

TRADE-OFFS IN SKILL ACQUISITION AND TIME ALLOCATION AMONG JUVENILE CHACMA BABOONS

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We hypothesize that juvenile baboons are less efficient foragers than adult baboons owing to their small size, lower level of knowledge and skill, and/or lesser ability to maintain access to resources. We predict that as resources are more difficult to extract, juvenile baboons will demonstrate lower efficiency than adults will because of their lower levels of experience. In addition, we hypothesize that juvenile baboons will be more likely to allocate foraging time to easier-to-extract resources owing to their greater efficiency in acquiring those resources.

We use feeding efficiency and time allocation data collected on a wild, free-ranging, non-provisioned population of chacma baboons (*Papio hamadryas ursinus*) in the Moremi Wildlife Reserve, Okavango Delta, Botswana to test these hypotheses. The major findings of this study are:

1. Juvenile baboons are significantly less efficient foragers than adult baboons primarily for difficult-to-extract resources.

We propose that this age-dependent variation in efficiency is due to differences in memory and other cognitive functions related to locating food resources, as is indicated by the greater amount of time juvenile baboons spend searching for food. There is no evidence that smaller body size or competitive disruption influences the differences in return rates found between adult and juvenile baboons in this study.

2. An individual baboon's feeding efficiency for a given resource can be used to predict the duration of its foraging bouts for that resource.

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These results contribute both to our understanding of the ontogeny of behavioral development in nonhuman primates, especially regarding foraging ability, and to current debate within the field of human behavioral ecology regarding the evolution of the juvenile period in primates and humans.

KEY WORDS: **Chacma baboons; Juveniles; *Papio hamadryas ursinus*; Primates; Skill acquisition; Time allocation**

In the journey to become a competent adult, juvenile primates face a series of trade-offs affected by features of the physical, biotic, and social environment that set individuals on one of a number of possible trajectories (Janson and van Schaik 1993; Pereira and Fairbanks 2003; Post, Hausfater, and McCuskey 1980). This article addresses the causes and consequences of an extended juvenile period with specific attention to the capabilities of juveniles and the learning curves associated with adult tasks. The role of experience and the time needed to learn intensive skills versus the time to grow to a sufficient body size to accomplish tasks are topics of current debate in human behavioral ecology (Bock and Sellen 2002; Leigh 2001). This study of juvenile foraging efficiency and time allocation contributes to the discussion by measuring the acquisition profile of juveniles versus adult females in the socially complex and risky environment of a troop of chacma baboons living in the Okavango Delta of Botswana.

If a juvenile is adept at procuring a fig but struggles at detecting, unearthing, and cleaning a root then how should she allocate her foraging time? Devoting time to acquiring figs will have the immediate, short-term benefit of providing energy but will have long-term costs because that time is not spent in developing skills needed to acquire resources that are more difficult to extract, which is essential because figs are only seasonally available. On the other hand, devoting time to acquiring roots has a short-term cost resulting from the low level of competence in this task although there is a long-term payoff through becoming more experienced and efficient at acquiring this resource. Throughout the juvenile period, time devoted to skill acquisition is a trade off with time spent on production (Bock 1995, 2002a, 2002b).

A juvenile's small size and lack of knowledge and skills affect (a) the amount of time it takes to search for food, (b) the ability to feed efficiently, and (c) the ability to maintain access to high-quality patches. The amount of time an individual spends searching for food depends on the distance between resource locations, the ability of the individual to remember and navigate to resources, and the travel speed of the individual. The small size of juveniles may affect search time through slower travel time between resources, lower competitive ability and therefore more difficulty in

locating a suitable area to feed, and/or less experience in locating nutrient-dense areas. Each bite of food may be more difficult for a juvenile than for an adult to acquire because the juvenile has less experience and is less skilled or because its small body size reduces access. In the quest for resources a juvenile perceives a landscape of energy and risk (Janson and van Schaik 1993; Post et al. 1980). The highest-quality patches may be associated with a higher density of adults, which confers protection from predators (Hamilton 1971; Roberts 1996) but can intensify the cost of competitive disruption (Barton 1993; Hall and Fedigan 1997; Ron, Henzi, and Motro 1996; van Schaik et al. 1983). In addition to having to perform the cognitive functions related to evaluating nutrient density and spatiotemporal mapping of resources, juveniles living in a competitive arena must evaluate the probability of maintaining access to a resource. In this environment, therefore, feeding efficiency is determined by both foraging skills and social skills.

Recent research within the field of human behavioral ecology on the evolution of the juvenile period has primarily focused on three models (Bock and Sellen 2002; Leigh 2001): the brain growth model (Bogin 1999), the adult mortality model (Charnov and Berrigan 1993), and the embodied capital model (Kaplan 1996; Kaplan and Bock 2001; Kaplan et al. 1995, 2000). The brain growth and embodied capital models both emphasize learning as a powerful selective force on the juvenile period in humans and see the large human brain and the long juvenile period as a response to the great amount of learning-based knowledge necessary to be a competent forager. The adult mortality model developed by Charnov (1993) and extended to humans by Blurton Jones, Hawkes, and O'Connell (1999) argues that organisms shift investment at some point from their own growth into producing offspring. In this case, natural selection is not directly acting to extend juvenility but is rather a consequence of slow growth. Knowledge and skills acquired during the juvenile period are beneficial according to this model, but those benefits are not sufficient selective pressure to have extended the juvenile period.

Empirical tests of these models have produced mixed results depending on the ecological milieu and tasks examined (Bock and Sellen 2002). In their study of children's foraging, Bliege Bird and Bird (2002; Bird and Bliege Bird 2002) found that Meriam children in Australia were far more constrained in their marine foraging returns by body size than by experience-based skill. In their study of Hadza adolescent skill development, Blurton Jones and Marlowe (2002) argue that both school attendees and non-attendees have similar skill levels. They found, for instance, that there was no difference in bow and arrow shooting accuracy. Other studies have found that experience has strong effects on performance of tasks related to food procurement. Ohtsuka (1989) found that age had a significant effect

on the hunting ability of Gidra Papuan men (after controlling for strength and body size). Walker and colleagues (2002) found strong age-effects among Ache foragers in male ability to locate potential prey. Bock (2004) has shown that among children in the Okavango Delta of Botswana body size and experience have independent or interacting effects on children's foraging efficiency depending on the task examined.

The ontogeny of skill acquisition in nonhuman primates has been studied in foraging behavior (Boinski and Fragasy 1989; Corp and Byrne 2002; Custance et al. 1999; Hauser 1993; Moura and Alonso 2000; Watts 1985; Whiten et al. 1996), social behavior (Bramblett and Coelho 1987; Fairbanks 1993; Pereira 1995; Pereira and Altmann 1985), vigilance (Alberts 1994; Cheney and Seyfarth 1990; Hauser 1988; Moura and Alonso 2000), and maternal care (Bard 1994; Berman 1990; Fairbanks 1996; Timmermans and Vosen 1996). The focus of study has been on social learning (King 1994) as well as maturational processes affecting the brain and physical attributes such as body size (Corp and Byrne 2002; Fairbanks 2000). Studies addressing the ontogeny of foraging skill in nonhuman primates have had mixed results. Juvenile nonhuman primates have foraging bouts of shorter duration with limited diet breadth relative to adults (Hauser 1993). The hypothesis that social learning contributes to the development of foraging ability has received limited support in studies of monkeys (Boinski and Fragaszy 1989; Hauser 1993). Recent research on apes has highlighted the importance of maturational processes while questioning the role of social learning because proximity to the mother has benefits to both mother and offspring in terms of energy maximization (Corp and Byrne 2002). The current study contributes to our understanding of the constraints on the development of foraging ability in a social, omnivorous cercopithecine species by evaluating the relative contributions of experience and physical attributes to feeding efficiency.

We examine the efficiency of feeding behavior as measured by bites per minute for a specific food type achieved by individual adult females and juveniles of both sexes. By categorizing food types based on the ease of extraction, we are able to assess the impact of juveniles' small size and/or lack of experience on their efficiency in processing. If size is linked to feeding efficiency, then juvenile males should be more efficient than juvenile females for resources that are more difficult to extract. This should be evident only after the age of 66 months, since in this population there are no significant size differences between males and females before that age (Johnson 2003). We expect that if search time is a function of experience and knowledge then age should be positively related to feeding efficiency in both males and females. We also expect there to be a series of trade-offs involved in the time allocated to different foraging-related activities. Feeding efficiency should be positively related to feeding time because we

would expect natural selection to result in optimal time allocation such that individuals engage in activities with the highest payoff (Bock 2002a, 2002b). We also expect, however, that there are additional constraints functioning in multiple time frames and with multiple currencies. For instance, an individual might be most efficient at foraging for one resource but constrained from pursuing that resource owing to competition from conspecifics in group foraging or because of the threat of predation in lone foraging. This would result in an individual foraging at less than maximum efficiency because of the trade-off between energy acquisition and risk.

METHODS

Study Population

The study population is a troop of approximately 75 chacma baboons (*Papio hamadryas ursinus*) in the Okavango Delta, Botswana, living within the boundaries of the Moremi Wildlife Reserve. This troop has been studied continuously since the early 1970s by Hamilton and associates (Hamilton, Buskirk, and Buskirk 1978) and continues to be the focus of research by Cheney and Seyfarth (1997; Cheney et al. 1995, 1996). The demography of the troop is known and the level of habituation is high, allowing for detailed focal follows of adults as well as juveniles. Close observation is required to record data such as bite rate and identification of resources (or food types) exploited. Data were collected through focal follows of twenty-three adult females, nine juvenile females, and thirteen juvenile males. Juvenile females ranged in age from 1½ to 4 years, and the age range for juvenile males was 2½–6 years at the start of the 19-month study.

Chacma baboons (*Papio hamadryas ursinus*) are one of five subspecies of savanna baboon in the genus *Papio*. The collective savanna species have been characterized as omnivorous generalists (Hamilton, Buskirk, and Buskirk 1978) and they are distributed across the African continent from Senegal in the east to Ethiopia in the west and south to South Africa (Dunbar 1992). Dietary preferences vary across sites (Whiten et al. 1991) and recent research suggests that diet also varies within sites for juveniles, adult males, and adult females (Barton et al. 1993).

Data Collection

Foraging behavior was measured during behavioral streams of foraging bouts which were recorded on focal individuals for 30 continuous minutes. Activity states were categorically scored as feed, scan, search, travel,

rest, and groom (definitions of activity states follow Dunbar 1992). Individuals were scored as searching when they were observed handling and discarding food items, digging, or in some way manipulating a substrate to uncover concealed resources. The beginning and ending times of activity states were recorded. In addition to activity states, the number of bites, food type consumed, and number of scans were also collected. Plant identification was facilitated through consultation with local research assistants with many years of experience and with botanist Peter Smith of the University of Botswana as well as through texts (Ellery and Ellery 1997; Palgrave 1983). Following Barton (1993) a bite was considered a hand to mouth action for items such as grass and leaves. For other foods, such as flowers, fruits, and corms, a bite was equated with the consumption of the entire food item. Data were recorded using an integrated microcomputer/GPS unit designed by Trimble Navigation, Inc.

Overall activity budgets for each individual were constructed from two types of time allocation data: behavioral streams (described above) and time point data collected during 2-hour focal follows. In addition to activity state, each point sample, at 10-minute intervals, included the number and identity of conspecifics within 0–5, 5–10, 10–15, and 15–20 m of the focal individual.

A supplant is defined as a displacement of one individual by another. The activity of the recipient of the supplant was disrupted and the recipient moved off its position. Each supplant involving the focal individual was recorded noting the identity of the interactants and whether the focal individual was the supplanter or supplantee.

Data Analysis

We ranked resources post hoc according to the difficulty of extraction based on detection and embeddedness. The seeds of *molapo* species (mixed grass), invertebrates, and roots were classified as “difficult.” This determination is based on the height of the seeds above the ground and the height, strength, and skill required to detect whether seeds are present on a particular stalk. The stalk must be bent down and seeds extracted dexterously to maximize efficiency. Invertebrates (mostly insects) are concealed, and they must be detected and pursued if necessary. In order to utilize roots a complex suite of sequential tasks must be completed. An appropriate digging site must be located and the substrate needs to be removed rapidly. The root must be extracted and cleaned prior to consumption. Grass stems and seed pods (predominantly *Acacia* spp.: *Acacia erioloba*, *A. hebeclada*, *A. nigrescens*, *A. sieberiana*, *A. tortilis*) were classified as “medium.” These resources are less embedded than those listed above, but they require a higher level of processing than the fruits categorized as “easy.” Jackelberry

(*Diospyros mespiliformis*), marula, and figs (*Ficus sycomorus*, *F. thonningii*) were classified as “easy” because they are picked up off the ground and do not require processing.

RESULTS

Age/sex class significantly affects allocation of time to different activities (Table 1). Adult females devote a significantly higher proportion of their time to feeding than juvenile females and juvenile males. There are multiple causes for this difference. It may be an effect of juvenile characteristics in that young males and females are both smaller and less experienced than adult females. Juvenile females and males spend a significantly higher proportion of time searching for food than adult females. Another source of variation in time allocation may be due to a different cost/benefit structure for the trade-offs faced by juvenile females and males. Juvenile males spend significantly more time in play and rest and significantly less time grooming than adult and juvenile females. For one activity, scanning, the time allocation profile of adult females and juvenile males is similar whereas juvenile females spend significantly less time scanning. There are no significant differences by age/sex class in the proportion of time devoted to travel.

Age has a significant effect on feeding efficiency (bites/minute), with younger animals having lower efficiency than adult females during foraging bouts on mixed grass, roots, grass stems, and figs. There are no significant effects of age on feeding efficiency for invertebrates, seed pods, jackelberry, and marula (Table 2). Lowess curve estimation on scatterplots illustrate the increase in efficiency with age for mixed grass (Figure 1). Although we predicted an effect of experience on feeding efficiency for invertebrates, there was no age effect (Figure 2).

Since no male baboons in the sample are older than 85 months, to

Table 1. ANOVA: Time Allocation Profile by Age/Sex Class

Activity	Adult Female	Juvenile Female	Juvenile Male	F	df	p-value
Feed	.63	.58	.55	4.527	497	0.011
Travel	.08	.06	.08	2.038	499	n.s.
Rest	.07	.05	.13	8.499	499	<0.0001
Groom	.04	.06	.01	5.898	499	0.003
Search	.08	.16	.12	8.89	496	<0.0001
Scan	.07	.05	.08	3.236	497	0.04

Table 2. OLS Regression: Effect of Age and Sex on Feeding Efficiency (Bites/Minute)

<i>Food Type</i>	<i>Extraction Difficulty</i>	<i>Covariate</i>	<i>N</i>	<i>Std β</i>	<i>adj r²</i>	<i>p-value</i>
Mixed grass	Difficult	age	164	0.394	0.150	<0.0001
		sex	76	0.081	0.007	n.s.
Invertebrates	Difficult	age	141	0.002	0	n.s.
		sex	63	-0.179	0.030	n.s.
Roots	Difficult	age	516	0.126	0.014	0.004
		sex	181	0.020	0.001	n.s.
Grass stems	Medium	age	134	0.242	0.051	0.005
		sex [†]	N/A	—	—	—
Seed pods	Medium	age	128	-0.027	0.001	n.s.
		sex	51	-0.027	0.002	n.s.
Jackelberry	Easy	age	109	0.114	0.004	n.s.
		sex	33	0.256	0.003	n.s.
Marula	Easy	age	81	0.024	0.001	n.s.
		sex	52	-0.050	0.003	n.s.
Figs	Easy	age	70	0.284	0.067	0.016
		sex	36	-0.203	0.054	n.s.

[†] Only one female under the age of 90 months was observed consuming grass stems.

examine the effect of body size on foraging efficiency we included sex as an independent variable controlling for age. In this population male and female body size does not significantly differ until 66 months of age (Johnson 2003). There were no significant effects of sex on feeding efficiency among juvenile baboons.

The probability of being supplanted shows a slight significant decrease with age for foraging bouts on invertebrates. The probability of being supplanted decreases slightly with age for foraging bouts on mixed grass and increases slightly for foraging bouts on seed pods; however, these differences are not statistically significant (Table 3).

In addition to the lack of significant differences in time devoted to travel (Table 1), there are no significant differences in travel speed across age/sex classes (Table 4).

The variation in feeding efficiency predicts variation in time allocation. For all resources except jackelberry, an individual's feeding efficiency for that resource measured in bites/min is a significant predictor of the proportion of time spent feeding on that resource (Table 5). This means that juveniles spend less time foraging for resources for which they are less efficient foragers.

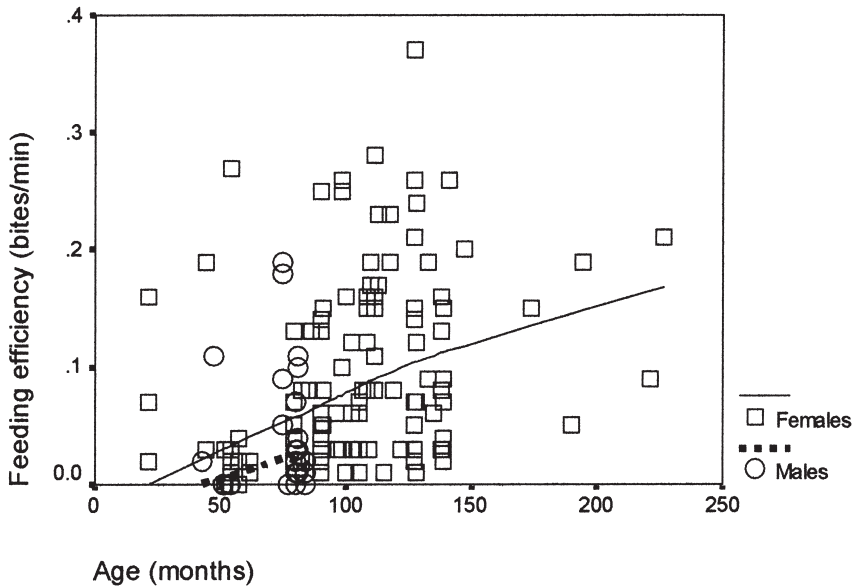


Figure 1. Comparison of female and male feeding efficiency (measured as bites/minute) for mixed grass. Squares represent individual foraging bouts for females and circles represent individual foraging bouts for males. Lowest curves were fit to the data (solid line for females, dashed line for males). There were no males over 85 months old in the sample.

DISCUSSION

Age and sex affect time allocation profiles, clearly reflecting differences in the costs and benefits of specific activities. The time allocation of juveniles in this study coupled with feeding efficiency data suggest novice ability in foraging. Juveniles spend a significantly larger proportion of time in food search than adult females (see also Agetsuma 2001; Hanya et al. 2003). However, they spend a smaller proportion of time feeding than adult females (see also Boinski and Fragaszy 1989; Hauser 1993; Post et al. 1980). For the youngest juveniles this may reflect smaller energy demands owing to smaller size, but it also may be due to the increased time required to locate a suitable patch. Alternatively, juveniles may be relegated to feeding in lower-quality patches, and although we did not address patch quality here, it is an important direction for future study. The cost of continuing to feed after the troop has moved on to a new location may be quite high in an area with a large number of predators. Younger animals may be more

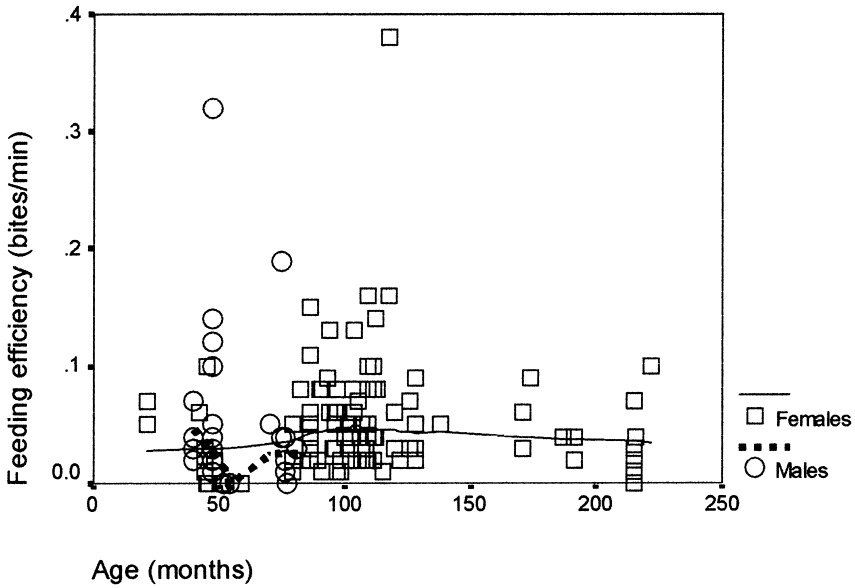


Figure 2. Comparison of female and male feeding efficiency for invertebrates. See Figure 1 for additional explanation.

Table 3. Logistic Regression: Probability of a Supplant Interrupting a Feeding Bout

Food Type	Odds Ratio	(95% LCI, UCI)	p-value
Mixed grass	0.989	(0.978, 1.001)	0.081
Invertebrates	0.979	(0.962, 0.996)	0.013
Roots			n.s.
Grass stems			n.s.
Seed pods	1.008	(1.000, 1.015)	0.059
Jackelberry			n.s.
Marula			n.s.
Figs			n.s.

Table 4. Mean Travel Speed by Age/Sex Class

Age/Sex Class	Mean Travel Speed (m/sec)
Adult female	37.6
Juvenile female	40.0
Juvenile male	42.8

Table 5. OLS Regression: Effect of Feeding Efficiency on Duration of Time Spent Feeding by Food Type

<i>Food Type</i>	<i>Std β</i>	<i>adj r^2</i>	<i>p-value</i>
Mixed grass	0.145	0.052	0.082
Invertebrates	0.585	0.345	<0.0001
Roots	0.106	0.01	0.015
Grass stems	0.174	0.015	0.051
Seed pods	-0.087	0.008	n.s.
Jackelberry	0.109	0.009	n.s.
Marula	-2.61	0.086	0.015
Figs	0.459	0.246	<0.0001

at risk of predation owing to their smaller body size and less experience at detecting and avoiding predators. More risk averse behavior will constrain the time devoted to alternate activities, especially feeding. Female juveniles spend significantly less time scanning than adult females or juvenile males. Perhaps female juveniles reap the benefits of shared vigilance by positioning themselves in proximity to more neighbors than either of the other two age/sex classes being examined (Johnson 2001).

This study demonstrates that juveniles have significantly lower feeding efficiency than adults. Our findings agree with that of Post and colleagues (1980), who showed that juvenile male and female yellow baboons have lower bite rates for grass stems, berries, and roots than adult females (see also Hanya et al. 2003 for Japanese macaques). Competitive disruption, attention diverted to scanning, travel speed, and distance limitations do not seem to contribute to this difference in efficiency. Juveniles are not more likely than adult females to be supplanted while they are feeding for most resources. Juveniles are not slower than adults. Juveniles do not spend more time scanning than adult females. We conclude that the differences between juvenile and adult efficiency are primarily due to differences in ability related to age-specific cognitive, memory, and fine motor performance.

Mixed grass and roots show the greatest difference in age-specific feeding efficiency. This variation may be due to effects of body size, experience, and skill, or competitive disruption by conspecifics. These extractive resources are more difficult to acquire owing to the skill needed to detect underground resources, the dexterity required to remove dirt, the ability to detect individual items of appropriate size in a clump of grass, and the difficulty in pulling down grain heads and removing the grains with the mouth. Contrary to our prediction regarding foraging for invertebrates, there was no support for the effect of experience on foraging efficiency for

this resource. Invertebrate foraging may be largely opportunistic, and prey are captured and consumed as they are startled by the baboons moving through an area. Likewise, there is no significant effect of age on feeding efficiency for jackelberry, marula, and seed pods. These resources can simply be picked up off the ground and are easy to consume. In contrast with our prediction, there was an age effect on feeding efficiency for figs. One potential explanation is that food quality is more uneven for figs than for other resources we have categorized as "easy," and the ability to detect quality may increase with age. The comparison of adult female and juvenile foraging patterns, in addition to the quantitative measurement of feeding efficiency, suggests that foraging ability develops over the juvenile period. Experience, therefore, is a major factor affecting the pattern of resource acquisition.

In this study we do not examine the component parts of experience and how each potential component, such as social learning, affordance learning, or imitation, is related to the development of foraging skill. Also, although we have a strong measure of body size in the sexual dimorphism of baboons over 66 months old, we do not directly assess the probability that unmeasured maturational processes that directly covary with age are responsible for some of the age effects in foraging efficiency. We believe, however, that there is little logical support for this latter interpretation since foraging efficiency for the most difficult to extract resources continues to improve throughout adulthood. This would mean that these putative unmeasured maturational processes would also continue throughout adulthood, a scenario that is not congruent with other aspects of baboon maturation, or indeed the age patterning of maturation in any primate. An interesting future direction would be to attempt to partial out the effects of various components of experience on age-dependent foraging efficiency.

CONCLUSION

The major findings of this study are as follows:

1. Juvenile baboons are significantly less efficient foragers than adult baboons. We propose that this age-dependent variation in efficiency is due to differences in memory and other cognitive functions related to locating food resources, as is indicated by the greater amount of time juvenile baboons spend searching for food. There is no evidence that smaller body size or competitive disruption affects the differences in return rates found between adult and juvenile baboons in this study.

2. An individual baboon's feeding efficiency for a given resource can be used to predict the duration of its foraging bouts for that resource.

These differences in feeding efficiency and time allocation are important means by which selection shapes the development and growth patterns of this species. The significance of characteristics of juvenile development can best be determined by placing them in the ecological context of a suite of alternate activities.

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