

Original Article

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Ecological Risk Aversion and Juvenile Ring-Tailed Lemur Feeding and Foraging

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Key Words

Life history · Feeding ecology · *Lemur catta* · Predation · Ontogeny

Abstract

The extended primate juvenile period has been linked to interactions between feeding ecology and sociality. However, accumulating field data on juvenile primates suggest variation in the linkages between foraging efficiency, group foraging and social behaviour. In many non-human primates, juvenile ability (strength, coordination and motor skills) does not limit foraging success. If predicted limitations in feeding are not found in juvenile monkeys, it is possible that the gregarious strepsirrhines may show foraging patterns similar to those implicated in the evolution of a life history where long juvenile periods are advantageous. To test these behavioural predictions, I present a mixed longitudinal sample of observations on feeding and foraging behaviour from ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve, Madagascar. Like several platyrrhine species, close proximity during foraging, low feeding efficiency and low dietary diversity are not typical of ring-tailed lemurs. The lack of ecological trade-offs in these species may indicate stronger common roles of sociality and social complexity in structuring the elongation of the primate juvenile period.

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The extended juvenile period (from the point at which an individual can survive without its mother to the age at first reproduction) [Pereira and Altmann, 1985] is one of the major life history characteristics of primates. Multiple hypotheses have attempted to explain juvenility as either a non-adaptive consequence of other aspects of primate life history, including brain mass, metabolic demands and demography [Pagel and Harvey, 1993; Godfrey et al., 2004], or as a product of selection to enhance learning complex foraging tasks or social roles [Joffe, 1997; Ross and Jones, 1999].

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The ecological risk aversion hypothesis (ERAH) [Janson and van Schaik, 1993] bridges these perspectives by incorporating growth, development and energetics of juvenility in an ecological context. Its authors propose that juveniles must simultaneously minimize mortality risks of predation and starvation. Juveniles mitigate predation risk by foraging in the centre of the group or closer to group members. Because of their inexperience, low feeding proficiency and lower competitive status, this decrease in proximity elevates feeding competition. Low juvenile feeding proficiency then requires decreased growth rates to minimize starvation risks borne by less competent and experienced feeders. The extended primate juvenile period, particularly in monkeys and apes, is then a result of selection favouring a single, non-maximal growth rate to compensate for this starvation risk that extends a nutritionally independent developmental period.

There is mixed support for the behavioural foundations of the ERAH in the haplorhines. Juveniles may forage closer to the centre of the group [Janson, 1990; van Noordwijk et al., 1993] but not necessarily closer to another group member to minimize predation risk [Stone, 2007], and in many species, juveniles are neither less efficient nor do they spend more time foraging than adults [Fragaszy, 1990; Hanya, 2003; Gunst et al., 2008; Bezanson, 2009]. This study uses ontogenetic behavioural data to test if the development of feeding in a gregarious strepsirrhine meets the predictions of the ERAH where studies in monkeys have yielded equivocal results. If juvenile ring-tailed lemurs forage in ways that are consistent with ERAH, then they will do so closer to group members (particularly in high-risk areas) and spend less time in high predation risk areas. Closer proximity will result in more aggression directed at juveniles and overall lower foraging efficiency.

Methods

Study Population

Data were collected on a mixed longitudinal sample of ring-tailed lemurs (*Lemur catta*) from May 2009 to March 2010 at the Beza Mahafaly Special Reserve (Beza: 23°40' S, 44°36' E). With the help of 4 field assistants, more than 2,000 observation hours were completed on 78 individuals from 7 study groups (for age categories, number of individuals and sampling details, see table 1). Individuals were assigned to age classes based on either known birth dates for animals born in 2006 or later or were designated as adults if born before 2006 or transferred from an unknown group [Sauter and Cuozzo, unpubl. data]. All feeding, foraging and agonistic behaviours were recorded continuously in JWatcher during 12-min focal animal sampling sessions (FAS). Interobserver reliability was periodically assessed using Cohen's kappa statistic included in the JWatcher package to maintain a $\kappa = 0.90 \pm 0.05$ [Coelho and Bramblett, 1981]. All methods were approved by the Institutional Animal Care and Use Committee at Arizona State University (08-983R) and by Madagascar National Parks (135/07; 257/09), and conformed to the Principles for the Ethical Treatment of Non-Human Primates of the American Society of Primatologists.

Spacing, Risk and General Activity

Distance to the nearest neighbour was categorically defined and translated to a numerical value representing increasing distance (touch = 0, within arm's reach = 1, within 1 m = 2, within 3 m = 3, and greater than 3 m away = 4) and position within the tree crown based on a 3 × 3 grid (interior, middle, exterior; lower, middle, upper) were recorded instantaneously at 3-min intervals during the FAS. This grid was used to assess potential predation risk [Janson, 1998]. The outer edges of a tree crown and the ground, regardless of distance to a tree or cover, were categorized as high-risk foraging from aerial (*Polyboroides radiatus*) and terrestrial predators (*Felis* sp.,

Table 1. Sample size for the number of individuals, total observation hours per age-sex category, the mean number of FAS per day and the mean number of hours (\pm SE) each individual was observed per day across the study period

Age category	Sex	Individuals, n	Observation, h	Mean FAS, n/day	Mean observation duration, h/day
Infant 1 (0–12 weeks)	female	14	93.4	5.0	1.02 \pm 0.06
	male	12	99	5.4	1.14 \pm 0.06
Infant 2 (13–24 weeks)	female	8	102.4	5.6	1.10 \pm 0.06
	male	10	112.2	5.8	1.12 \pm 0.07
Juvenile 1 (25–52 weeks)	female	4–6	152.2	7.7	1.52 \pm 0.08
	male	1–3	46.2	7.3	1.44 \pm 0.14
Juvenile 2 (1–2 years)	female	3–6	186.4	6.4	1.29 \pm 0.07
	male	1–6	136.8	6.6	1.30 \pm 0.07
Subadult (2–3 years)	female	3	82.4	5.1	1.04 \pm 0.07
	male	6–8	272.4	5.7	1.16 \pm 0.05
Adult (>3 years)	female	23–26	693	4.1	0.82 \pm 0.02
	male	11–17	337	4.0	0.80 \pm 0.02

Number of individuals includes animals that have passed from one age category to the next.

Canis familiaris, *Cryptoprocta ferox*, *Acrantophis dumerili*). This categorization also reflects ring-tailed lemur bias toward higher vigilance while on the ground [Gould and Sauther, 2007]. All other areas (i.e. tree crown interior) were grouped together as low risk. Agonistic encounters were recorded as events during the FAS, and only aggression that would disrupt feeding and foraging was included (e.g. move to displace, spat, lunge, cuff).

Feeding and Foraging

Feeding was defined as the ingestion of food and foraging as the active searching for and processing of food items and includes sniffing, licking and cracking. Ring-tailed lemur foods do not require extensive processing and are typically ingested in a single bite by all age categories. Some fruits such as *Tamarindus indica* and *Crataeva excelsa*, however, may require a minimum of strength or postcanine occlusal surface area to open [Cuozzo and Sauther, 2004], and insects may take coordination and practice to capture. Bite counts were conducted for each individual throughout the 12-min FAS sessions to measure intake rates [Johnson and Bock, 2004]. Average bite count rates were then calculated for each individual per day of observation. Plants were identified to species and parts were categorized into unripe fruit, ripe fruit, young leaves, mature leaves, flowers and flower buds. Arthropods were identified to species when possible and minimally to taxonomic order.

Analysis

Data were summarized per individual per day, generating a mixed-longitudinal data set of individual days. Logistic generalized linear mixed models with a binomial error distribution and logit link identity were fit to proportional data using the *lme4* package in R 2.13 [Bolker et al., 2009; R Core Development Team, 2011]. Individual animal identity, sex and reproductive season were included as random effects to control both for the repeated sampling of individuals, previously identified sex differences [O'Mara and Hickey, 2012, 2014] and seasonal fluctuations in food availability [Sauther, 1998; O'Mara and Hickey, 2014]. Age effects in the variables of interest were evaluated by comparing nested models differing in the factor of interest with a likelihood

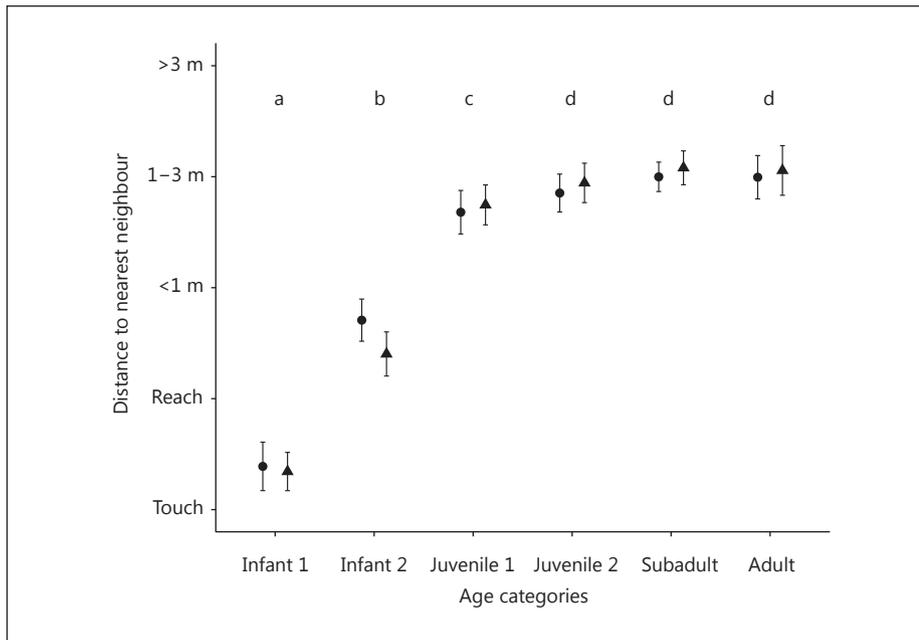


Fig. 1. Distance to nearest neighbour (mean \pm SD) while feeding and foraging for all observations (triangles) and in high predation risk areas (circles). Shared letters denote age categories that are not significantly different.

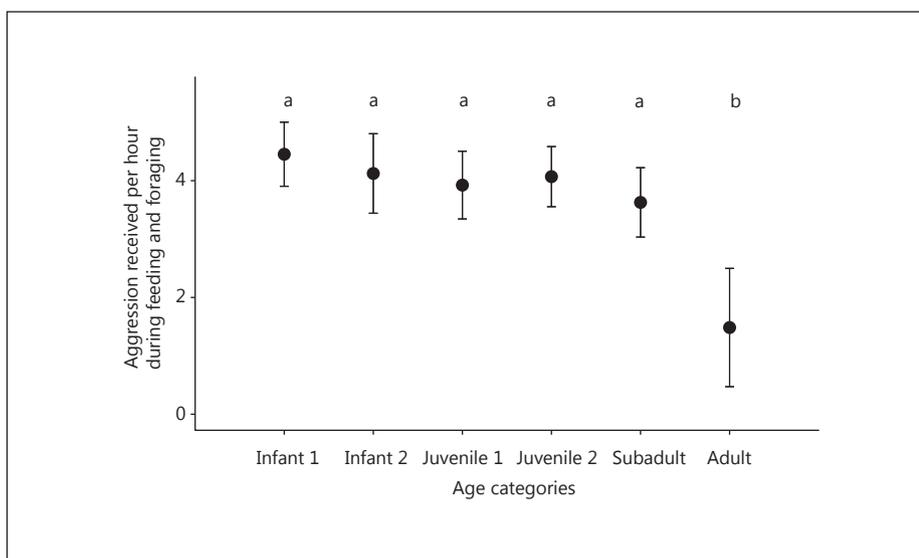


Fig. 2. Aggression received during feeding and foraging (mean \pm SD). Shared letters denote age categories that are not significantly different.

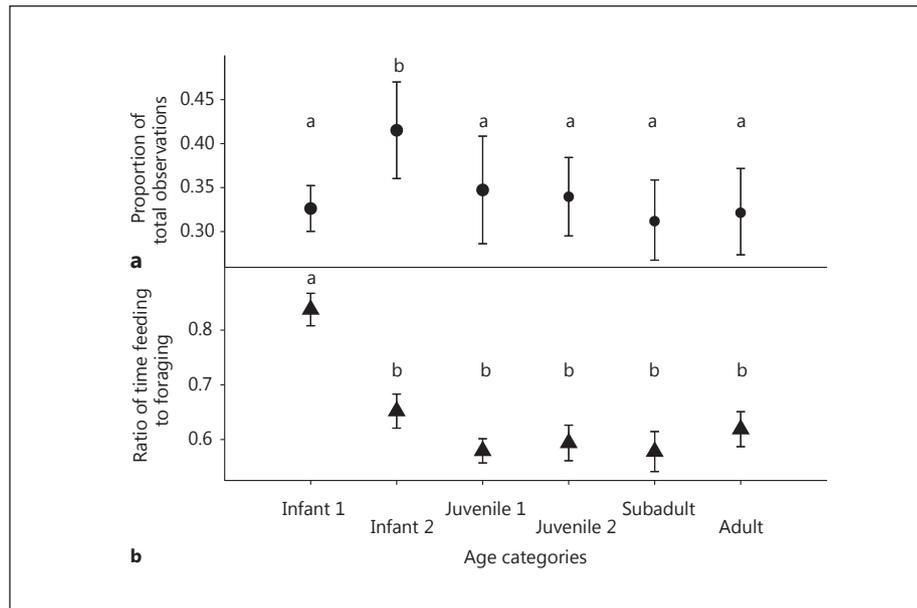


Fig. 3. Time engaged feeding and foraging (mean \pm SD). Shared letters denote age categories that are not significantly different. **a** Percent of total observations observed feeding and foraging. **b** Ratio of time observed feeding to time observed foraging.

ratio test of the two nested models (χ^2). Tukey's post hoc tests identified differences among age categories. Significance for all tests was evaluated at $\alpha = 0.05$, and means are presented with standard deviation.

Results

Infant categories 1 and 2 spend less time in areas of high predation risk than older animals (fig. 1; $\chi^2 = 97.56$, d.f. = 5, $p < 0.001$). Typical adult distances of 1–3 m to the nearest neighbour are reached by the beginning of juvenile category 2 ($\chi^2 = 1.1548$, d.f. = 3, $p = 0.8855$). Spacing while feeding and foraging are similar in areas of high predation and when all observations are grouped together, and show a general trend of increased spacing as animals age (fig. 1).

Young animals experience higher rates of aggression directed at them while feeding and foraging than do adults (fig. 2; $\chi^2 = 98.609$; d.f. = 11, $p < 0.001$), and males receive more aggression than females at all ages ($\chi^2 = 46.612$; d.f. = 6, $p < 0.001$). Infant males receive the most aggression (4.67 ± 0.27 events/h) and adult females the least (0.98 ± 0.70 events/h). Aggression directed at an individual while feeding or foraging does not affect the ingestion rate of each food type ($\chi^2 = 9.381$; d.f. = 5, $p = 0.110$).

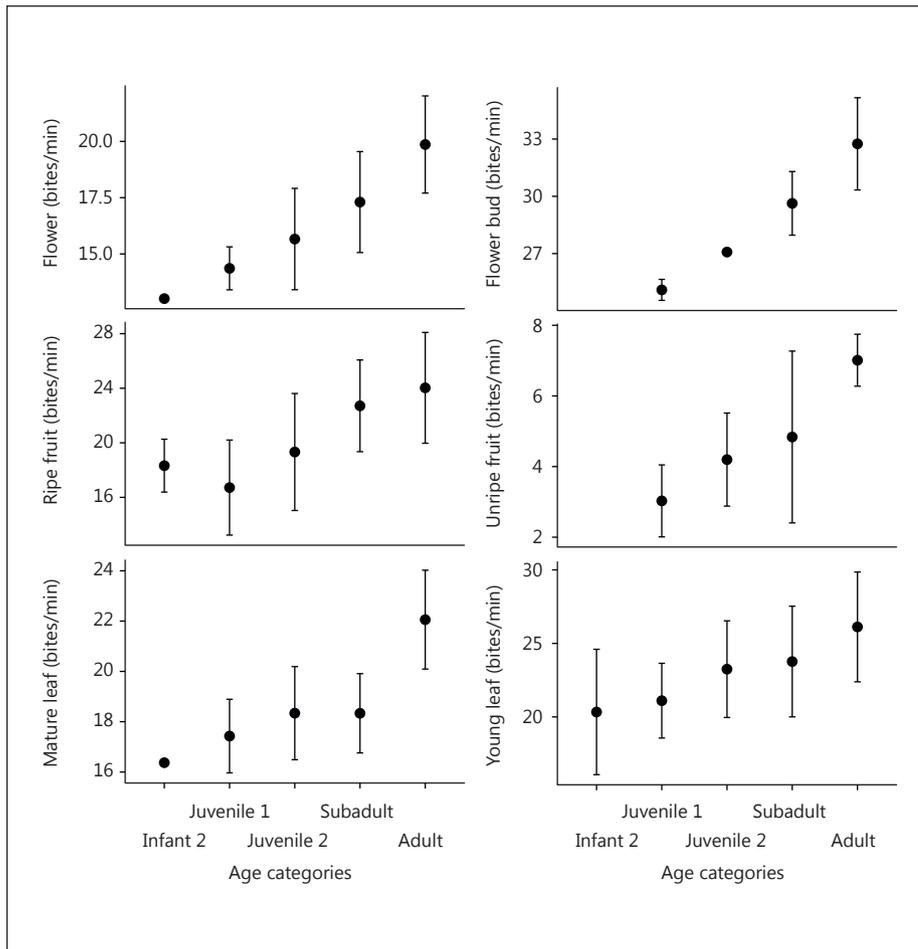


Fig. 4. Bites per minute for ring-tailed lemur food types (mean ± SD).

Infants show high ratios of time feeding to foraging and devote a larger proportion of their time to feeding (including nursing) than to foraging relative to other age classes (fig. 3; $\chi^2 = 652.3$, d.f. = 5, $p < 0.001$). All other age classes do not differ in the ratio of time spent feeding to time spent foraging (fig. 3; $\chi^2 = 9.501$, d.f. = 4, $p = 0.060$). Bite count rates increase with age across all food types (fig. 4; $\chi^2 = 207.92$, d.f. = 30, $p < 0.001$). Infants and young juveniles are generally slower feeders than adults, but there is large variation in bite count by food part (fig. 4). By juvenile stage 2, differences in bite rates in leaf ingestion disappear, but bite rates for ripe fruits and flowers remain low until the subadult category. Adults are the most proficient at capturing caterpillars that escape by dropping on silk and flying insects, including cicadas (fig. 5).

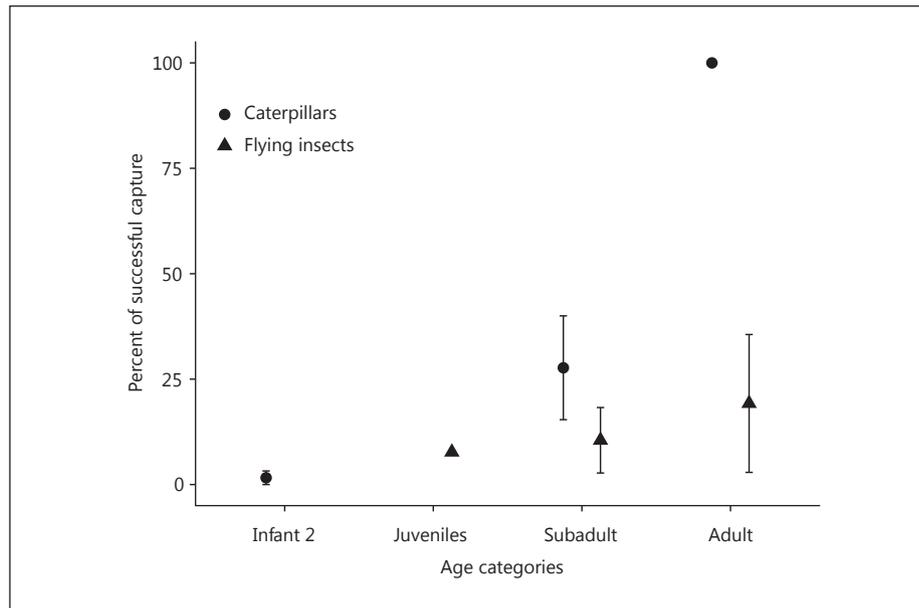


Fig. 5. Percent of capture success (mean \pm SD) for arthropod prey. Some prey types were not available during a given age stage.

Discussion

The ERAH predicts that ‘slow and steady wins the race’ to balance the mortality risks of predation and starvation [Janson and van Schaik, 1993]. Like some platyrrhines [Stone, 2007; Bezanson, 2009], ring-tailed lemur juveniles do not seem to trade reductions in predation risk for increased starvation risk in a risk averse manner and only partially meets the predictions of the ERAH. They forage as often as adults in high-risk areas and do not forage closer to group members when doing so. Juveniles receive more agonism than older group members, but this does not lower feeding efficiency. Infants and juveniles have lower ingestion rates for most foods, however, but age differences for young leaf consumption, which constitutes a large portion of the diet, are absent once individuals reach juvenile stage 2.

Juvenile ring-tailed lemurs were not observed to forage closer to group members or invest more time foraging in low-risk areas. Infant mortality rates for lemur species average between 30 and 70% [Overdorff et al., 1999; Wright, 1999; Gould et al., 2003], and juvenile mortality for this population is typically between 6 and 30% [Gould et al., 2003; O’Mara, unpubl. data]. It is possible that the instantaneous mortality risk is low for lemurs once they reach the juvenile stage, but there is still considerable predation, likely as a consequence of the large proportion of time that ring-tailed lemurs spend on the ground. The majority of predatory species at this site are terrestrial (e.g. dogs, cats, snakes, fossa), but lemurs are also exposed to aerial predation from owls and harrier hawks. Furthermore, ring-tailed lemurs are more vigilant

while on the ground than anywhere in the tree canopy [Gould and Sauther, 2007]. During this study I observed wild cats (*Felis* sp.) prey on infant ring-tailed lemurs twice from ambush positions on the ground. Alternatively, foraging in the same area as adults and not necessarily foraging closer to them is enough to limit predation attempts through dilution effects and may present the best options when trying to maximize social learning opportunities [O'Mara and Hickey, 2012]. This may be particularly true for juvenile ring-tailed lemurs that are balancing increased aggression rates against access to food and predator exposure.

By 1 year of age, juveniles are equally efficient as adults, even though they experience higher rates of aggression during foraging than adults. Additionally, at all ages males receive more aggression than females, except during the cold dry season with the lowest food availability [O'Mara and Hickey, 2014]. Rates of aggression, however, may not be an adequate measure of feeding competition [Johnson and Bock, 2004]. Beginning at juvenile stage 1, ring-tailed lemurs do not spend more time foraging relative to feeding than do adults and dedicate the same proportion of their total daily budget (30–35%) to feeding and finding food. In primate species where juveniles devote more time to foraging relative to feeding, it is generally due to limitations in strength, cognition and/or fine motor skills [Johnson and Bock, 2004; Lonsdorf, 2005; Gunst et al., 2008]. These same limitations were found in juvenile ring-tailed lemurs which were less effective at capturing insects and opening hard and tough fruits, likely due to dental and gape restrictions [Eaglen, 1985; Yamashita, 2002; Sauther and Cuozzo, 2009]. The lower juvenile ingestion rates of flowers and flower buds are likely due to social displacement from this highly prized resource that appears during seasons of low overall food abundance [Sauther, 1998; O'Mara and Hickey, 2014].

Juvenility is a period of life where individuals acquire the behavioural skills that are necessary as an adult, and it is generally characterized by a progressive refinement of skill and knowledge when learning complex foraging tasks, spatial maps or social rules that may require a long period of learning [Joffe, 1997; Ross and Jones, 1999]. Juveniles must focus on what it takes to survive this vulnerable stage [Bezanson and Morbeck, 2013] and show behavioural repertoires unusual for adults. They play, have more diverse diets and use positional behaviour modes that are either rare or absent in adults [Pereira, 1993; O'Mara and Hickey, 2014]. While juvenile ring-tailed lemur feeding behaviour is much like that of adults, they do show some distinct differences and have the most diverse diets in their groups, and they show a moderate degree of overlap with adults in their social groups [O'Mara and Hickey, 2014]. Many studies now show that juvenile primates do not meet the ERAH's behavioural predictions of being inefficient in executing their own feeding and foraging, and doing so in a particularly predation-sensitive way [Fragaszy and Boinski, 1995; Stone, 2006; Bezanson, 2009]. It is possible that the non-maximal growth rate of primates is not dependent on minimizing the ecological risk across the entire juvenile period but is a result of minimizing risk during particularly sensitive modules of the immature period [Pereira and Leigh, 2003]. Alternatively, ecological risk aversion may not play any role in the evolution of this non-maximal growth, and other aspects of primate ecology and physiology are more important. The low energetic throughput of primates [Pontzer et al., 2014], coupled with large brains and increased social complexity may exert significant pressure on delaying maturation. Future work that integrates the energetics of development within an ecological and social context will better test whether juveniles use behaviourally risk averse strategies and whether these help mitigate starvation risks and energetic deficits.

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