assistance of Marvin Lopez Morales, while a sizeable portion of the list was adapted partially from A. Skrinyer (in progress).

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Common Name</th>
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<tbody>
<tr>
<td>Araceae</td>
<td>Spathiphyllum silvicola</td>
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<tr>
<td>Arecaceae</td>
<td>Acromia aculeata</td>
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<tr>
<td></td>
<td>Astrocaryum standleyanum</td>
<td>Pejibaye del monte</td>
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<td>Attalea butyraceae</td>
<td>Palma real</td>
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<td></td>
<td>Cocos nucifera</td>
<td>Palma de coco</td>
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<td></td>
<td>Elaeis oleifera</td>
<td>Palmiche</td>
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<td>Anacardiaceae</td>
<td>Anacardium excelsum</td>
<td>Espavel</td>
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<td>Spondias mombin</td>
<td>Jobo</td>
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<td></td>
<td>Tapirira myriantha</td>
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<td>Celastaceae</td>
<td>Cuervea kappleriana</td>
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<tr>
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<td>Clusiaceae</td>
<td><em>Symphonia globulifera</em></td>
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<td>Combretaceae</td>
<td><em>Terminalia catappa</em></td>
<td>Almendra</td>
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<td>Convulvulaceae</td>
<td><em>Maripa nicaraguensis</em></td>
<td>Sangre del toro</td>
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<td>Euphorbiaceae</td>
<td><em>Hieronima alchorneoides</em></td>
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<td>Fabaceae</td>
<td><em>Inga spp.</em></td>
<td>Guaba</td>
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<tr>
<td>Malvaceae</td>
<td><em>Hibiscus pernambucensis</em></td>
<td>Majagua</td>
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<tr>
<td>Moraceae</td>
<td><em>Ficus spp.</em></td>
<td>Chilamate</td>
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<td><em>Vantanea barbourii</em></td>
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