Nutritional Ecology and Growth in Juvenile Phayre's Leaf Monkeys

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Abstract of the Dissertation

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Primates exhibit slow growth and an extended juvenile period relative to other similar-sized mammals. Certain evolutionary explanations have linked the costs or benefits of bigger primate brains to slow life histories in general, although a link specifically to the length of juvenility is less clear. The ecological risk aversion hypothesis singles out the juvenile period as a target of selection, positing that slower growth rates and smaller size provide juveniles with an energetic buffer (i.e., lower absolute metabolic demand) against starvation risk during a critical period of heightened vulnerability. This greater vulnerability is attributed largely to juveniles' lower foraging and competitive abilities, making them more susceptible to nutritional stress particularly during seasonal shortages in resource availability.

Folivorous primates have been described as having a relatively lower risk of starvation due to their reliance on a seasonally abundant, less contestable resource. In addition, a lower quality, leaf-based diet has less foraging complexity and therefore a lower threshold for skill

acquisition. Such arguments, however, do not account for the greater mechanical demands of a folivorous diet. Increased dietary toughness and fiber content pose potential food-processing pitfalls for juveniles, who may be hampered by lesser masticatory strength, smaller gape size, or lack of complete permanent dentition.

This dissertation explored feeding behavior and growth during the juvenile life stage for a folivorous primate, Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*), in a seasonal forest at the Phu Khieo Wildlife Sanctuary in Thailand. Between November 2006 and May 2008, I collected data on juvenile, subadult and adult subjects from three habituated groups of Phayre's leaf monkeys to form three main datasets: 1) adult and juvenile feeding behavior data including instantaneous recording of dietary composition and continuous recording, whenever possible, of intake rates (i.e., bites per minute), 2) dietary characteristics, specifically, food plant fracture toughness and nutritional content profiles, and 3) juvenile growth and pseudo-velocity curves of distal lower limb length. I combined these datasets to achieve three main study goals: 1) compare feeding efficiency (i.e., bite rates) across age classes with a specific focus on the effect of dietary toughness, 2) investigate age-related differences in feeding behavior and the consequences for juveniles' nutritional and energetic intake, and 3) characterize juvenile limb growth patterns for a wild colobine species and test for developmental correlates of individual variation in size-for-age.

In investigating juvenile feeding ability, I predicted that juveniles – due to size- and strength-related constraints – would be less efficient (i.e., slower bite rates), would be disproportionately negatively affected by food toughness, and thus would consume less-tough foods. Via focal animal and ad libitum sampling, I counted bites (or number of whole items consumed depending on food type) per minute during feeding bouts as the measure of feeding

efficiency. While bite rates varied depending on the food being consumed, age also played a significant role: both younger and older juveniles fed significantly more slowly than adults. Similarly, while increasing dietary toughness slowed bite rates for all age classes, younger juveniles but not older juveniles experienced steeper declines in efficiency with tougher foods. Yet, neither younger nor older juveniles eschewed tough foods, consuming diets no different in overall toughness from those of adults based on both dietary composition and feeding times.

Next, to assess whether reduced efficiency led to energetic consequences for juveniles, I compared energy, protein and fiber intake scaled according to metabolic mass for each age class using two datasets: the first, a 7-month dataset encompassing fruiting and flowering peaks was used to compare juveniles to adults, and the second comprised three seasonal blocks across a 17-month span for known-aged immatures (16 to 65 months). I predicted that, in order to meet energetic requirements, juveniles would compensate for reduced efficiency by increasing feeding effort or by altering dietary composition. I also expected that seasonal increases in food processing demand (i.e., dietary toughness and fiber intake) would more severely affect juveniles' energy intake rates. Plants eaten by the monkeys were collected, dried and analyzed for macronutrient content (n = 95 food items). I used these nutritional data to estimate hourly rates of energy and nutrient intake for each focal individual. Juveniles typically had higher rates of energy (kilocalories/hour) and protein consumption (grams (DM)/hr) per unit of metabolic mass than subadults and adults, although age classes did not differ in their fiber intake (NDF grams (DM)/hr). I found no significant age differences in dietary proportions according to food type (i.e., young and mature leaves, seeds, fruits, and flowers). Juveniles ensured adequate intake by spending more time feeding than adults, rather than by consuming higher-quality or less-tough foods.

There was one exception to the pattern: in one month with relatively higher NDF intake, younger juveniles (i.e., those closest to average weaning age) had the lowest nutritional intake rates among all four age classes even controlling for their smaller metabolic mass. However, there was no significant age effect of either fiber intake or dietary toughness on energy and protein intake rates. More specifically, even though younger juvenile feeding efficiency was disproportionately slowed by dietary toughness, these individuals did not show an equivalent proportionally greater increase in feeding time relative to toughness; instead, comparable rises in feeding effort occurred for younger and older subjects alike. Interestingly, NDF intake was the only dietary rate variable to exhibit a decline relative to dietary toughness, although this was likely due to the fact that measures of toughness but not NDF included seed pods and casings that were processed but discarded rather than consumed.

Finally, to describe the patterns of limb length growth for Phayre's leaf monkeys, I employed non-invasive photogrammetric methods to measure distal lower limb lengths for all juvenile subjects and a subset of adults and older infants. Cubic spline regressions were used to fit curves to the limb length data at known ages for males and females as well as individual curves for subjects with longitudinal data (i.e., 5 or more datapoints across a 10-16-month time span). Pseudo-velocity curves depicted a steady decline in growth rate for juvenile females and a more gradual decline for juvenile males, although when plotted individually, males seemed to exhibit a possible acceleration, or growth spurt, right around the start of subadulthood. Although variation in dietary quality has been shown to affect growth rates in other primates, here I found no significant relationship between variation in juvenile growth rates controlling for age and nutritional intake. Yet, longer term growth consequences were apparent: in particular, individuals with later weaning ages had significantly longer length-for-age as older juveniles. This finding

contrasts with results from baboon studies, for example, where maternal rank and condition were stronger determinants of female size-for-age, and high-ranking mothers actually were able to wean offspring at earlier ages. Also juvenile females with longer length-for-age showed a trend toward earlier dispersal ages, which may indicate these larger females had or would reach sexual maturity sooner than their smaller counter parts.

Overall, juvenile Phayre’s leaf monkeys exhibited reduced bite-rate efficiency, and dietary toughness disproportionately suppressed bite rates for younger juveniles. Yet juveniles did not avoid high-toughness foods, and, relative to metabolic mass, typically managed to maintain nutritional intake rates significantly above those of adults and subadults with one possible exception. They were able to do so largely due to greater feeding effort as well as the metabolic buffer of smaller body size. The month in which younger juveniles’ intake dropped below that of other age classes highlights the quickly changing risks, especially for those just transitioning from maternal dependence. I surprisingly found no response of individual growth velocity to nutritional intake among juveniles. However, maternal investment earlier in life did affect size-for-age. Likewise, faster growth rates in females may have fitness benefits if younger dispersal ages are an indication of earlier reproductive maturity. Thus, understanding factors that influence variation in growth rates and size-for-age offers insight into early selective pressures, which likely have long-term consequences for reproductive success.

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For Finn—
for being so true.

For my parents—
for being there always no matter what.

For Tim—
for your strength when I needed it most,
and for your love.
I am the luckiest

For Willa and Edie—
for singing our songs,
for the love and laughter that bring light to my life.
I love you both to JUPITER and back.

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CHAPTER 1.

Extended juvenility and feeding competence: the folivore perspective

It is well known that primate life histories are distinctively slow compared to those of similar-sized mammals (Harvey et al., 1987; Charnov and Berrigan, 1993; Ross, 1998), and yet, their extended juvenile period still stands out. While the risks and associated costs of such a delay in reproduction are clear (Pereiera, 1993), the adaptive "benefits" are less well understood. In describing the challenges of the juvenile period, Pereira and Fairbanks (2002, p. ix) state: "Surviving the period before reproduction can even begin is the single greatest challenge in most life histories." Thus, neglecting the study of juveniles ignores the role of selection during this critical period in shaping eventual outcomes. Across primate species, immatures can grow at different rates and durations to achieve similar adult size (Leigh, 1992, 1995). Similarly, within a species or a population, male and female juveniles (or high- vs. low-rankers) already exhibit numerous differences in diet, patterns of skill acquisition, social partners, activity budget, and even mortality risk (Rowell and Chism, 1986; van Schaik, 1992; Crockett and Pope, 1993; Strier, 1993; van Noordwijk et al., 1993; Rose, 1994; Nikolei and Borries, 1997; Maestripieri and Ross, 2004; Agostini and Visalberghi, 2005; Lonsdorf, 2005). Juveniles who do not survive to reproduce have an effective fitness of zero, making research on adult subjects the study of the already successful (Pereira and Leigh, 2003). Only by including juvenile subjects can we further our understanding of variation in developmental trajectories, their social and ecological correlates, and the consequences for long-term fitness.

Evolutionary explanations for slow primate life histories

The juvenile period is the time between the end of maternal dependence (i.e., weaning) and the age at sexual maturity or the start of adulthood. In general, life history theory recognizes the key tradeoff between investing more in growth up front to improve eventual production potential and the concomitant risk of dying before reproducing; depending on species-specific mortality and production rates, natural selection regulates the tradeoff, optimizing age at maturity (i.e., the transition between energy allocation toward growth and body size versus reproduction) and possibly also body size (Charnov, 1991; Kozlowski and Weiner, 1997). This idea relies on the fact that life history characteristics are interrelated (Harvey and Clutton-Brock, 1985; Read and Harvey, 1989; Purvis and Harvey, 1995); taking years to develop to maturity only to die shortly thereafter (i.e., long juvenile periods but short overall lifespans) clearly would be sub-optimal. As such, many evolutionary explanations for slow primate life histories do not address long juvenility specifically, instead viewing it as a correlated consequence of an overall shift. Yet other approaches allow for some wiggle room, with the potential for variation in the timing and duration of juvenility independent of body size or other life history traits (Pagel and Harvey, 1993; Kozlowski and Weiner, 1997; Roff et al., 2006). Indeed, within the life history framework, some traits appear to be more phylogenetically conserved (i.e., gestation length), while others may be more malleable to environmental changes and selection pressures, such as weaning age (i.e., the start of juvenility) (Kamilar and Cooper, 2013).

The link to bigger brains

Over the past decades, researchers have undertaken broad interspecific comparative analyses to explore relationships between primate life history and brain and body size as well as proxies for dietary and social complexity (Harvey et al., 1987; Joffe, 1997; Ross and Jones, 1999; Deaner et al., 2003; Barrickman et al., 2008). The evidence for an evolutionary link to brain size is robust, however, results and conclusions often differ as to which aspect of life history (e.g., the juvenile period vs. life span vs. periods of maternal dependence) shows the strongest relationship. Likewise, over time, analyses have changed and improved in the methods employed to control for confounding factors such as body size, phylogeny and even other life history traits themselves (i.e., holding life span constant when analyzing age at maturity). Here I describe several of the main hypotheses for the evolutionary relationship between primate brains and life histories.

The skill-learning or needing-to-learn hypothesis was one of the few early explanations to focus explicitly on the juvenile period. It viewed extended juvenility as an adaptive response to increasing social and ecological complexity associated with primate encephalization, allowing time to practice the complex skills necessary for adulthood (Poirier and Smith, 1974; Pereira and Altmann, 1985; Joffe, 1997; Ross and Jones, 1999; van Schaik et al., 2006). This argument claimed that the short-term costs of reproductive delay pay off in the long run. That is, “the returns on investments in development occur at older ages” (e.g., embodied capital: Kaplan et al. 2000), by improving survival during adulthood, increasing longevity and improving reproductive performance enough to compensate for the delay to sexual maturity (van Schaik et al., 2006). Juvenile primates certainly learn and acquire skills; however, as the evolutionary impetus for delayed maturity, this argument has several weaknesses. For one, it does not adequately account for the costs of juvenile mortality (Bogin, 1999). Nor does it explain slow growth; as Pereira and Fairbanks (1993) question: if skill acquisition alone was driving this shift, why not learn skills at full adult size?

The skill-learning hypothesis has given way to others that emphasize the role of larger primate brains in slowing life histories in general, typically with a scope less specific to the juvenile period. These tend to belong to one of two camps, emphasizing either the developmental costs of bigger brains or the cognitive benefits (Barton and Capellini, 2011). The cognitive buffer hypothesis highlights the adaptive benefits of greater cognitive capacity and learning ability, enabling flexible behavioral responses to relatively rare or unexpected ecological risks or crises, thereby providing a "buffer" against mortality and the evolution of longer life spans (Allman et al., 1993; Deaner et al., 2003; Sol, 2009). Allman and colleagues (1993) describe the resulting feedback loop in which longer-lived species not only have more opportunities to learn but are more likely to encounter environmental changes in a lifetime, thus benefiting from learned information. Likewise, mortality becomes very costly for long–lived species in terms of reproductive success (Janson, 2003). Using brain size as a proxy for cognitive ability (Reader and Laland, 2002; Deaner et al., 2007), comparative analyses have demonstrated a significant positive correlation with primate life span to the exclusion of other life history variables (Deaner et al., 2003). However, Sol (2009) argued that an association between brain size and longevity (as opposed to mortality rates) only indirectly supports the cognitive buffering hypothesis; instead, he provided evidence from bird studies indicating that larger-brained species survive better than smaller-brained species when introduced to novel environments, which he suggests is more powerful validation of the hypothesis.

Others have argued instead that the high metabolic costs of growing larger brains have constrained the pace of development earlier on, with subsequent slowing of overall primate life histories (Martin, 1996; Ross and Jones, 1999; Barrickman et al., 2008; Barton and Capellini, 2011). Whether or not brain tissue is more energetically expensive than other organs, as brain size increases relative to body size, the brain metabolic rate constitutes a relatively greater proportion of energy intake (Armstrong 1983; Hofman 1983). These greater metabolic costs, according to the brain-growth constraint hypothesis, result in a tradeoff in overall energetic allocation with less available for growth and reproduction (Ross and Jones, 1999; van Schaik et al., 2006; Barrickman et al., 2008). Ross and Jones (1999) found a significant relationship between adult brain size and the age at maturity, and suggested extended juvenility was a result of growing or maintaining larger brains, although, as mentioned, the lack of controls in these earlier methods cast some doubt on conclusions spotlighting one phase of life history over others. In addition, there has been debate about the duration of potential developmental costs as primate brains actually tend to achieve adult size well prior to the end of juvenility, about the time of weaning (Leigh, 2001; Bolter, 2004). However, other aspects of neural development continue, for example, processes of myelination and dendritic growth (McKinney, 2000), although the relative energetic costs and the associated duration of such costs are less clear. Still others link developmental pace to brain size and growth via maternal investment: the maternal energy hypothesis suggests fetal and postnatal brain growth and eventual adult brain size are limited by the mother's available energetic turnover mediated by variation in the timing of gestation and lactation (Martin, 1996; Barton and Capellini, 2011). Indeed, fetal brain development showed high sensitivity to maternal nutritional restriction, with little or less apparent effects on maternal body mass and fetal somatic growth (Antonow-Schlorke et al., 2011). Barton and Capellini (2011) suggest that developmental-constraint explanations are validated by the significant relationships between the duration of gestation and lactation with patterns of fetal and postnatal brain growth respectively across mammals.

The link to energetic demand

Rather than *maternal* energy regulating brain size, Pontzer and colleagues (2014) recently suggested that selection on energy requirements themselves, separate from brain size, may have contributed to slow primate life histories. They found that total energy expenditure in primates was far lower than in other eutherian mammals controlling for size and phylogeny, although primate basal metabolic rates were no different. In an earlier study, they described low energy expenditure among orangutans as an adaptive response mitigating starvation risks in forests characterized by periodic extreme resource shortages (Pontzer et al., 2010). The trade-off for low energy throughput (i.e., daily caloric intake and expenditure) is reduced reproductive rates and, presumably, overall slow life history, although among the life history traits tested, only reproductive rate showed a significant relationship to total energy expenditure after controlling for phylogeny.

The ecological risk aversion hypothesis singles out the extended juvenile period and slow growth rates as a similar adaptive means of energetic buffering. Janson and van Schaik (1993) propose that slow growth and smaller size allow juveniles in particular to lower their relative metabolic demand. Along these lines, Clutton-Brock and colleagues (1985) attributed sex-biased juvenile mortality in sexually dimorphic mammals to the fact that larger-bodied males have greater energetic requirements and are therefore more likely to suffer from nutritional stress and starvation. With heightened feeding competition, the sex bias grew with greater mortality among larger males, particularly in the year following weaning. Similarly, Janson and van Schaik (1993) stress the elevated mortality risks following the transition to nutritional independence, largely attributed to juveniles' smaller body size and inexperience, which hamper their feeding ability and render them more vulnerable to predation and costs of feeding competition. Younger juveniles typically enjoy greater adult tolerance and, therefore, can mitigate predation risk by engaging in less risky foraging closer to the group center and to fellow group members. However, this tactic concurrently intensifies resource competition and, consequently, the risk of starvation. As stated then, “natural selection favors a single, nonmaximal value of the growth constant if mortality increases more than linearly with the growth constant” (Janson and van Schaik 1993, p. 70). Deaner and colleagues (2003) later adjusted the model so that it applied to brain growth and the risk of brain malnutrition rather than the more general starvation risk. They cited the more rigid patterns of brain growth relative to the potential flexibility in somatic growth rates as well as evidence for accelerated or catch-up growth following periods of nutritional stress or deprivation. However, non-primate research seemed to suggest that extreme growth-rate fluctuations and catch-up growth in particular likely have serious negative consequences for fitness in the long-term (Boersma and Wit, 1997; Metcalfe and Monaghan, 2001; Mangel and Munch, 2005).

The ecological risk aversion hypothesis predicts that developmental rates should vary relative to risk, suggesting that faster life history in folivores may be the result of relatively low starvation risk associated with a folivorous diet, which relies on a seasonally abundant, less-contestable resource. In support, Leigh (1994) found that folivorous anthropoids grew at faster rates and achieved adult body mass at earlier ages than non-folivorous taxa. Likewise, cross-species comparative analyses detected a negative trend between the degree of folivory and length of juvenility (Ross and Jones, 1999). However, comparisons among lemurids showed that frugivores actually grew at faster rates than folivores (Godfrey et al., 2004). Along similar lines, developmental life history pace was no faster among folivorous Asian colobines than it was for more frugivorous macaque species (Borries et al., 2011). And more and more, research on folivorous taxa has provided evidence for within and between group feeding competition (Snaith and Chapman, 2005; Harris et al., 2010), as well as seasonal shifts in resource availability (Dasilva, 1992; Koenig et al., 1997; Sayers and Norconk, 2008). Demonstrating both the important influence of energetic risk on developmental pace and the oversimplification of broad dietary categories, Stoinski and colleagues (2013) demonstrated that western lowland gorillas, relying on more dispersed and temporally variable resources, have significantly later weaning ages than mountain gorillas, characterized by a diet of abundant herbaceous vegetation with relatively little variation in availability over time.

Juvenile foraging competence

Needing to learn as the evolutionary impetus for extended juvenility has garnered little direct support from studies of primate foraging ontogeny (e.g., Boinski and Fragaszy, 1989; Stone, 2006; van Schaik et al., 2009); nevertheless, achieving foraging competence is clearly a critical aspect of primate development. The relatively complex primate dietary niche potentially involves extractive foraging (Gibson, 1986), daily ranging decisions based on spatial memory and mapping (Cunningham and Janson, 2007; Di Fiore and Suarez, 2007), and differentiating plant foods with high nutrient quality relative to toxic or other secondary compounds (Glander, 1982; Magliocca and Gautier-Hion, 2002; Wasserman and Chapman, 2003). As an individual transitions to nutritional independence, the ability to consume a higher quality diet at this early age may have lasting consequences in terms of survival and reproductive success (Altmann, 1991, 1998).

Learning foraging competence

Determining the precise timing of the onset of adult-level foraging competence likely is not possible in group-living taxa as immatures typically do not make ranging and foraging decisions independently of other group members (van Schaik, 2003). Instead, proximity to fellow group members provides opportunities for observation and socially facilitated learning in foraging contexts (van Schaik, 2003; Visalberghi and Addessi, 2003; Fragaszy and Visalberghi, 2004; Humle and Snowdon, 2008; Rapaport and Brown, 2008). Active teaching occurs rarely if at all in non-human primates (Boesch, 1991; Lonsdorf, 2006), yet young individuals often show high interest in adult foods, particularly when the food being eaten is a rare resource or an item otherwise difficult to obtain or process (e.g., King, 1999; O'Malley and Fedigan, 2005; Jaeggi et al., 2008). Even without active teaching, infants and juveniles may benefit from social facilitation in that those in proximity to foraging adults are more likely to explore, manipulate and consume similar foods (e.g., Whitehead, 1986; Addessi and Visalberghi, 2001; Tarnaud and Yamagiwa, 2008). Species for which young spend more time in proximity to like-sexed adults tend to develop sex-typical foraging behaviors early on (van Noordwijk et al., 1993; Agostini and Visalberghi, 2005) and even acquire skill sets more quickly (e.g., termite-fishing proficiency in female chimpanzees: Lonsdorf, 2005).

Behaviors that facilitate skill acquisition, such as play-feeding behaviors and heightened interest in foraging adults, are already common in infancy (Nowell and Fletcher, 2008; Tarnaud and Yamagiwa, 2008), which serves as a reminder of the value of acquiring basic foraging skills *prior* to weaning and the start of juvenility. Indeed, many studies have found that juvenile diets (i.e., food items consumed, including mechanically challenging foods), and sometimes even foraging techniques, already closely mirror those of adults well prior to the end of the juvenile period marked by the transition to sexual maturity (Watts, 1985; Byrne and Byrne, 1993; Fragaszy and Boinski, 1995; Inoue-Nakamura and Matsuzawa, 1997; Lonsdorf, 2005; Stone, 2006; Nowell and Fletcher, 2008; Raguet-Schofield, 2010).

Constraints on juvenile feeding efficiency

Still, baseline knowledge of what to eat and how to eat it only take an individual to a certain point. Feeding speed as well as bite size ultimately determine energetic intake for a particular food (Schülke et al., 2006). Research has shown that for specific foods, feeding efficiency continues to improve with age sometimes throughout juvenility and into subadulthood (Johnson and Bock, 2004; Sousa et al., 2009; Gunst et al., 2010a). The time required to achieve adult-level efficiency varies according to the type of foraging demand: for capuchin foods that required strenuous, physically demanding foraging, such as palm fruits, adult-level proficiency correlated with growth and dental development, and juveniles appeared to achieve this physical-strength threshold around three years of age (Gunst et al., 2010b). In contrast, more cognitively demanding foraging, such as the search for and selection of bamboo stalks containing embedded larvae, proficiency continued to improve up until six years of age, twice as long (Gunst et al., 2008, 2010a; b).

Juveniles' smaller body sizes pose potential problems for foraging ability (Fragaszy and Boinski, 1995). For one, smaller size can lower competitive ability (Fragaszy and Boinski 1995; Janson and van Schaik 1993), which determines an individual's ability to maintain access to a preferred food patch. Thus, even if a juvenile identifies a preferred food source, inability to maintain sustained or uninterrupted access can have a substantial negative impact on foraging success and intake rates (Janson 1990; Johnson and Bock 2004). In addition, smaller size may be associated with measures of lesser masticatory strength. In an ontogenetic sample of capuchin monkeys, Chalk (2011) found reduced resistance capabilities in the crania of younger individuals. Body size may also constrain intake rates due to smaller gape size and bite volume (Perry and Hartstone-Rose, 2010; see also juvenile banded watersnakes: Vincent et al., 2006). Finally, the eruption and occlusion of permanent dentition should allow for increased molar surface area. Until then, juveniles are likely at a processing disadvantage as molar surface area showed allometric increases across herbivourous mammals, and improved food processing times (Shipley et al., 1994; Wright, 2004).

Ontogeny of folivore feeding behavior

Although research into foraging ontogeny has expanded greatly in recent decades, among these studies, folivorous taxa tend to be represented exclusively by howler monkeys and gorillas. From this work, the earlier studies found that infants were more likely to feed synchronously with their mothers (mountain gorillas: Watts 1985; mantled howler monkeys: Whitehead 1986), from the same plant item at the same time. Whitehead (1986) reported behavioral differences between infant leaf and fruit-eating, which were attributed to differences in the likelihood of plant toxicity: young howlers were more independent when eating fruits than leaves, and infants were more often in proximity to an adult when leaf–eating. Milton (1988) reported taxonomic differences between howler and spider monkeys that echoed these findings, with greater reluctance toward novel foods on the part of the folivorous howler monkeys.

The diets of young mountain gorillas mirrored those of adults at an early age, even prior to weaning (Watts, 1985). Observations of western lowland gorillas feeding in a bai habitat suggested a similar timing for the acquisition of basic independent feeding skills (Nowell and

Fletcher, 2008). Infants showed the greatest variability in processing relative to feeding time, and were more likely to focus on plant parts that required less processing; within the juvenile period, individuals already exhibited preference for roots and rhizomes, and proportions of plant parts consumed changed very little after weaning age and into sub-adulthood. When feeding on well-defended leaves such as stinging nettles, mountain gorillas employ complex processing techniques to minimize the effect of the plants' defenses (Byrne and Byrne, 1993). By weaning age, functionally equivalent elements used in the overall processing technique were in place, yet the repertoire of techniques (i.e., the sequential ordering of processing actions) significantly increased with age beyond juvenility (Byrne and Byrne, 1993).

For both howlers and gorillas, juveniles spent significantly more time feeding than adults (*Alouatta palliata*: Raguet-Schofield, 2010; *A. pigra*: Amato et al., 2014; *Gorilla beringei* juveniles vs. silverback male: Rothman et al., 2008). For howler monkeys at least, this difference is likely a result of their reduced efficiency as indicated by higher ratios of foraging to feeding time (Raguet-Schofield, 2010). For both taxa, comparisons of nutritional intake indicated that juveniles achieved higher daily energy and nutrient intake per unit of metabolic mass relative to adults or at least adult males (Rothman et al., 2008; Amato et al., 2014). Because gut size scales isometrically with body size, smaller-bodied animals are expected to have shorter gut passage times and thus reduced digestive efficiency (Demment and van Soest, 1985; but see Clauss et al., 2008). However, fecal analysis in mountain gorillas showed no differences in digestive efficiency across juveniles, adult females and silverback males despite the relatively large body size variation (Rothman et al., 2008). Amato and colleagues (2014) found age differences in the makeup of the gut microbial community and suggested that the particular taxonomic pattern for juveniles may provide benefits in terms of added microbial energy production.

Traditionally, the folivorous diet has been thought of as less complex than a frugivorous diet, with little to no extractive foraging for embedded resources – a characterization often used to explain associations between folivory and smaller brain size and faster life histories (e.g., Ross and Jones, 199). However, folivores make use of dental and gut adaptations (Chivers, 1994; Lucas and Teaford, 1994; Lambert, 1998; Willis and Swindler, 2004) to specialize on fibrous food items with greater mechanical demand, which could be more challenging for juveniles. As an indication of such challenges, folivorous taxa have been found to have accelerated dental development, particularly relative to weaning age (Harvati, 2000; Godfrey et al., 2001; Dirks, 2003), which may be decoupled from somatic developmental rates. The resulting dental advantage may serve to better equip young juveniles for the high-processing demands of a folivorous diet, which might otherwise delay nutritional independence. The consequences of processing demands on young juvenles can be severe: in mantled howler monkeys, juvenile mortality rose during the lean season when overall dietary toughness increased (Raguet-Schofield, 2010).

Phayre's leaf monkeys

Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) are medium-sized Asian colobines. In contrast to the aforementioned folivores relying on caeco-colic fermentation, colobines are fore-gut fermenters, characterized by complex, multi-chambered stomachs allowing for microbial fermentation of ingested foods prior to digestion, including otherwise toxic or digestion-inhibiting secondary compounds (Chivers, 1994; Lambert, 1998). Phayre's leaf monkeys at the Phu Khieo Wildlife Sanctuary in northeastern Thailand consumed a diet of roughly 46 percent leaves, though they also relied on unripe fruits and seeds, flowers, bamboo shoots and insects (Suarez, 2013). Dietary composition for the species varies seasonally (Aziz and Feeroz, 2009; Suarez, 2013) and the presence of immature fruits in the diet negatively correlated with the consumption of young leaves.

For the groups studied here at PKWS, the study site within the sanctuary sits at an elevation of 600 to 800m asl and experiences relatively high annual variation in minimum and maximum temperatures (Koenig and Borries, unpublished; see also Grassman et al., 2005). A dry season occurs roughly between November and March each year. In conjunction with annual weather variation, Phayre's leaf monkeys exhibited seasonal birth peaks with more infants born between November and April (Borries and Koenig, unpublished). Among other factors, conceptions may be linked to changing resource availability as the likelihood of conception increased with improving physical condition for adult females (Lu et al., 2011). Seasonality and changes in resource availability and dietary composition are important for understanding juveniles' ecological risks. Among colobines, nutritional conditions or proxies thereof (e.g., group size, high seasonality) have been linked to rates of development (Borries et al., 2001, 2008). At PKWS, Phayre's leaf monkeys were weaned at 19 months on average (Borries et al., 2014a) and had average ages at reproductive maturity of 5.3 years (Borries et al., 2011). The site also was home to an intact and diverse predator community including eight felids (Grassman et al., 2005; Koenig and Borries, 2012), which posed a documented threat to juvenile Phayre's leaf monkeys in particular (Borries et al., 2014b).

Study Overview

This study aimed to investigate two major aspects of the juvenile period critical to an individual's survival and future success: 1) feeding behavior and associated dietary competence and 2) growth rates and size-for-age variation. Here I will outline the objectives specific to each of the three data chapters.

The second chapter investigated a measure of feeding proficiency (i.e., bite-rate efficiency) with the goal of parsing out limitations due specifically to reduced masticatory strength or ability. I predicted that if juveniles were constrained by size and strength, they would be less efficient feeders for higher toughness foods. To test this, I used a field mechanical tester to measure fracture toughness for as many foods in the leaf monkey diet as possible (n=115 food items, 77 species) and paired this with feeding data for juvenile and adult leaf monkeys. Juveniles were split into younger and older age classes to better ascertain the potential duration of any inefficiencies relative to maturity.

Next, the third chapter built on questions of reduced efficiency to determine whether juveniles managed to achieve adequate energetic and nutritional intake for their metabolic mass as compared to adults. Food plants were collected, dried and analyzed for macronutrient content (n=95 items). I used these corrected for final dry weight along with feeding rates and bite weights to determine hourly rates of energy, protein and NDF intake for juveniles and adults across months. Because of their smaller size and the metabolic costs of growth, juveniles should have greater relative energetic needs than adults. Thus if they are attaining sufficient intake, their hourly rates should exceed those of adults after scaling for metabolic mass. Further, if seasonal shifts in dietary toughness and fiber content occur, there should be a coordinated reduction in energetic intake with the strongest effect on the youngest individuals.

Fourth, I characterized the growth pattern during juvenility for male and female distal lower limb lengths. To do so, I fit cubic spline-estimated curves to limb lengths measured via non-invasive, photogrammetric methods for immatures of known age and adults of estimated ages. Previous research on primate growth rates in the wild has found a relationship between food availability and growth rates with consequences for reproductive success, namely faster growth allows an individual to reach reproductive maturity at an earlier age. It has also shown that the timing of maternal investment varies relative to offspring size; that is, mothers with smaller offspring will invest longer such that variation in size at weaning is reduced. Yet this work has tended to focus on taxa characterized by strong matrilineal dominance hierarchies. Here, I investigated the correlates and consequences of limb growth in a taxon with female-biased dispersal and a less stable dominance hierarchy.

Finally, the last chapter synthesizes the main results and the broader implications of this research. It also touches on the use of a non-invasive photogrammetric method that has given way to a similar but less error-prone method. I conclude by describing avenues for future research, particularly in regard to wild colobines.

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CHAPTER 2:

Juvenile feeding behavior and the role of dietary toughness in Phayre's leaf monkeys

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Abstract

For many primate species, juveniles tend to be less competent feeders and foragers than adults, often due to size- and/or experience-related constraints. Disentangling the relative roles of small size vs. inexperience has proven difficult for obvious reasons: as immatures age, they also get larger, stronger and more experienced. Also, while certain foods are easily classified as difficult to eat, comparing objectively across all foods in the diet becomes problematic. As a step toward unraveling these constraints, I chose a study species that relies little on extractive foraging and instead exploits a mechanically demanding diet. I examined the influence of dietary toughness on feeding behavior in adult and juvenile Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) at the Phu Khieo Wildlife Sanctuary in northeastern Thailand. Focal feeding data, including bites-to-mouth per minute, were collected on adults, older juveniles and younger juveniles from three groups for 14 months. During eight of these months, corresponding dietary fracture toughness was measured using a portable mechanical tester for testing fresh samples in the field within 24 hours of collection (N=115 items). As expected, younger and older

juveniles were significantly less efficient feeders than adults overall, taking fewer bites per minute. Incorporating dietary toughness into the models revealed a constraining effect on feeding efficiency even for adults, however, more mechanically demanding foods took a significantly greater toll on younger juvenile feeding efficiency than on either older juveniles or adults. Unexpectedly, juveniles did not appear to compensate by adjusting their dietary composition and avoiding the toughest foods as we found no significant age differences in overall dietary toughness. These results suggest that even young juvenile leaf monkeys are equipped to exploit a mechanically demanding diet albeit less efficiently than adults. And the constraining effect of dietary toughness does not persist throughout the entire juvenile period.

Introduction

Weighing the costs and benefits of primates' distinctively long juvenile period (Pereira and Altmann, 1985; Pereira and Fairbanks, 1993; Walters, 1987) is a life history puzzle that continues to spur new research. Certain evolutionary explanations have highlighted potential selective advantages of primates' developmental slow-down, particularly as it relates to foraging complexity and the acquisition of ecological competence (e.g., ecological risk aversion: Janson and van Schaik, 1993; skill learning: Pereira and Altmann, 1985; Ross and Jones, 1999; humans: Kaplan et al., 2000). More recent hypotheses have shifted toward the idea that extended immaturity – rather than a target of selection – is, instead, a consequence of selection either for larger primate brains (Barrickman et al., 2008; Barton and Capellini, 2011; Deaner et al., 2003; Sol, 2009) or for lower energy expenditure (Pontzer et al., 2014); yet Altmann's pivotal work (1991, 1998) established the importance of diet from a very early age and the long-term consequences for fitness. Research focused on adults is the study of the already successful

(Pereira and Leigh, 2003). Detailed study of dietary ontogeny can identify variation in developmental trajectories within and across species, better informing our understanding of factors influencing survival and lifetime reproductive success.

The stakes are especially high during the transition to nutritional independence that typically marks the start of the juvenile period. Primates exploit a relatively complex environment (Clutton-Brock and Harvey, 1980), and both the ‘ecological risk-aversion’ and the ‘skill learning’ hypotheses assume that juveniles exhibit reduced foraging ability relative to adults as they gain the size, strength or experience necessary to successfully exploit a more complex dietary niche (Janson and van Schaik 1993; Pereira and Altmann, 1985; Ross and Jones, 1999). Until they achieve feeding and foraging competence, juveniles face increased starvation risk (or brain malnutrition risk: Deaner et al. 2003), particularly during periods of food scarcity (Janson and van Schaik 1993; e.g., Raguet-Schofield, 2010). And as mentioned previously, even during the earliest stages of independent feeding, individual variation in diet and foraging ability serves as an indicator of eventual long-term fitness (e.g., dietary variation in yearling baboons: Altmann, 1991, 1998).

Numerous studies of foraging ontogeny in both primates and non-primates have found evidence for lower immature foraging ability including slower intake rates as well as differences from adults in dietary composition and in time spent feeding, handling or searching for food (Boinski and Fragaszy, 1989; Chalk, 2011; Corp and Byrne, 2002; Daunt et al., 2007; Gunst et al., 2008; Hanya, 2003; Hauser, 1993; Johnson and Bock, 2004; Marchetti and Price, 1989; Post et al., 1980; Raguet-Schofield, 2010; Robl, 2008; Rolseth et al., 1994). In regard to the evolutionary hypotheses, there are two key questions surrounding age differences in foraging ability. The first is about timing – do these differences persist beyond infancy and, in fact, throughout the entire juvenile period such that they could have a role in setting the age at maturity? The second concerns the constraints – does inexperience limit foraging ability such that practice and observational learning are essential to achieving adult-level competence or are juveniles instead limited by physical aspects of smaller size such as lesser manual and masticatory strength and mixed deciduous and adult dentition? Of course, these are not mutually exclusive, so both smaller size and inexperience may constrain juvenile feeding and foraging performance.

Timing of adult-level foraging ability

If selection has favored a longer juvenile period to allow time to master foraging skills as the 'skill-learning' hypothesis contends, then juveniles should not become fully competent until just prior to age at maturity. For some species at least, this does not appear to be the case. Juvenile squirrel monkey (*Saimiri sciureus*) foraging behavior was "nearly indistinguishable" from that of adults (Stone, 2006, p 105). Apes exhibit even longer periods of immaturity, yet prior to the age at reproductive maturity, juvenile gorillas are not only capable of meeting estimated nutritional requirements (Rothman et al., 2008), but they do so using feeding and foraging patterns and rates similar to those of adults (Nowell and Fletcher, 2008; Watts, 1985). Likewise, juvenile and even older infant chimpanzees are able to successfully perform complex foraging tasks such as nut-cracking and termite fishing (Inoue-Nakamura and Matsuzawa, 1997; Lonsdorf, 2006) as well as forage on very large fruits (Corp and Byrne, 2002).

Other studies, however, highlight the importance of differentiating between simply being able to perform a foraging task versus foraging with adult-level efficiency, for which longer-lasting age differences have been reported. In chacma baboons (*Papio ursinus*), bite-rate efficiency (i.e., number of bites per feeding bout) on mixed grasses continued to improve with increasing age throughout the juvenile period (Johnson and Bock, 2004). Chimpanzees successfully make leaf tools for drinking water starting around 3.5 years of age, however, in terms of efficiency, the leaf dippers made by juveniles and even adolescents are smaller and carry less water per dip than those made by adults (Sousa et al., 2009). A detailed study of feeding behavior in capuchins (*Sapajus apella*) in Suriname found that efficiency during extractive foraging for embedded larvae (i.e., number of larvae found per hour spent searching) continued to increase with age up until subadulthood, while older juveniles had already achieved adult-level efficiency for palm-fruit feeding – a less complex but more physically constrained foraging task (Gunst et al., 2008; 2010a,b). These examples illustrate the difficulty in disentangling the effects of small size on foraging ontogeny from those of inexperience since both factors are tightly correlated with age and are not necessarily mutually exclusive.

Size-related constraints on feeding and foraging

A few detailed studies have managed to document the importance of experience in acquiring specific foraging skills (e.g., chimpanzee termite fishing: Lonsdorf, 2005; aye-aye larval extraction: Krakauer, 2005). Practice and experience certainly contribute to the development of foraging competence, especially for more complex, more skill-dependent foraging tasks (Gibson, 1986; van Schaik et al., 2006). However, Janson and van Schaik (1993) argued that smaller size rather than lack of skill is the greater limitation to juvenile primate foraging efficiency. And because of primates' extended growth period, the disadvantages of small size could persist throughout juvenility until closer to sexual maturity when individuals approach adult body size (Bercovitch et al., 1998; see also Leigh, 1994).

Experimental research has shown that feeding variables such as maximum bite size and chew cycle duration scale with body mass across many primate species as well as non-primate herbivorous mammals (Perry and Hartstone-Rose, 2010; Ross et al., 2009; Shipley et al., 1994). Estimated bite force – as approximated by physiological cross-sectional area of various jaw adductor muscles – also scaled with body mass, suggesting larger animals are able to generate greater muscle force (*Macaca*: Anton, 1999; 34 primate species: Perry et al., 2011). Similarly, during development, ontogenetic changes in size and shape should impact a juvenile's ability to exploit the adult diet. Among non-primates, juvenile watersnakes (*Nerodia fasciata*), for example, had relatively smaller gapes and weaker cranial muscles than adults (Vincent et al., 2007). Likewise, the craniodental configuration in adult opossums (*Monodelphis domestica*) conferred a mechanical advantage in masticatory function over that of juveniles' (Thompson et al., 2003). For two New World monkeys, examination of ontogenetic size and shape changes in mandibular and cranial morphology indicated greater resistance abilities for adults relative to younger juveniles (Chalk, 2011; Chalk et al. in review; but see Vinyard and Ravosa, 1998), suggesting that biomechanical performance during feeding improves with age.

More broadly, size determines whether or not an individual can access a particular resource at all (Agostini and Visalberghi, 2005). For example, Corp and Byrne (2002) concluded that infant chimpanzees were limited by smaller hands and mouths when foraging on large fruits, which required greater effort to detach, carry and manipulate. Similarly, "the larger its body mass, the more effectively a capuchin is able to perform strenuous foraging actions successfully, such as bashing open hard-husked fruits, and biting open bamboo stalks" (Gunst et al., 2008, p 200). Indeed, Fragaszy and colleagues (*Sapajus libidinosus*: 2010) managed to weigh individual subjects and found that heavier individuals were more efficient in nut-cracking foraging tasks.

Such direct body size comparisons related to foraging ability are rare due to the risks and challenges of weighing wild animals, especially arboreal species. Instead, researchers have documented size-related feeding variation by comparing males and females in taxa that exhibit sexual size dimorphism (e.g., *Cacajao calvus*: Bowler and Bodmer, 2011; *Cebus capucinus*: Rose, 1994; see also Kamilar and Pokempner, 2008) as well as comparing across species with similar diets but differing body size (e.g., *Chiropotes* and *Pithecia*: Kinzey and Norconk, 1993). In ontogenetic samples, researchers have sometimes chosen to document detailed foraging skill development for a single foraging task or for food deemed to be strength dependent (e.g., Corp and Byrne, 2002; Gunst et al., 2010a). With greater regularity, food mechanical properties have been used to describe dietary mechanical demand within and across species (Bowler and Bodmer, 2011; Chalk, 2011; McGraw et al., 2011; Norconk et al., 2009; Raguet-Schofield, 2010; Robl, 2008; Taylor et al., 2008; Wright, 2004). While some have relied on descriptive labels or rankings (e.g., subjective five-point scale of food hardness: Bowler and Bodmer, 2011), a field mechanical tester kit for measuring food mechanics (e.g., Darvell et al., 1996; Lucas et al., 2001) provides a more objective method for quantifying detailed variation in the mechanical demand of the diet as a whole.

Food mechanical properties

Just as experience-related constraints are most evident with extractive foraging, strength-related constraints should manifest for mechanically demanding foods. For example, red uakari males (*Cacajao calvus*) ate harder fruits than the smaller-bodied females, and juveniles appeared to eschew the hardest fruits eaten by adults (Bowler and Bodmer, 2011). More generally, food mechanical properties are known to influence primate feeding behavior and dietary composition

(Kinzey and Norconk, 1990; Hill and Lucas, 1996; Teaford et al., 2006). Fracture toughness, Young's modulus (or stiffness) and hardness (a composite measure) are particularly informative measures of plants' defenses against being eaten (Lucas et al., 2000, 2003).

Diets that include tough or hard foods place greater demand on the masticatory apparatus and therefore dietary mechanics have likely influenced selection on craniodental morphology, with specialized jaws and dentition found in species utilizing mechanically demanding foods (Wright, 2004, 2005). The relationship between the two, however, is not always a direct one (e.g., Daegling and McGraw, 2001; Ross et al., 2012) and appears to be mediated by a number of factors (e.g., maximum dietary toughness or reliance on tough fallback foods: Taylor et al., 2008; Wright et al., 2009; repetitive vs. heavy loading regime or processing tactics: Ledogar, 2009; Wright et al., 2008a,b). In his study, Ledogar (2009) identified multiple craniodental features that correlate positively with diets requiring repetitive loading (i.e., folivorous diets), such as zygomatic arch size, mandible length and height of the ascending ramus above the occlusal plane.

So far, results from the few recent studies that have incorporated food mechanical demand into examinations of dietary ontogeny highlight the somewhat equivocal role of mechanical properties in explaining age-related feeding differences. Most research, has focused on species that can be classified as hard-object feeders; these have found that the overall toughness or hardness of juvenile diets did not significantly differ from those of adults (*S. libidinosus*: Chalk, 2011; *Pithecia pithecia*: Robl, 2008; top five foods for *Cercocebus atys*: McGraw et al., 2011) and juveniles did not have to avoid consuming the toughest food in the adult diet. However, for mantled howler monkeys, the only folivorous species examined thus far, juveniles' overall toughness profiles tended to be lower than those of adults, though the difference was not significant (*Alouatta palliata*: Raguet-Schofield, 2010). Results are somewhat mixed as to whether food mechanical properties affect juveniles' feeding behavior such as intake rates or processing techniques. Adult and non-adult sooty mangabeys exhibit broadly similar use of oral processing behaviors in overall comparisons but significant age differences became apparent within some food species, for example, non-adults employed post-canine crushing less often to process the nuts of *Sacoglottis gabonensis*, one of the most mechanically demanding items in the mangabey diet (McGraw et al., 2011). Tufted capuchin juveniles at Fazenda Boa Vista, Brazil had longer average feeding times and slower feeding rates than adults for the overall diet, largely due to longer oral processing times (i.e., opening or preparing foods but excluding mastication) (Chalk, 2011). These differences, however, were not always consistent with food mechanical properties: for example, adult and juvenile ingestion times did not differ for bark, one of the toughest food items in the diet, but differed significantly for flowers, the food tissue with the lowest toughness values.

Study goals

As a step toward unraveling size-related constraints from those of experience, we chose to study a folivorous species that engages in little to no extractive foraging to lessen the potential impact of experience on foraging competence. Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) are medium-sized colobines whose diet includes more than 45 percent leaves (Aziz and Feeroz, 2009; Suarez, 2013). Like all colobines, they are equipped with both craniodental and gut adaptations to exploit a more mechanically demanding diet (Chivers, 1994; Lucas and Teaford, 1994), however, Wright and colleagues (2008a,b) have described the genus as ingestive folivores, relying more heavily on efficient oral processing of foods to reduce particle size prior to digestion in the gut.

The goal of this study was to examine juvenile diet and feeding efficiency in Phayre's leaf monkeys relative to dietary mechanical demand, serving as a proxy indicator of potential strength-related constraints on accessing and processing foods in the overall diet. Because of the nature of the diet of our study animals – thinner tissues such as leaves and unripe leguminous seeds – this study describes their diet using toughness alone. Toughness is defined as the work performed in extending a crack for a certain unit area (Lucas et al., 2012). A tough food resists crack propagation even at high strains; for example, "…leaves are the quintessential displacement limited foods in the diets of primates,… they demand repetitive slicing with the molars to produce enough small pieces for adequate breakdown by gut flora"(Wright et al., 2009, p690). We made three main predictions: 1) juveniles feed less efficiently than adults in general (i.e., consume less food per unit time measured via intake rates), 2) smaller juveniles have greater difficulty than adults processing mechanically demanding foods and therefore their intake rates decline more steeply as food toughness increases, and 3) juveniles must exclude the toughest foods eaten by adults because of limited masticatory strength, leading to overall lower dietary toughness for juveniles compared to adults. For all three of these predictions, we expect a developmental progression, whereby younger, smaller juveniles are, for example, slower feeders (in terms of food intake) than older, larger juveniles, who, in turn, are slower than adults.

Methods

Study site and subjects

This study took place at the Phu Khieo Wildlife Sanctuary (PKWS) in northeastern Thailand. Within the sanctuary, the study site (16°27'N, 101°38'E) was a 1,300 ha area of dry and hill evergreen forest as well as patches of dry dipterocarp forest (Koenig and Borries, 2012). KOL followed three groups of habituated Phayre's leaf monkeys for 17 months between October 2006 and May 2008. Because most of the analyses included here involve food mechanical properties, they come from a smaller 8-month dataset, split into two 4-month periods from two consecutive years. In both 2006-07 and 2008 seasons, these two 4-month periods roughly overlapped with the end of the dry season and the start of the rainy season (details below).

Focal subjects included all juveniles present in the three groups and a subset of adults (including subadult males) from each group. Breeding is mildly seasonal in this population with most births occurring between November and April (Koenig and Borries, unpublished), therefore, juveniles could be split into two age categories based on birth cohorts at the start of the study. Younger juveniles (J1s) were those who had ended nipple contact or had reached average weaning age (19.0 months: Borries et al., 2014). Their ages ranged from 16 months (the youngest individual weaned from nipple contact in this sample) to 29 months. The older juvenile age class (J2s) started at age 30 months and ended at the time of reproduction or dispersal for females and at subadulthood for males. The oldest focal juvenile female was 51 months, though juvenile females often dispersed or disappeared from the natal group prior to four years, well before reproduction (average age for disperal is approximately 4 years: Larney, 2013). Older juvenile males transitioned into subadulthood when their head-body length reached that of an adult female (average age at subadulthood for focal sample was about 4.5 years). By this definition, subadult size and presumably strength would be equivalent to those of an adult female, thus, for the purposes of these analyses, subadult males were included in the adult age class. The number of focal individuals per age class varied across months as individuals disappeared/dispersed or aged into the next category with an average of 13.4 focal adults (including subadult males) per month (range: 12-15), 7.4 focal J1s (4-10) and 8.3 focal J2s (5-11).

Data collection

Behavioral data were collected during full- and half-day follows, and KOL was with each of the three groups five to six days per month for a total of 1,383 contact hours in the eight-month period. We used three main datasets to carry out the analyses: 1) standardized intake rates (bites per minute), 2) food toughness and 3) instantaneous focal feeding data.

Intake rates

KOL counted bites per minute opportunistically while conducting both focal and ad libitum sampling. A bite was defined depending on the food item: as hand-to-mouth motion for most leaves with number of leaves noted when possible, as whole items for small fruits and flowers, and as the proportion of fruit consumed per time interval for larger fruits (Barton and Whiten, 1993; Janson and van Schaik, 1988; Johnson and Bock, 2004; Stone, 2004). Bites were counted at any point during a feeding bout for at least three consecutive minutes as long as the animal continued to actively put food to mouth or was clearly masticating food. A count was truncated if these behaviors ceased and/or when searching or handling interrupted active feeding for more than a few seconds.

The variable of interest for comparing efficiency is the actual amount of food eaten per unit time. Because wet weights were available for a smaller subset of food species, we instead standardized bite rates relative to average adult bite size when necessary. For example, if adults ate two leaves per bite on average for a particular food species, while a juvenile ate only one leaf per bite, the juvenile's bite rate was halved to better control for the difference in grams ingested per bite. If variation in bite size could not be determined during an observation period, those counts were excluded or left unstandardized. Of the initial 4,959 bite rates counted, 1,488 bite rates for 50 food items were included in the final dataset (see additional exclusion criteria in data analysis description below), 16 of which required bite-size standardization (mostly leaves: 13 of 16).

Dietary fracture toughness

KOL collected data on the toughness of leaf monkey foods using a portable mechanical tester kit (Darvell et al., 1996; Lucas et al., 2001), available onsite from December 2006 through March 2007 and then again from February through May 2008. With the help of a field assistant, plant samples were collected either from fallen foods as the monkeys ate or by using a telescoping pole after the group had moved or, if necessary, returning to the patch within a 5-day period. Samples were stored in plastic bags and tested within 24 hours of collection following Teaford and colleagues (2006), though typically samples were tested within 6 to 12 hours. For almost all foods, KOL measured toughness (R, in Joules/m^2) via a scissors test, used for items that are rod-shaped (e.g., leaf midribs) or sheet-like (e.g., leaf laminae, flower petals, exocarp, thin seeds) (Lucas et al., 2003). Although this covered the majority of the diet, the leaf monkeys did eat pulpy fruits and thicker seeds at times, and for these foods we used the corresponding wedge test to estimate toughness. For most foods, KOL tested at least two samples per food or food tissue when tissues could be separated and tested individually (e.g., fruit endosperm, endocarp, mesocarp and exocarp). The protocol differed slightly when testing leaves, which vary in toughness across the leaf (i.e., tip, middle, base) as well as for different anatomical features (i.e., midvein, secondary veins and lamina) (Dominy et al., 2003; Lucas et al., 2001; Teaford et al., 2006). Following a protocol described by Lucas and colleagues (2001), KOL made three cuts per leaf at the tip, midleaf and base except if precluded by leaf size (e.g., small leaf buds or bipinnate leaves), in which case one cut was made. The cuts were made perpendicular to and including the midvein and a secondary vein when possible. This allowed for each cut to be further dissected using the on-screen force displacement curve to isolate the peaks from the relatively flat area in between and determine separate values for the midvein, secondary vein and lamina. For all food types, values for multiple tissues or leaf parts were averaged and used to determine the overall average and the maximum toughness values per food item (n=115 food items, 77 species with some species repeated because, for example, the leaf monkeys ate the flowers, leaves and fruits of the same species).

Focal data

KOL conducted 20-minute focal animal samples using instantaneous recording at one-minute intervals (Martin and Bateson, 2007) on juvenile and adult subjects totaling 507 hours for the eight months of data included here (30,418 instantaneous sample points; average monthly focal hours per juvenile = 5 hours (297 sample points); per adult = 3.9 hours (234 sample points)). A long-term project assistant also collected focal animal data on adult subjects for two of the groups and an additional 77.3 hours of his data (3 months: Jan-Mar2007) were included in the analysis to determine proportion of time spent feeding. If a focal individual fed at the one-minute sample point, plant category (e.g., fruit, leaf, flower, etc.), part (e.g., whole, pulp, seed, petiole) and plant age as well as genus and species (or a unique ID number) were noted. These instantaneous data were used to calculate focal individuals' monthly feeding proportions per food item (i.e., number of samples per specific food item divided by total feeding samples).

Data analysis

Feeding efficiency

We tested the prediction that juveniles were less efficient feeders by comparing intake rates (bites per minute standardized by bite size) across age classes. We averaged bite rates per age class for each food item within each month, and then excluded foods for which we did not have multiple bite counts for each of the three age classes within a given month (n= 50 food items; mean count per food for adults = 9.0 (range: 2-34), for older juveniles = 11.0 (2-37), and for younger juveniles = 9.9 (2-30)). We used a linear mixed model (LMM; Quinn and Keough 2002) to test for age variation in bite rates with food item at the species level included as a random factor.

The influence of toughness on feeding efficiency

To explore the influence of toughness on feeding efficiency, we first analyzed adult bite rates alone to determine whether toughness constrained efficiency even for proficient feeders at full adult body size. For this analysis, we used a linear model including food type (i.e., leaves, flowers, small whole fruits, large pulpy fruits, and seeds) as a categorical predictor to account for variation in bite sizes and ingestion behaviors (e.g., the plucking speed of small fruits and flowers vs. leaves) as well as the potential range of food toughness (i.e., the toughest flower petals are less tough than most leaves).

To test whether toughness imposed greater efficiency costs on younger age classes, we created a new dependent variable: instead of bite rates, we used bite-rate ratios to represent the degree of difference between age classes within a single food item. For the three age-class pairings (adults vs. J2s, adults vs. J1s, J2s vs. J1s), we calculated a ratio for each food item/species with the older age class always in the numerator (i.e., adult bite rates over J2 bite rates, adults over J1s, J2s over J1s). We used the ratio rather than the difference because foods with lower toughness were more likely to have higher bite rates as well as greater variability, which tended to inflate differences among the age classes for these foods. Ratios were calculated using monthly bite-rate averages and these were matched to corresponding toughness data for that food from the same month (n=36 food items). We excluded data on foods for which toughness values and multiple bite counts for all three age classes could not be matched within a month.

We then ran separate general linear regression models of bite-rate ratio on food toughness for each age-class pairing including food type as a categorical predictor. If toughness has a stronger negative influence on the younger age class in a pairing, then we would expect toughness to be a significant positive predictor of the bite-rate ratio (i.e., the difference in efficiency becomes more pronounced between the two age classes as toughness increases).

Finally, we ran a combined analysis to test for differences in the relationship to food toughness across age pairs. Here, we conducted a homogeneity-of-slopes model, once again with bite-rate ratios as the dependent variable, toughness as the covariate and age pairs (Adult-J2, Adult-J1, J2-J1) as an additional fixed factor along with food type. In contrast to a traditional

ANCOVA, which assumes homogeneous slopes, this design tests whether regression lines for the categorical predictors (within-group regressions) are heterogeneous (Quinn and Keough, 2002), i.e., whether the continuous and categorical predictors interact affecting the bite-rate ratios.

The influence of toughness on diet composition

Lastly, we looked at the potential role of toughness on dietary differences to determine whether juveniles might consume a diet lower in toughness than that of adults or avoid the toughest foods altogether. We did this analysis in two ways: first looking simply at dietary presence/absence from focal data, that is, any food observed being eaten regardless of frequency, and second, using dietary composition to incorporate time spent feeding on each food species. Because we were sometimes unable to identify foods eaten during focal sampling or because some foods were not tested for mechanical properties, we did not always have useable data for 100 percent of an individual's focal diet. We therefore set a threshold level for the analyses: only individuals with dietary coverage (i.e., the proportion of the focal diet with corresponding toughness data) of at least 50 percent per month were included, although the lowest average dietary coverage for included individuals ended up at 73.2 percent ranging up to 97.2 percent (mean=87.8%). This exclusion threshold left fewer than 3 adults for the month of December 2006, so the whole month was excluded from analysis.

We calculated a monthly toughness mean for each individual, first, by averaging the maximum toughness values of any food the individual was observed consuming in any amount regardless of feeding time. For the second analysis, we calculated a weighted toughness value by taking a food's maximum toughness value in a given month times the proportion of instantaneous focal feeding samples that each individual spent on that particular food for that month. Because we included only individuals for which we had identified a majority of their focal diet, we summed the weighted values for all foods in an individual's focal diet to describe an overall monthly toughness profile. Maximum toughness was used instead of average toughness to better explore the peak values an age class was willing to exploit. Then, we used linear mixed models to compare toughness profiles across age classes, again including month and focal individual as random factors as well as adding group ID to the random factors because differences in group size may affect feeding times (Caraco, 1979; Janson, 1988).

Data were not normally distributed; therefore continuous variables (i.e., bite rates and toughness values) were $\log_{10}$-transformed for all analyses. Residuals were then plotted and analyzed to verify normality (Sokal and Rohlf, 1995). Potential outliers were identified using studentized residuals, leverage and Cook's distance (Quinn and Keough, 2002). Datasets were reanalyzed without outliers to ensure results did not change. We conducted all tests in Statistica 10.0 (©Statsoft. Inc 1984–2011). All tests were two-tailed and significance was set at alpha ≤ 0.05 except planned comparisons between age classes for which the alpha level was adjusted per pairwise comparison using Holm's sequential Bonferroni procedure (Abdi, 2010).

Results

Age differences in feeding efficiency

Feeding efficiency significantly differed across age classes (LMM, age class: $F_{(2,96)}=128.85$, $p<0.001$, Figure 2.1). With food item included as a random factor to better control for influences related to tissue type or food size, the model accounted for 97 percent of the variation in intake rates. Pairwise comparisons corrected using Holm's sequential Bonferroni adjustment (Abdi, 2010) revealed significant differences between each of the three age classes (Table 2.1) with J1 intake rates consistently the slowest, followed by J2s and then adults with the highest rates.

The influence of toughness on feeding efficiency.

We found toughness was a significant negative predictor of adult intake rates with juveniles excluded (univariate test: $F_{(1, 40)}=12.55$, $\beta=-0.401$ $p=0.001$). The model as a whole, including food type as a factor, accounted for 70 percent of the variation in adult feeding efficiency (Figure 2.2), establishing our baseline for tougher foods imposing a cost regardless of age or size.

For all pairwise age-class comparisons, the bite-rate ratio increased significantly as toughness increased, indicating that as foods became tougher, the younger age class' bite rates (denominator of the ratio) slowed significantly more than those of the older age class (numerator) (Figure 2.3). However, visual inspection of the regression coefficients suggests that the adult-J1 pair had the steepest slope of the three age-class pairings (i.e., the greatest degree of difference in bite rates as foods got tougher) as well as the greatest F and R^2 values (Table 2.2), with toughness and food type accounting for 60 percent of the variation in the overall model versus 31 and 29 percent respectively for the adult-J2 and J2-J1 pairings. While results for the two models that included younger juveniles (adult-J1 and J2-J1) were robust to the removal of outliers (i.e., remained significant upon reanalysis), reanalyzing the adult-J2 model without two outliers (two fruits identified via leverage) changed the results such that toughness was no longer a significant predictor of bite-rate ratio (tables and figures reported with outliers included).

When bite-rate ratios for all three age pairs were combined in a single model and tested for homogeneity of slopes (Figure 2.3), the overall model was significant (GLM: $R^2=0.567$, $F_{(8, 99)}=16.23$, $p<0.001$) and the univariate results indicated a significant difference in slopes (age pair by toughness interaction effect: $F_{(2)}= 4.25$, $p<0.016$). Pairwise comparisons point to the weaker relationship between toughness and bite-rate ratio for the adult-J2 pairing (as suggested by the loss of significance upon removal of outliers) as driving the overall slope difference across age-class pairs. The adult-J2 pair significantly differed from the adult-J1 ($t=-6.98$, $p<0.001$) as well as from the J2-J1 pair ($t=5.71$, $p<0.001$) but the two pairs that included younger juveniles (adult-J1 and J2-J1) did not significantly differ from each other ($t=-1.27$, $p=0.206$).

Toughness and juvenile diet composition

Foods eaten by Phayre's leaf monkeys exhibited notable variation in toughness, ranging from a mean value of 154.6 Jm^{-2} for mature fruit pulp to 2,666 Jm^{-2} for the average mature leaf midrib and up to a mean value of 5,423 Jm^{-2} for pith (Table 2.3). We predicted that juveniles would consume a diet lower in toughness; this was not the case, however. In the first analysis, monthly maximum toughness based on presence/absence for juveniles was no different from that of adults ($F_{(2, 862)} = 0.61$, $p=0.54$, Figure 2.4) with the overall model explaining just 9 percent of variation in dietary toughness (Table 2.4). To better assess actual diet composition, we incorporated individual focal feeding times into the second analysis, but this provided similar results with no significant difference in weighted toughness profiles across age classes ($F_{(2,110)}=0.29$, $p=0.75$, Figure 2.5).

Discussion

Our results suggest that juvenile Phayre's leaf monkeys do not consume a diet lower in overall toughness than that of adults. Instead, as the foods they eat get tougher, juveniles, particularly younger juveniles, feed less efficiently than adults, consuming less per unit time. By the older juvenile period, significant differences from adult-level efficiency are reduced for most foods, suggesting the necessary size/strength threshold can be reached prior to adulthood. These results add to a growing consensus that juvenile primates do not have to eschew the tougher foods eaten by adults (Chalk, 2011; McGraw et al., 2011; Raguet-Schofield, 2010; Robl, 2008; but see Bowler and Bodmer, 2011), however, juvenile Phayre's leaf monkeys experience greater efficiency costs when feeding on these mechanically challenging foods.

Juveniles consume tough foods

Counter to our predictions, neither younger nor older juveniles ate a diet lower in overall toughness than that of adults. This was the case both when we examined the diet in terms of presence/absence of food species as well as overall dietary composition incorporating time spent feeding on each item. In this, leaf monkeys differ from a non-primate example; juvenile big brown bats (*Eptisicus fuscus*) consumed diets with softer foods than adults (Hamilton and Barclay, 1998). However, our results confirm those found for other primates, particularly hard-object feeders for which juvenile diets resembled those of adults in terms of mechanical properties (*S. libidinosus*: Chalk, 2011; *Pithecia pithecia*: Robl, 2008). Likewise, folivorous mantled howler monkey juveniles consumed diets similar to adult diets in terms of the presence/absence of foods (Raguet-Schofield, 2010). While juvenile howlers had a lower overall toughness profile when feeding times were included and tended to eat only the tips of mature leaves more often, neither of these age differences was significant.

Although our results are based on a seasonal sample, throughout 17 months of observation, we observed only one food item eaten regularly by adults and older juveniles that was not also eaten by younger juveniles. Adults processed unripe *Afzelia xylocarpa* fruits by repetitively gnawing on the thick-husked pod to expose the young seeds inside. Although the *A. xylocarpa* husk was one of the tougher items in the diet (mean R = 6,371 J/m^2; n=3, range 4,970 – 9,069), even younger juveniles regularly ate the seeds of at least two other species with equivalent or greater toughness values for their pods. *A. xylocarpa*, however, was a very large fruit, roughly 15 or more centimeters in length, and by far the heaviest fruit eaten by the leaf monkeys. Although we did not include fruit size as a variable, Robl (2008) measured weight and diameter of fruits in the red uakari diet and found that as foods became larger, juveniles fed significantly less than adults. Similarly, older tufted capuchins (adults and subadults) processed fruits with larger diameters than those processed by juveniles (Chalk, 2011). Chalk (2011) also found a positive relationship between fruit diameter and mechanical properties, thus, it could be the size of *A. xylocarpa* combined with its greater mechanical demand that rendered the fruit inaccessible to younger juveniles still limited by smaller gapes or even small hands and lesser manual strength. Yet overall, smaller size and lesser strength did not affect juveniles' capacity to exploit tough foods. Instead, they exhibited dietary toughness profiles no different from those of adults.

Reduced juvenile efficiency

While their overall diets did not differ as a result of toughness, juvenile leaf monkeys were disadvantaged in their intake efficiency for these tougher foods. Our results demonstrate that dietary toughness constrains feeding rates to some extent regardless of age or size, however, the toll on younger juveniles was far greater than for older individuals. To some extent, age differences in efficiency persisted even for some lower-toughness foods, such as flowers. Slower intake rates, in general, could be due to a number of factors including age differences in vigilance while feeding or longer handling times due to smaller, less dexterous hands (e.g., slower picking rate for flowers). However, these variables alone do not explain the fact that as food toughness increased, juvenile efficiency became more and more impaired relative to adult efficiency. For folivorous species that emphasize repetitive loading for food breakdown (Ledogar 2009), the constraining role of food toughness highlights the importance of variation in the time dedicated to masticating foods, which depends on chewing rates as well as bite size.

In their study of two colobine genera, Wright and colleagues (2008a) found a trend for longer chewing bout lengths when feeding on tougher leaves. Ross and colleagues (2009) found that food mechanics had only minimal impact on temporal variables related to mastication time (i.e., chew cycle duration, number of chews, chewing sequence duration) across primate species of different body sizes. However, any impact was more noticeable among lab animals than among zoo animals included in the study. The authors attributed this difference to the fact that experimenters controlled bite sizes for lab animals but not for zoo animals. The zoo subjects were therefore free to adjust their bite sizes according to each food's physical properties. Another experimental feeding study on strepsirrhines found that bite sizes were smaller for the two more mechanically demanding foods (n=3) included in the study (Perry and Hartstone-Rose, 2010). Additionally, bite size in general scaled with body size as well as mandible length (Perry and Hartstone-Rose, 2010; see also Shipley et al., 1994). For leaf monkeys, the importance of bite size likely shifts depending on the type of food being eaten. For example, bite size rarely, if ever, varied for seed-eating since most seeds in the diet are small enough to be eaten in a single bite. For leaves, however, younger juveniles frequently consumed noticeably smaller bites than adults, particularly for larger, more mature leaves that adults often consumed by picking several leaves at once and eating all together.

Greater toughness also dampened the feeding efficiency of older juvenile leaf monkeys to some extent, but, again, younger juvenile efficiency relative to that of older juveniles was more toughness-limited than was older juvenile efficiency relative to adults'. Constraints related to food mechanics might not persist throughout the entire juvenile period. Because our group of older juveniles included individuals from 2.5 years up to 4 years, these results could indicate that the oldest in the age class have reached sufficient size and strength to be able to consume tough foods nearly as efficiently as adults.

Alternatively, the ontogenetic threshold in question could have more to do with dental development or smaller tooth size than with smaller body size or lesser strength per se. Chewing produces stress that depends on the relationship between the force of the masticatory muscles as well as the occlusal area of the molars (Shipley et al., 1994), and molar surface area has been associated with masticatory effort and/or efficiency (Lucas and Teaford, 1994; Willis and Swindler, 2004; Wright et al. 2008). Folivores have larger relative tooth size compared to frugivores (Kay, 1975), and *Trachypithecus* spp., in particular, exhibit larger molar area relative to *Pygathrix* spp. (Wright et al., 2008). Thus, juvenile chewing efficiency could be disadvantaged prior to the emergence of all permanent molars.

Folivorous primate species tend to have accelerated dental development including greater dental endowment (i.e., percentage of exposed occlusal area for permanent dentition) (Dirks, 2003; Godfrey et al., 2001, 2004). In their food-processing hypothesis, Godfrey and colleagues (2001) proposed that selection for a faster pace of dental development among folivores better equipped weanlings to consume a more mechanically demanding diet. Harvati's (2000) study of dental eruption sequence found that *Trachypithecus* spp, like most other Asian colobines, showed early eruption of the second molars, particularly M^2, and some indication of intermittent accelerated third-molar eruption. For a wild-shot sample of *Trachypithecus cristatus*, a species closely related to our study species and of similar body size, M1 erupts between age 1 and 2 years (estimated ages: Bolter, 2004), overlapping with our younger juvenile sample, which ranges from 1.3 to 2.4 years. Eruption of M2 occurs between 2 and 3 years of age (Bolter, 2004). Assuming Phayre's leaf monkey development roughly tracks that of *T. cristatus*, nearly all older juveniles in our sample (i.e., 2.5 to 4.25 years) would already have their permanent second molars, while the oldest J2s might have permanent M3s as well (M3 eruption between 3 and 3.75 years in *T. cristatus*: Bolter, 2004). Considering the importance of postcanine dentition in the breakdown of tough foods (Lucas and Teaford, 1994), the timing of *Trachypithecus* dental development relative to our age classes could explain why younger juveniles, still lacking permanent second and third molars, feed less efficiently on tougher foods while older juveniles tend to be more competent.

Indeed, even compared to other colobines, food processing tactics among some members of the *Trachypithecus* genus depend more heavily on larger tooth size and faster chewing (Wright et al., 2008a). This greater emphasis specifically on postcanine mastication of the leaf monkey diet may help to explain the incongruence of our feeding efficiency results with those reported for the omnivorous capuchin monkey (*S. libidnosus*). Chalk (2011) found no consistent overall relationship between mechanical properties and age differences in feeding rates for either younger or older juveniles. In addition, when rates were examined independently of mechanical properties, time spent *masticating* foods did not differ between adults and juveniles; rather, rate differences were due to juveniles' significantly longer oral ingestion times (i.e., getting the food into position for postcanine mastication).

If for juvenile leaf monkeys, eruption and endowment of permanent molars is the critical factor in consuming a tough diet as efficiently as do adults, then we would expect to see a similar effect of toughness in the largely folivorous howler monkeys for which adults also exhibit specialized dental adaptations. In fact, Wright and colleagues (2008b) suggest that mandibular shape is more similar between *Trachypithecus* spp and *Alouatta* spp than between the more closely related *Trachypithecus* spp and *Pygathrix* spp. Interestingly, Raguet-Schofield (2010) found that juvenile mortality among mantled howler monkeys (*A. palliata*) spiked during the lean season when overall dietary toughness increased. Even more telling, DeGusta and colleagues' (2003) examined a sample of wild howler monkey crania (*A. palliata*) (found dead and collected over a 10-year period), and found that individuals with the smallest molars (permanent M1s) had significantly higher mortality rates around the age of weaning.

Conclusion

Like juveniles of most other primate species studied thus far, juvenile Phayre's leaf monkeys did not exclude mechanically demanding foods, and they exhibited dietary toughness profiles similar to those of adults. While toughness did constrain feeding efficiency regardless of age, its impact was most severe for younger juveniles. This greater toll of food toughness on younger juveniles exploiting a folivorous diet points to the limiting role of lesser masticatory strength on efficiency, likely due to reduced resistance abilities of smaller skull morphology and/or to reduced molar surface area in individuals for which permanent molars have yet to fully erupt. Future work will incorporate analysis of nutritional intake across age classes in order to test whether younger juveniles' lower feeding rates translate into added nutritional stress.

Tables and Figures

Table 2.1. Holm's-corrected pairwise comparisons of intake-rates by age class.

Age pair	*t(df)*	*p*
Adult vs. J2	7.16(96)	<0.0001
Adult vs. J1	-16.02(96)	<0.0001
J2 vs. J1	-8.86(96)	<0.0001

Table 2.2. The relationship between intake-rate ratio (older age class vs. younger) and food toughness (both variables $\log_{10}$-transformed). (Holm's sequential Bonferroni procedure sets alpha levels at 0.017, 0.025 and 0.05 respectively). Significant *p* values in bold.

	Toughness			Full Model
Age pair	F	*p*	β	R^2 (df)
Adult vs. J1	27.42	**<0.001**	0.669	0.595 (4,31)
Adult vs. J2	9.53	**0.004**	0.515	0.310 (4,31)
J2 vs. J1	5.56	**0.025**	0.398	0.292 (4,31)

Table 2.3. Toughness (Joules/meter^2) for plant parts of leaf monkey foods. (Food part: la=lamina, mdrb=leaf midrib; Plant age: ma=mature, yo=young; SE=standard error).

Food part	Plant age	Mean R	SE	Maximum R	Minimum R	Species [n]	Samples [n]
exocarp	ma	371.99	57.78	995.40	19.80	6	18
exocarp	yo	908.96	65.80	3209.5	99.9	21	60
exocarp (pods)	ma	3130.65	824.87	9964.1	447.9	5	9
exocarp (pods)	yo	2879.21	382.20	11589.4	92.3	14	54
fruit pulp	ma	154.62	22.53	297.50	42.90	4	7
fruit pulp	yo	1028.68	109.16	3707.10	28.70	18	41
seed	ma	776.29	94.14	2084.00	234.00	9	19
seed	yo	519.03	38.89	3133.90	33.10	38	130
whole fruit	ma	186.64	21.70	459.00	43.20	3	19
whole fruit	yo	1053.82	171.09	3173.90	221.80	6	19
flower (bud)	yo	516.80	36.22	1852.40	47.00	22	95
flowers	ma	238.57	20.38	660.40	24.30	12	34
flower stem		873.71	99.48	3484.40	68.10	17	42
leaves (la)	ma	653.3	104.67	4945.35	12.90	17	59
leaves (mdrb)	ma	2666.08	107.10	7872.80	75.20	25	80
leaves (la)	yo	378.78	21.00	3099.20	25.40	38	165
leaves (mdrb)	yo	1384.15	56.25	7708.70	26.00	38	161
Pith/bark	yo	5113.1	1301.38	9581.5	1751.4	1	6

Table 2.4. Comparison across age classes of mean maximum dietary toughness defined by presence/absence of foods in the diet and weighted by feeding proportions.

	Dietary toughness					
	presence/absence			weighted by feeding proportion		
Variable	*F*(df)	*P*	Whole model R^2	*F*(df)	*P*	Whole model R^2
Age class	0.61(2,110)	0.54	0.091	0.29(2,862)	0.75	0.469

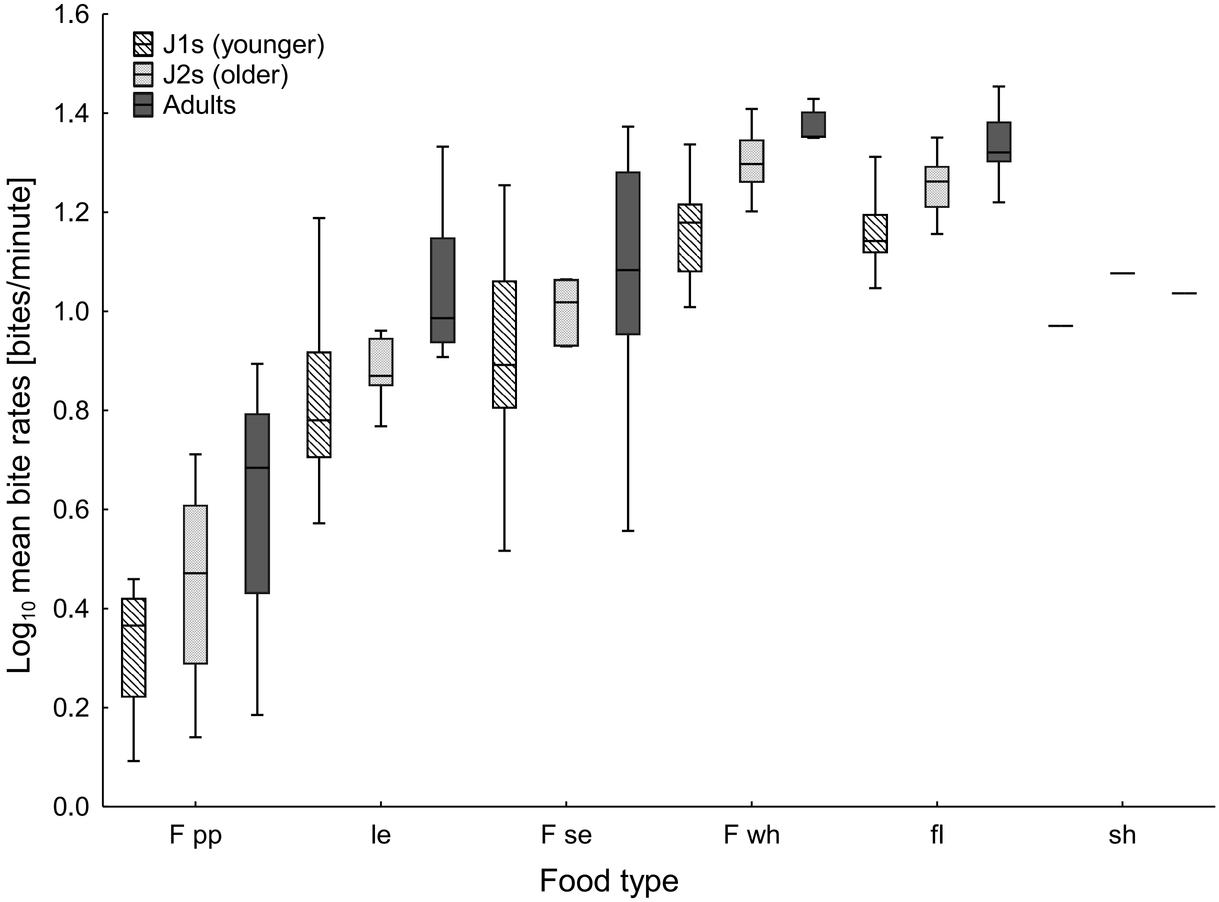

Fig. 2.1. Age-class differences in bite-rate efficiency ($\log_{10}$-transformed). For illustrative purposes, bite rates are grouped by food type rather than specific food (as in the analysis). Food type abbreviated as: F pp = fruit pulp, le = leaves (combined bud, young and mature), F se = seeds (combined young and mature), F wh = whole fruits, fl = flowers (buds included) and sh = shoots (only bamboo used in analysis). Depicted are mean, standard error (box), and standard deviation (whisker).

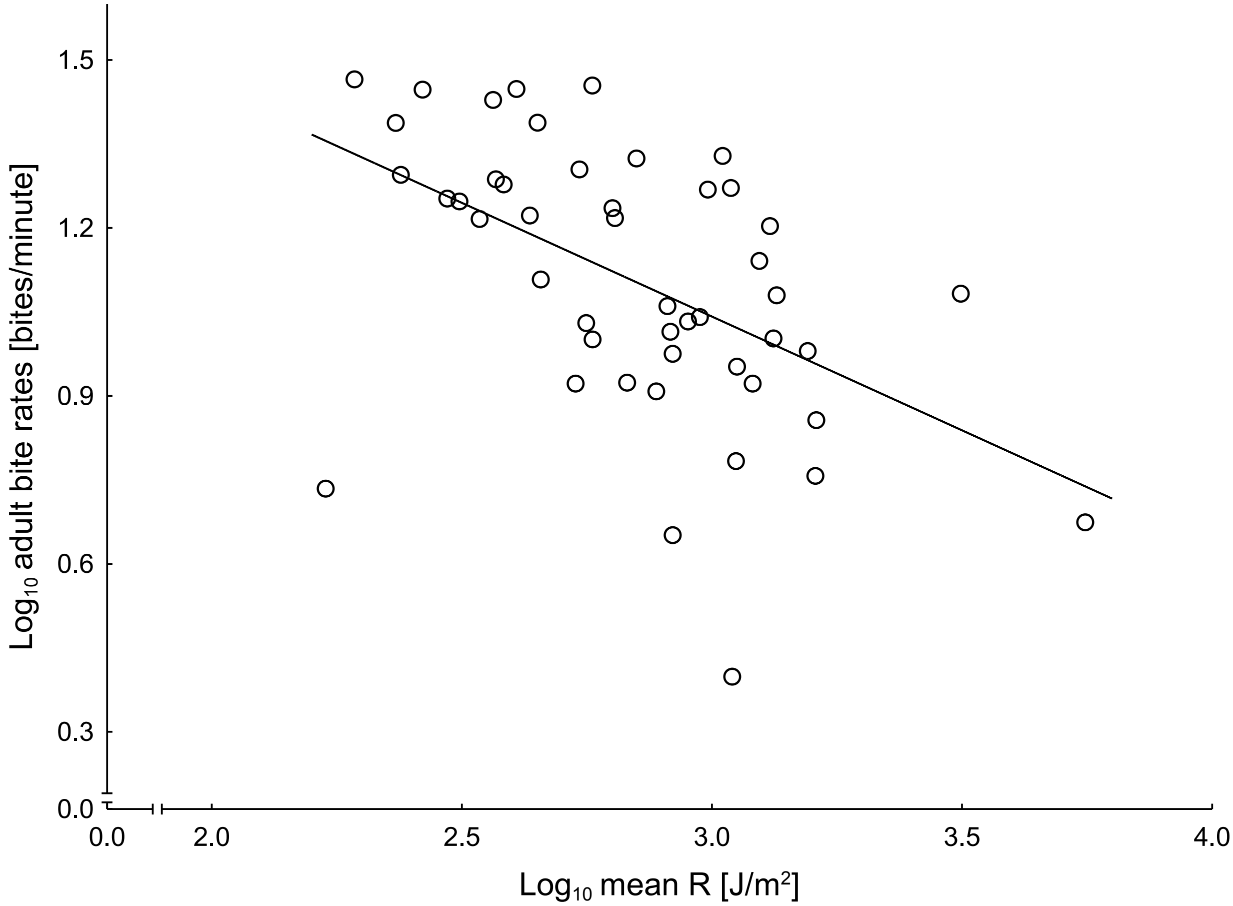

Fig. 2.2. Relationship between dietary toughness (log$_{10}$-transformed) and bite-rate efficiency (log$_{10}$-tranformed) for adult individuals.

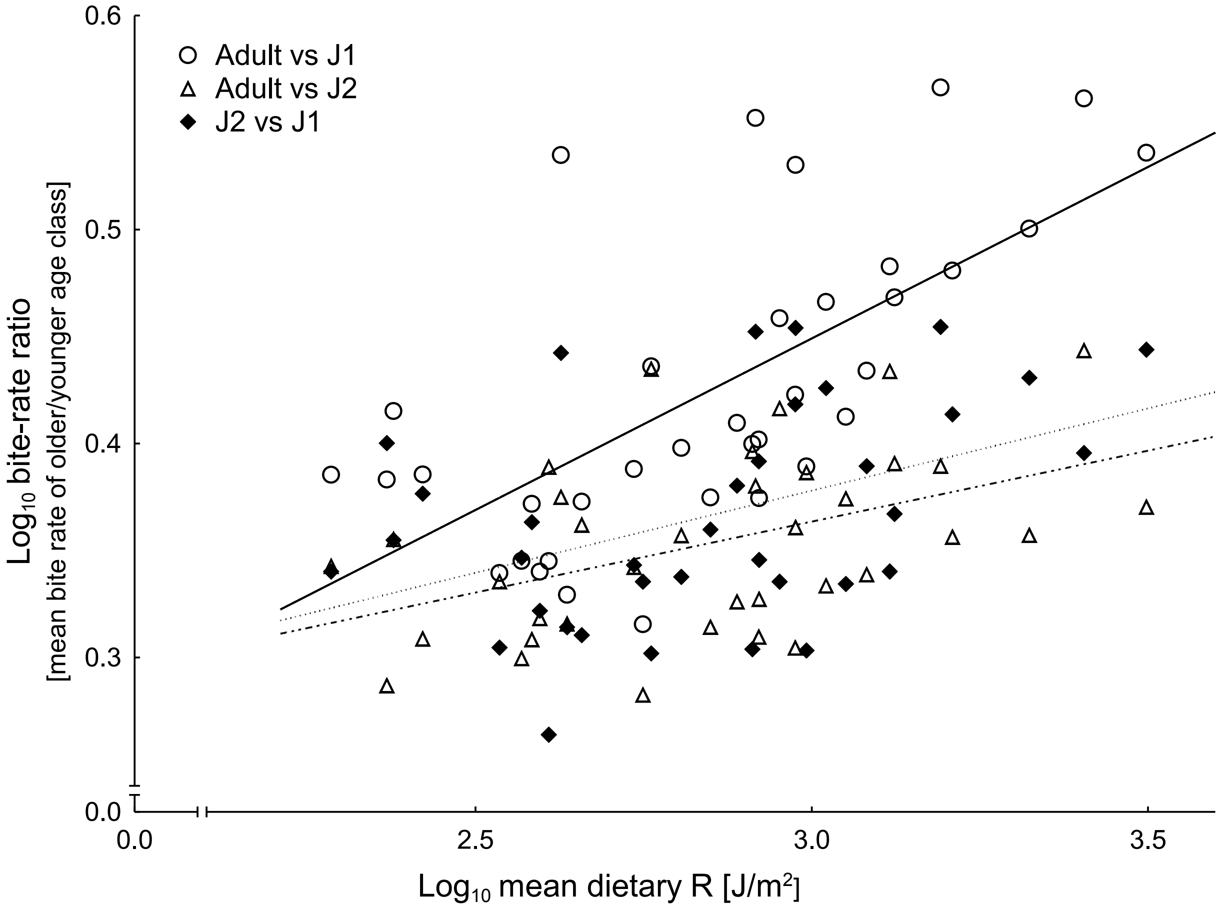

Fig. 2.3. Bite-rate ratios ($\log_{10}$-transformed; i.e., the degree of difference in bite rates between age-class pairs) in relation to dietary toughness ($\log_{10}$-transformed) (Ad to J1: solid line, Ad to J2: dotted line, J2 to J1: hatched line).

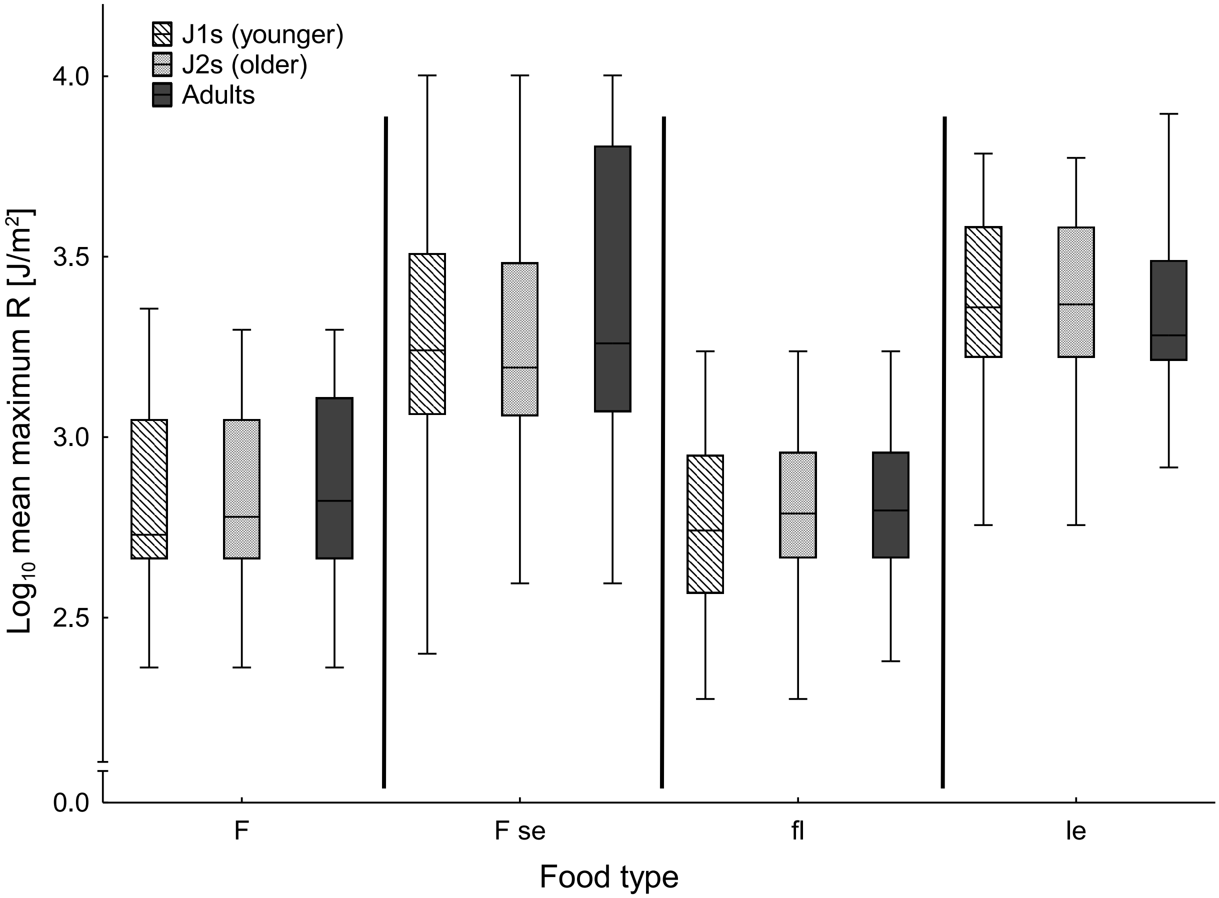

Fig. 2.4. Maximum dietary toughness (based on presence/absence of items in the diet) for each age class by food type (food type not included in analysis but depicted here for illustrative purposes). Depicted are mean, standard error (box), and standard deviation (whisker).

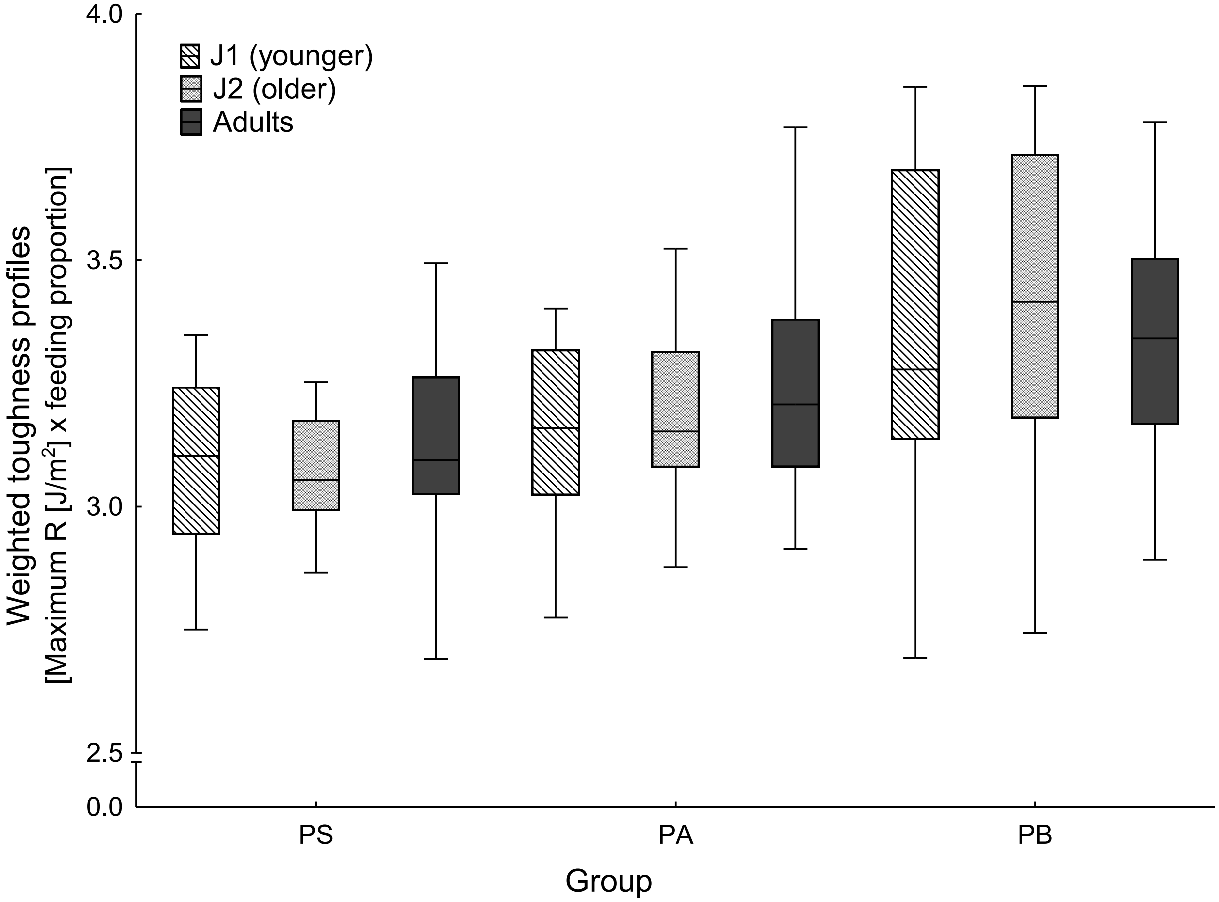

Fig. 2.5. Individual dietary toughness profiles (maximum monthly R [J/m^2] weighted by feeding time and $\log_{10}$-transformed) by age class for each study group. Depicted are the mean, standard error (box), and standard deviation (whisker).

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CHAPTER 3.

Age-related differences in nutrient and energetic intake in Phayre’s leaf monkeys

Abstract

Some evolutionary explanations for slow primate life histories have highlighted the risk-reducing benefits of lower energetic demand. For juveniles especially, slow growth rates and smaller body size provide a metabolic buffer as they develop adult-level foraging competence, which otherwise makes juveniles more vulnerable to starvation, particularly during periods of food scarcity. The diet of folivorous primates has been described as relatively low-risk, with an abundant resource to exploit or fall back on. In addition, a leaf-based diet should be less complex with less extractive foraging and therefore a lower threshold for attaining competence. Both factors have been cited to explain folivores’ (sometimes) faster growth rates and life history pace. Such arguments, however, do not account for the greater mechanical demand of a folivorous diet, which poses potential pitfalls for smaller, weaker juveniles still lacking full permanent dentition as they transition to nutritional independence. Here, I explore age-related differences in nutrient and energetic intake in Phayre’s leaf monkeys (*Trachypithecus phayrei crepusculus*) at the Phu Khieo Wildlife Sanctuary in Thailand. Between January 2007 and May 2008, I collected feeding behavioral data on younger and older juveniles, sub-adults and adults during three time blocks (3 to 4 months each) representing seasonal variation at the site. Plants eaten by the monkeys were collected, dried and analyzed for macronutrient content, which I used to calculate monthly energy and nutrient intake for each focal individual. Juveniles, younger juveniles especially, typically consumed greater energy (kilocalories/hour) and protein (grams

(dry matter)/hr) per unit body mass than did sub-adults and adults, however, age classes did not differ in their fiber intake (NDF grams(dry matter)/hr). While juveniles benefited from the reduced metabolic demand of smaller size, they also appeared to compensate for slower ingestion rates by spending significantly more time feeding than adults. Unexpectedly, individual growth velocity did not show a significant response to variation in nutritional intake on a monthly basis, however, more robust data regarding colobine growth rates in the wild are needed to better understand the relationship between growth and folivorous diets.

> *"Because the nutrient demands of growth and reproduction are spread out over time, it appears that primates do not need to seek out foods of particularly high nutrient density, except perhaps during weaning," (Oftedal et al., 1991, p161).*

Introduction

Since the skill-learning hypothesis first linked the length of primate juvenility to the timing of ecological (and social) skill acquisition (Poirier and Smith, 1974; Pereira and Altmann, 1985; Pereira and Fairbanks, 1993), more recent decades have seen an uptick in research focused specifically on juvenile diets and feeding behavior. Needing time-to-learn as an explanation for delayed maturity has given way to other hypotheses, such as those suggesting selection for primate encephalization led to slower life histories (e.g., developmental costs: Barrickman et al., 2008; Barton and Cappellini, 2011; cognitive buffer: Deaner et al., 2003; Sol, 2009). Others posit slower life histories as a consequence of primates' reduced energetic expenditure (Janson and van Schaik, 1993; Pontzer et al., 2014), with the ecological risk aversion hypothesis pointing to slow juvenile growth as the target of selection due to the associated survival benefits of reduced metabolic demand during the critical transition to nutritional independence when individuals likely are most vulnerable to starvation risks (e.g., higher infant/juvenile mortality: Altmann et al., 1985).

Greater juvenile risk linked to reduced foraging proficiency

Initial research on foraging ontogeny tended to focus more on infant rather than juvenile age classes (Post et al., 1980; Boinski and Fragaszy, 1989). As focus turned more toward juveniles in particular, results were equivocal as to whether juvenile diets and feeding behavior really differed all that much (Corp and Byrne, 2002; MacKinnon, 2006; Stone, 2006, 2007), and sometimes varied depending on whether the question involved what, where or how to eat. Age-related niche differentiation on a spatial scale within primate groups is possible, for example, when younger individuals capitalize on smaller body size by exploiting smaller foraging substrates too small to support adult body mass (e.g., Nakayama et al., 1999; Agostini and Visalberghi, 2005). However, for most group-living primates, it is often not necessary (or possible) for juveniles to make independent decisions regarding what or where to eat, and proximity to fellow group members provides ample opportunities for observation in foraging contexts and socially facilitated learning (van Schaik, 2003; Visalberghi and Addessi, 2003; Fragaszy and Visalberghi, 2004; Humle and Snowdon, 2008; Rapaport and Brown, 2008). This tends to minimize age differences in dietary composition, especially because immature individuals in proximity to foraging adults are more likely to explore, manipulate and consume similar foods (e.g., Whitehead, 1986; Addessi and Visalberghi, 2001; Tarnaud and Yamagiwa, 2008). Likewise, the early development of sex-typical foraging behaviors has been attributed to greater proximity to like-sexed adults (e.g., chimpanzee termite-fishing: van Noordwijk et al., 1993; Lonsdorf, 2005), and, in some cases, sex differences have outweighed age differences in feeding behaviors (e.g., tufted capuchins: Agostini and Visalberghi, 2005).

Indeed, many studies have found that juvenile diets (i.e., food items consumed, including mechanically challenging foods), and sometimes even foraging techniques, already closely mirror those of adults well prior to the end of the juvenile period marked by the transition to sexual maturity (Watts, 1985; Byrne and Byrne, 1993; Fragaszy and Boinski, 1995; Inoue-Nakamura and Matsuzawa, 1997; Lonsdorf, 2005; Stone, 2006; Nowell and Fletcher, 2008; Raguet-Schofield, 2010; Chalk, 2011). Infants moreso than juveniles have been reported to engage in play-feeding behaviors as well as intense observation of foraging adults (Tarnaud and Yamagiwa, 2008; Nowell and Fletcher, 2008), highlighting the importance of achieving basic foraging competence *prior* to rather than during the post-weaning period of nutritional independence. And yet more quantitative dietary descriptions have unearthed finer grained differences between juveniles and adults. In particular, juveniles exhibited reduced intake efficiency relative to adults when feeding on the same or similar food species, differences which may persist into mid- or late juvenility (Nakayama et al., 1999; Johnson and Bock, 2004; Sousa et al., 2009; Gunst et al., 2010 a; b; see also Chapter 3). Body size may constrain intake rates due to smaller gape size and bite volume (Perry and Hartstone-Rose, 2010; see also juvenile banded watersnakes: Vincent et al., 2006) or due to lesser manual or masticatory strength or even the impact of reduced molar surface area on processing times (Shipley et al., 1994; Wright et al., 2008; Chalk, 2011). Among tufted capuchins, Gunst and colleagues (2010) attributed age differences in processing behaviors to size-related constraints, particularly for hard or fibrous foods, but cited experience as the limiting factor for age differences in foraging success on foods requiring search and extraction (see also Johnson and Bock, 2004). In addition, competitive risks potentially slow feeding rates, for example, a captive study of rhesus macaques found that low-ranking juveniles had feeding bouts interrupted more often due to startle, which, in addition to lowering intake rates, the authors suggested also added to social stress for lower ranking individuals (Peláez et al., 2000).

Juvenile feeding strategies

These age differences in foraging success contribute differentially to tradeoffs in time allocation. Some studies have found that juveniles dedicate proportionally more time to feeding and/or foraging behaviors (Janson and van Schaik, 1993; Nakayama et al., 1999; Amato et al., 2014; but see Hanya, 2003; Johnson and Bock, 2004), possibly to offset their lower intake efficiency. Likewise, juveniles might concentrate feeding effort differently depending on their expected foraging success as well as specific nutritional requirements. For example, in juvenile chacma baboons, feeding proficiency on an item positively predicted the proportion of feeding time, such that juveniles spent less time feeding on difficult food resources (Johnson and Bock, 2004). Similarly, juvenile Japanese macaques in a predator-free environment consumed more animal matter while adult males relied more heavily on fibrous plant matter (Hanya, 2003), a difference that also might be mitigated by variation in protein content relative to digestibility. As Janson and van Schaik (1993) described, predation risk factors into behavioral tradeoffs, such that juveniles may accept higher competitive costs associated with foraging in the group center in exchange for the safety benefits that come with neighbor proximity. The expected net result of such strategies for juveniles would be to increase dietary similarity with adults by feeding from the same or nearby food patches, while also further encumbering intake rates due to increased social vigilance and faster patch depletion.

Metabolic demand in relation to age and growth

For all wild animals, energy intake (often measured as field metabolic rate) must cover the energetic costs of cell maintenance and repair, thermoregulation, losses to waste products via digestion and food detoxification, activity costs (i.e., locomotion, feeding, vigilance behaviors), and finally production (of new cells), that is growth or reproduction depending on maturity (Nagy, 1987). Across placental mammals, the ¾ power scaling factor typically describes the allometry of metabolic rate (Kleiber, 1961; Nagy, 1987, 1994; Savage et al., 2004; but see Glazier, 2005), meaning that smaller-bodied juveniles experience lower metabolic demand on an absolute basis yet require more energy per unit mass than larger adults. In addition, juveniles must divert energy toward growth. Adult females experience greater energetic costs during gestation and moreso during lactation, typically described for primates as averaging from 20 to 60 percent more than the energy expenditure of a non-reproductive female (Portman, 1970; Key and Ross, 1999). And even for slow-growing primates, the available data suggest that growth is as or even more costly than lactation, with daily energy requirements 30 to 50 percent greater per unit mass than those of adults (NRC, 2003; Nicolosi and Hunt 1979).

Recent research comparing adult and juvenile nutritional intake has shown that, on average, juveniles appear to maintain adequate energy balance and nutrient intake, with their relative daily values exceeding those of adults, particularly adult males (e.g., Japanese macaques: Hanya, 2003; mountain gorillas: Rothman et al, 2008; black howler monkeys: Amato et al., 2014). For gorillas, Rothman and colleagues (2008) specified that juveniles’ greater protein intake, for example, was achieved by consuming more per unit body mass rather than selecting for higher protein foods.

Juveniles' seasonal disadvantage

While juveniles' reliance on tactics such as spending more time feeding or targeting "easier" foods facilitates sufficient nutrient and energy balance when foods are relatively abundant, they likely are less effective during periods of seasonal shortage when social tolerance declines and competition increases across all ages (Janson and van Schaik, 1993). In a highly seasonal environment characterized by winter energy deficits, Nakayama and colleagues (1999) found that both juveniles *and* adult females significantly increased feeding time during the lean winter months, but for juveniles, this was in addition to already higher annual feeding rates. Both age classes experienced energy deficits during this extended period of resource scarcity, and the authors suggested that the animals survived by relying on energy stores from fat. However, as fat relative to body mass typically increases with age (i.e., age reduction in fat-free mass: NRC, 2003), the younger individuals would have had lower so-called energy stores, making them more vulnerable to starvation. Indeed, the youngest juveniles – those just transitioning to nutritional independence – appear to suffer the greatest mortality during lean periods (e.g., Altmann et al., 1985).

Again, slow and flexible growth rates likely alleviate some of this nutritional burden, and experimental research has shown significant growth-rate responses to energy and/or protein supplementation and restriction (e.g. rhesus macaques: Terasawa et al., 2012; heifer calves: Brown et al. 2005; deer mice: McAdam and Millar, 1999; rats: Parks, 1970). Growth rates varied according to food availability for wild baboon troops living in different environments (Alberts and Altmann, 2005). Among primates in seasonal environments, researchers found evidence for growth-rate suppression during leaner seasons, particularly in faster-growing taxa (e.g., ring-tailed lemurs: Pereira, 1993; golden lion tamarins: Dietz et al., 1994).

Of course, while limited food resources constrain growth, improved nutritional intake can result in accelerated growth velocity (catch-up growth) (Prader et al., 1963; Boersma and Wit, 1997; Farnum et al., 2003). However, there is debate as to whether catch-up growth can fully compensate and allow an individual to attain typical adult size (Kerr and Waisman, 1970; reviewed in: Boersma and Wit, 1997). Mounting evidence suggests that catch-up growth has significant fitness consequences in terms of longevity and reproductive success (Metcalfe and Monaghan, 2001; Mangel and Munch, 2005; but see: Lochmiller et al., 2000). More importantly, perhaps, slower growth rates are associated with later ages at sexual maturity (McAdam and Millar, 1999; Setchell et al., 2001; Johnson, 2003; Altmann and Alberts, 2005). Thus, while flexible growth responses likely mitigate nutritional stress, there are associated costs. Altmann's work with yearling baboons so effectively demonstrated the importance of dietary quality at a young age and the costs of a relatively poor-quality diet early on to eventual long-term fitness (Altmann, 1991; 1998).

Folivores and seasonal stress?

In terms of the ecological risk aversion hypothesis, folivorous primates, with a diet comprised of more abundant and evenly distributed resources, should face diminished starvation or nutritional risk, allowing for faster developmental rates (Janson and van Schaik, 1993). Support in this regard is equivocal: while captive folivorous anthropoids grew at faster rates than non-folivores (Leigh, 1994), folivorous versus frugivorous lemurids exhibited the reverse pattern (Godfrey et al., 2004). In addition, developmental life history pace did not differ according to dietary category for Asian colobines relative to macaques (Borries et al., 2011). More and more, in fact, research on folivore feeding ecology suggests active within and between group competition for food (reviewed in Snaith and Chapman, 2007) as well as seasonal shifts in resource availability (Dasilva, 1992; Koenig et al., 1997; Sayers and Norconk, 2008).

Thus, even among folivores, the potential for ecological risks likely varies according to degree of dietary diversity or flexibility and environmental seasonality. For example, Wasserman and Chapman (2003) studied multiple groups of red colobus and black-and-white colobus and determined that no group was energy-limited. In contrast, gray langurs in Nepal experienced seasonal reductions in resource availability and energetic intake, resulting in increased travel times and reduced nutritional condition for adult females (Koenig et al., 1997; Koenig and Borries, 2001). Furthermore, nutritional condition affected reproductive cycles and likelihood of conception (Koenig et al., 1997; Ziegler et al., 2000; Koenig and Borries, 2001) and reproductive rates for this population were suppressed compared to a food-provisioned population (Borries et al., 2001), suggesting fitness consequences related to nutritional stress. Seasonal shortages often lead to dietary shifts toward non-preferred resources (e.g., fallback foods: Doran-Sheehy et al., 2009; Marshall et al., 2009), which can result in a greater proportion of or reliance on mechanically challenging foods (e.g., capuchins: Wright et al., 2009; mantled howler monkeys: Raguet-Schofield, 2010), with potentially greater detrimental effect on juveniles.

Study goals

In an effort to gauge the relative nutritional and energetic adequacy of the juvenile diet, this study compared the nutritional ecology of juvenile and adult Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*). These medium-sized colobines exhibit seasonal variation in dietary composition (Aziz and Feeroz, 2009; Suarez, 2013), with considerable feeding time dedicated to consuming young leaves, but also to mature leaves and unripe seeds, foods typically characterized by greater mechanical demand. Juvenile Phayre's leaf monkeys have lower bite-rate efficiency than adults, and younger juveniles, in particular, are adversely affected by food toughness, yet they do not appear to avoid the tougher resources. Therefore, I explored whether juvenile nutritional strategies and presumed ability to meet nutritional requirements varied according to dietary fiber content and toughness as well as in relation to changes in energy and protein content. I made two main predictions in this regard: First, I expected juveniles to have lower overall intake rates than adults per time spent feeding as well as greater proportions of time spent feeding as a strategy for ensuring equivalent nutrient intake. Second, if plant defenses are a greater hindrance to juvenile intake, I predicted steeper negative slopes (significant interaction effect) between nutrient intake and both fiber intake and dietary toughness at younger ages. Although fracture toughness should correlate with fiber content for foods such as leaves, seed predators, such as Phayre's leaf monkeys, often discard rather than consume the toughest parts of a plant. In addition, as the external indicator of a potential food's mechanical characteristics, fracture toughness may actually serve as a better predictor of food selection than fiber content (Hill and Lucas, 1996). Next, because juveniles have greater energetic requirements per unit of body mass, I expected that juvenile energy and protein intake scaled for metabolic mass would exceed that of adults. Lastly, if juvenile growth rates are sensitive to changing nutritional risk, then seasonal or individual variation in energy and/or protein intake should predict relative growth rate controlling for age.

Methods

Study site and subjects

This study took place at the Phu Khieo Wildlife Sanctuary (PKWS) in northeastern Thailand. Within this 1,570 km^2 park, the 1,300-ha study site (16°27'N, 101°38'E) is an area of dry and hill evergreen forest with patches of dry dipterocarp forest (Grassman et al., 2005; Koenig and Borries, 2012). Annual temperature averages 21.2°C and annual rainfall averages 1,144mm (Borries et al., 2011), with a dry season typically occurring between November and March. I collected behavioral and food nutritional data from three habituated groups of Phayre's leaf monkeys for 17 months between October 2006 and May 2008. Here I used data from three time blocks (January through March 2007, July through September 2007, and February through May 2008) representing aspects of seasonal variation at the site: on an annual cycle, January and February encompass the late dry season with a generally low availability of flowers and fruits, plant-flowering characterizes March and April, July and August overlap with the end of a peak in fruit abundance, and the seasonal availability of bamboo shoots peaks in September. Complementary detailed focal observation of adult subjects began in July of 2007, therefore, nutritional comparisons by age class were restricted to the latter two blocks (n=24 focal individuals in mid-2007; 25 in 2008).

Focal subjects included all juveniles and sub-adults present in the three study groups and a subset of adults from each group (Table 3.1 and 3.2). Because breeding is mildly seasonal in this population – most births occur between November and April (Koenig and Borries, unpublished) – birth cohorts were used to assign immatures to one of three age classes: younger juveniles (J1s), older juveniles (J2s), and sub-adults. Based on the age ranges of cohort members within each observation block, I set the cut-off age marking the transition from younger to older juvenile after 25 months, which is about 4 months younger than the 2.5 years used in previous chapters. This has the added benefit of restricting the J1 category to better represent the period of initial nutritional independence. Of course, weaning is a gradual process rather than an abrupt transition (Lee et al., 1991; Lee, 1999; Borries et al. 2014). Individuals from the same birth cohort varied in their weaning ages, and therefore, at times, focal animals were still observed in nipple contact. However, because I cannot account for the nutritional contribution of time spent suckling, for these analyses I excluded individuals from the sample until focal animal sampling indicated zero time in nipple contact. The three youngest J1 subjects were actually two to three months younger than average weaning age of 19 months, yet all three had younger siblings and were never observed in nipple contact. However, an individual from the same birth cohort was still regularly in nipple contact (24.8% of focal time during the 2008 block) and was therefore excluded from these analyses. This is the only age class for which subjects shift across observation blocks: by 2008, the focal J1s from the 2007 period were older than 2 years of age and therefore considered J2s. In 2008, the focal J1s comprised individuals who were still considered infants in regular nipple contact during the 2007 observation block.

With the 2-year starting age, the older juvenile sample averaged 33.6 months of age (range: 26 to 45 months, n=9 per observation year). Subjects from the oldest birth cohort in the sample were all older than 4 years during this period and were considered sub-adults (mean age=54 months; range: 49-65 months, n=6). The sub-adult age class was comprised mainly of natal males as most older females had emigrated from their natal groups (average dispersal age is approximately 4 years: Larney, 2013). There were two exceptions: In early 2007, an older natal female (B4.1) was sampled prior to emigrating (presumed) at age 48 months and a known-aged non-natal female (S2.1) from the same birth cohort dispersed between habituated groups and was sampled during the 2007 collection period . Again, age class transitions are difficult to define and, by the 2008 period, some of the older sub-adults arguably could have been considered young adults. However, there was a minimum of a 2-year age gap between the oldest sub-adults and the youngest adult male (known age) and female (estimated age based on study population average age at first birth (5.3 years: Borries et al., 2008)). In addition, although both males and females in this age class had attained or were close to attaining adult limb length (Chapter 4), most primates, males especially, continue to grow in muscle mass beyond cessation of statural growth (e.g., Setchell et al., 2001), therefore, metabolically, these individuals were distinct from full-grown adults.

The adult sample was comprised of three males and five females all of unknown age except for the youngest adult male (Am5.1) – a natal male between 6.5 and 7.2 years during this timeframe. For the two older adult males (M3 and M4), I estimated minimum ages of at least 10 years based on their initial descriptions as sub-adult or young adult when first observed in 2001 (Borries and Koenig, pers. comm.). Rough ages were estimated for adult females by using the average age at first birth (5.3 years: Borries et al., 2011) as a starting age from the birth month of the presumed first offspring, resulting in an age range of 6.7 years to just over 10 years of age. Adult female reproductive status, including conception dates, could be reconstructed retroactively based on offspring birth dates and known gestation length (Lu et al., 2010; Borries, pers. comm.). For both observation periods, the majority of females was neither pregnant nor in early lactation (i.e., no infants younger than 6 months, the time when lactation is presumbably the costliest). Again, there were two exceptions: the 2007 observation period coincided with early gestation for one female (S5), and the 2008 period with early lactation (infant age 2-6 months in nipple contact) for the same female and gestation for a second female (S2) whose conception date was in March 2008.

Data collection

Focal feeding data and intake rates

I collected feeding data via focal animal sampling with a combination of instantaneous and continuous recording (Martin and Bateson, 2007). I chose focal subjects by adhering as closely as possible to a monthly pre-assigned semi-random order. Days were divided into seven roughly 90-minute blocks between 6:45 and 17:45 and each focal individual was sampled at least once per block per collection period for a total of 576.3 focal hours across the 10 months (453 hours from the dataset with adults; monthly means: 2.3 focal hours per adult; 2.6 hours on average per non-adult).

During each 20-minute sample, I recorded feeding bout start and stop times continuously. Activity was noted at one-minute intervals, and more specifically, during feeding bouts, I noted whether the focal animal was actively feeding (i.e., putting hand to mouth or masticating food), reaching for food, or handling food (i.e., oral or manual manipulation to access food parts). In addition, I recorded plant category (e.g., fruit, leaf, flower, etc.), part (e.g., whole, pulp, seed, petiole) and maturity as well as the plant species. Unknown plants were collected for later identification. During feeding bouts, bites per minute were counted for at least three consecutive minutes whenever visibility allowed. Counts were truncated if active feeding stopped or was interrupted by searching or handling for more than several seconds. After three minutes, counts and additional behavioral data were noted, and then counting would resume at the start of the next minute if the animal was still feeding and visibility allowed. A bite was defined depending on the food item: as hand-to-mouth motion for most leaves with number of leaves noted when possible, as whole items for small fruits and flowers, and as the proportion of fruit consumed per time interval for larger fruits (Barton and Whiten, 1993; Janson and van Schaik, 1988; Johnson and Bock, 2004; Stone, 2004). When differences in bite size were noted, intake rates were scaled accordingly. For example, if leaves were typically eaten one at a time but a juvenile ate only half a leaf per bite, the juvenile's bite rate was halved. If variation in bite size was suspected during an observation period but could not be accurately determined due to poor visibility, those counts were excluded. All others were left unstandardized.

Using collected plant samples, I replicated observed bite sizes (i.e., whole items or a cluster of smaller items) ten times and weighed these to determine the average wet weight per bite or food unit. These weights were multiplied by number of bites or items eaten per minute and by time spent feeding to obtain individual wet weight intakes (g/min). For determining individual intake, I used an individual's average bite rate if the number of bite counts and feeding time were roughly equivalent, for example, 14 minutes spent feeding and 12 bite counts. Typically, this was more likely for short feeding bouts of fewer than five minutes. Otherwise, I substituted the average bite rate for a particular age class or birth cohort. In the previous chapter investigating size-related constraints on intake efficiency, adults and sub-adults were pooled citing the definition of sub-adults as having attained head-body length equivalent to adult females. For determining overall nutrient intake, however, I have calculated sub-adult bite rates separately whenever possible to account for any possible social or competitive constraints influencing their intake rates. Each age class averaged at least 10 separate bite counts per food for the foods included here (80 items or more depending on age class).

Plant nutritional analysis and calculating nutrient intake

With the help of assistants, I collected plant samples immediately following feeding bouts whenever possible. To obtain sufficient sample sizes, we often had to mark and re-visit patches within the week for additional collection. We always made the effort to collect plants from the same or a nearby patch as well as of the same maturity as what was eaten by the monkeys. Plant items were processed to match only the parts eaten by the monkeys. For example, when feeding on seeds, the monkeys not only discarded the husks but, in some cases, also spit out the thin seed cases. These samples then were dried in a field oven at approximately 40° - 55°C until the dry weight remained constant. After drying, samples were packed air tight and stored with silica gel until they could be transported to the Animal Science Department at Kasetsart University in Bangkok where samples were analyzed for macronutrient content (crude protein (CP), lipids(LP), neutral detergent fiber (NDF), ash and moisture). Crude protein was measured via the Kjeldahl procedure as total nitrogen times a 6.25 conversion factor. Lipid content was determined using petroleum ether extraction, and the neutral detergent fiber fraction was measured via detergent fiber analysis (van Soest et al., 1991; van Soest, 1994). The laboratory at Kasetsart University repeated the analyses three times per sample and reported the average values. For the observation period analyzed here, nutritional data were available for 95 distinct food items from 70 species, accounting for an average of 82.7 percent of the diet. Effort was made to re-collect and re-analyze items eaten frequently over time or consumed in different seasons or years, resulting in a total of 118 samples.

To estimate metabolizable energy, I first calculated the dry matter percentage of total non-structural carbohydrates (TNC) as the difference after subtracting each nutrient measure from 100%: TNC% = 100-%CP-%LP-%NDF-%ash. Following Conklin-Brittain and colleagues

(2006), the energetic contributions from protein, fats and carbohydrates were weighted according to physiological fuel values based on human energetics (National Research Council, 2003): 4 kcal/g protein, 4 kcal/g carbohydrate and 9 kcal/g fat. Lastly, I incorporated the energetic contribution from fiber fermentation by using a genus-specific fiber digestibility coefficient; Nijboer and Clauss (2006) reported an average NDF digestibility of 59.1% for three *Trachypithecus* species (*obscurus*, *auratus* and *francoisi*) based on feeding experiments using natural browse to better equate the fiber content of wild diets. Conklin-Brittain and colleagues (2006) used 3 kcal of available energy/g fiber after subtracting 1kcal/g lost to anaerobic microbial activity. This value is weighted by the NDF digestibility coefficient of 0.591 to get an overall physiological fuel value of 1.77. The final equation for estimated metabolizable energy is:

EME (kcal/g) = [(4*%DM TNC) + (4*%DM CP) + (9*%DM LP) + (1.77*%DM NDF)]/100

Rothman and colleagues (2012) suggested that alternative coefficients based on data from small ruminants rather than human-derived data may be used for colobines due to digestive similarities, they concede that the issue requires further research and substituting data from small ruminants may not be appropriate. Thus, the estimates used here may underestimate metabolizable energy by excluding potential energy from fermentation, however, this would be more of a concern for cross-species comparisons rather than the within-species comparisons carried out in this chapter. Of greater concern, when comparing age classes of different body size, is the possibility that size-related differences in gut capacity will affect dietary digestibility (Demment and van Soest, 1985). However, a recent comparative analysis of 19 primate species found no significant correlation between mean retention time (i.e., time available for digestion) and body mass (Clauss et al., 2008), although this was across dietary types. More importantly, analysis of fecal ADL (acid detergent lignin) in mountain gorillas detected no difference in dry matter digestibility across adult males, adult females and juveniles, suggesting a lack of age-related differences in digestive efficiency despite significant body size differences (Rothman et al., 2008), although it is possible that the situation might be different in a foregut fermenter such as a colobine monkey.

Monthly energy and nutrient intake on a dry matter basis was determined for each focal animal by multiplying 1) the age-class-specific number of bites or items per minute, 2) the weight of that item (g DM based on the proportion of moisture-corrected dry weight) 3) the number of minutes spent feeding on that food, and, finally, the property of interest: a) energy (kcal/g DM), b) CP (%DM/100), c) NDF (%DM/100). For each focal animal, total energy or nutrient intake was pooled for each month and divided by the number of focal hours. Not all foods in the leaf monkey diet were analyzed for nutritional content. Therefore, individual data points were excluded from analysis if less than 65 percent of the diet was accounted for in that given month or time block.

Dietary toughness

Between December 2006 through March 2007 and again from February through May 2008, I collected data on the toughness of leaf monkey foods using a portable mechanical tester kit (Darvell et al., 1996; Lucas et al., 2001). Mechanical testing required far less for testing than was required for chemical analyses; typically plant samples were collected either from fallen foods as the monkeys ate or gathered directly from the patch or tree after the group had moved. All samples were tested fresh within 24 hours or less of collection following Teaford and colleagues (2006). For most leaf monkey foods, toughness (R, in Joules/m^2) was measured via a scissors test, although pulpy fruits and larger seeds were tested with the wedge test. In either case, effort was made to test at least two samples per food or food tissue when tissues could be separated and tested individually (e.g., fruit endosperm, endocarp, mesocarp and exocarp). The protocol for testing leaves with multiple cuts followed Dominy and colleagues (2003; see also Lucas et al., 2001). See Chapter 2 for additional details. For all food types, values for multiple tissues or leaf parts were averaged and used to determine the overall average and the maximum toughness values per food item (n=115 food items, 77 species). For the early 2007 and the 2008 observation blocks, I estimated individual dietary toughness by matching each food item in an individual's diet with the corresponding maximum dietary toughness (if available for that item). The toughness values were weighted by the number of minutes the individual spent feeding on that item in that month. Weighted values were summed across each individual's monthly diet and divided the total number of minutes spent feeding.

Metabolic scaling and estimating body mass

To control for size-related metabolic differences, I created a second set of intake variables by dividing hourly intake rates by metabolic body mass (MW) (Table 3.3). Here I have relied on the ¾ power scaling factor for body weight ($W^{0.75}$)(Kleiber, 1961; Savage et al., 2004). Although I recognize that some researchers have questioned the universality of the ¾ exponent within narrower taxonomic clades, including for primates specifically, as well as for intraspecific ontogenetic scaling (Bokma, 2004; Glazier, 2005; Snodgrass et al., 2007), without detailed metabolic data across age classes and across multiple colobine species, I chose to follow standard practice. First, adult body mass was taken from the literature (females: 6.3kg, males: 7.87kg: Smith and Jungers, 1997). Bolter (2004) has reported body mass for immature male and female silvered langurs, a closely related species. These would likely underestimate juvenile size for the Phayre's leaf monkey sample because adult silvered langurs are smaller (females: 5.8kg, males: 6.6 kg). Similarly, using the distal lower limb lengths measured for all non-adult focal animals in this study population (Chapter 4) to determine a percentage of adult size achieved would likely overestimate juvenile mass owing to the fact that skeletal lengths mature to adult size earlier than does body mass. Therefore, assuming growth patterns are similar between the two species, I used silvered langur data to create a length-to-mass conversion factor. In addition to body mass, Bolter (2004) also reported for silvered langurs the percentage of adult tibial length achieved for each of three age classes (Class 1: 1-2 years, 2: 2-3 years, 3: 3-3.75 years; ages dentally determined). Using these data, I calculated a ratio based on the percentage of adult tibial length achieved divided by the percentage of adult mass achieved. For example, 2-3-year old male tibial length was 82 percent of adult length but average mass for that age class was 46.2 percent. The ratio of 82 to 46.2 provided a scaling factor of 1.77. Then for the Phayre's leaf monkey sample, I divided percent of adult length attained by the age-class-appropriate conversion factor to estimate a percent of adult weight attained. The resulting proportion multiplied by the published adult male or female weight provided an estimate of average juvenile body mass. Because growth velocity decelerates with age, conversion factors were calculated for each of the three age classes available in the published literature and applied based on average age of each birth cohort and sex for each sampling year. For example, during the 2008 sampling period, older J2 males from my sample had achieved approximately 85.2 percent of adult distal lower limb length. Dividing this percentage by the 1.77 scaling factor suggested J2 males were roughly 48.1percent of adult mass (7.87kg), resulting in an estimated body mass for J2 males of 3.78kg. For comparison, juvenile silvered langurs at 59 percent of adult mass were roughly

3.6kg. This conversion was performed based on average limb length for males and females of each birth cohort in each sampling year.

Measuring and modeling limb growth

I used non-invasive photogrammetric methods (primates: Emery and Whitten, 2003; Deschner et al., 2004; Breuer et al., 2007; Rothman et al., 2008; whales:Jaquet, 2006; elephants: Morgan and Lee, 2003; Shrader et al., 2006) to estimate distal lower limb length for all juvenile and sub-adult focal subjects at regular intervals between November 2006 and September 2007 and again between February and May 2008. Prior to fieldwork, segments of known length were photographed at each of seven different distances and digitized to determine a centimeter-to-pixel relationship via OLS regression (Shrader et al., 2006). I relied on this relationship, along with distances from the camera to the subject measured using a high-precision laser distance meter, to predict a photograph-specific conversion factor, which I then used to convert pixel counts measured in Image J (version 1.46r) to length in centimeters. I took digital photographs in the field opportunistically whenever subjects descended to roughly observer eye-level, that is, a height perpendicular to my (the camera's) horizontal plane of vision. Photographs were carefully screened in an effort to use only those for which the subject and camera height were in horizontal orientation as well as those with parallel orientation of the limb segment. Ultimately, 726 photographs (mean within-photo CV = 0.864%, SE=+/-0.021, between-photos: mean CV = 0.926%; range: 0.002 – 3.12, n=110) were used to determine limb lengths for 35 non-adult, known-age Phayre's leaf monkeys. On average, each individual contributed 6.7 monthly measures to the dataset (range: 1-13 datapoints per individual). See Chapter 4 for further details on the methods and potential error associated with counting and converting pixels to centimeters.

Data analysis

Feeding/intake variables. To compare intake by age or age class, I employed linear mixed effects models in the "lme4" package (nmle: Pinheiro et al., 2012) in R 3.1.0 (R Core Team, 2014) including individual nested within group as well as month as random factors. Although typically month was included as a random factor due to likely temporal autocorrelation, when testing for seasonal effects, month was used as a fixed factor I used age as a continuous variable in the longer 10-month dataset of known-aged immatures and age class as a fixed factor in the smaller 7-month dataset including adults. To determine the significance of age or age class to the overall model, I used likelihood ratio testing to compare each full model to a null model excluding age or age class as a factor but retaining random factors. The latter adult-included dataset comprised the majority of comparisons, and I conducted post-hoc tests for pairwise differences in age classes by using the "multcomp" package (Hothorn et al., 2008) in R with Holm's method for p-value adjustment. When testing proportional data (i.e., dietary proportions by food type or proportion of observation time spent feeding), I used either logit transformations or generalized linear mixed models with a Gamma distribution. When datasets contained zeros, I added a small constant (0.001) to each value and then ran generalized linear mixed models on otherwise untransformed data in the MASS R package (Venables and Ripley, 2002) using the glmmPQL function, which uses a penalized quasi likelihood procedure for parameter estimation (Bolker et al., 2009).

Intake relative to growth rate. For focal individuals with sufficient longitudinal data, I fit individual growth curves using natural cubic spline regression using the "splines" package, which requires a minimum of 4 datapoints for curve fitting (mean number of datapoints per individual = 8.1 monthly length measures, range =6-12, n=14 individuals). Individual growth velocity data (i.e., first derivatives) were calculated using the “sfsmisc” package (Maechler et al., 2014). To standardize growth velocity relative to age, the dependent variables were residuals from a cubic regression of velocity on age. Because growth velocity was highly dependent on neighboring data points, residuals were averaged and intake values were pooled across observation blocks. Individual intake was paired with growth velocity in subsequent months, that is, if an individual’s average velocity with an observation block was based on limb measures from February and March, then intake values were pooled for January and February. In most cases, data were log-transformed and standardized as z-scores prior to analysis. Residual diagnostics suggested the data adhered to assumptions of parametric testing (i.e., normality, homoscedasticity, independence). Tests were two-tailed and alpha values were set at $p<0.05$.

Results

Dietary composition and monthly variation

Dietary proportions by food type based on wet weight intake varied across months (Figures 3.1 and 3.2), but the pattern of monthly variation was similar across age classes. I found no significant age-class difference across seven months in the proportion of dietary wet weight made up of young leaves (F = 1.74; likelihood ratio test comparing full vs. null model: $X^2 = 2.17$, df=12, $p > 0.9$), mature leaves (F = 0.362; $X^2 = 1.062$, df=12, $p > 0.9$), whole fruits or pulp (F = 1.80; $X^2 = 2.106$, df=12, $p > 0.9$), seeds (F = 2.61; $X^2 = 4.82$, df=12, $p > 0.9$), or flowers (F = 0.384; $X^2 = 0.937$, df=12, $p > 0.9$).

Despite monthly variation in food type, I found no seasonal effect in the shorter 7-month dataset on any of the intake variables (i.e., energy, crude protein or NDF intake all scaled for metabolic weight) for adults and sub-adults only (energy: $F_{(6, 65.99)} = 0.311$, $X^2 = 2.06$, df=6, $p >$

0.91; crude protein: $F_{(6, 64.47)} = 0.702$, $X^2 = 4.572$, df=6, $p > 0.5$; and NDF: $F_{(6, 65.99)} = 1.65$, $X^2 = 10.33$, df=6, $p = 0.11$). As Table 3.4 highlights, with the exception of fat content, nutrient and energy content tended to be relatively consistent across broad food categories. Likewise, when using the 10-month dataset of known-aged non-adults, controlling for age as a continuous variable, energy intake again did not significantly vary across months (LMM of energy: $F_{(9,123.81)} = 1.68$, n = 143 observations; likelihood ratio test with and without month: $X^2 = 14.99$, df=9, $p = 0.091$, Figure 3.3). However, crude protein intake did show significant monthly variation (LMM of protein: $F_{(9,122.88)} = 3.35$, n = 143 observations; likelihood ratio test with and without month: $X^2 = 28.015$, df=9, $p < 0.001$, Figure 3.4) as did NDF intake (LMM of NDF: $F_{(9,131.98)} = 5.67$, n = 143 observations; likelihood ratio test with and without month: $X^2 = 47.816$, df=9, $p < 0.0001$, Figure 3.5). Crude protein intake was lowest in January 2007, a month when the leaf monkeys consumed a relatively high proportion of seeds. The only significant pairwise differences were between January and March 2007 ($p < 0.01$) as well as April 2008 (p=0.011). NDF intake was higher in July and September 2007 and April 2008 but, of those months, July's intake was far and away the highest and, except for September and April, differed significantly from every other month in pairwise comparisons (see Table 3.5, Table 3.6a-c).

Age differences

On average, juveniles consumed less food (measured in grams of wet weight per hour) than did sub-adults and adults: J1s: 38.85g (SE= 2.89), J2s: 40.08g (SE= 2.42), sub-adults: 55.58g (SE= 4.81), adults: 48.10g (SE= 3.66) ($F= 3.048_{(3, 135.1)}$, LRT: $X^2 = 9.09$, df=3, $p = 0.028$). However, inspection of pairwise tests indicated that age class differences were actually less than predicted and, in fact, only sub-adults and J2s showed a significant pairwise difference in wet weight intake ($p = 0.03$; all other pairs: $p>0.2$, adjusted *p*-values). Controlling for proportion of time spent feeding shed some light on age-class differences: at a particular feeding time, adults had significantly greater intake than either J2s or J1s ($p < 0.0001$) but their intake was not significantly different from sub-adults ($p=0.289$) (Figure 3.6). For younger juveniles, feeding time never dips below a threshold of about 24 percent of observation time, and, indeed, both younger and older juveniles spent significantly more time feeding compared to adults (age class: $X^2 =16.8$, df=3, $p < 0.001$), Figure 3.7, Table 3.7).

In testing for age-related variation in nutrient and energetic intake, I first included sex in the model along with age class. Sex was not a significant effect based on model comparison via likelihood ratio tests (model with sex: AIC= -53.6, df =18; model without sex: AIC=-55.37, df=17, $X^2 = 0.234$, p=0.629), therefore, I excluded sex from all models. However, because some adult females may experience greater reproductive costs than males (see Methods), I typically separated adult males and females and presented both for illustrative purposes.

Energy and nutrient intake. In comparison to adults and sub-adults, juveniles, younger juveniles especially, had significantly higher hourly energy consumption per kg of body mass (age class: $X^2 =17.694$, df = 3, $p < 0.001$; Figure 3.8, see Table 3.7). Likewise, juveniles had significantly greater crude protein intake for their metabolic mass ($X^2 = 27.473$, df=12, $p < 0.01$, Figure 3.9, Table 3.7). The pattern was fairly consistent across all months with one exception: in September, 2007, younger juveniles exhibited lower intake of both energy (Figure 3.10a; $X^2 = 8.66$, df=3, $p = 0.34$; J1s < J2s ($p=0.015$) and J1s<adults ($p < 0.001$)) and protein (Figure 3.10b; $X^2 = = 5.395$, df=3, $p=0.145$). It is important to note that post-hoc testing within each month would require a correction for the familywise error rate, which would set alpha below the *p*-values reported here.

The pattern shifted somewhat for NDF intake with no significant age difference in metabolically scaled rates (X^2 = 12.062, df=12, p >0.4, Figure 3.11). In testing fiber intake as a potentially disproportionate deterrent on juveniles, I found no evidence of an interaction between NDF rates and age class on either time spent feeding or on energy or protein intake (likelihood ratio test of model with interaction vs. no interaction: feeding time: X^2 = 3.35, df=3, p > 0.3; energy: X^2 = 0.659, df=3, p > 0.8 (Figure 3.12); and protein: X^2 = 2.579, df=6, p > 0.4 (Figure 3.13). However, incorporating weighted dietary toughness offered additional insight. Toughness data were not available during the July – September period, therefore these analyses are based on the early 2007 plus 2008 time period. With toughness as the covariate instead of NDF intake, I still found no significant interaction with age on feeding time; instead, feeding time increased significantly with increasing dietary toughness across all non-adult ages (with and without toughness: X^2 = 16.63, df=1, p<0.001, Figure 3.14). Just as with NDF rates, there was no significant relationship between toughness and either protein intake or energy intake, nor was there an interaction effect on age. However, dietary toughness was a nearly significant negative predictor of NDF intake : (X^2 =5.94 df=2, p=0.051). Visual inspection of the plot (Figure 3.15) suggested that with increasing dietary toughness, J1s' fiber intake decreased more rapidly, however, after controlling for random factors, the likelihood ratio test comparing the models with and without an interaction effect was not significant (X^2 = 2.23, df=1, p=0.136).

Intake and growth velocity. Finally, contrary to predictions, individual growth velocity residuals did not appear to exhibit a coordinated response with either energy intake (LRT of model vs. null model: X^2 = 0.217, df=1, p>0.6, Figure 3.16) or crude protein intake (X^2=0.223, df=1, p>0.6, Figure 3.17).

Discussion

This study demonstrated the ability of juvenile colobines to exceed adults in their energetic and protein intake scaled for metabolic differences. Generally, this seemed to be achieved by a combination of increased time spent feeding as well as the relative reduction in metabolic demand due to smaller body mass and slower growth, in line with predictions from the ecological risk aversion hypothesis. Despite some seasonal variation in dietary composition over the longer time span, juveniles' dietary proportions by broad food category did not differ from adults, suggesting, at least indirectly, that they did not seek out higher quality foods.

Age differences

Juveniles devoted significantly more time to feeding than older age classes; and only with feeding effort held constant did their hourly wet weight intake drop significantly below that of sub-adults and adults. Thus it seems that juveniles, younger juveniles especially, compensated for lower feeding efficiency via ramped-up feeding effort, a tactic employed by juveniles in other primate species as well (e.g., Nakayama, 1999; Amato et al., 2014). For a species with a mechanically demanding diet such as Phayre's leaf monkeys, increased feeding effort may be the key to meeting energetic demand for juveniles. Overall, they were successful: both younger and older juveniles consumed significantly greater energy and protein per unit body mass than adults.

For fiber intake, the consistent pattern shifted such that juveniles' rates of NDF intake were similar to those of adults and sub-adults. Similarly, juvenile mountain gorillas consumed significantly more energy per metabolic mass than both adult females and silverback males, but exhibited less pronounced differences for both protein and fiber intake: juveniles differed from silverbacks but not significantly from adult females (Rothman et al., 2008). Juvenile mantled howler monkeys also had higher relative macronutrient intake compared to adult males but did not differ from adult females (Amato et al., 2014).

Compared to these two taxa, Phayre's leaf monkeys exhibited more pronounced differences between juveniles and both adult sexes rather than just males. The authors attributed the greater similarities between adult females and juveniles in their study to the shared elevated energetic demand of growth and reproduction, particularly lactation and gestation for adult females. Rothman (2008) also concluded that the higher rates in juveniles and adult females were not due to those individuals selecting for higher quality foods but rather related to the metabolic benefits of reduced body size, which are drastically different for highly sexually dimorphic gorillas. Although much less extreme, *Alouatta pigra* also exhibits greater mass dimorphism than do Phayre's leaf monkeys (1.77 vs 1.07: Smith and Jungers, 1997). The contrast therefore demonstrates the key role of body mass in alleviating nutritional risks while also emphasizing the importance of incorporating meaningful size differences for accurately evaluating age-specific energetic and nutritional success.

Seasonal constraint?

The findings here suggest that juvenile diets for Phayre's leaf monkeys, on a broad scale, have higher protein-to-fiber ratios than either adults or sub-adults, though it is unclear whether this is a result of active selection or constraint. Despite seasonal variation in dietary toughness and, to a lesser extent, NDF intake, neither juveniles nor adults for that matter suffered any corresponding reduction in energetic or protein intake. Instead, young juveniles, older juveniles and sub-adults alike all increased feeding time with increasing dietary toughness. Similar increases in lean-season foraging effort and feeding time have been described for other taxa (e.g., Nakayama, 1999; Stone, 2007). At least for the leaf monkeys, increased effort seemingly enables them to maintain relatively consistent energetic intake despite seasonal variation in plant parts available and consumed. However, months characterized by greater dietary toughness also had significantly lower intake of NDF (e.g., January 2007), and, although not significant, the relationship appeared to be strongest for younger juveniles. This could be an indicator of reduced juvenile efficiency, if, when foods are both tough and higher in fiber content, this youngest age class exhibits a stronger negative response despite equivalent increases in feeding effort. In addition, it is important to recognize that increased feeding effort and activity has energetic costs, likely resulting in greater variation that was has been accounted for here by excluding comparative measures of energy expenditure.

Weighted dietary toughness peaked in January, 2007, yet younger juveniles did not appear to suffer energetically that month with scaled intake still exceeding that of sub-adults (no adult focal data available from early 2007). Instead, the one exception arose in September, 2007, when intake per metabolic mass of younger juveniles actually dipped below other age classes. This month was one of three with relatively higher NDF intake across the 10 months. July had far higher NDF intake, but in July a greater proportion of the diet was whole fruits and pulp. Instead, September was characterized by greater reliance on bamboo shoots and *Afzelia xylocarpa* seeds, both of which may present challenges to young juveniles. *Afzelia* seeds were the one food that younger juveniles were never observed actually consuming. Although some younger juveniles made attempts, the large pods were eventually always dropped unopened. At other times, J1s sat in close proximity to adults (usually mothers) feeding on *Afzelia*, observing or, when possible, stealing scraps of dropped or discarded fibrous mesocarp. As for bamboo, leaf monkeys specialized on the very soft, young bamboo shoots, and mechanical data from a previous year indicated these shoots had rather low toughness (mean=381 J^*m^{-2}). In terms of actual feeding time, bamboo ingestion rates did not differ greatly across age classes. Yet foraging for and processing bamboo prior to eating is time-consuming as well as risky as it requires the individual to descend to the ground to retrieve the just emerging shoot – all factors weighing against young juveniles.

Of course, low J1 intake values for September could be an artifact of small sample size, however, it is then surprising that there is not more variability across the other months. Indeed, one of the three younger juveniles (S5.1) disappeared within two months of this September energetic dip and was presumed to have died as her mother remained present in the group. S5.1 was almost exactly at the point of transition from maternal dependence to nutritional independence, that is, although she was occasionally observed in nipple contact in September, it was minimal and she was not observed suckling during any focal observations after July 2007. Although just an anecdote, her likely death following a potentially energetically challenging time highlights the elevated nutritional stress and associated risks faced during the transition from infancy even for a folivore.

In a study of young mantled howler monkeys approaching weaning age, Raguet-Schofield (2010) documented not only increased dietary toughness during the lean season, but also a corresponding increase in the time young individuals spent in nipple contact, which she proposed was being used as a fall-back resource of sorts. Even more telling were the documented disappearances attributed to increased mortality due to nutritional stress. Also for *Alouatta palliata*, de Gusta and colleagues (2003) found a relationship between smaller molar size (permanent M1s) and likelihood of death at weaning age based on measurements taken from a sample of individuals found dead. Although indirect, these examples highlight the fact that, despite dietary abundance, seasonal increases in mechanical demand may disproportionately stress young juveniles.

Finally, if growing juveniles do experience shortfalls or peaks in energy or protein intake, these should be reflected in growth velocity. However, on an individual basis, I found no significant relationship between variation in either energy or protein intake and the subsequent month's growth response. Aside from September, energetic intake remained relatively even across all three observation blocks and protein intake varied only a little. Thus, it is possible that juveniles are maintaining an energetic surplus, allowing growth to progress relatively unchecked. Unfortunately, no growth data are available between October 2007 and January 2008, therefore the analyses here did not directly incorporate any short-term effects on growth from the potential energetic shortfall in September. Considering what is known about growth-rate responses to energy and/or protein supplementation and restriction (e.g. rhesus macaques: Terasawa et al., 2012; heifer calves: Brown et al. 2005; deer mice: McAdam and Millar, 1999; rats: Parks, 1970), it seems likely that the limited dataset used here does not have sufficient resolution to detect finer-grained variation amidst confounding factors such as age-related variation in growth velocity.

Tables and Figures

Table 3.1. Focal animals by sex and age class for the seven-month dataset including adults with ages or estimated ages for age class comparisons. [a.] Adult ages were not known but were estimated based on average age at first birth for females (see text for further detail). Young adult and subadult males were known to birth month or birth season. [b.] A non-natal female of known age (S2.1) from the same birth cohort as the natal subadult males. [c.] The younger juvenile age class is the only one for which individuals shift between 2007 and 2008 (see further detail in Methods).

	2007		2008			
AgeClass	Males	Females	Males	Females	Mean age (yrs)	Age range
Adults[a]	3	3	3	5	9.0	6.5 - 11.8
Subadults	5	1[b]	5	0	4.7	4.1 – 5.4
Older juveniles	3	6	5[c]	5	2.8	2.2 - 3.8
Younger juveniles[c]	2[c]	1	1	2	1.6	1.3 - 1.8

Table 3.2. Focal juveniles and subadults from the expanded dataset by group and sex.
[a.] Subadults are all male except one non-natal female of known age among PA subadults.

Group	Juvenile males	Juvenile females	Subadults
PA	1	4	2[a]
PB	4	6	3
PS	2	4	1

Table 3.3. Data taken from Bolter, 2004 for *Trachypithecus cristatus* age classes.

Age class	Age (estimate)	% of adult tibial length		Mass (kg)		% of adult mass		Conversion factor % AD tibia/% AD mass	
		Female	Male	Female	Male	Female	Male	Female	Male
2	1-2yr	77	70	2.3	2	0.396	0.302	1.949	2.318
3	2-3yr	90	82	3.4	2.8	0.585	0.463	1.539	1.773
4	3-3.75	98	96	5	5.4	0.860	0.814	1.140	1.179
5 Adults	>4yr	100	100	5.8	6.6				

Table 3.4. Mean nutrient content and standard error by food type. EME= estimated metabolizable energy, CP = crude protein, NDF = neutral detergent fiber, LP = lipids, TNC = total non-structural carbohydrates. Species/items included more than once if analyzed in different states of ripeness or in two different years.

Food type	N	EME	SE	CP	SE	NDF	SE	LP	SE	TNC	SE	Ash	SE
Young leaves	26	3.16	0.06	22.87	1.49	32.84	2.06	0.31	0.17	37.22	2.31	10.42	2.03
Mature leaves	11	2.92	0.07	14.23	2.15	37.72	2.55	0.51	0.44	35.54	3.55	12.00	1.19
Young seeds	29	3.48	0.14	14.00	1.70	38.01	3.66	5.56	1.98	39.03	2.66	3.56	0.30
Mature seeds	2	4.58	1.27	14.47	3.22	32.75	4.75	25.00	24.37	24.15	16.54	3.63	0.13
Flowers	14	3.26	0.04	18.29	1.66	28.71	1.59	0.67	0.36	44.90	2.59	7.43	0.73
Unripe fruits	21	3.20	0.06	11.72	1.36	37.77	2.50	1.74	0.68	42.52	3.16	6.25	0.58
Ripe fruits	12	3.22	0.33	10.12	1.86	39.30	3.58	6.51	2.58	40.11	5.56	5.85	1.36
Petiole	1	2.80		3.82		50.64		0.00		37.10		8.44	
Pith	1	2.90		3.95		45.12		0.41		44.02		6.49	
Bamboo sh	1	3.00		30.59		31.00		0.00		21.71		16.70	

Table 3.5. Monthly means plus standard error of combined juvenile and sub-adult intake rates for energy (Kcal/hr/MW), protein (CP(g(DM)/hr/MW) and fiber (NDF(g(DM)/hr/MW).

	Kcal/MW	SE	CP/MW	SE	NDF/MW	SE	n
Jan07	9.233	0.758	0.427	0.054	0.704	0.109	14
Feb07	11.582	1.278	0.639	0.069	1.097	0.121	15
Mar07	11.708	1.146	0.768	0.091	1.150	0.120	17
Jul07	14.239	1.366	0.496	0.052	2.137	0.215	14
Aug07	10.469	1.849	0.499	0.079	1.361	0.355	12
Sep07	11.756	1.503	0.486	0.047	1.428	0.269	13
Feb08	10.905	0.872	0.614	0.060	1.110	0.103	15
Mar08	9.036	0.875	0.492	0.046	0.783	0.074	15
Apr08	11.532	1.316	0.711	0.079	1.295	0.160	14
May08	9.259	0.762	0.517	0.050	0.989	0.085	14

Table 3.6a. Matrix depicting significant monthly pairwise comparisons of hourly energy intake (Kcal/MW). Holm's adjusted *p*-values reported. *** indicates < 0.001, ** < 0.01, * < 0.05.

	Jan-07	Feb-07	Mar-07	Jul-07	Aug-07	Sep-07	Feb-08	Mar-08	Apr-08	May-08
Jan-07										
Feb-07	ns									
Mar-07	ns	ns								
Jul-07	0.155	ns	ns							
Aug-07	ns	ns	ns	ns						
Sep-07	ns	ns	ns	ns	ns					
Feb-08	ns	ns	ns	ns	ns	ns				
Mar-08	ns	ns	ns	ns	ns	ns	ns			
Apr-08	ns	ns	ns	ns	ns	ns	ns	ns		
May-08	ns	ns	ns	ns	ns	ns	ns	ns	ns	

Table 3.6b. Matrix depicting significant monthly pairwise comparisons of hourly crude protein intake (CP/MW). Holm's adjusted *p*-values reported. *** indicates < 0.001, ** < 0.01, * < 0.05.

	Jan-07	Feb-07	Mar-07	Jul-07	Aug-07	Sep-07	Feb-08	Mar-08	Apr-08	May-08
Jan-07										
Feb-07	ns									
Mar-07	**	ns								
Jul-07	ns	ns	ns							
Aug-07	ns	ns	ns	ns						
Sep-07	ns	ns	ns	ns	ns					
Feb-08	ns	ns	ns	ns	ns	ns				
Mar-08	ns	ns	ns	ns	ns	ns	ns			
Apr-08	*	ns	ns	ns	ns	ns	ns	ns		
May-08	ns	ns	ns	ns	ns	ns	ns	ns	ns	

Table 3.6c. Matrix depicting significant monthly pairwise comparisons of hourly fiber intake (NDF/MW). Holm's adjusted *p*-values reported. *** indicates < 0.001, ** < 0.01, * < 0.05.

	Jan-07	Feb-07	Mar-07	Jul-07	Aug-07	Sep-07	Feb-08	Mar-08	Apr-08	May-08
Jan-07										
Feb-07	ns									
Mar-07	ns	ns								
Jul-07	***	***	***							
Aug-07	ns	ns	ns	**						
Sep-07	*	ns	ns	ns	ns					
Feb-08	ns	ns	ns	**	ns	ns				
Mar-08	ns	ns	ns	***	ns	ns	ns			
Apr-08	*	ns	ns	0.08	ns	ns	ns	ns		
May-08	ns	ns	ns	***	ns	ns	ns	ns	ns	

Table 3.7. Model parameters for each dietary variable: feeding time, energy intake/MW, protein intake/MW, fiber intake/MW. Likelihood ratio tests compare full model (with age class as main effect) to null model without. Post-hoc pairwise comparisons were made using Tukey contrasts. Adjusted *p*-values reported.

Intake (dependent) variable					
Feeding Time [logit proportion]			Estimate	SE	*p*-value
χ^2(df) 16.802 (3)	*p* value <0.001	Intercept	-0.413	0.171	
		Paired contrasts			
		AD v J1	-1.062	0.277	<0.001
		AD v J2	-0.5809	0.195	0.015
		AD v SA	-0.4122	0.219	>0.17
		SA v J1	-0.650	0.291	>0.1
		SA v J2	-0.169	0.219	>0.4
		J2 v J1	-0.481	0.275	>0.17
Log$_{10}$ Energy [kcal/hr/MW]			Estimate	SE	*p*-value
χ^2(df)	*p* value	Intercept	0.676	0.246	
17.694(3)	<0.001	Paired contrasts			
		AD v J1	-0.959	0.283	0.003
		AD v J2	-0.565	0.199	0.018
		AD v SA	-0.027	0.222	> 0.6
		SA v J1	-0.959	0.297	0.006
		SA v J2	-0.5382	0.219	0.042
		J2 v J1	-0.0267	0.280	>0.2
Log$_{10}$ Protein [g(DM)/hr/MW]			Estimate	SE	*p*-value
χ^2(df) 27.473 (12)	*p* value <0.01	Intercept	0.872	0.267	
		Paired contrasts			
		AD v J1	-1.314	0.398	<0.01
		AD v J2	-0.514	0.187	0.03
		AD v SA	-0.021	0.224	>0.9

		SA v J1	-1.293	0.481	0.03
		SA v J2	-0.492	0.244	0.09
		J2 v J1	-0.801	0.361	0.08
Log$_{10}$ NDF [g(DM)/hr/MW]			Estimate	SE	*p*-value
χ^2(df) 12.062 (12)	*p* value >0.4	Intercept	0.528	0.323	
		Paired contrasts			
		AD v J1	-0.718	0.371	>0.2
		AD v J2	-0.337	0.236	>0.4
		AD v SA	-0.003	0.277	>0.9
		SA v J1	-0.721	0.322	0.15
		SA v J2	-0..340	0.215	>0.4
		J2 v J1	-0.381	0.325	>0.4

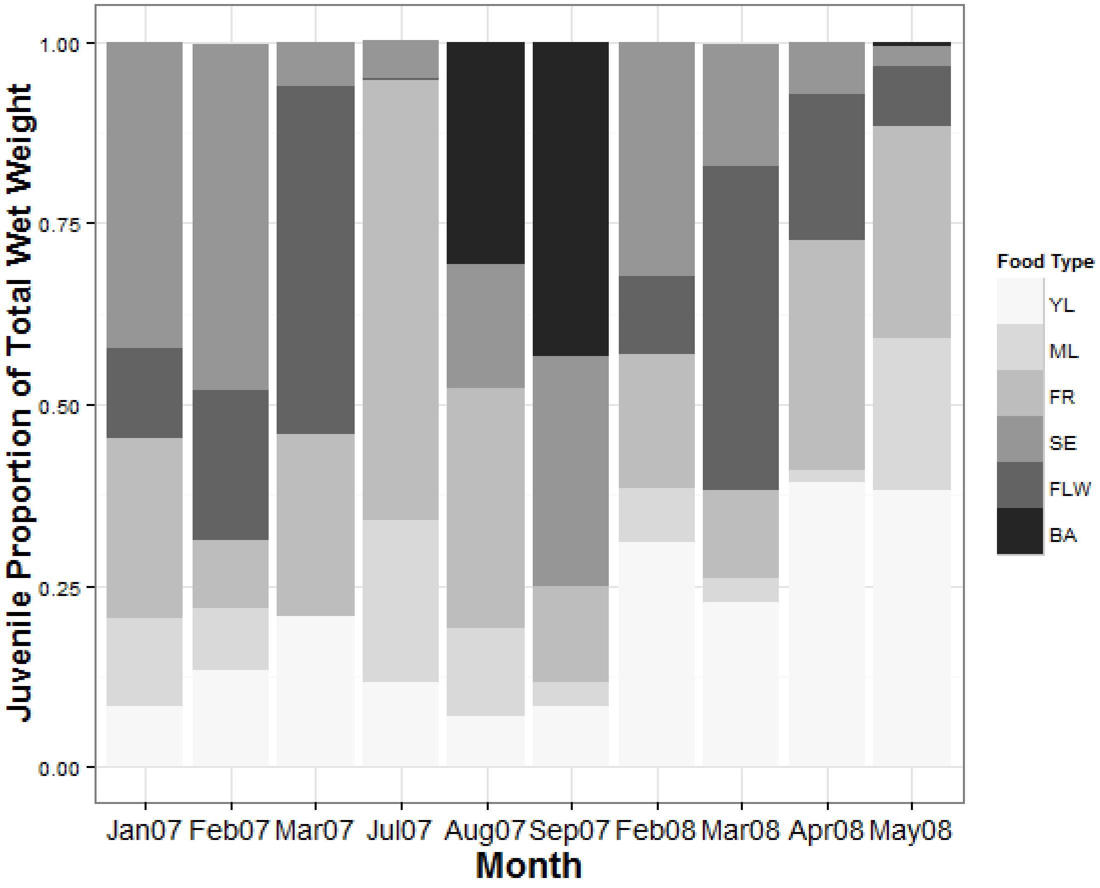

Fig. 3.1. Juvenile dietary proportions by food type based on wet weight intake across three time blocks: January – March 2007; July-September 2007 and February – May 2008. . YL=young leaves, ML=mature leaves, FR=fruit pulp or fruits eaten whole, SE=seeds, FLW=flowers including buds, and BA=bamboo shoots.

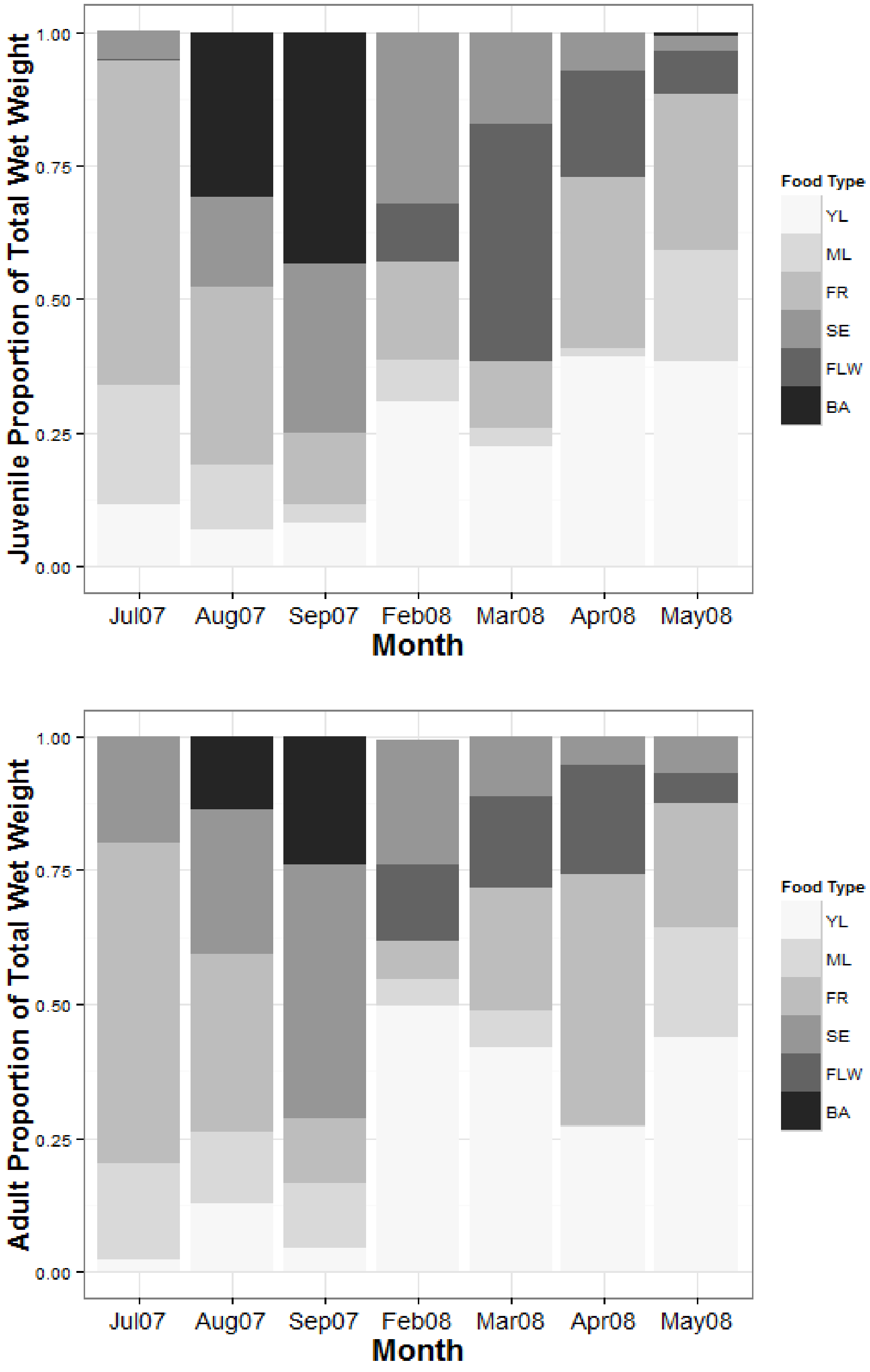

Fig. 3.2. Dietary proportions based on wet weight intake for the shorter 7-month period with a separate plot for juveniles (top) and adults (bottom) for visual comparison.

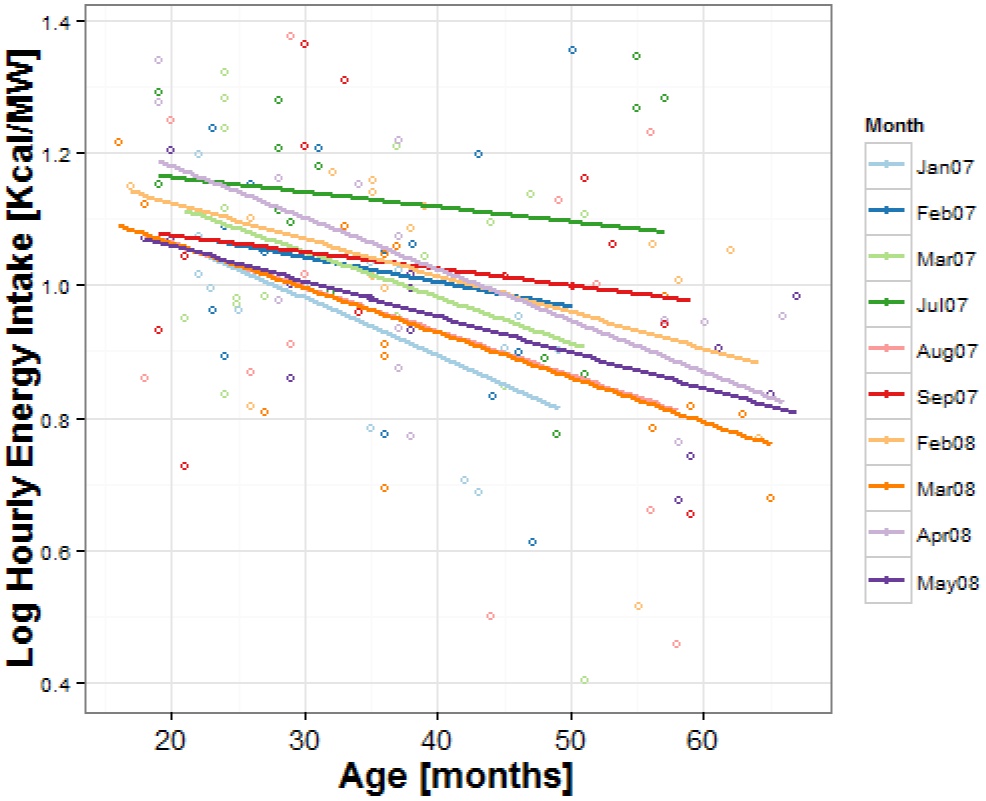

Fig 3.3. Hourly energy intake (log$_{10}$-transformed Kcal/hr/MW) by month relative to age

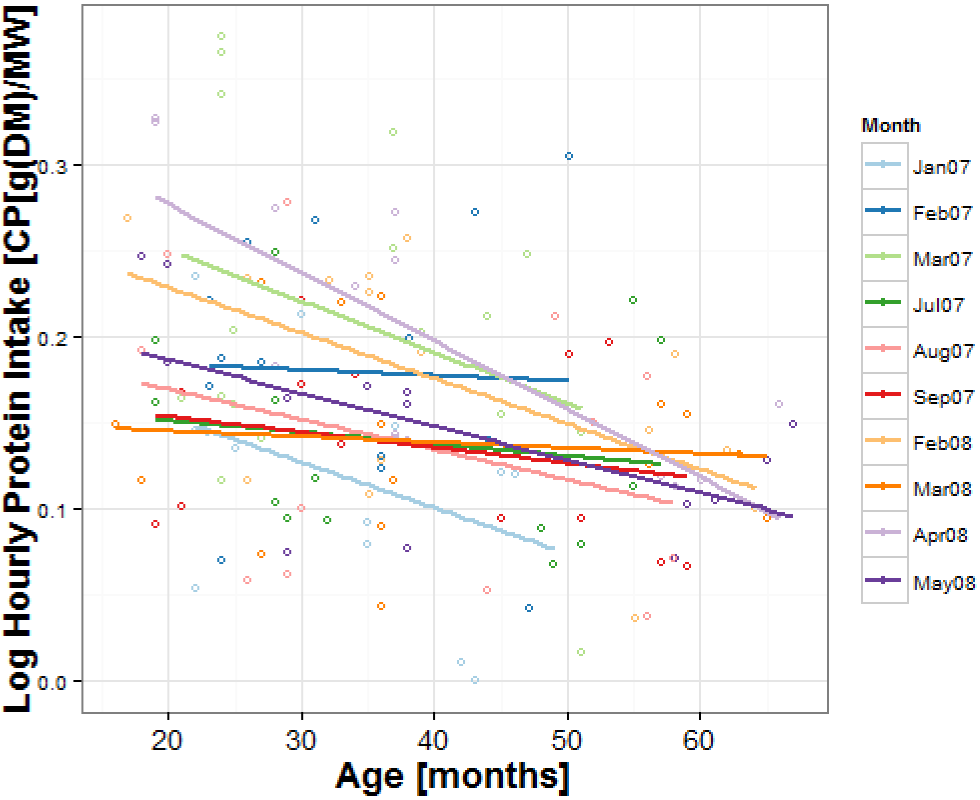

Fig. 3.4. Hourly protein intake (log$_{10}$-transformed g(DM)/hr/MW) by month relative to age

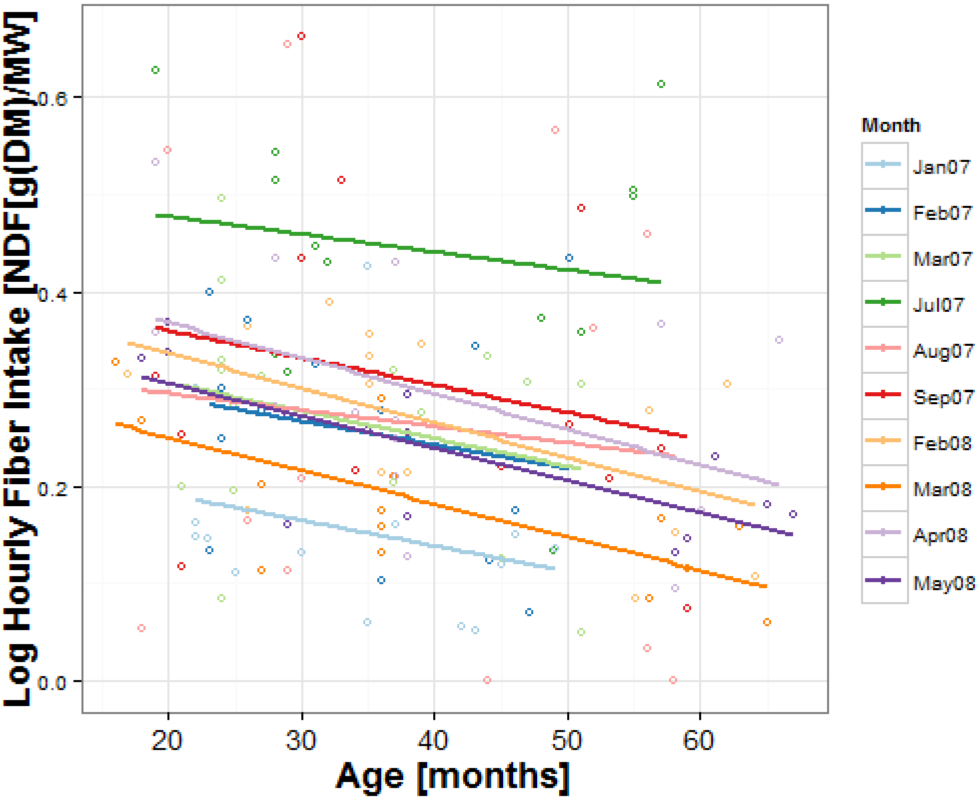

Fig. 3.5. Hourly NDF intake ($\log_{10}$-transformed g(DM)/hr/MW) by month relative to age

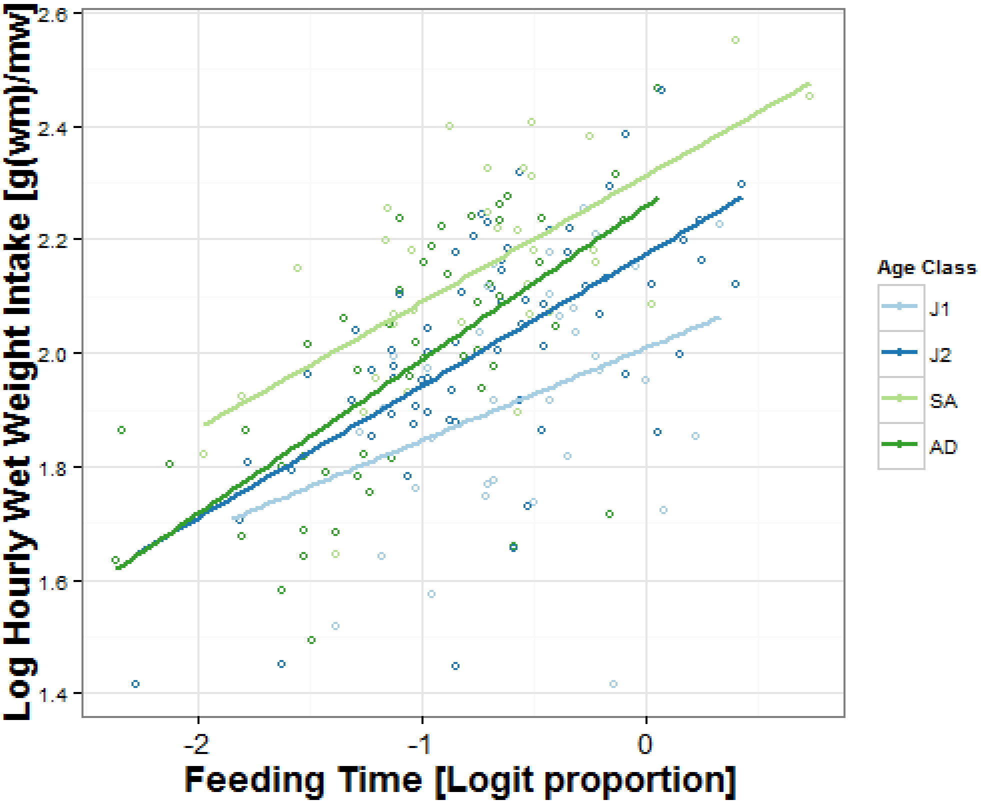

Fig. 3.6. Wet weight intake ($\log_{10}$-transformed g/hr) relative to feeding time (logit-transformed proportion of total observation time) for each age class. Mean intake by age class: J1s: 38.85g (SE= 2.89), J2s: 40.08g (SE= 2.42), subadults: 55.58g (SE= 4.81), adults: 48.10g (SE= 3.66)

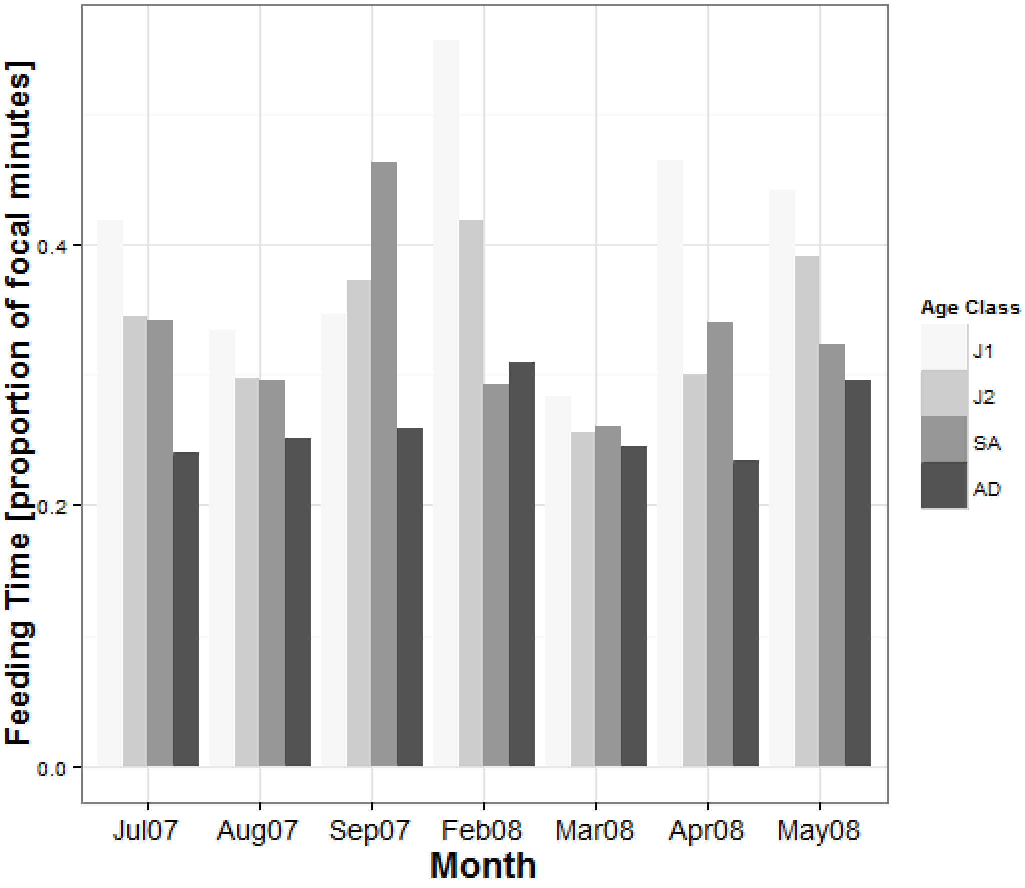

Fig. 3.7. Mean monthly feeding time (logit-transformed) by age class.

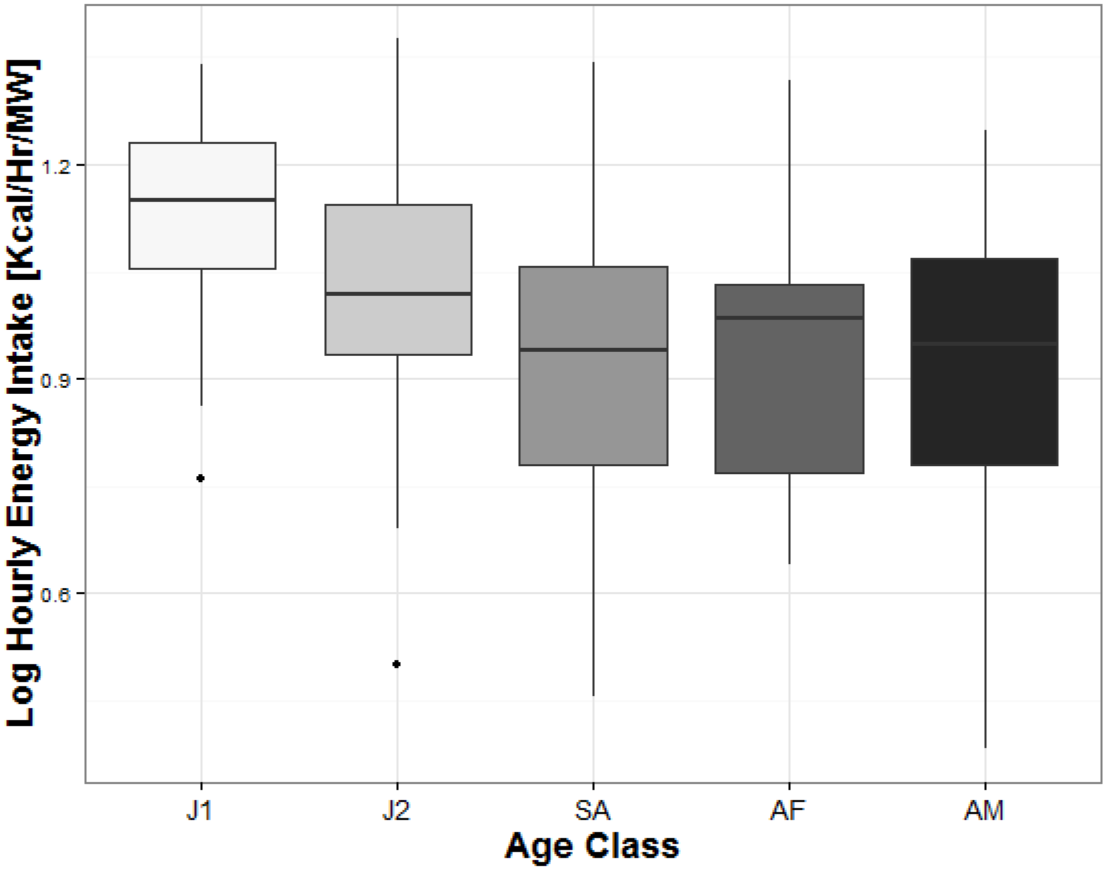

Fig. 3.8. Hourly energy intake scaled for metabolic weight ($\log_{10}$ kcal/hr/MW) by age class and age-sex class for adults.

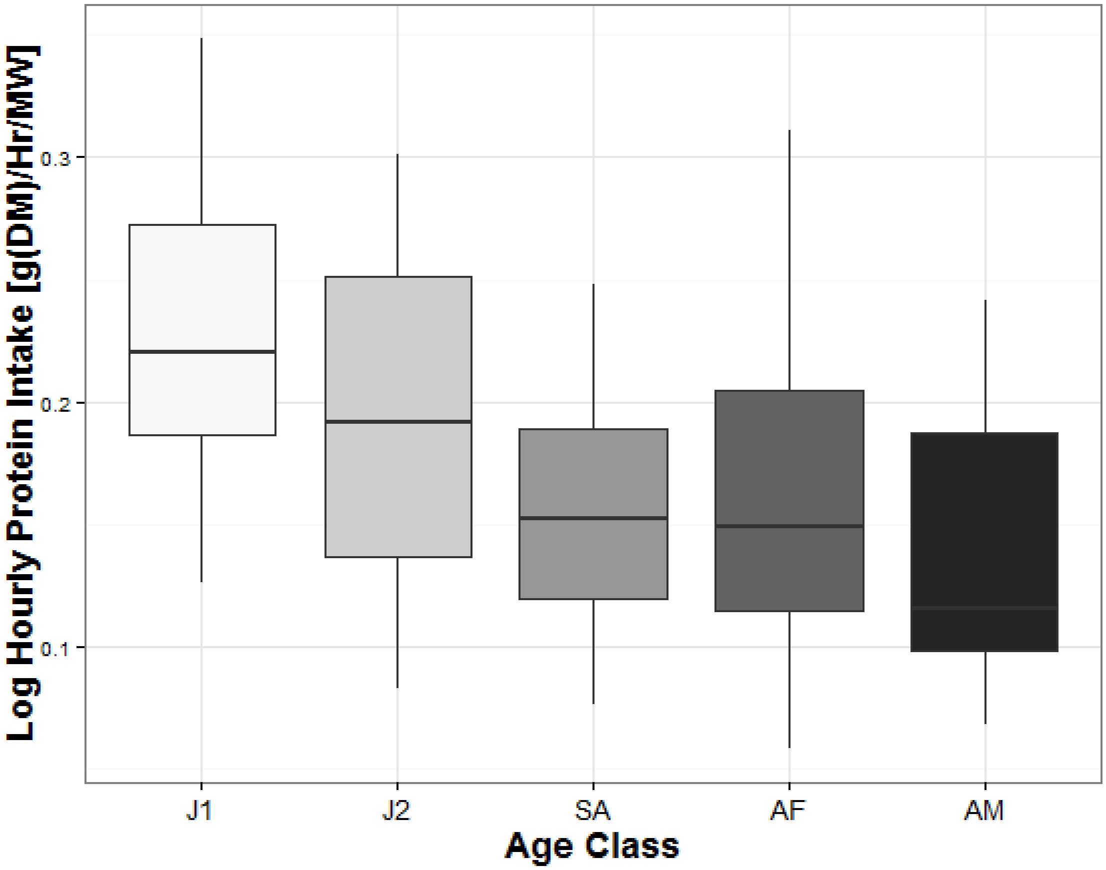

Fig. 3.9. Hourly protein intake weighted for metabolic weight ($\log_{10}$-transformed g(DM)/hr/MW) by age class and age-sex class for adults.

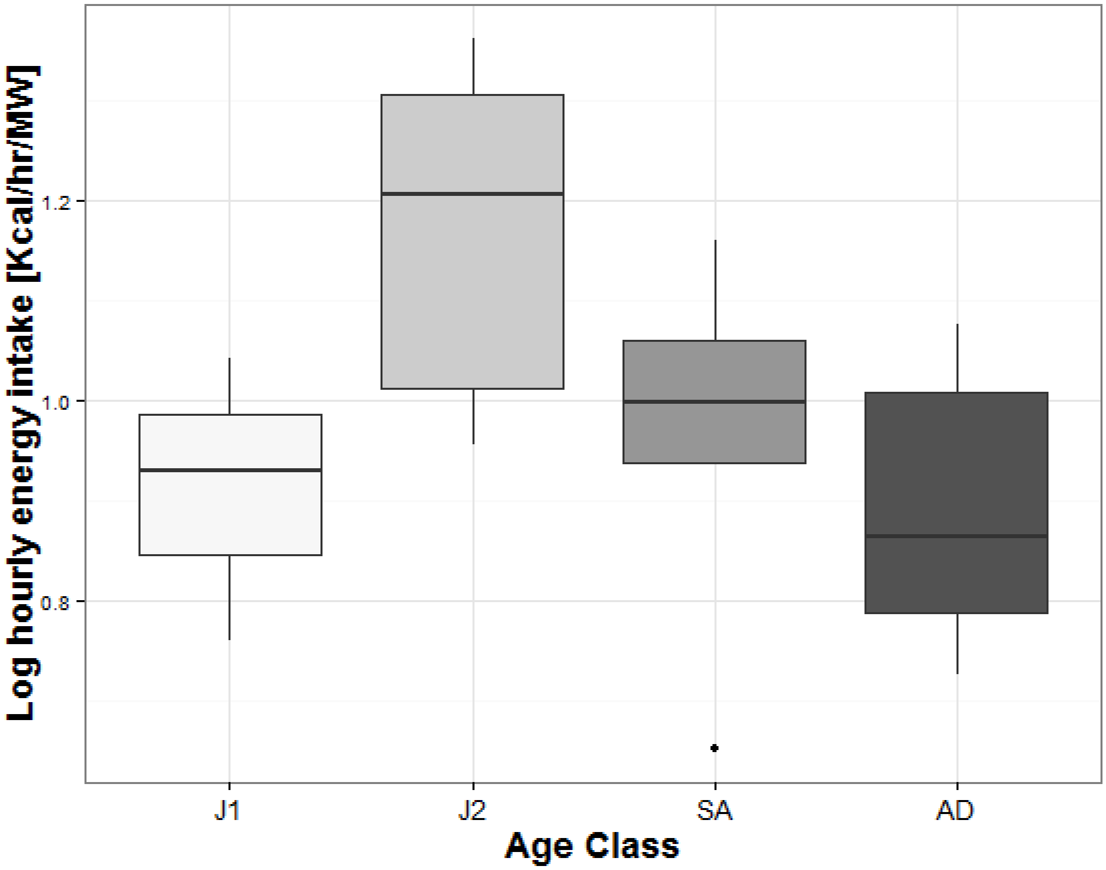

Fig. 3.10a. For September 2007 only, hourly energy intake scaled for metabolic weight ($\log_{10}$ kcal/hr/MW) by age class.

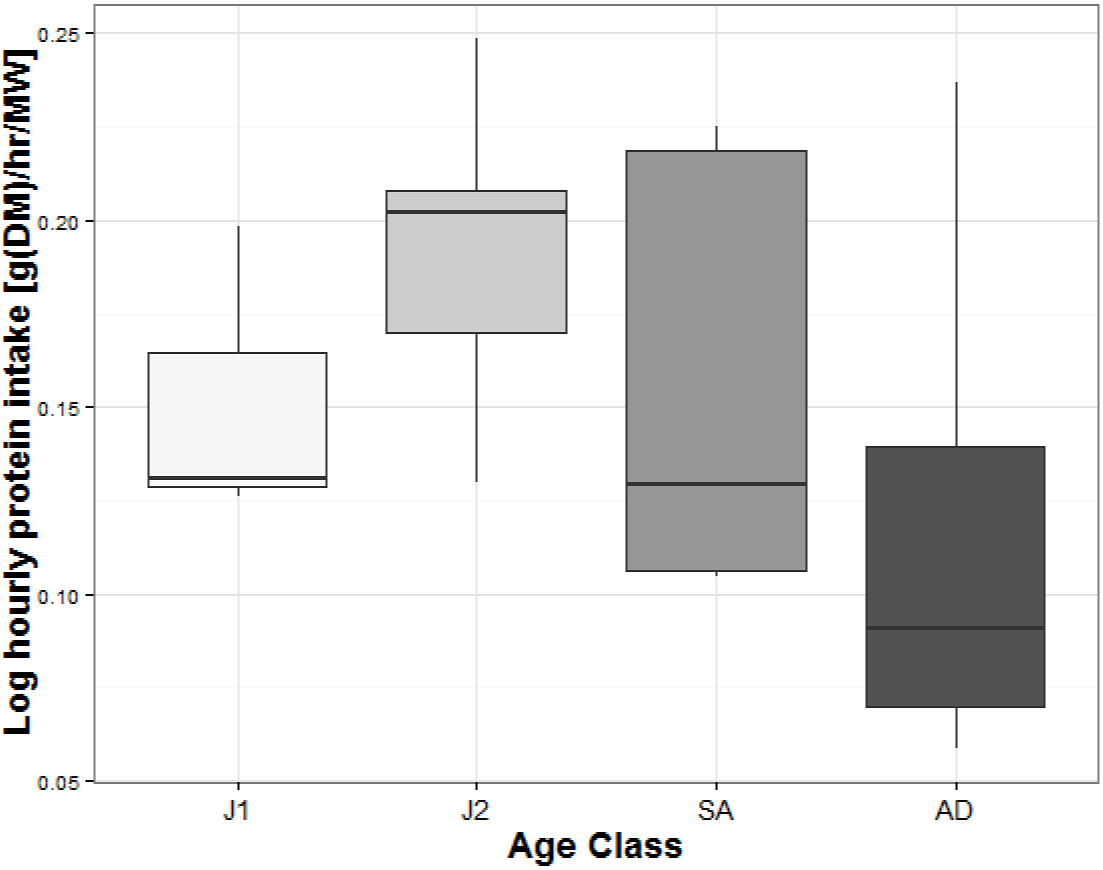

Fig. 3.10b. For September 2007, hourly protein intake scaled for metabolic weight ($\log_{10}$ kcal/hr/MW) by age class.

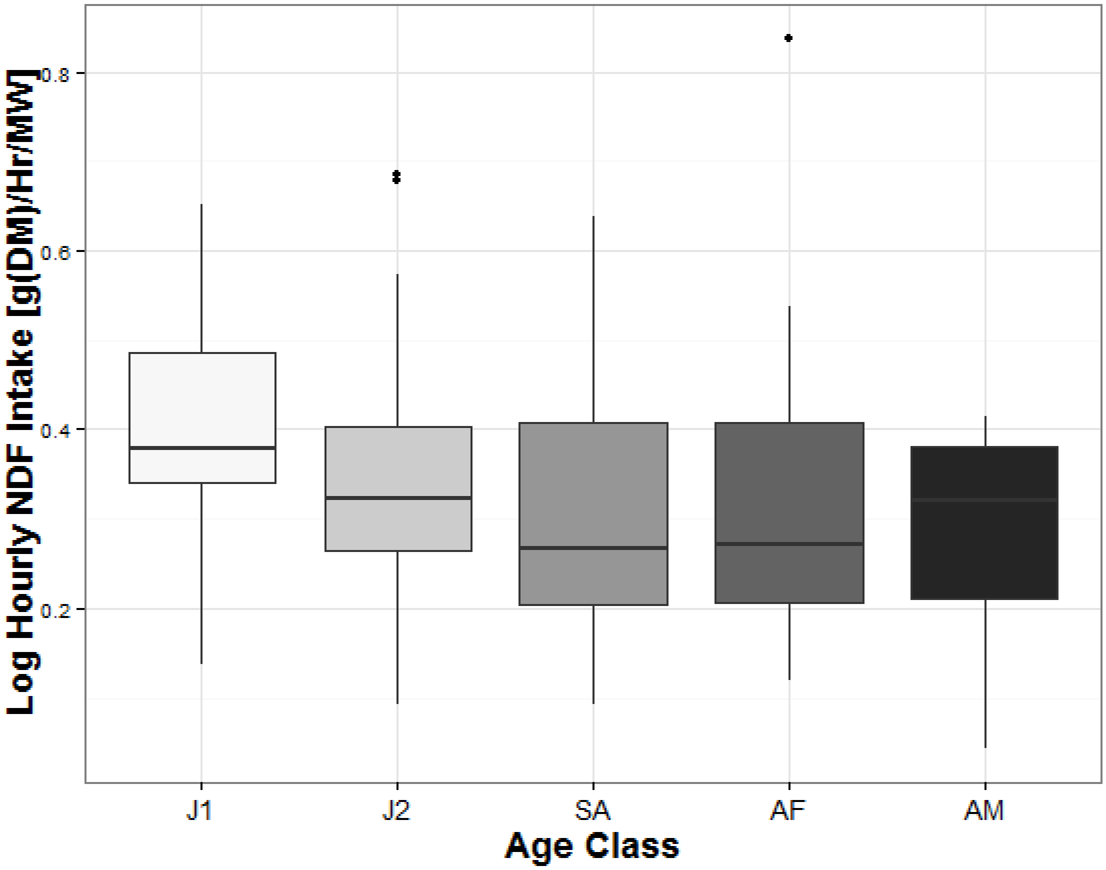

Fig. 3.11. Hourly NDF intake ($\log_{10}$-transformed NDF/hr/MW) by age class and age-sex class for adults.

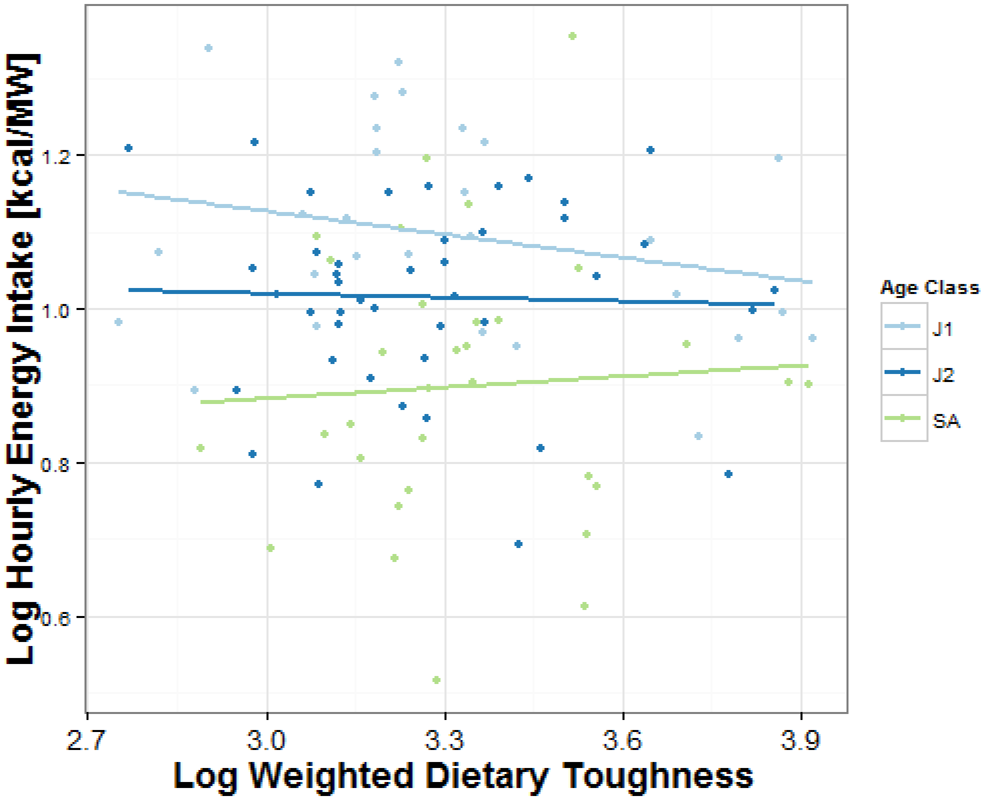

Fig. 3.12. Energy intake relative to dietary toughness (both $\log_{10}$-transformed and scaled for metabolic mass) by age class, excluding adults (dataset: Jan-Mar 2007, Feb-May 2008).

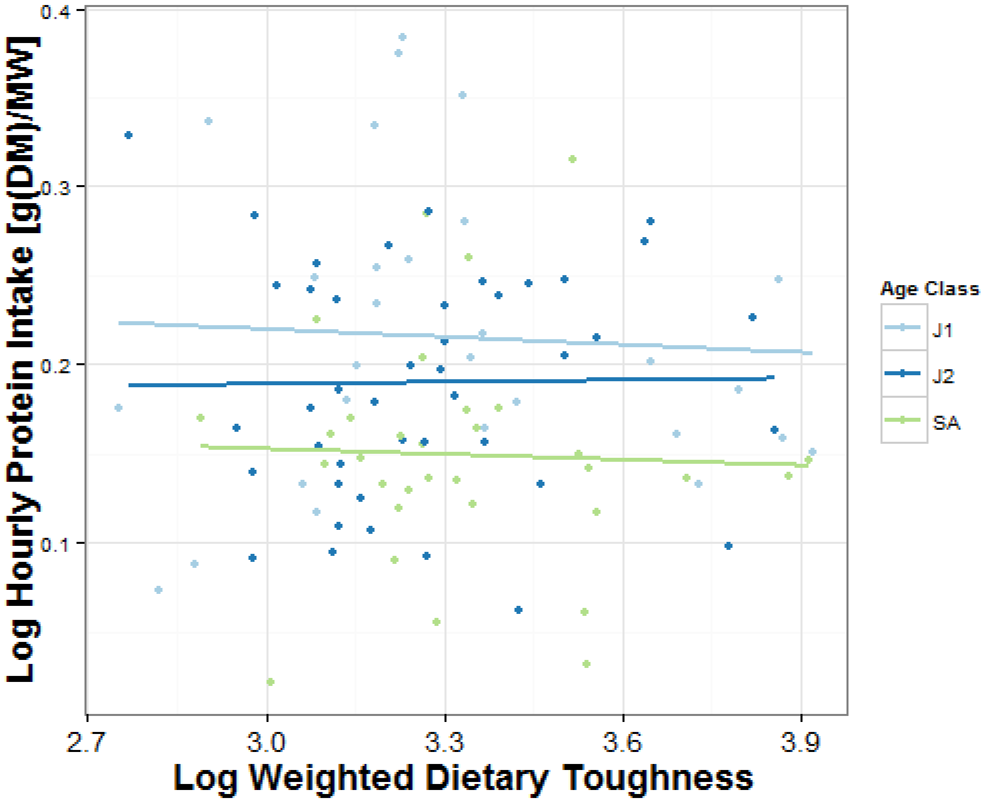

Fig. 3.13. Protein intake relative to dietary toughness ($\log_{10}$ transformed and scaled to metabolic mass) by age class excluding adults (dataset: Jan-Mar 2007, Feb-May 2008).

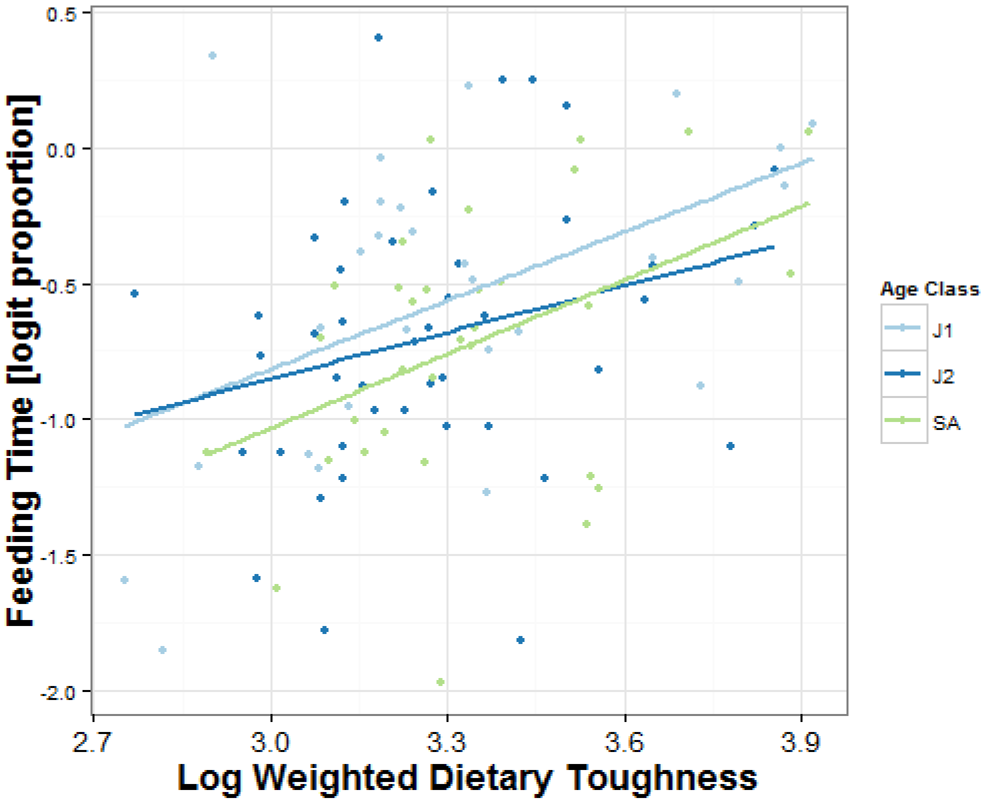

Fig. 3.14. Proportion of time spent feeding relative to dietary toughness (logit- and $\log_{10}$-transformed respectively).

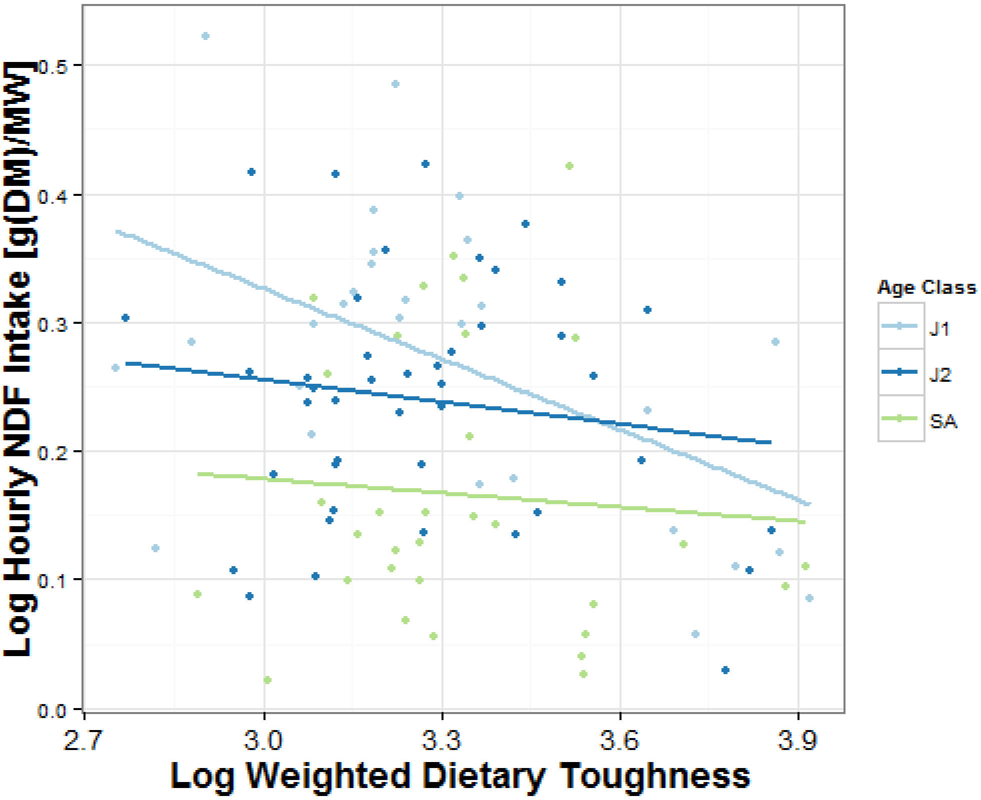

Fig. 3.15. NDF intake rates relative to weighted dietary toughness weighted by time spent feeding with a stronger negative slope for younger juveniles. (X^2=3.72, df=1, *p*= 0.054). Both variables $\log_{10}$-transformed.

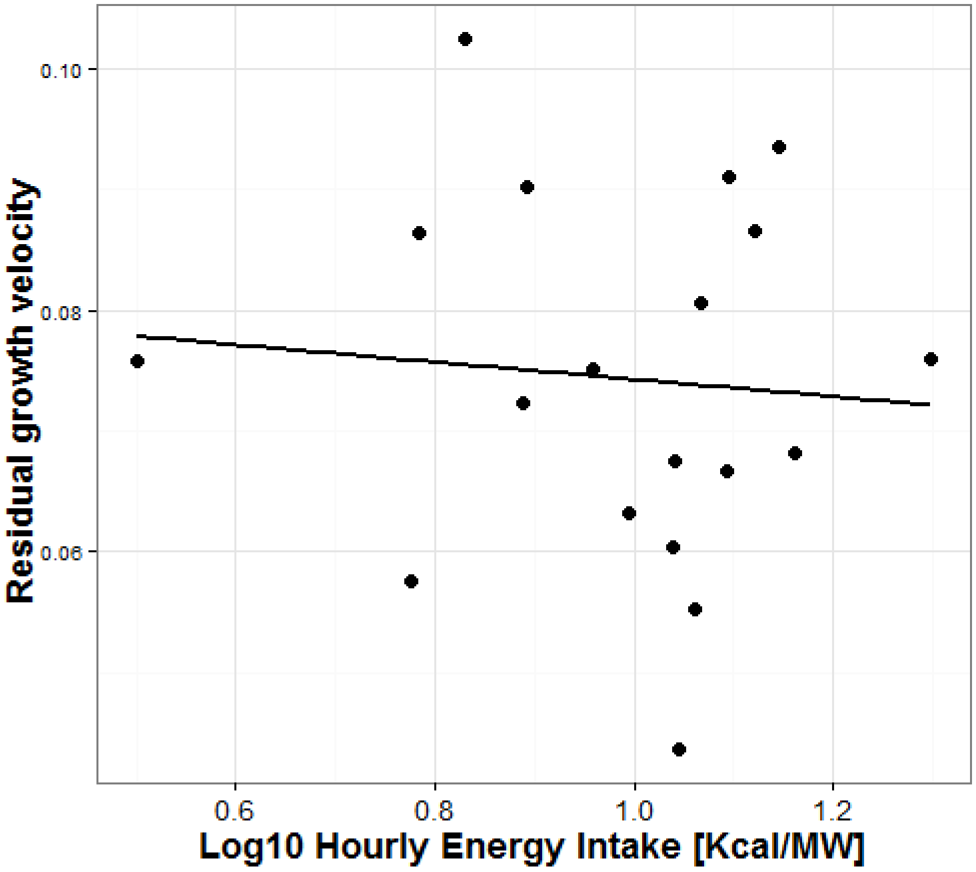

Fig. 3.16. Growth velocity for age (residuals from a cubic polynomial regression of velocity for age) relative to individual energy intake in the previous month (or pooled across the observation block if matching multiple growth residuals were available).

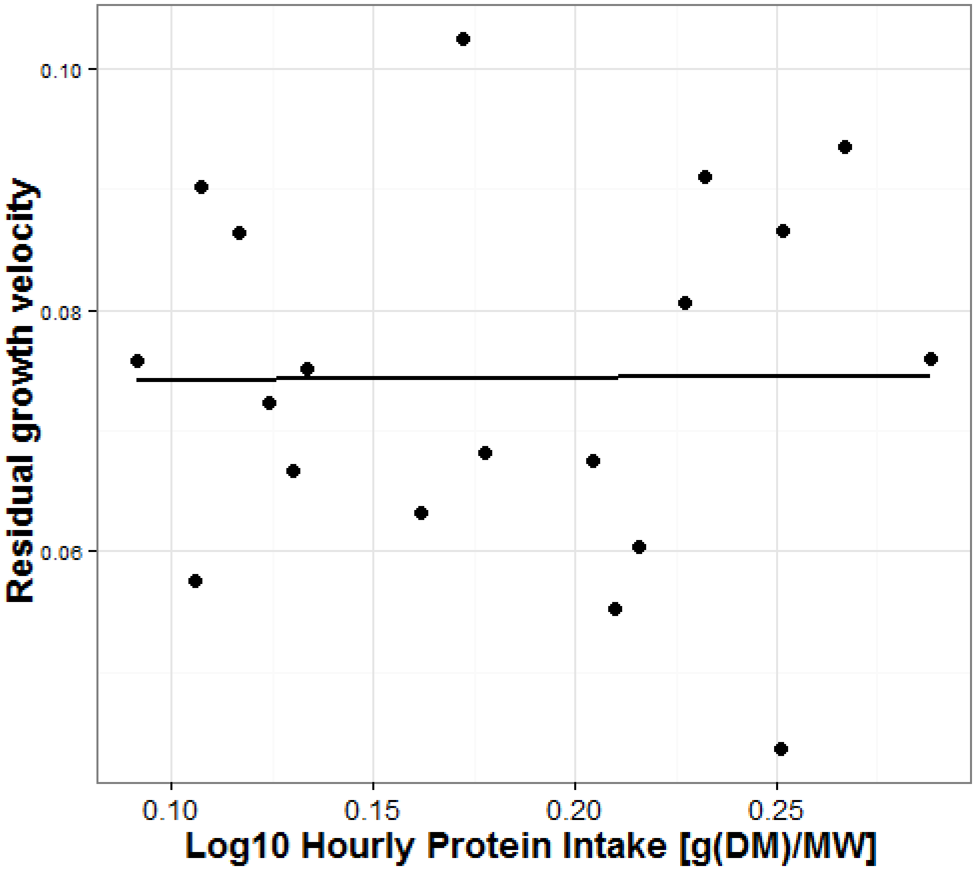

Fig. 3.17. Growth velocity for age (residuals from a cubic polynomial regression of velocity for age) relative to individual protein intake in the previous month (or pooled across the observation block if matching multiple growth residuals were available).

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CHAPTER 4.

Growth and correlates of size-for-age in Phayre's leaf monkeys

Abstract

Primate growth patterns have been shown to respond flexibly to socioecological variation on both ultimate and proximate scales; the former contributes to our understanding of primate life history evolution, while the latter marks growth rate as a potential proxy for fitness variation in pre-reproductive individuals. Yet concurrent size and behavioral data of immature primates from wild populations – folivores in particular – are relatively scarce, therefore, our current understanding of growth patterns is based largely on captive datasets. Here, I present growth curves fit to distal lower limb lengths of known-aged Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) at the Phu Khieo Wildlife Sanctuary in northeastern Thailand. Between November 2006 and May 2008, I photographed individuals from three habituated groups and collected corresponding laser-measured distances-to-subject. Following photogrammetric methods, I determined knee-to-heel length for 51 individuals (19 males, 32 females), including 35 of known age and four with age estimated from known birth season. Growth and pseudo-velocity curves were fit via cubic spline regression to the overall mixed longitudinal and cross-sectional dataset, and size-for-age residuals were generated from cubic polynomial regressions run separately for male and female immature leaf monkeys. Growth curve patterns indicated that females were slightly larger than males during the initial post-weaning period. Juvenile males grew at faster rates with a possible acceleration around four years of age to attain longer adult limb length. Sexual dimorphism in adult limb length was mild (1.07) and on par with what has been reported for mass dimorphism in this species. In relating size-for-age to life history

measures, I found a significant positive correlation between weaning age and individual size-for-age later in juvenility, which differs from patterns reported for cercopithecine species. Female Phayre's leaf monkeys emigrate from their natal groups prior to reproductive maturity. Most females emigrated well before reading adult length, however, juvenile females who were longer-limbed for their age tended to disperse at earlier ages, a trend in line with research showing that larger, presumably good-condition females reach sexual maturity earlier. Distal lower limb growth cessation in males took place between 4.5 and 5.5 years. Because statural measures tend to mature earlier than body mass, this finding, albeit based on a small sample, might indicate that ages of colobine mass growth cessation used in the literature based on captive data are underestimated.

Introduction

Decades of research have established the strong relationship between life history and body size (Calder, 1984; Harvey et al., 1987), while also demonstrating that life history traits, and growth rates in particular, can vary across and within taxa even when body size is held constant (e.g., growth rates in birds: Starck and Ricklefs, 1998). Compared to other similar-sized mammals, primates grow more slowly and for longer (Charnov and Berrigan, 1993; Mumby and Vinicius, 2008). Life history theory suggests that age at maturity, and likewise the timing of growth cessation, depends, in part, on selective trade-offs between metabolic investment in growth versus reproduction (Charnov, 1993; Kozlowski and Weiner, 1997; West et al., 2001). As with life history pace, numerous factors – including age-specific mortality risk, metabolic rates, ecology and diet, and brain size – have been cited to explain variation in the duration and the pace of growth on both proximate and ultimate scales (Case, 1978; Fraser and Gilliam, 1992;

Charnov and Berrigan, 1993; Janson and van Schaik, 1993; Ross, 1998; Lochmiller et al., 2000; Roff et al., 2006; Mumby and Vinicius, 2008; Pontzer et al., 2014).

For primates specifically, longer, slower growth simply may be the developmental tradeoff resulting from encephalization and the associated costs of growing larger brains (Armstrong, 1983; Charnov and Berrigan, 1993; Ross and Jones, 1999; van Schaik et al., 2006; Barton and Capellini, 2011; but see Leigh, 2004), particularly since somatic growth and neural growth have proven difficult to decouple on an evolutionary scale (Barton and Capellini, 2011). Similarly, the cognitive buffering hypothesis proposes that the selective advantage of greater cognitive flexibility has led to longer primate life spans, and slow development is merely a correlated consequence of living longer (Deaner et al., 2003; Sol, 2009). In contrast, the ecological risk aversion hypothesis suggests that growth rates themselves are the target of selection (Janson and van Schaik, 1993). Their argument posits that selection for slower growth reduces energetic requirements at a critical time of increased ecological vulnerability. That is, smaller, inexperienced juveniles typically are more vulnerable both to predation and starvation. Socio-spatial tactics employed to reduce predation risk – such as positioning in the group center or in proximity to more neighbors – put juveniles at a greater competitive disadvantage, further hampering foraging efforts for these newly nutritionally independent individuals. Lowering energetic demand via slower growth mitigates juveniles' risk of starvation (or brain malnutrition: (Deaner et al., 2003), particularly during periods of food scarcity.

In seeming support, comparisons of growth data from captive anthropoids show folivorous taxa tended to grow more rapidly and completed growth earlier than non-folivores of similar size (Leigh 1994; see also African apes: Leigh and Shea, 1996), a difference that has been attributed to the reduced energetic/starvation risks associated with consuming a readily available, less-contested food resource such as leaves. Similarly, in terms of developmental pace, the highly herbivorous/folivorous mountain gorillas weaned their infants as much as a full year earlier than the more frugivorous western gorillas (Stoinski et al., 2013). However, the relationship remains ambiguous; for example, among small-bodied platyrrhines, factors such as infant care strategies rather than feeding competition better predicted variation in growth rates (Garber and Leigh, 1997). Folivorous lemurs, while dentally advanced, actually grew more slowly in terms of somatic growth than similar-sized frugivores (Godfrey et al., 2004). Comparing life history pace in general, Asian colobines (folivores) were no faster than macaques (non-folivores), with similar interbirth intervals, ages at sexual maturity and, in fact, longer gestation periods (Borries et al., 2011).

Short-term tradeoffs between growth and ecological risk

In the short-term, individual or population-level growth rates have shown flexible responses to varying ecological risks (growth vs. mortality tradeoffs reviewed in Mangel and Stamps, 2001). As expected, limited food availability can dampen the pace of growth (e.g., rats: Lochmiller et al., 2000). Likewise, killfish of a certain length (>80mm) exhibited suppressed growth rates in the presence of predators compared to those in predator-free pools (Fraser and Gilliam, 1992). Studies documenting such condition-related growth variation tend to be limited to relatively faster-growing, non-primate or even non-mammalian subjects (e.g., damselflies: De Block and Stoks, 2008; lizards: Stamps and Eason, 1989), or else take place under experimental or lab-based conditions (e.g., Lochmiller et al., 2000 but see 40-year elephant study: Lee et al., 2013). Altmann and Alberts (2005), however, described a natural experiment comparing intraspecific growth among wild savannah baboons living in different conditions with varying degrees of resource availability. They found that individuals in groups relying solely on “wild-foraging” grew more slowly, were less sexually dimorphic and reached sexual maturity later than those in a “food-enhanced” condition (Altmann and Alberts 2005; see also Japanese macaques: Mori 1979, vervets: Turner et al., 1997). Broader life history comparisons within and across taxa likewise indicate faster developmental and reproductive rates in provisioned or captive populations compared to those in the wild (Borries et al., 2001; Borries et al., 2011). Highlighting the potential flexibility of growth rates, Dietz (1994) documented seasonal variation within a population, with young tamarins growing more slowly during the dry season, a period of food scarcity, as compared to more favorable wet-season conditions.

Such developmental plasticity on a short-term scale may be especially adaptive in more unpredictable environments. Indeed, primates’ longer growth duration allows for growth rates to have even greater flexibility in response to external conditions (Altmann and Alberts 2005). Plasticity in the face of changing ecological as well as social conditions marks growth rates as significant sources of potential fitness variation during immaturity. Previous work has shown a relationship between body size and age of maturity or first conception such that larger animals reach sexual maturity earlier (Bercovitch et al. 1998; Setchell et al. 2001; Altmann and Alberts 2005). Age at maturity is a major determinant of reproductive span, and, as such, an important factor for lifetime reproductive success (Altmann et al. 1988; Kaar et al. 1996; Johnson 2003). Furthermore, larger adult body size may offer advantages in terms of competitive ability (e.g., birds: (Oddie, 2000) as well as reduced predation risk (Janson and van Schaik, 1993; Johnson and Bock, 2004; Agostini and Visalberghi, 2005). Chimpanzee predation on red colobus troops highlights the greater vulnerability of immature individuals; infants and juveniles comprised 75 percent of the red colobus deaths with only 22 percent of young surviving to maturation

(Stanford, 1995). To some extent then, larger body size confers advantages: if reaching a certain threshold size sooner allows juveniles to reduce predation or even competitive risks, selection should act to speed up growth. Of course, as the previous discussion of growth-vs.-mortality tradeoffs suggests, these potential advantages of rapid growth have to be weighed against the associated costs that would make maximum growth rates sub-optimal (Case, 1978; Janson and van Schaik, 1993; Mangel and Stamps, 2001).

Some evidence suggests that individuals may be able to make up for short-term periods of slower growth during resource scarcity by growing at accelerated rates once ecological conditions improve (e.g., Prader et al., 1963; Boersma and Wit, 1997; Farnum et al., 2003). This so-called catch-up or compensatory growth would potentially negate long-term fitness variation related to early growth suppression (e.g., cotton rats: Lochmiller et al. 2000). However, recovery does not come for free and the costs of catch-up growth likely have lasting fitness consequences, for example, delay to age at maturation and shortened lifespan as well as (or due to) greater accumulation of cellular damage (Mangel and Munch, 2005; De Block and Stoks, 2008; see also review in Metcalfe and Monaghan 2001). Indeed, Altmann and Alberts (2005) found no evidence for catch-up growth in wild baboons: juveniles that started out small-for-age remained small-for-age. The authors speculate that wild-feeding conditions do not offer sufficient energetic opportunity for accelerated growth or else the intensity of matrilineal dominance hierarchies is such that the advantages or disadvantages of maternal rank persist even after nutritional independence.

Maternal influences on growth

The social environment also influences growth and offspring outcomes, particularly via phenotypic maternal effects. In baboons, maternal dominance rank had a positive relationship with immatures' size for their age as well as growth rates (Setchell 2001; Johnson 2003). In addition, multiparous mothers (i.e., typically larger and/or more experienced) tended to have offspring that were large for their age, grew more quickly or had increased survivorship (Setchell et al., 2001; Johnson, 2003; elephants: Lee et al., 2013). Maternal factors such as these and others (e.g., maternal body mass and condition) have been firmly linked to growth during fetal and infant periods when individuals are still nutritionally dependent (Martin, 1996; Garcia et al., 2009; Antonow-Schlorke et al., 2011) as well as having consequences for infant behavior (e.g., relationship to mother's available milk energy: Hinde and Capitanio, 2010). Yet studies including juvenile subjects have found that maternal effects on mass growth tend to persist post weaning and throughout juvenility (Setchell et al., 2001; Johnson, 2003; Altmann and Alberts, 2005). Maternal rank or condition, therefore, can provide a long-term fitness advantage, especially for taxa characterized by stable matrilineal dominance hierarchies.

The lasting influence of maternal rank and condition might lead to the assumption that mothers who invest longer will have relatively larger offspring. However, both intraspecific and interspecific research suggests this is not the case. In baboons, higher-ranking, better-condition mothers actually had shorter lactation durations, while lower-ranking, poorer condition females invested longer, seemingly to allow infants to reach weights similar to the weanlings of high-ranking mothers (Johnson, 2003; Altmann and Alberts, 2005). Lee and colleagues (1991) proposed that the timing of weaning depends on infants reaching a threshold weaning weight, roughly four times infant birth weight (see also Bowman and Lee, 1995). Under this premise, higher-ranking, better-condition, and/or more experienced mothers –rather than investing longer in offspring – instead are able to invest more per unit time allowing for faster infant growth rates and younger weaning ages. For example, in captive rhesus macaques, multiparous mothers produced greater milk yields than primiparous mothers, enabling their infants to grow at faster rates (Hinde et al., 2009).

Sex differences

Primates exhibit wide variation in adult size dimorphism, and, as Leigh (1992) suggested, further study of the ontogenetic pathways leading to adult size might elucidate the selective pressures driving this variation. He described multiple developmental pathways for achieving adult size dimorphism. Commonly, two basic patterns, or a combination of the two, have been observed by which males achieve larger body size: 1) males grow for longer periods than females known as bimaturism, leading to sex differences in the age of reproductive maturity, or 2) males grow at faster rates, or 3) both patterns may occur (Shea, 1985; Leigh, 1992; O'Mara et al., 2012). For taxa achieving dimorphism via growth-rate differences, males tend to exhibit growth spurts, often resulting in more highly dimorphic adults (Leigh 1992).

Starting from the adult perspective, the selective pressures leading to variation in primate size dimorphism have been difficult to pinpoint. Research has investigated potential relationships of dimorphism with factors such as phylogeny, diet, and degree of arboreality finding varying levels of support, while the sexual selection hypothesis focuses on the strong link to variation in male-male competition (Leigh, 1992; Ford, 1994; Plavcan and van Schaik, 1997; but see lemurids: Leigh and Terranova, 1998). Plavcan and van Schaik (1997) initially suggested that colobines were an exceptional case, exhibiting high variation in the degree of dimorphism as well as a number of taxa with less dimorphism than would be predicted by their higher levels of male competition. However, in their reanalysis, Grueter and van Schaik (2009) argued that differentiating Asian colobines based on social organization and degree of home range overlap (i.e., multi-male—multi-female vs. modular societies (OMUs with high overlap) vs. non-modular societies (OMUs with low overlap)) better represented actual variation in the *frequency* of male competition, thereby enabling a better fit to models explaining size dimorphism as a consequence of sexual selection.

Of course, the selective pressures shaping the evolution of adult size dimorphism are at work long before age at maturity, and can affect male and female growth differently. For example, Leigh (1995; see also Jarman, 1983) described delayed maturation as a possible risk-aversion strategy, in which case, divergent developmental pathways may reflect sex-specific and/or taxon-specific strategies depending on the type of risks and the timing of when risks arise for maturing individuals. Using captive data, Leigh (1995) noted that males exhibited faster growth rates than females in species characterized by one-male—multi-female groups, but in multi-male—multi-female taxa, dimorphism occurs via bimaturism with males growing for longer but not necessarily faster than females. If adult body size signals entry into the adult competitive realm as Leigh suggested, slower growth for longer periods may delay the associated competitive risks. For one-male groups, the timing of growth spurts later in juvenility or subadulthood may be coordinated with a more sudden rise in risk, such as heightened adult male aggression associated with breeding seasonality. For some taxa, especially one-male groups, the breeding male may aggressively evict maturing juvenile or sub-adult males (e.g., Mohnot, 1978; Rajpurohit and Sommer, 1993; eviction of both sexes: Glander, 1992). In multi-male—multi-female groups, targeted aggression does not necessarily precede natal male dispersal events (Pusey and Packer, 1987; e.g., white-faced capuchins: Jack and Fedigan, 2004).

Indeed, whether due to eviction or other proximate causes, natal dispersal – typically at or prior to physical and reproductive maturity (e.g., Alberts and Altmann, 1995; Strier and Ziegler, 2000; Nishida et al., 2003) – can bring with it significant additional risk for immatures of the dispersing sex. First off, leaving the protective benefits of group life exposes young emigrants to greater predation risk either due to time spent alone or to travel in unfamiliar environments (Isbell, 1994; Alberts and Altmann, 1995; Isbell and van Vuren, 1996). In addition, dispersers, females especially, often face costs associated with entry into a new group, as resident females tend to target immigrant females for aggression, sometimes resulting in serious injury or secondary dispersal (e.g., mantled howlers: Glander, 1992; chimpanzees: Kahlenberg et al., 2008).

Potential sex differences in the socioecological risks during development not only shape growth patterns on an evolutionary scale, but might also contribute to sex-differential responses to changing ecological conditions in the short term. Among baboons, for example, food-enhanced conditions led to greater magnitude of adult size dimorphism, likely due to the greater differences between males between the two ecological conditions. That is, while growth rates for both sexes respond positively to more abundant resources, males benefited the most, exhibiting a relatively greater growth-rate improvement than females as well as earlier growth spurts (e.g., wild-foraging vs. food-enhanced: Altmann and Alberts, 2005; wild vs. captive: Johnson 2003). Among vervets, however, females exhibited the more significant response to improved ecological conditions; females from a food-enhanced population were significantly heavier than females living under poorer ecological conditions but males showed no significant difference

(Turner et al., 1997), perhaps because, as the dispersing sex, they had fewer opportunities than females for crop-raiding opportunities.

Study goals

Growth data from wild primates are scarce. The majority of primate growth data comes from captive subjects, and the energetic surpluses typical of captivity or provisioning are known to influence developmental rates and even eventual adult sizes (Turner et al., 1997; Borries et al., 2001; Johnson, 2003; Altmann and Alberts, 2005; Borries et al., 2011). Considering the equivocal results on the relationship between a leafy diet and faster or slower growth rates (Leigh, 1994; Godfrey et al., 2004), more data from folivorous taxa – especially wild populations – are needed to further test hypotheses linking diet to developmental and overall life history variation. Colobines, in particular, are underrepresented in comparative analyses of primate growth. Thus, I aimed to measure and describe an aspect of skeletal growth (lower limb length) in a wild colobine, the Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*). In addition, simultaneously collected demographic data allowed for further investigation of potential interrelationships with and consequences of growth. Finally, most size data are based on measures of body mass. Bolter and Zihlman (2003) describe a mosaic pattern to development with different body systems maturing at different times (e.g., completion of skeletal maturation before that of muscle mass). Within the skeletal framework, postcranial regions also vary in growth rates and durations, for example, the timing of when long bones reach adult length or skeletal elements fuse (Bolter and Zihlman, 2003). The developmental patterns typical of body systems other than muscle mass (e.g., skeletal lengths and fusions) is less well understood and more ontogenetic data are needed to better explore relationships between postcrania and locomotor patterns (e.g., Bolter, 2011).

In particular, studies of sexual dimorphism frequently rely on measures of body mass for which subadult growth spurts have been well-documented (Leigh, 1996; Setchell et al., 2001), yet the occurrence of growth spurts in measures of non-human primate body length is less certain (and even disputed: Bogin, 1999). Growth spurts in body mass detected among toque macaques and mandrills were not apparent in statural measurements from the same populations (Cheverud et al., 1992; Setchell et al., 2001). Instead, their growth patterns pointed to skeletal bimaturism as the basis for adult length differences (see also Asian colobine sample: Bolter, 2004). Linear measures in Japanese macaques, however, showed seasonal adolescent growth spurts (Hamada et al., 1999), and the authors suggested that longitudinal datasets with frequent measurements afford better opportunities for detecting such spurts. For example, growth spurts were not apparent in cross-sectional analysis of captive chimpanzee length measures, however, longitudinal analysis of individual curves indicated adolescent growth accelerations for a subset of individuals (Hamada and Udono, 2002).

Phayre's leaf monkeys are medium-sized Asian colobines, and adults exhibit mild sexual dimorphism in body mass (6.3kg for females and 7.9kg for males: Smith and Jungers, 1999). The limited growth data available for colobines in general indicate the presence of body mass growth spurts for males and females (e.g., captive data on *Semnopithecus entellus*, *Trachypithecus obscurus* (male data only) and *Colobus guereza*: Leigh 1996) as well as skeletal bimaturism based on dentally aged specimens in a wild-shot post-mortem sample of *T. cristatus* (Bolter, 2004; 2011).

Koenig and Borries (2012) recently described *T. phayrei* as having a unique and dynamic social organization even among colobines. Their long-term study, of which this study is a part, characterized the species as having female-biased dispersal (Borries et al. 2004) and as capable of shifting between one-male and multi-male arrangements with no evidence for male group takeovers (Gibson and Koenig, 2012; Koenig and Borries, 2012). Genetic and behavioral analyses confirm that inbreeding avoidance is a main driver of female natal dispersal in this population of Phayre's leaf monkeys (Larney, 2013). On average, natal females disperse around 4 years of age (Larney, 2013), which is roughly a year prior to the average age of first birth (5.3 years: Borries et al., 2011).

Using longitudinal and cross-sectional limb length data measured via photogrammetry for known-aged immature Phayre's leaf monkeys, I examined differences in growth between sexes as well as group-related and individual variation in size-for-age. I expected adult dimorphism in lower limb length based on known differences in body mass. Predictions regarding growth patterns depend, in part, on sex-differential socioecological risks, which are complicated by the fact that maturing male Phayre's leaf monkeys may either emigrate or remain philopatric. Therefore, I instead predicted that male and female lower limb growth would exhibit evidence of bimaturism based on evidence for this pattern in skeletal measures of a closely related species (Bolter, 2004).

As with other primate taxa for which size remains relatively consistent throughout immaturity, I predicted that juveniles who were large- or small-for-age at the start of the study would remain so at the end of the study. The pace of growth and other aspects of life history often can be correlated, and evidence suggests that variation in growth rates can serve as an indicator of fitness. Therefore, I made two life history-related predictions in regard to inter-individual variation in size-for-age: 1) if better condition mothers invest more per unit time allowing for shorter lactation periods, individuals weaned at earlier ages should be larger for their age as older juveniles and subadults; and 2) because faster growth and larger body size have been linked to earlier reproductive maturity (Bercovitch et al., 1998; Altmann and Alberts, 2005), and might also confer greater competitive advantage upon immigration in a new group, natal juvenile females who are large for their age should emigrate at younger ages.

Methods

Study site and subjects

This study took place at the Phu Khieo Wildlife Sanctuary (PKWS) in northeastern Thailand (16°5'-35' N, 101°20'-55' E). Within the sanctuary, the study site (16°27'N, 101°38'E) is a 1,300 ha area of dry and hill evergreen forest with patches of dry dipterocarp forest (Koenig and Borries, 2012). I studied three groups of habituated Phayre's leaf monkeys for 17 months between October 2006 and May 2008.

The three study groups varied in size with the small group (PS) averaging 15 individuals between the study start in late 2006 and the end of the study in mid-2008, the large group (PB) averaging 27 and the mid-sized group (PA) averaging 22 individuals (Table 4.1). Individuals were considered juvenile if they had ended nipple contact or had reached average weaning age (19 months: Borries et al. 2014). Ultimately, the limb-length dataset included 51 individuals from these three groups: 16 adults and 35 known-aged immatures comprised of 29 juveniles and 6 older infants, the youngest of which was already 10 months of age. Of the 51, 32 were female and 19 were male.

Juvenile subjects were split into younger and older classes (referred to as J1s and J2s respectively) based on the age composition of birth cohorts at the start of the study (breeding is mildly seasonal in this population with most births occurring between November and April: Koenig and Borries, unpublished). The J1 age class ranged from 16 months (the youngest individual weaned from nipple contact in this sample) to 29 months. The older juvenile age class (J2s) started at age 30 months based on the inclusion of immatures from older birth cohorts at the start of the study. For females, the J2 period ended at the time of first reproduction (i.e., mean age = 5.3 years: Borries et al., 2011) or, more commonly for this sample, at dispersal (mean age = 4 years: (Larney, 2013), after which known-aged subjects could no longer be followed except for rare occasions when they dispersed between habituated groups. During this study period, average dispersal age tended to be younger than the overall average with only a single focal female reaching 48 months of age prior to her disappearance and presumed dispersal. By definition, pre-reproductive immigrant females were classified as J2s, however, they were not included in this sample because ages could not be determined with the exception of one individual who transferred between habituated groups and, therefore, was known from birth (S2.1). For males, older juveniles transitioned into subadulthood when their head-body length reached that of an adult female upon visual inspection (average age at subadulthood for focal sample was about 4.5 years). The number of juveniles varied across months as individuals disappeared/dispersed or aged into older age classes with a monthly average of 7.4 J1s (range: 4-10) and 8.3 J2s (range: 5-11).

Ages for all infants and J1s and nearly all J2s were known to the exact day (n=11), week (n=12), or month (n=11). Birth month was estimated for two of the older J2s – both very young infants when first observed – and for one subadult male first observed as an older infant 1 (i.e., all still exhibited the orange natal coat, which gradually changes to the adult gray color over about the first six months: Borries et al. 2008). These three individuals were among seven young infants observed when group PB was first contacted in March 2003 by Andreas Koenig and Carola Borries. They were assigned with confidence to the 2002-2003 birth season. With seven infant 1s present in group PB at the time, comparison of individual developmental differences facilitated estimates of birth month, with the very youngest individuals (the two J2s) assigned February 2003 birthdates, the month just prior to first observation (Borries, pers comm).

All adult ages were unknown, except for one young adult female (A7.1) who did not disperse and eventually reproduced in her natal group. This individual was first observed as an infant in 2000 and, thus, could be assigned to the previous birth season although her exact birth month was not known. Based on the roughly 6-month birth season, her birth month was assigned to the average month (February), which would make her 5.4 years at the time of her first birth, fitting well with the population average of 5.3 years (Borries et al. 2011). Again, using the average age at first birth, a second adult female – determined to be nulliparous in late 2000 based on nipple size and stature relative to other adult females – was estimated to be about 10 years of age based on the known date of her first birth. All other adult ages were unknown. For purposes of anchoring the growth curve, they were assigned an average adult age of 12 years. For adults with multiple measurements, their age was averaged based on 12 years of age for the initial measurement and the added number of months for the subsequent measurement.

Photogrammetric methods

Lower limbs (knee-to-heel) were measured non-invasively via photogrammetric methods (primates: Emery and Whitten, 2003; Deschner et al., 2004; Breuer et al., 2007; Rothman et al., 2008; whales:Jaquet, 2006; elephants: Morgan and Lee, 2003; Shrader et al., 2006), allowing for limb length estimates to be determined using distance to the subject and pixel counts from digital photographs. Subjects were photographed opportunistically from November 2006 to September 2007 and again between February and May 2008 using a Panasonic Lumix digital camera (8.0 megapixels) at maximum focal length (89mm). For each photograph, a high-precision laser distance meter (Leica Disto5; reported accuracy +/-3mm) was used to measure distance to the lower limb. In advance of fieldwork, a centimeter-to-pixel ratio was calibrated for the camera by photographing a yardstick at various distances (7 distances, 2.5 – 25m). The known lengths were measured in Image J 1.46r to obtain corresponding pixel counts (each photo was measured three times and pixel counts were averaged) across the range of distances (Shrader et al., 2006). I used distance-to-the-object (X) and the resulting cm/pixel ratios (Y) in an OLS regression; the resulting regression equation then was used to predict cm/pixel ratios for the measured distances specific to each photograph.

This method relies on the parallel orientation of the subject (in the sagittal plane) relative to the camera as well as the horizontal orientation in a plane perpendicular to the camera (i.e. subjects photographed at eye-level) (see sources of error below). Phayre’s leaf monkeys are arboreal and tended to remain well above eye level. Therefore, photographs were taken opportunistically on occasions when subjects descended to near observer eye level (i.e., heights relatively parallel to the plane of the camera). These opportunities occurred during: 1) extended foraging bouts at low heights due to either shorter/shrubbier patches (e.g., bamboo) or in trees in low-lying areas but in proximity to higher elevation lookouts, or 2) drinking bouts during the dry season (November – February/March) when individuals came to the ground to drink from streams or standing pools. Subjects were typically photographed from a lateral view while sitting, which allowed for the lower limb segment to remain still long enough to obtain corresponding distance measures. When time allowed, distance to the subject was measured to both endpoints repeatedly (i.e., once to the knee and to the foot before the photograph and again to both endpoints after the photograph) and then the distances were averaged. Individuals were photographed as often as conditions allowed during each group month with emphasis given to focal juveniles, often to the exclusion of adults and infant. All photographs were taken at maximum focal length (89mm).

During the height of the rainy season, frequent downpours as well as a tendency for groups to utilize higher canopy heights (particularly groups PA and PS) caused gaps in photographic coverage for several individuals between April and July 2007 and again in May 2008. Ultimately, after all photographs were screened (see below), monthly limb lengths were determined for an average of 6.7 months per immature individual (range: 1-13 months) based on an average of 2 useable photographs per month (range: 1-6 photos). The much more limited photographic sample for a subset of available adults and infants resulted in individual measures for an average of 1.4 months (range: 1-2), based on an average of 1.2 photos per individual per month (range: 1-2).

Prior to digitizing, all photographs were visually screened; those that clearly deviated from the relative horizontal or sagittal planes as well as those for which limb segments were obscured or were too blurry for precise endpoint identification were discarded (n=938 discarded out of 1,686 photographs). The more than 700 photographs remaining were assigned 2 separate scores on a scale of 1 to 5. First, the distance score was based on the number of distance measures (1 to 4) obtained for that particular photo. Repeated distance measures to both the knee and foot not only ensured the accuracy of the distance but could also be used to gauge the parallel orientation of the limb for the second score. This orientation score was based on the subject's orientation in a horizontal plane relative to the camera (i.e., height) as well as the limb segment's parallel orientation in the sagittal plane. These were judged using visual inspection and, for parallel orientation of the limb, using the standard deviation for the knee and foot measures to better determine whether the limb was photographed at a tilt.

The whole lower limb, from knee to heel, was chosen as the segment to measure because the endpoints were less likely to be obscured by hair and were not dependent on positioning (as opposed to ending at the ankle or using the forearm segment), thereby improving repeatability of landmark identification. Each image was digitized to obtain pixel counts four to five times and the resulting values were averaged per photograph (mean within-photo CV = 0.864%, n=726, SE=+/-0.021, range = 0.038-4.63%). When multiple photographs were measured for a single individual within a month, the average CV was 0.926% (range: 0.002 – 3.12, n=110).]

Several sources of measurement error are possible with this method including distance accuracy, difficulty identifying anatomical landmarks and problems of parallax (Spencer and Spencer, 1995; Jaquet, 2006). In a study using digital photogrammetry to measure sperm whale flukes, Jaquet (2006) determined that significant measurement error resulted when the subject was at an angle of 20° or greater outside of the horizontal plane. As described, great effort was made to reduce these sources of error. In a brief validation study conducted with silvered langurs at the Bronx Zoo, I determined that average lengths obtained via photogrammetry did a fairly good job of approximating actual physical measurements of seven juvenile males (Figure 4.1). Despite the fact that only a single distance measure was taken per photograph, of the 23 photographs measured (2-5 per individual), average deviation from actual measures – physical measurements taken during medical examinations performed within a 2-month period by zoo staff – was 0.10cm (SE=0.06, range: 0.001-0.77). In addition, comparing physical measurements from medical examinations of pilot study subjects showed that lower limb length as defined for this study (i.e., knee-to-heel) significantly correlated with body weight (Kendall's tau = 0.593, $p<0.05$; n=8 (7 juvenile males aged 23-48 months plus one female, 60 months), Figure 4.2).

Modeling growth with cubic spline regressions

Traditionally, lowess and cubic spline regressions (non-parametric, non-linear regression analyses) have been used to model growth, combining longitudinal and cross-sectional data (e.g., primates including humans: Poirier, 1973; Cheverud et al., 1992; Leigh, 1992, 1994; Johnson, 2003; Setchell et al., 2001; Altmann and Alberts, 2005; O'Mara et al., 2012; domestic cattle: Meyer, 2005). Cubic spline regression represents the fit of the data as piecewise cubic polynomials (Hastie and Tibshirani 1990), allowing knots or breakpoints to be assigned to the curve. By stringing together separate cubic polynomials for each segment between the knots, each datapoint ends up having "a local rather than a global influence" (Meyer, 2005) (p.480), which is important when using a dataset that combines longitudinal and cross-sectional data (Besse et al., 1997). At the same time, Leigh (2001) describes splines as less sensitive to "localized differences in data abundance" (p. 228) than lowess and are therefore less likely to overfit the data. Overall, 209 datapoints from the 51 individuals were used in the growth curve estimation. Due to the sparseness of datapoints at the ends of the growth curve (i.e., fewer adult datapoints relative to juveniles and no infants younger than 10 months), I employed natural cubic regression spline, which forces the end segments of the piecewise curve to be linear (Zuur et al., 2009).

Curve estimation during the growth phase only did not require modeling a breakpoint at growth cessation, therefore, I used cubic curve estimation after comparing the fit of linear regression with quadratic and cubic polynomial regression. Among growing females, quadratic and cubic curve estimations both provided a better fit to the length data than a simple linear regression (linear: $R^2 = 0.773$; quadratic: $R^2 =0.797$, quadratic term: $p < 0.01$; cubic: $R^2 = 0.819$, cubic term: $p < 0.01$). For males, all three seemed to do just as well (R^2s respectively =0.926, 0.926, 0.930), though the cubic term showed a trend toward significance ($p = 0.067$), and visual inspection suggested a more flexible fit to the data points at the ends of the data range for this model. Thus, to maintain consistency with females, I represented individual size-for-age for both sexes by calculating residuals from a curve fit using cubic polynomial regression.

To depict the rate of change in growth with age, first *derivatives – the* slope of a function at a particular value of the independent variable – were estimated from the natural spline regression curves excluding adults of unknown age. These were plotted against corresponding age and were fit with spline-smoothing curves to visualize changes in growth velocity and allow detection of potential growth spurts. The timing of growth spurts and/or growth cessation may be influenced by risk-aversion strategies (Leigh, 1995). Within a population, co-existing alternative strategies may lead to male bimaturism (e.g., mandrills: Wickings et al., 1993; orangutans: Utami et al., 2002). Therefore, in an attempt to detect growth patterns otherwise obscured by individual variation – for example, growth spurts with differences in age at onset – I examined juvenile and subadult males individually. This data subset comprised only male subjects with a longitudinal sample of at least a 14-month span (n=9, 5 younger males (J1s to J2s), 4 older (J2s to subadults); mean timespan between first and last measurements = 15.5 months). At the individual level, I attempted to reduce any noise from measurement error by selectively omitting monthly datapoints such that individual limb measurements were at least 3 months apart (mean = 5.2 month span, range: 3-8.5 months) resulting in 4 measurements per individual. To visually check for similar patterns in growth velocity across individuals, I fit smoothing splines to individual pseudo-velocity curves.

Demographic data

Age at cessation of nipple contact. Nipple contact was noted on a one-zero basis for each day of contact with a group following Borries and colleagues (2014), which defined nipple contact as occurring when the nipple could be seen in the infant's mouth for at least several consecutive seconds. Age at cessation was based on the last month in which consistent nipple contact was observed for each individual. For older juveniles and subadults weaned prior to the start of this study, these ages were determined using long-term study data (Borries, pers comm). For younger individuals weaned during the course of this study, cessation ages were based on one-zero observations supplemented by observations of nursing behavior recorded during focal animal sampling.

Female dispersal age. Actual observed dispersal events were rare during the study period. More often, female disappearances from month to month were noted but immigration into a new group could not be confirmed. Of the 12 natal females who disappeared without returning during this study, four were confirmed dispersal events because the subjects immigrated into other habituated groups, at least temporarily (secondary dispersal is common in this species: Borries et al., 2004; Larney, 2013). Of the other disappearances, seven were presumed dispersal events based on females' ages and the fact that several had previously temporarily dispersed only to return to their natal group. One female disappeared at age 27 months, an age still considered to be a younger juvenile and far younger than the average dispersal age. Her disappearance may have been due to mortality, therefore, I ran the analysis involving dispersal ages both with and without this female.

Data analysis

I used R 3.1.0 (R Core Team, 2014) to run cubic spline regressions to fit growth curves and corresponding first derivatives to model pseudo-velocity curves using the included "splines" package as well as the package "sfmisc" (Maechler et al., 2014). Additional analyses were performed using Statistica 12 (©StatSoft, Inc. 1984-2013). As previously described, I calculated individual residuals from cubic regression analysis as continuous measures of individual size-for-age and tested individual consistency of size-for-age two ways: first by running an ANOVA and comparing across- and within-individual variation based on the sums of squares, and second, via Wilcoxon signed ranks for matched pairs. Then, to control for possible group-related genetic influences on size-for-age, I tested the relationship between size-for-age and weaning age using a general linear model including group as a factor. Group ID could not be included in the analysis of female dispersal ages due to small sample sizes. Instead, juvenile females who dispersed/disappeared during the study were classified as either large- or small-for age (i.e., positive or negative average residual during J2 period), and I conducted a Mann-Whitney U test for difference in dispersal age between the two size categories. Tests were two-tailed and alpha values were set at $p<0.05$.

Results

Sex differences in growth and velocity curves

Adult Phayre's leaf monkeys exhibited mild sexual dimorphism in knee-to-heel length (male-female ratio: 1.068, Figure 4.3) with an average adult length for males of 21.15cm (range: 20.17-21.84cm, SD = 0.827, n=3) and 19.81 cm for adult females (range: 19.19-20.37cm, SD = 0.413, n=11). By average weaning age of 19 months, juvenile male lower limbs averaged 14.66cm or about 72.75 percent of adult male length (Figure 4.4a). Similarly, juvenile females had achieved roughly 75.66 percent of adult female length with lower limbs averaging 14.99cm (Figure 4.4b). At the average dispersal age of female subjects (41 months), females had achieved, on average, 90.52 percent of adult female length.

Young juvenile males and females follow relatively similar growth trajectories until growth curves diverged between 34 and 37 months of age (Figure 4.5) with females starting to level out earlier than males. Although, younger juvenile females tended to be slightly larger than males of similar ages, the difference is not significant prior to 30 months of age (ANCOVA: F=2.852, p=0.097). An ANCOVA for older juveniles and subadults (30-59 months) indicates significant sex differences in limb length (F=88.33, p<0.001). However, average male and female lengths for shorter time spans (4-5 months for younger juveniles; 8-10-month spans as sample sizes decrease for older juveniles and subadults) do not show significant differences until after 3.6 years of age (Table 4.2, Figure 4.6).

Age at growth cessation was determined definitively for only a single male and estimated for four additional males and one female (Table 4.3). For S2.1, the only older juvenile female of known age, her last three measurements came at about 50, 57 and 65 months of age. Between the earlier two measures (a 7-month span), she gained approximately 0.77 cm in length, while during the later 8-month span, she gained a mere 0.15cm and attained a length in the range of the adult female average. Unfortunately, due to the gap in data points, I can estimate her age at growth cessation only as sometime between 57 and 65(+) months of age.

For the males, the youngest age at growth cessation was 54 months. The largest male (Bm10.1) had three subsequent length measures at 55, 61 and 62 months of age with no increase in limb length. Although Bm10.1 is one of the males whose birth month was estimated, it seems unlikely that his age has been significantly underestimated. For one, the same birth month was assigned to another young infant first observed with Bm10.1, and based on her estimate age, in contrast, she was small for her age. In addition, using this estimated birth month, Bm10.1 had one of the oldest weaning ages on record among study individuals (29 months vs. the estimated population average of 19 months), in opposition to the conclusion that age has been underestimated (Borries, pers comm). The individual with the oldest age at growth cessation (Sm1.1) was measured only twice during the study: at 59 and 71 months with a 1.2cm-length increase between the two to reach his presumed adult length of 21.1cm. From 59 months of age, even growing at peak velocity for older males (estimated as 0.36cm/mo, see below), Sm1.1 would need a minimum of 3.4 additional months to add more than 1cm in length. Thus, his age at growth cessation was estimated as 63 months at the earliest, though he likely was even older.

Plotting first derivatives against age for known-aged non-adults illustrates steadily declining average growth velocity over time though female velocity declines at a steeper rate than that of males (Figure 4.7). There is no indication of a growth spurt in limb length for either sex using the dataset that includes cross-sectional data. At all ages, males appear to grow at faster rates than females. To detect possible evidence of growth spurts obscured by individual differences in timing, the peak velocities determined for individual males indicated that the maximum values (0.36 and 0.31 cm/mo, Figure 4.8) occurred in older juvenile males, ages 42 and 41 months respectively, while the next highest values (0.24 cm/mo for both) were found for younger individuals aged 24 and 18 months.

Consistency and correlates of individual size-for-age

Individual size-for-age exhibited greater variation across individuals compared to within-individual variation (ANOVA: across-individual sum of squares = 34.51, within-individual (error) sum of squares = 7.39, n=20 individuals with 4 or more monthly measures, Figure 4.9). Individual size-for-age also remained relatively consistent over time using only individuals with data available from the start and the end of the study period (mean time span = 14.6 months, range: 10-17 months, n=14). From this longitudinal sample, an individual's younger and older size-for-age residuals were significantly correlated (tau=0.636, T=54, $p < 0.003$, Figure 4.10), suggesting significant though not perfect consistency over time. .

Counter to predictions, age at cessation of nipple contact showed a significant positive relationship with average size-for-age as an older juvenile, controlling for potential group differences ($F_{(1,14)} = 9.38$, $p < 0.01$; whole model $R^2 = 0.52$, $p<0.05$, n=18 excluding individuals with estimated ages, Figure 4.11). That is, individuals weaned at later ages were larger for their age by late juvenility. As predicted for dispersal timing, large-for-age females were more likely to emigrate at earlier ages than those who were small-for-age (MWU: U=3.5, Z=-2.01, $p<0.05$, n=11). However, this significant result becomes merely a trend upon removal of a female whose disappearance occurred at 27 months, far younger than the average age of dispersal (MWU: U=3.5, Z=-1.78, $p=0.076$, Figure 4.12).

Discussion

Sex differences

Adult male and female Phayre's leaf monkeys exhibited mild dimorphism in lower limb length with a male-to-female ratio of about 1.07, less than the mass dimorphism ratio of 1.25 based on body mass measures for the species from Smith and Jungers (1997). Longer adult male limb lengths were achieved, in part, by faster male growth during juvenile and subadult periods. Skeletal bimaturism might also be a factor as suggested by pseudo-velocity curves showing the continuation of male growth beyond the cessation of female growth, however, additional data from sub-adults and young adults of known ages are needed to be certain.

During the younger post-weaning period (19 to 30 months), young males tended to be smaller than females of similar ages, which mirrors findings for closely related *T. cristatus*, in which females had higher average body mass than males during dentally estimated younger age classes 1-3 (up to about 3 years: Bolter, 2004). For Phayre's leaf monkeys, these early juvenile sex differences were not significant, however, and male and female growth trajectories were rather similar prior to 3 years of age. Minimal sex difference early on is common for primate growth patterns. For example, male and female body mass and segment lengths in wild vervets did not start to diverge until around two years of age (Turner et al., 1997), while significant sex differences in body mass in wild baboons did not occur until 5 to 5.5 years (Johnson, 2003; Altmann and Alberts, 2005). In free-ranging mandrills, one of the most size-dimorphic primate species, young males tended to be heavier than females as early as 12 months of age and were longer in stature (crown-rump length) starting between 18 and 24 months, however, significant differences did not become consistent until around four years of age or later (Setchell et al., 2001).

The growth trajectory in male Phayre's leaf monkeys showed its first clear divergence from females closer to the three-year mark, and significant differences in average male and female limb lengths became apparent after 3.7 years of age. Based on growth and pseudo-velocity curves, the emergence of significant sex differences were due, at least in part, to faster growth rates in juvenile males. For older juvenile females, the growth curve started to level out while the male curve maintained steepness. The male pseudo-velocity curve remained consistently above that of females, though both showed steady declines throughout the juvenile period and no accelerations that would indicate a growth spurt in limb length. This contrasts with the available growth data for colobine body mass, by which measure both males and females exhibited mass growth spurts (Leigh, 1996).

Yet primate male growth spurts in body mass often show high variability in the peak velocities reached as well as in the age of growth spurt onset (Leigh, 1996; seasonal impact: Hamada et al., 1999). For that reason, the variation in individual velocity curves noted here – though based on very small samples sizes – nonetheless, hints at the possibility of male growth spurts being obscured when all data are combined and examined cross-sectionally. Across individual males with sufficient longitudinal spread, the highest peak velocities (0.36 and 0.31 cm/mo) occurred in older males, ages 42 and 41 months respectively, while the highest peak velocity in younger juveniles was 0.24 cm/mo for two individuals aged 24 and 18 months. Unfortunately, no male subject spanned ages 37 to 41 months partly due to age clusters in the dataset resulting from the mild birth seasonality. And only two males – the two with the highest relative peak velocities for all growing males in the longitudinal sample – contributed data between the ages of 41 and 45 months. Therefore, if the onset of a growth spurt occurred around 40 months of age, using derivatives from the spline-generated curve that interpolates among the complete set of datapoints may have failed to detect it. That said, large male growth spurts in primates tend to be associated with high degrees of adult size dimorphism (Leigh 1992); and although male mandrills experienced marked growth spurts in body mass, even this highly dimorphic taxon did not appear to have spurts in the statural measure crown-rump length (Setchell et al. 2001). Instead, female mandrill growth velocity declined more steeply and growth was completed at an earlier age than in males. Considering the mild dimorphism in adult Phayre's leaf monkeys, distinctive male growth spurts in limb length might be unlikely. Leigh (1992) suggested that male growth tends to follow either a pattern of prolonged growth or else a pattern involving a growth spurt. Therefore, the individual variation in male Phayre's leaf monkey growth velocity may simply be an indicator of males' maintaining steady growth rates for longer while the somewhat earlier decline in females could be illustrative of earlier growth cessation. In other colobine species, Bolter (2004) documented greater increases in skeletal length for males than females during the older juvenile period (estimated age of 3 to 4 years), however, the cross-sectional sample did not allow for differentiating between the possibility of a male growth spurt or earlier female growth cessation.

More data are needed to confidently identify bimaturism in Phayre's leaf monkey limb lengths. Based on only a single older juvenile female with available measures during the time period in question, female age at growth cessation could occur sometime between 57 and 65 months. This particular female gave birth at 61 months of age, suggesting female lower limbs achieve adult length roughly around the time of reproductive maturity if not before. This appears to be typical of cercopithecoid females, including colobines, who are capable of becoming pregnant or giving birth to their first offspring prior to completing either body mass or skeletal length growth (e.g., 3 colobine species: Bolter, 2004). For example, in a colony of captive tufted capuchins, females had achieved roughly 90 percent of adult weight at the time of first conception (Fragaszy and Adams-Curtis, 1998), while female mandrills were only 74 percent of adult mass at age at first birth (Setchell et al., 2001).

Age at growth cessation for males may occur as early as 54 months while the upper range remains less clear but likely upwards of 63 months. For most if not all of these 6 subadult males, adult limb lengths were achieved well prior to either attaining dominant status or alternatively emigrating from the natal group. As mentioned, different body systems grow in a mosaic pattern with statural length measures typically completing growth earlier than body mass (Bolter and Zihlman, 2003). Of the 6 subadult males for which age at growth cessation could be roughly estimated, the two that completed growth earliest were the only individuals with multiple male cohort members. Leigh (1995) highlighted the potential for different growth strategies relating to risks associated with male subadulthood (i.e. male competition; dispersal-related risk). Male Phayre’s leaf monkeys face two very different possibilities as they approach adulthood: 1) remain and breed in their natal group or 2) emigrate and eventually recruit females to form a new group (Koenig and Borries 2012). As both solitary males and small all-male bands have been observed in the study area (Koenig, pers comm), the latter scenario, in particular, inevitably incurs the increased predation risks associated with dispersal. Although sample sizes here are admittedly small, inter-individual variation in age at growth cessation as well as growth velocity during late juvenility or subadulthood may relate to alternative growth strategies among males for mitigating potential competitive and/or dispersal risks (e.g., Leigh, 1995); that is, a scaled-down version of the patterns of male bimaturism in some primate taxa (e.g., mandrills and orangutans: (Wickings et al., 1993; van Adrichem et al., 2006)). Subadult males with no similar-aged male cohort members might be able to employ a crypsis-style strategy of slower growth to delay entry into the competitive arena of adult males, which potentially mitigates the need for or delays the timing of emigration. However, multiple like-aged males approaching subadulthood together might not be able to afford such a delay and, instead, might have an earlier need for the competitive or predator-avoidance advantage that comes with growing faster and achieving adult size earlier.

Possible causes and consequences of variation in size-for-age

Size-for-age is a relatively consistent trait over time, and individuals who are small-for-age during one age class tend to remain so during the later age class. However, there are exceptions, and it is possible for individuals who start out below average size, for example, to end up closer to average or slightly above average size. The individual with the greatest change over time was a juvenile female in group PB. PB6.2 was small for her age and still in nipple contact at 23 to 24 months of age, at which time her next sibling was born. In September 2006, based on instantaneous focal sampling, B6.2 spent 11 percent of the time in nipple contact with her mother. Yet just prior to her sibling's birth and in the three subsequent months, B6.2 spent, on average, 33 percent of focal time in nipple contact. She was eventually weaned completely at the late age of 28 months. As an older juvenile – her last measurement was taken at 39 months – B6.2 had become large for her age relative to other females.

The case of B6.2 highlights the possibility of catch-up or accelerated growth, which might also explain the unexpected positive relationship of weaning age with size-for-age as an older juvenile. Previous research has demonstrated that variation in maternal investment mitigates individual variation in size at weaning age (Bowman and Lee, 1995; Lee, 1999). Good-condition mothers presumably have higher milk yields or higher quality milk (Hinde et al., 2009;

Hinde and Milligan, 2011), enabling infants to grow at faster rates and reach threshold weaning sizes at earlier ages, while poor-condition mothers must prolong lactation to allow offspring to reach similar threshold sizes prior to weaning (e.g., Johnson, 2003). Much of this research, however, has focused on cercopithecines with matrilineal dominance hierarchies that are stable long-term (e.g., macaques, mandrills, baboons: Bowman and Lee, 1995; Setchell et al., 2001; Johnson, 2003; Alberts and Altmann, 2005). The long-term effect of variation in maternal investment should be investigated further in other taxa with female dominance hierarchies less stable over time, which would allow for a decoupling of maternal effects during infancy from the potentially correlated post-weaning benefits of maternal rank inheritance.

Of the 12 juvenile females who emigrated or disappeared during this study, those who were larger-for-their-age tended to leave their natal group at younger ages. Larger body size and faster growth rates have been associated with earlier ages at reproductive maturity (Bercovitch et al., 1998; Johnson, 2003). In this population of Phayre's leaf monkeys, average emigration age was approximately 4 years (Larney, 2013), about a year prior to average age at first birth (Borries et al., 2011). In her research, Larney (2013) linked female natal emigration in Phayre's leaf monkeys to inbreeding avoidance. Thus if body size is one factor signaling the transition to reproductive maturity, larger natal juveniles might disperse earlier to avoid reproducing with their presumed fathers.

On a more proximate level, dispersal timing might be linked to risk-reduction strategies, as most confirmed dispersal events (i.e., transfer of known individuals between habituated groups) have coincided with inter-group encounters, as seemed to be the case among female Thomas langurs (Sterck, 1997). While transfer decisions for Thomas langurs were linked to infanticide avoidance, male takeover and infanticide have not been observed in Phayre's leaf monkeys (Koenig and Borries, 2012). Instead, such timing might allow females to avoid or greatly reduce the amount of time spent solitary, which has been associated with increased predation risk (Isbell et al., 1993; Isbell, 1994). As with other female-dispersal species (Glander, 1992; Kahlenberg et al., 2008), the greater risk for transferring Phayre's females comes upon entry into a new group. New immigrant females face the risk of injury from resident females, who often chase or are otherwise aggressive toward extra-group females (Koenig, Borries, Larney, Ossi-Lupo unpublished data). So while actual timing of dispersal depends to some extent on proximity of neighboring groups, large-for-age juvenile females might have a better competitive advantage, and therefore take advantage of inter-group encounters when they arise, transferring at earlier ages than smaller females. Along these lines, Glander (1992) suggested that body weight among mantled howlers influenced an immigrant female's likelihood of success. He found that successful immigrant females tended to be heavier (though not significantly so) than those who remained as extra-group individuals for longer, likely because a female faced two possibilities: fight her way to the top of the female dominance hierarchy or leave the group and try again elsewhere.

In his comparative study indicating faster growth and earlier ages of growth cessation for folivorous taxa, Leigh's dataset (1992) showed closely related Asian colobines (*T. obscurus, T. cristatus*) completing mass growth around or before 5 years of age. Although small sample sizes here preclude definitive determination of age at lower limb growth cessation, preliminary results at the individual level point to similar ages ranging from 4.5 to 5.4 years, while predicted velocity based on cross-sectional analysis indicated small length increases for males beyond 6 years of age. Primates attain adult lengths for skeletal segments far earlier than they reach adult body mass: averaging across a sample of juvenile silvered langurs, Bolter (2004) determined that when limb segments are 84 percent of adult size, juvenile body mass is only 59 percent of average adult mass. Therefore, it seems likely that 4.5-to 5 years is too young for age at cessation of body mass growth for wild populations. At the same time, however, considering the mild sexual dimorphism, it seems unlikely that Phayre's leaf monkeys continue to gain muscle mass as long as the males of more dimorphic taxa such as mandrills and baboons (12 years and 8 to 9 years respectively: Setchell et al., 2001; Altmann and Alberts, 2005). Additionally, the unexpected results linking later weaning ages to above-average-sized juveniles highlights the need for developmental studies outside of cercopithecine taxa, including subjects with greater dietary variation as well as differences in social organization and social systems.

Tables and Figures

Table 4.1. Group composition at study start in November 2006.

Group	Ad male	Ad female	SubAd male	J2 male	J2 female	J1 male	J1 female	Infants	Total
PS	1	5	1	1	1	1	2	2	14
PA	3	5	1	1	6	1	2	3	22
PB	1	10	2	2	3	2	3	6	29
Total	5	20	4	4	10	4	7	11	65

Table 4.2. Female and male average limb length by age class. Sexes compared via MWU. Significant results in bold.

Age Class	Sex	Mean length	N	SE	U	Z	*p*
10-14	M	13.538	5	0.189			
10-14	F	n/a	0				
15-18	F	14.368	8	0.315			
15-18	M	14.678	5	0.203	18.0	0.22	0.826
19-24	F	15.422	9	0.294			
19-24	M	15.141	6	0.209	17.0	1.12	0.263
25-30	F	16.627	7	0.124			
25-30	M	16.120	6	0.220	10.0	1.5	0.134
31-36	F	17.262	10	0.136			
31-36	M	17.348	3	0.280	15.0	0.0	1.00
37-43	F	17.518	7	0.127			
37-43	M	17.820	5	0.263	10.0	-1.14	0.256
44-51	**F**	**18.284**	**4**	**0.247**			
44-51	**M**	**20.010**	**4**	**0.420**	**0.0**	**-2.17**	**0.030**
52-60	F	19.72	1				
52-60	M	20.838	6	0.290			
61-71	F	19.735	1				
61-71	M	21.328	4	0.170			
83-120	F	19.758	4	0.264			
83-120	M	21.456	1				
>11 years	F	19.826	7	0.133			
>11 years	M	21.003	2	0.833			

Table 4.3. Age or age range of individuals at growth cessation. [a] Ages are estimated by known birth season (see Methods). [b]S2.1 gave birth to her first infant at 61 months.

Subadult ID	Sex	Age at growth cessation (mos)	Total months with measures	No. of measures with no increase
Am3.2	M	58-60	5	2
Bm12.1[a]	M	≥54	2	1
Bm10.1[a]	M	54	11	3
Bm5.1	M	≥58	12	0
Sm1.1	M	>63	2	0
Sm3.1	M	≥58	10	1
S2.1[b]	F	57-65	5	0

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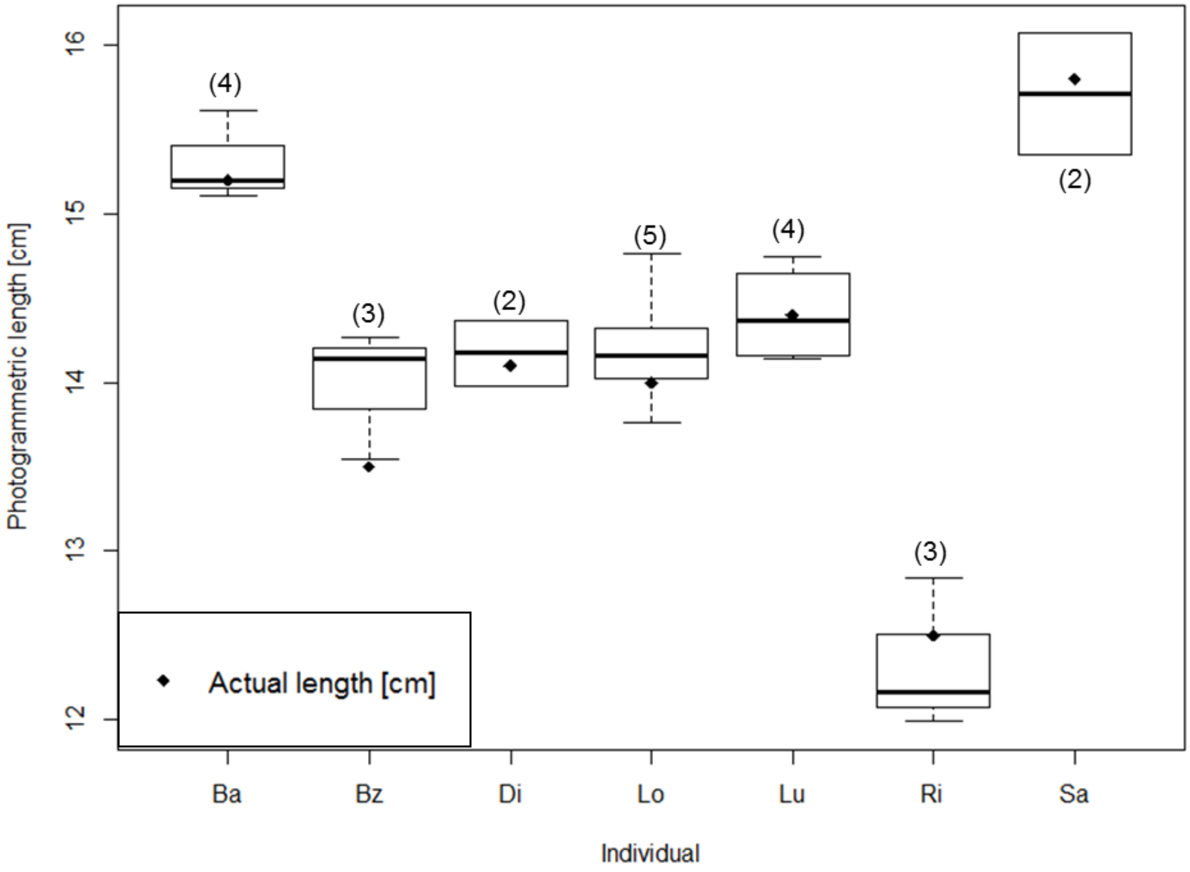

Fig. 4.1. Repeated measures of photogrammetric forelimb lengths for silvered langur juveniles relative to physically measured forelimb length indicated by diamond shape. () indicates number of photographs measured.

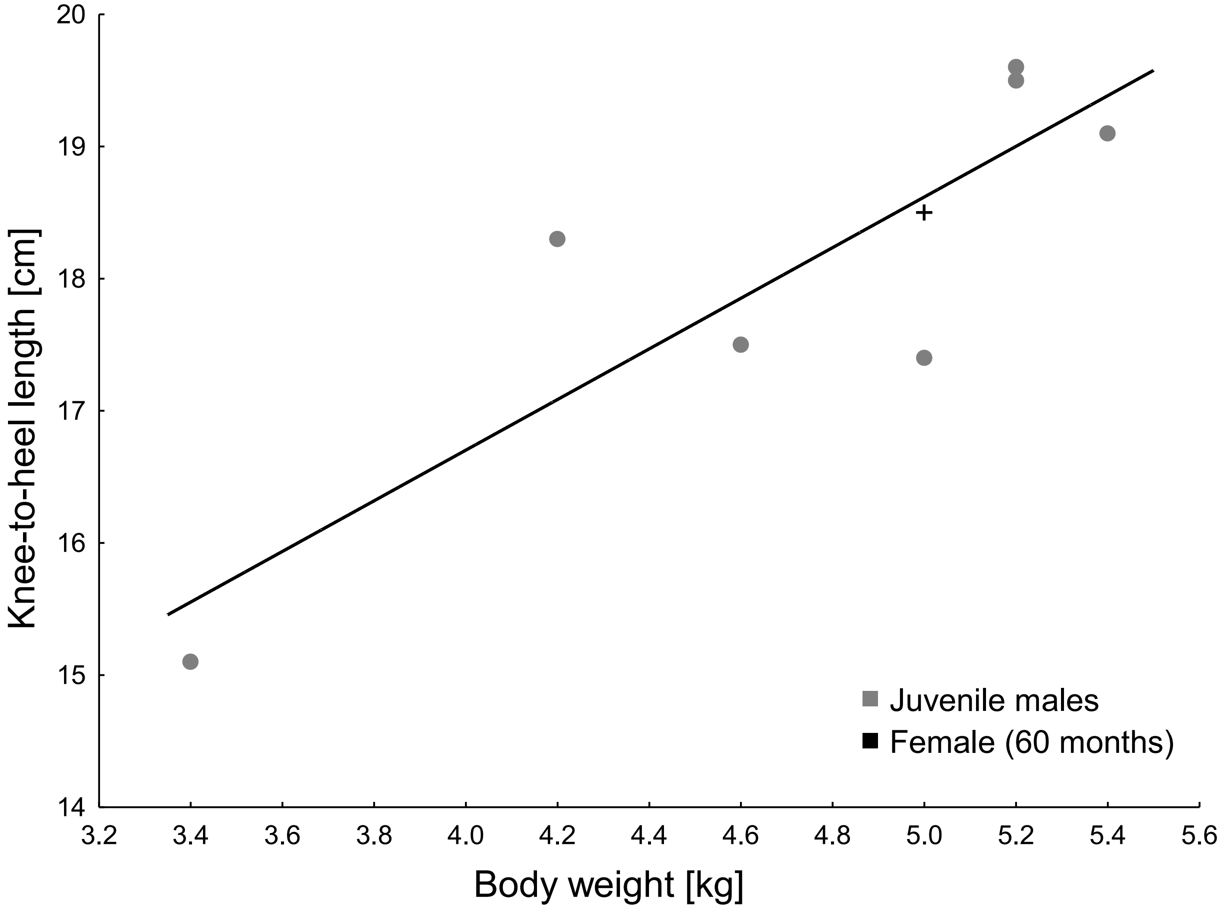

Fig. 4.2. Relationship between lower limb length and body weight for juvenile silvered langurs formerly housed at the Bronx Zoo. + indicates the one older female subject.

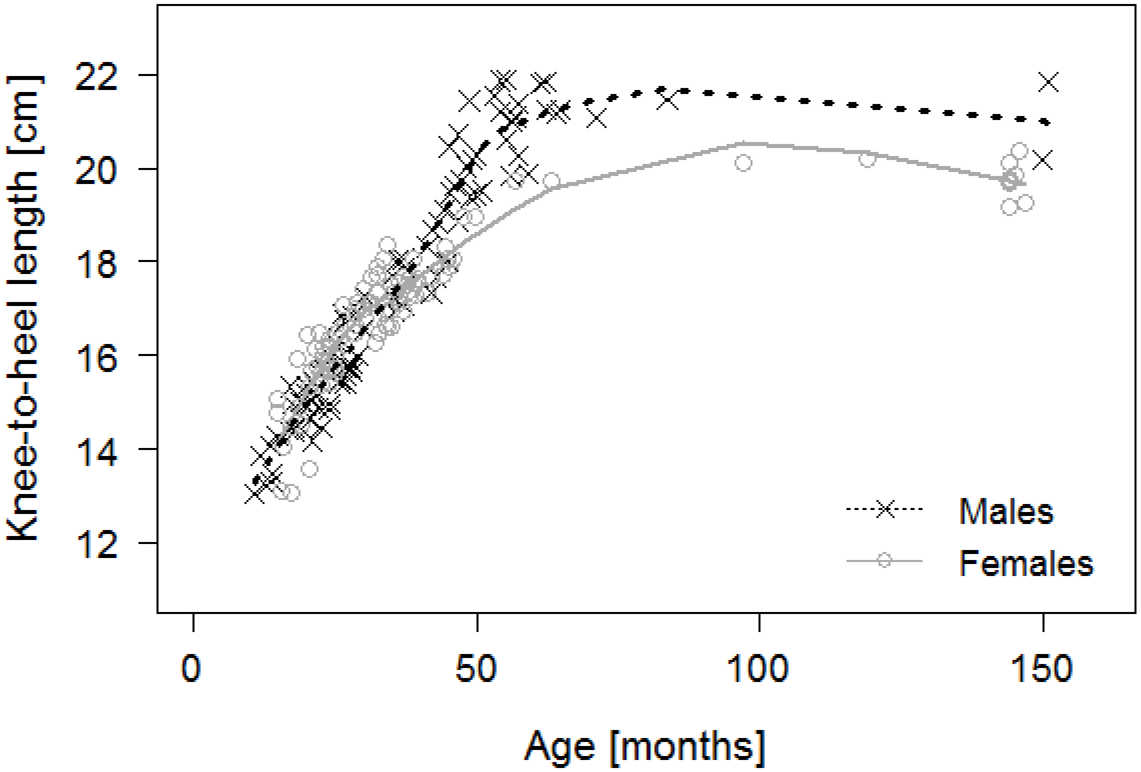

Fig. 4.3. Cubic spline curve fit to male and female knee-to-heel lengths plotted by age.

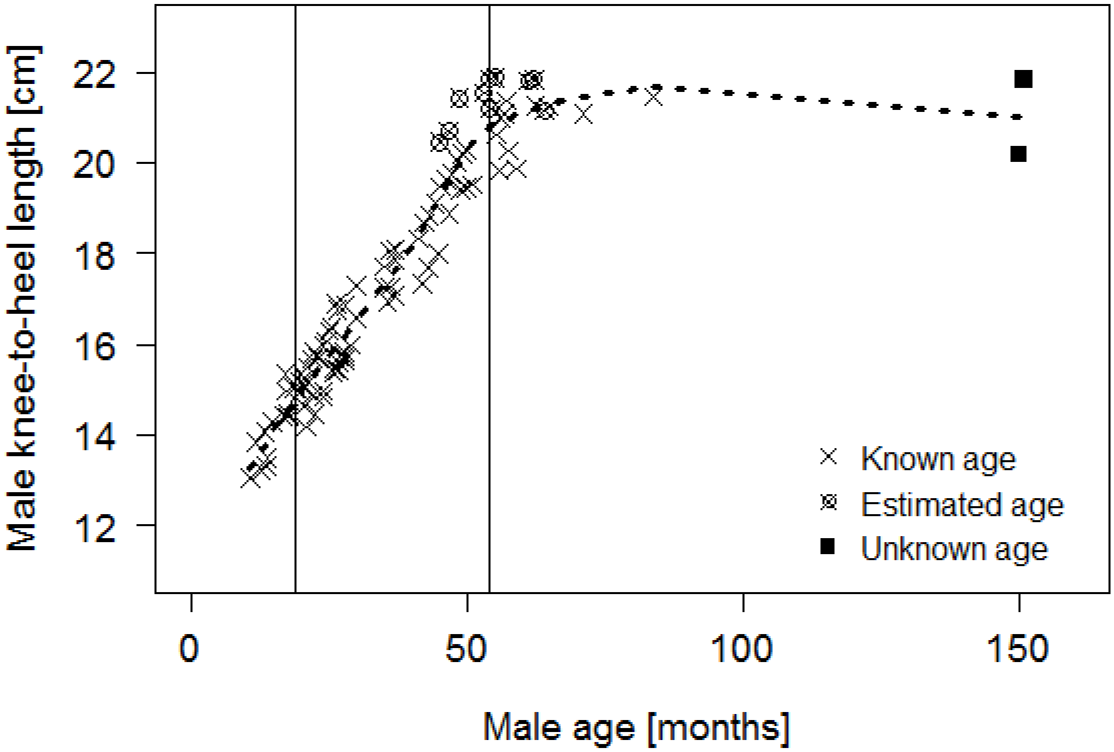

Fig. 4.4a. Cubic spline curve fit to male lower limb lengths plotted by age starting at 10.7 months of age. Estimated ages are for two subadults with repeated measures. Vertical lines in black denote average weaning age (19 months) and earliest age at growth cessation (54 months).

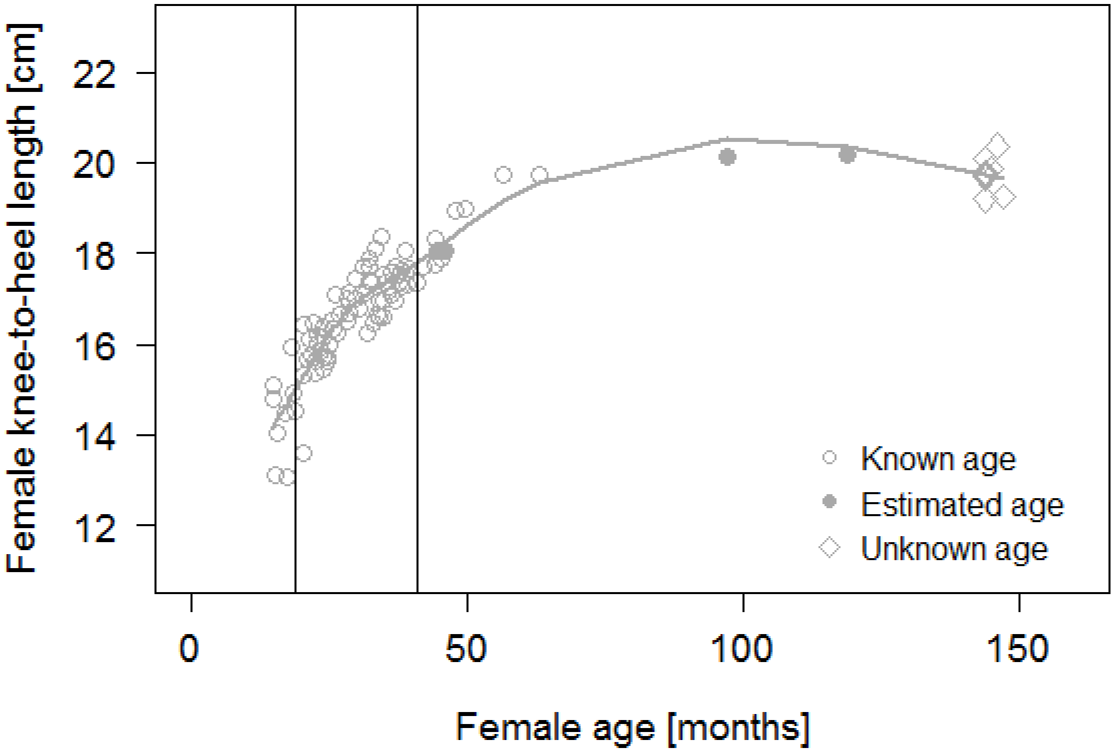

Fig. 4.4b. Cubic spline curve fit to female lower limb lengths plotted by age starting at 14.8 months of age. Vertical lines in black denote average weaning age (19 months) and average age at dispersal for study period (41 months).

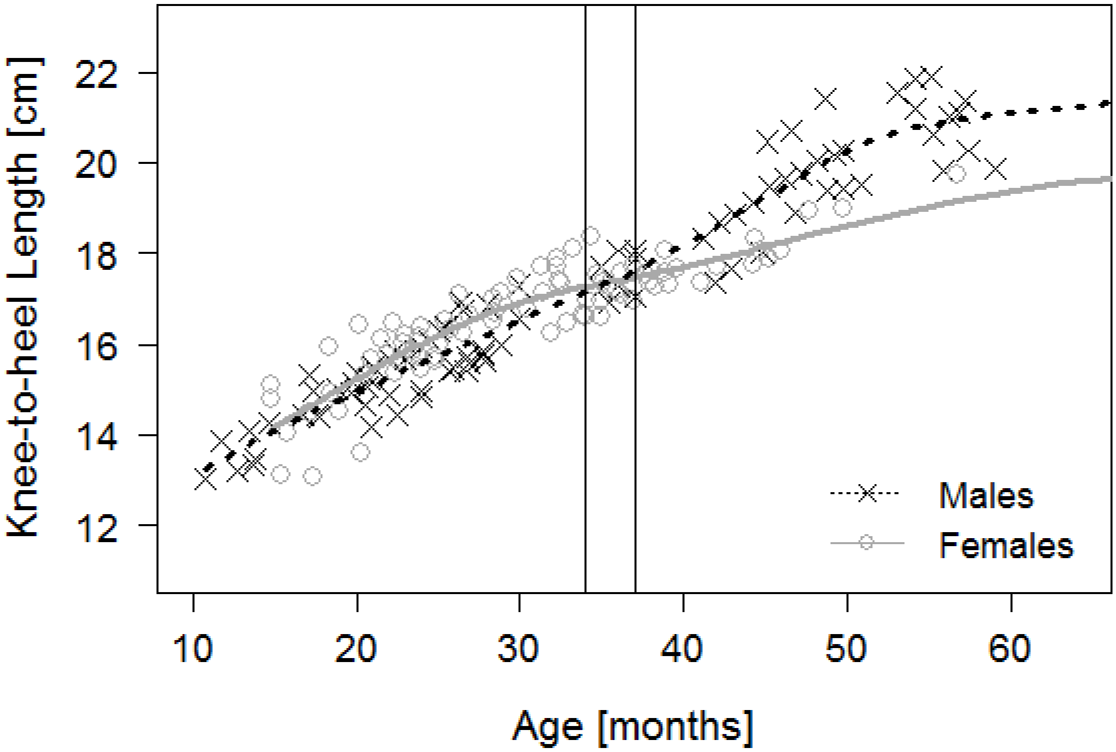

Fig. 4.5. Male and female limb lengths by age for juveniles and subadults. Black bars bracket the age range where male and female growth trajectories diverge.

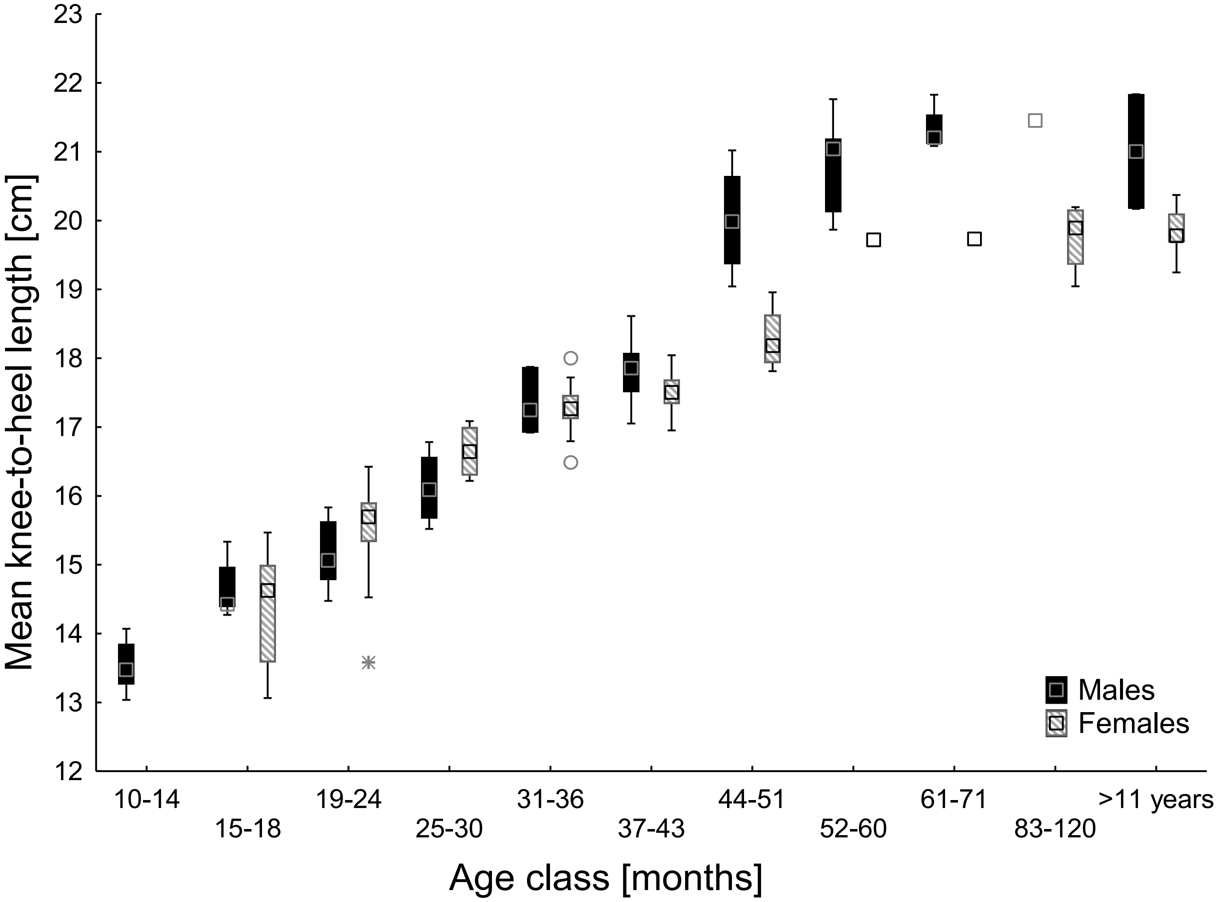

Fig. 4.6. Male and female mean limb length by age class.

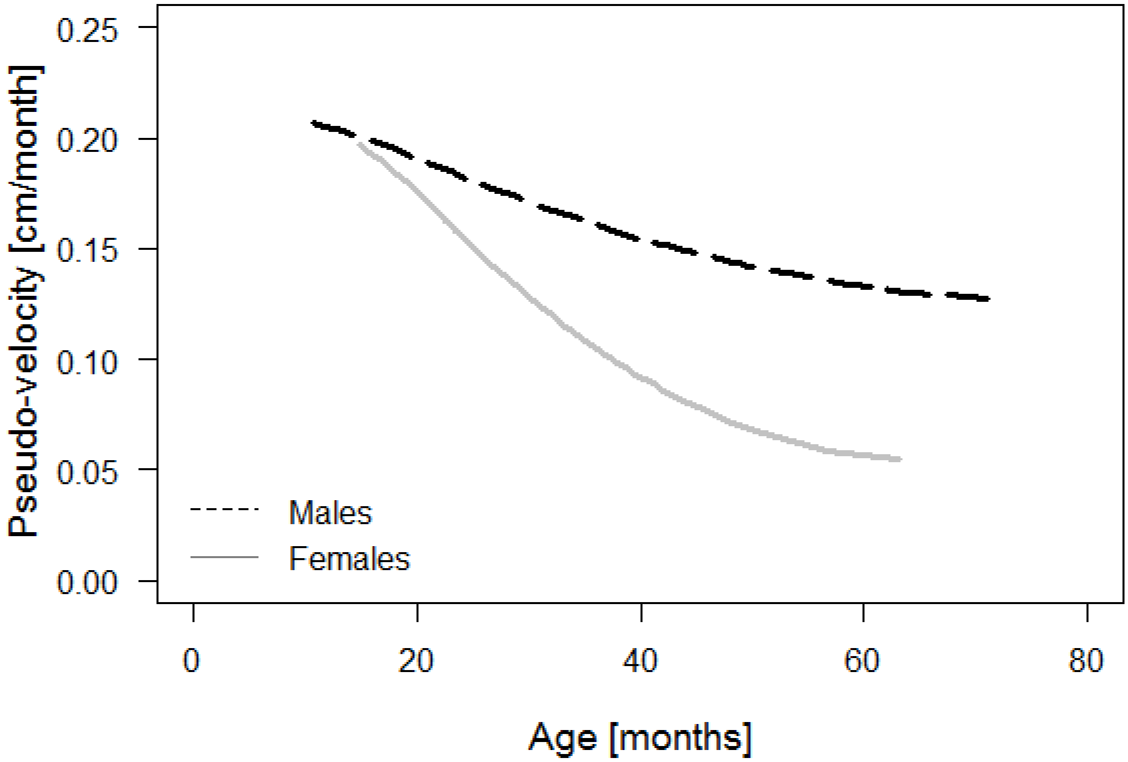

Fig. 4.7. Male and female pseudo-velocity curves excluding adults of unknown age.

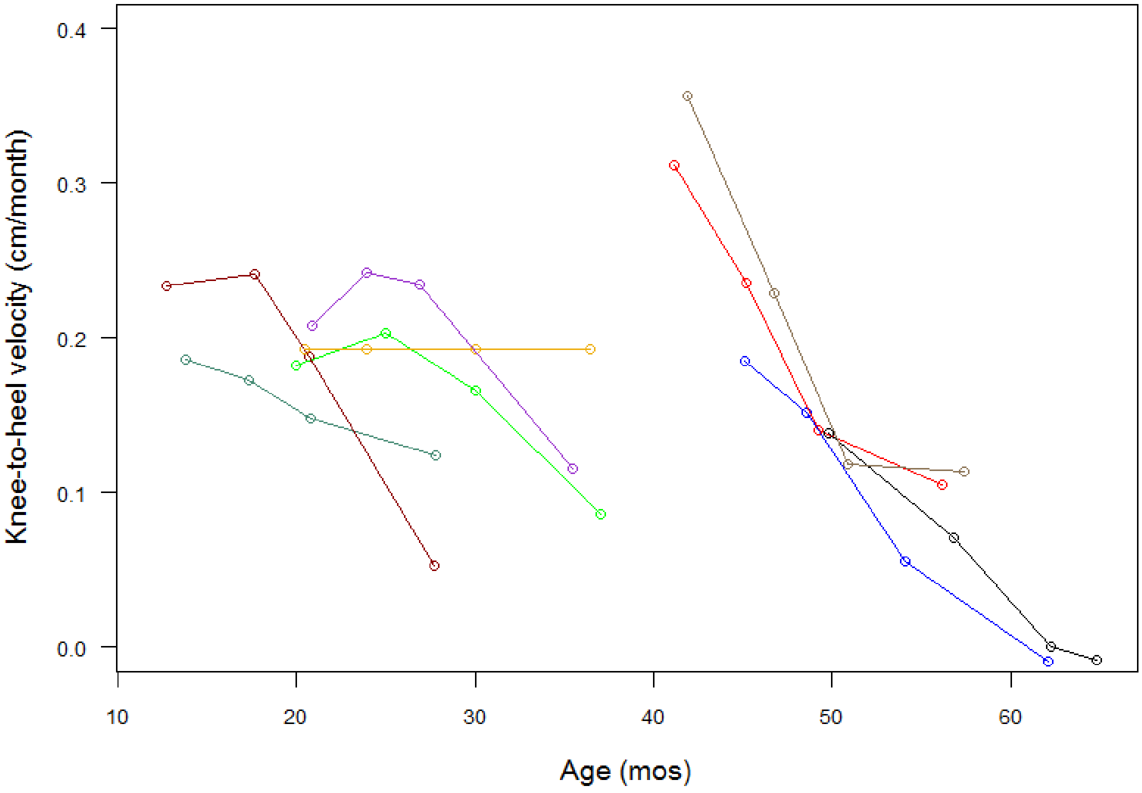

Fig. 4.8. Individual pseudo-velocity curves for 9 males (5 juveniles, 4 subadults) with longitudinal data (across a minimum time span of 14 months).

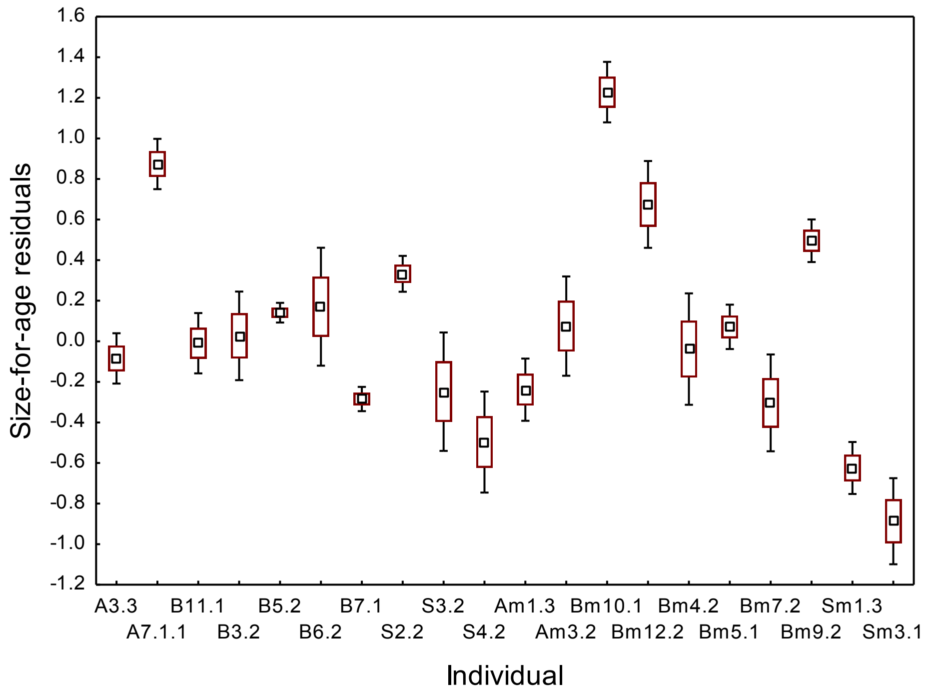

Fig. 4.9. Variation in individual size-for-age residuals. Only individuals with data deemed sufficiently longitudinal (at least 4 monthly measures) are included.

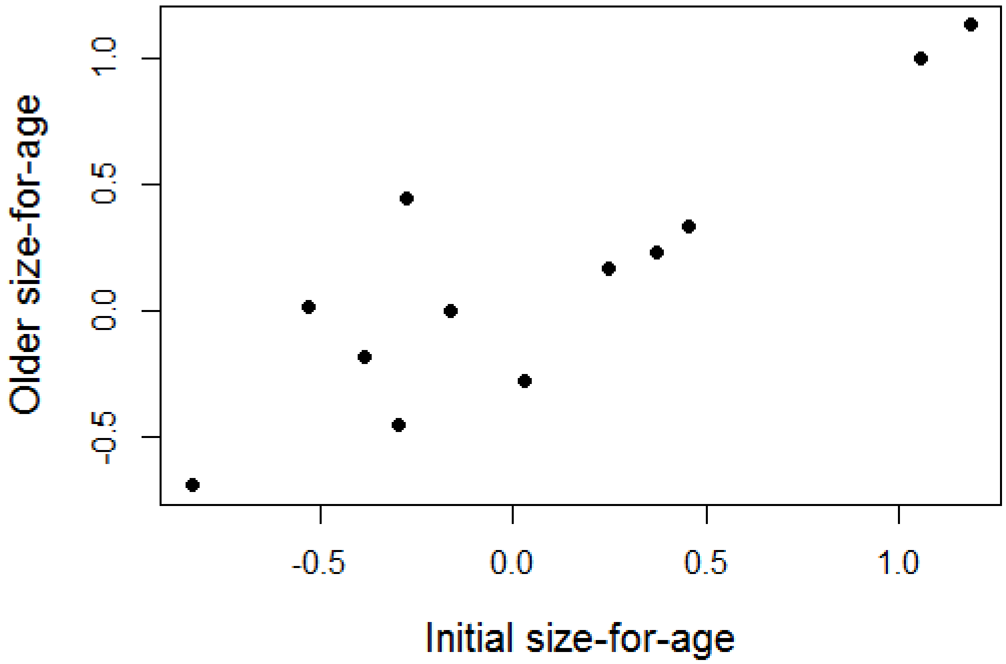

Fig. 4.10. Positive correlation between individuals' initial size-for-age residuals and older size-for-age.

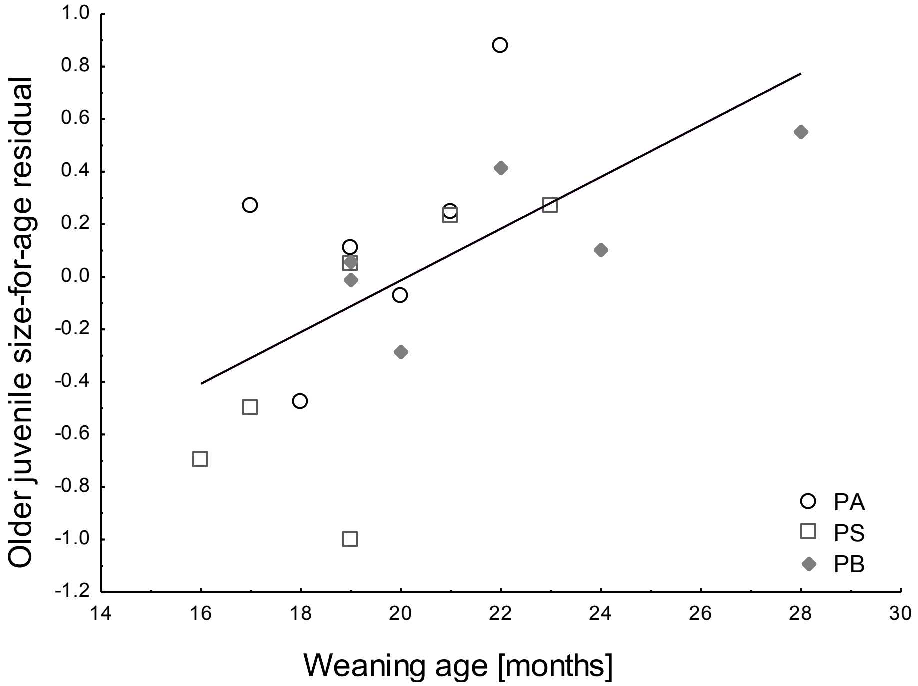

Fig. 4.11. Average size-for-age as older juveniles only and age at cessation of nipple contact.

Fig. 4.12. Median age at dispersal or disappearance for large-for-age and small-for-age females. Excluding individual B5.2 who disappeared at 27 months.

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CHAPTER 5.

Understanding ecological risks and counter-strategies in juvenile primates

This dissertation provides some of the first insight into the feeding behavior and potential fitness-related outcomes for juveniles in a wild colobine species. Previously, comparative analyses have reported faster somatic growth rates and faster dental developmental rates for folivorous taxa, and authors have linked their findings back to the reduced starvation risks and the greater mechanical demands respectively of leafy diets (Leigh, 1994; Godfrey et al., 2001). Yet outside of gorillas and howler monkeys, field data on feeding behavior for young folivorous anthropoids are sorely lacking. The distribution of colobine taxa covers a highly variable environmental range from tropical forests to dry, deciduous forests to high-altitude temperate forests (Oates et al., 1994), and the corresponding socioecological diversity (Bennett and Davies, 1994; Kirkpatrick, 2007) offers ample fodder for more thorough testing of links between diet and developmental pace on an evolutionary scale. Although the results here cannot speak directly to the evolutionary conclusions regarding juvenility and the relationship between diet and risk, they are another step toward improving our understanding and refining those conclusions.

Overview and Conclusions

For one, the findings described here lend credence to assertions that broad dietary categories oversimplify actual variation. In particular, this dissertation has demonstrated that folivores' ability to consume more abundant, less monopolizable resources does not necessarily alleviate ecological risks outright for juveniles. For example, younger juvenile intake rates should be disadvantaged in months where tougher foods comprise a larger part of the diet, such as during part of the dry season, regardless of whether or not these seasonal dietary shifts heightened feeding competition (not explicitly tested here). Nevertheless, during the time span of this study, reduced feeding efficiency did not appear to have nutritional consequences for juveniles, as they were able to maintain metabolically weighted rates of energetic and protein intake above those of adults. The same was true for both mountain gorilla and howler monkey juveniles with greater daily nutrition per unit of metabolic mass relative to adult males but not necessarily adult females (Rothman et al., 2008b; Amato et al., 2014). The intake similarity between juveniles and adult females in these two taxa was attributed to the greater energetic demands of lactation and gestation in elevating adult females over males (e.g., Dufour and Sauther, 2002), but perhaps also owing to the far higher degree of sexual dimorphism in mountain gorillas and, to a lesser extent, black howlers (but see Key and Ross, 1999).

Surviving ecological risks

Juveniles ensured adequate intake, in part, by spending more time feeding than adults, rather than by consuming higher-quality or less-tough foods. In general, juveniles did not avoid the toughest foods eaten by adults. Likewise, despite seasonal shifts in dietary composition (Suarez, 2013; this study), juveniles showed no differences from adults across months in their dietary proportions by food types (i.e., young and mature leaves, fruits, seeds, and flowers). Yet a strategy of shifting time allocation, on its own, could not account for younger juveniles' ability to maintain nutritional equivalence even in months for which dietary toughness spiked. More specifically, even though younger juvenile feeding efficiency was disproportionately slowed by dietary toughness, these individuals did not show a parallel proportionally greater increase in feeding time relative to toughness; instead, comparable rises in feeding effort occurred for younger and older subjects alike. Thus, juveniles were able to counterbalance their inefficiency via other means, most likely the reduced absolute metabolic demand afforded by smaller body size. On an absolute rather than a per-metabolic-mass basis, juvenile intake was either equivalent to or lower than adult intake, underscoring the metabolic advantage of meeting the maintenance requirements for less mass. Other studies comparing dietary characteristics across age-sex classes have found mixed results in this regard. Neither juvenile howler monkeys nor tufted capuchins eschewed high-toughness foods eaten by adults (Raguet-Schofield, 2010; Chalk, 2011), and juvenile (and adult female) mountain gorillas consumed more relative dry matter than silverbacks but did not select differentially for protein-rich foods (Rothman et al., 2008). In contrast, small- and medium-sized juvenile geladas did appear to select for lower toughness foods compared to large juveniles and adults (Venkataraman et al., 2014).

For Phayre's leaf monkeys, the one exception to the pattern of higher intake rates for the smallest individuals occurred for younger juveniles in a month characterized by relatively greater fiber intake. Anecdotally, this exception may represent the propensity for newly weaned juveniles to be the individuals most vulnerable to temporal changes in the diet. Raguet-Schofield (2010) found that as dietary toughness increased during the dry season, juvenile mantled howlers exhibited an uptick in suckling behavior. Species in highly seasonal habitats – lemurs especially – may time reproduction such that offspring weaning transitions align with peaks in fruit abundance (Sauther, 1998; Richard et al., 2000). Similarly, Nowell and Fletcher (2008) suggested that western lowland gorilla mothers cued in to offspring feeding ability, and as offspring processing-to-feeding ratios began to stabilize toward sub-adult levels, mothers showed an increasing tendency to terminate suckling bouts. Thus it would seem Phayre's leaf monkeys mothers could aid their offspring by timing weaning such that it occurs outside of the dry season, when dietary toughness may be greatest. Yet, initial inspection of weaning months gives no indication of a seasonal pattern (Borries and Koenig, unpublished).

Despite the lack of evidence for seasonally timed weaning, the findings here suggest that offspring benefit – in terms of size-for-age – from longer periods of maternal dependence: that is, individuals with later weaning ages were significantly longer-limbed later in juvenility. Whether or not these size gains translated into concrete fitness benefits (i.e., earlier reproductive maturity) remains to be seen, though a positive trend toward larger females dispersing at earlier ages might offer indirect evidence that they do. The positive relationship between later weaning ages and limb length, despite making intuitive sense, actually contrasts with findings of other studies. In baboons, for example, duration of maternal dependence was negatively correlated with the mother's rank (Johnson, 2003; Altmann and Alberts, 2005) such that only low-ranking mothers had to invest for longer to allow their offspring to achieve a threshold weaning weight (Bowman and Lee, 1995). The net result was that low-ranking baboon offspring had later weaning ages but remained small for their age. Clearly, more research on the topic are needed, especially in taxa without stable matrilineal hierarchies.

By the latter half of the juvenile period, dietary toughness has become less of an obstacle to efficiency, and this difference may relate to dental development and the relative molar surface area available for masticating tough foods. Tests of the food-processing hypothesis (Godfrey et al., 2001) indicate accelerated dental development and greater dental endowment relative to weaning ages for taxa with greater dietary mechanical demand, such as folivores. This combined with other studies of dental eruption schedules (e.g., earlier eruption of second molars among colobines: Harvati, 2000; earlier initiation of slowest forming molar in folivores: Dirks, 2003) suggest selection at work during ontogeny, and highlight the adaptive benefit of increased postcanine surface area at the time of transition to nutritional independence. Indeed, individual variation in this type of dental trait has been shown to correlate with likelihood of mortality; specifically, mantled howler monkeys with smaller permanent first molars were more likely to have died at younger ages, around weaning age in particular (DeGusta et al., 2003). As immatures may exhibit individual variation in the timing as well as the sequence of dental eruption, not just tooth size per se but the pace of development can lead to individual differences in processing ability around the critical weaning period. In closely related *T. obscurus*, M1 was considered in the process of erupting at 1 year of age (Godfrey et al. 2001); for the somewhat smaller-bodied *T. cristatus*, M1 was determined to have erupted between 1 and 2 years of age (Bolter, 2004). If Phayre's leaf monkeys are characterized by an equivalent eruption schedule, then M1 should be erupting just prior to or at weaning (average weaning age = 19 months: Borries et al., 2014). To explain the behavioral evidence for reduced efficiency among the youngest juveniles, it would seem that only with the eruption of permanent M2s (roughly 2 to 3 years of age: Bolter, 2004) are juveniles equipped for adult-level processing of a mechanically demanding diet. Such a conclusion reinforces the importance of accelerated dental development and the food processing hypothesis (Godfrey et al., 2001). Furthermore, their analyses of dental development and developmental landmarks including age at maturity highlight evidence for possible evolutionary decoupling of these rates, such that fast rates of the dental development do not necessarily demand equivalently fast rates of growth.

Future directions: a call for longitudinal ontogenetic data

Assessing dental development in the wild

The timing of M1 emergence for silvered and dusky leaf monkeys used here were largely based on measures from individuals of unknown or estimated age. While the sample from Godfrey and others (2001) appeared to include some known-aged individuals and soft tissue markers include coat color, the age assignments for skeletal specifments in Bolter (2004) were made according to developmental breaks; that is, the potential influence of birth peaks in distinguishing breakpoints in the patterns of dental eruption across immatures. Yet, this method has the potential to obscure individual variation at particular ages: faster or slower individuals could be mistakenly assigned to older or younger age classes respectively. Likewise, Smith and colleagues (Smith et al., 2013) point out that dental developmental data gleaned from captive subjects can result in misleading associations with life history markers and development of adult-typical feeding behaviors. Instead, they assessed dental development in young chimpanzees using a uniquely suited dataset of high-resolution photographs taken of open-mouthed individuals of known ages. Even with a small sample of 5 individuals, they documented far greater variation in age of M1 emergence than had been reported previously. They also found that differences from captive data were less than expected. While the emphasis on longitudinal data from known-aged individuals in the wild represents an important stride forward, the applicability of the method for use with smaller-bodied, more arboreal primates is questionable.

Measuring growth rates in the wild: the rise of non-invasive photogrammetric methods

For research on pre-reproductive subjects, knowledge of growth rates represents one important way of assessing individual fitness variation (e.g., Altmann and Alberts, 2005).

Longitudinal growth data from wild subjects of known age are still rare, largely due to the difficulty of obtaining them. Although trapping wild individuals for weighing and measuring is possible and has been done (Wolf, 1984; Cheverud et al., 1992; captive colony: Setchell et al., 2001), the costs of anesthetizing as well as the dangers of doing so (e.g., subjects have fallen to their deaths after being darted: Wolf, 1984) make trapping impractical for obtaining frequent longitudinal measures on multiple individuals. Importantly, in some countries capturing is not allowed. Other researchers have had success with baiting scales to lure study animals, specifically baboons, on for weighing (Johnson, 2003; Altmann and Alberts, 2005), which may be effective for terrestrial subjects. My own efforts to obtain body mass measurements for the highly arboreal leaf monkeys failed to collect even a single measure. The challenges were twofold: 1) when using a more permanent platform structure hung in advance, it was nearly impossible to predict precisely enough the locations where study groups would descend from the canopy to lower heights that would facilitate accurate scale readings, and 2) the use of a more portable hanging scale structure allowing quick placement was only attempted a couple of times as it appeared to stress subjects, with one juvenile male alarm calling in response.

Photogrammetric methods are not new to studies of animal behavior (Lee and Moss, 1995; Bräger et al., 1999; Shrader et al., 2006), however, their use with non-human primate field studies has been on the rise (Emery and Whitten, 2003; Breuer et al., 2007; Kurita et al., 2012), particularly since the publication of Rothman and colleagues' validation of the parallel-laser method (2008). This method improves on the one employed in this study, particularly in its use of a clinometer (see also triple-laser arrangement: Knuepfel and Vidich, 2010) to quantitatively account for non-perpendicular angles between the camera and the subject. The relative ease of use of this or similar methods will hopefully facilitate collection on longitudinal size measures from wild subjects. To date, the majority of primate mass and statural measurements have come from skeletal remains (e.g., Bolter and Zihlman, 2003) or from captive animals (e.g., Leigh, 1994; O'Mara et al., 2012). For the first, the data are cross-sectional only, individual ages are often estimated rather than known, and coordinating behavioral data are, obviously, lacking. The captive data represent what might be best-case scenarios rather than natural variation in growth patterns because provisioned animals tend to grow faster, reach maturity earlier and achieve larger sizes than their wild counterparts. Also, studies of growth rates sometimes rely only on cross-sectional data though also on a combination of cross-sectional and longitudinal data (Cheverud et al., 1992; Leigh, 1994; Bolter, 2011). While cross-sectional datasets with large enough samples have been effective for studying coarse-grained patterns (e.g., body mass growth spurts typically in subadult males: Leigh, 1996; Setchell et al., 2001; Altmann and Alberts, 2005), they are less effective in detecting subtler patterns, for example, growth spurts in length measures. Bogin (1999) has suggested that statural growth spurts are a derived characteristic unique to humans. Although length measures are rare compared to body mass, those studies that have analyzed statural growth using cross-sectional data sets tend to support Bogin's assertion (e.g., Cheverud et al., 1992; Setchell et al., 2001; Bolter, 2004). Furthermore, in the absence of growth spurts or significant rate differences, these studies often conclude that length dimorphism, in contrast to mass dimorphism, is achieved via bimaturism or sex differences in the duration of growth. Yet studies that have managed to fit velocity curves using both types of datasets have found that longitudinal data allow for detection of the smaller-scale growth spurts that may be obscured otherwise by individual differences in the timing of growth acceleration (Hamada et al., 1999; Hamada and Udono, 2002; implied in this study). Thus, growing attention to and implementation of non-invasive photogrammetric methods in the field will not only further our understanding of the ontogeny of sexual dimorphism, but also variation in developmental trajectories by facilitating detailed comparisons of socioecological data with growth outcomes.

The ontogeny of energetics

In this study, as in others that have made both inter- and intra-specific comparisons of energy intake, I have relied on the ¾ power law describing the scaling relationship between body mass for eutherian mammals and metabolic rates (Kleiber, 1961; Nagy, 1994; Savage et al., 2004). Other studies have gone a step further to incorporate energy *expenditure* (Leonard and Robertson, 1997; Wright et al., 2014). Taxon-specific measures of daily energy expenditure for primates are scarce, largely due to the expense (time and cost) of doubly labeled water methods for calculating field metabolic rates (Milton, 1998) (but see burgeoning data compilations: Pontzer et al., 2014), therefore, these studies again rely on BMR calculated via ¾ power scaling plus the energetic costs of specific activities as well as production costs.

Some researchers continue to tout the power relationship, particularly based on comparative analyses at broader taxonomic levels (Nagy, 1987, 1994; West et al., 1999; Savage et al., 2004), but more recent studies have raised questions regarding its universality at narrow taxonomic units, including whether the same scaling relationship holds within species across ontogenetic variation in body mass (Bokma, 2004; Glazier, 2005; Snodgrass et al., 2007). Glazier (2005) describes a 2/3-power scaling as potentially more appropriate for intraspecific relationships. If supported, such a reduced power relationship actually would diminish the metabolic differences between age classes. In addition, others have cited evidence for variation in basal metabolic rates beyond body mass, pointing to diet and lifestyle (e.g., degree of arboreality) as factors shaping metabolism (McNab, 1986; Sibly and Brown, 2007; McNab, 2008). Folivores, for example, have been singled out among primates as low-energy strategists predicted to have lower than expected basal metabolic rates for their body size. The limited evidence from howler monkeys would suggest otherwise (Nagy and Milton, 1979; Milton, 1998), though, outside of lemurs (Drack et al., 1999), there is, so far, too little evidence to confidently link diet and metabolic variation. In addition, conflicting results between studies highlights the potential issues surround intra- vs. inter-specific scaling differences. For example, field metabolic rates measured in red-tailed sportive lemurs via the doubly labeled water method suggested that the ratio of FMR to BMR mirrored the relationship found for eutherian mammals in general. However, more recently, Pontzer and colleagues (2014) cross-species analyses concluded that primates were unique in their extremely low total energy expenditure (roughly FMR) yet did not differ from other mammals in terms of BMR allometric scaling. How these factors may or may not influence intraspecific scaling relationships remains to be seen. While recent work has ramped-up efforts to measure FMR in a greater number of taxa (see Pontzer et al., 2014), this research should focus on compiling samples large and diverse enough to test for possible scaling variation within and between species.

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