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Life-History Correlates of Enamel Microstructure in Cebidae (Platyrrhini, Primates)

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ABSTRACT

Previous studies have examined tooth eruption as it relates intrinsically to body mass, brain mass, and other life history variables, and extrinsically to ecological factors (e.g., age at foraging independence, environmental risk aversion, and maternal investment). Different models have been explored wherein each of these variables impacts ontogeny. However, anthropoid and strepsirhine primates exhibit interesting differences in the relationships of these ecological and life history variables with tooth eruption. Moreover, interactions between ecological variables and dental tissue growth have only been explored in the lemurs. This study examines dental microstructure of the New World monkey family, Cebidae, to provide further insight into forces influencing the evolution of primate dental ontogeny. The Cebidae were chosen because they are a diverse group which is distinct in ecology and phylogeny from the better known catarrhines of the Old World. Using phylogenetic generalized least squares analyses (PGLS), we test whether brain mass, body mass, or the three above-mentioned ecological variables have stronger correlations with enamel growth. Results show that ecological factors have stronger relationships with cebid dental growth rates than brain or body mass. Foraging independence has the most impact on overall enamel growth as it has the strongest correlation with enamel extension rates. However, another estimate of enamel growth, rate of secretion, has the highest correlation with maternal investment. Our results suggest that an overarching ecological model encompassing the three current ecological hypotheses is needed to further understand the evolution of dental ontogeny within primates. Anat Rec, 294:2193–2206, 2011. © 2011 Wiley Periodicals, Inc.

Key words: Cebidae; life history; enamel growth; foraging independence; risk aversion; maternal investment

Dental increment research over the last several decades has shown that dental development is an excellent indicator of mammalian life history evolution and provides a means to make inferences regarding ecology and adaptation (e.g., Bromage and Dean, 1985; Beynon and Dean, 1987; Beynon and Wood, 1986; Beynon et al., 1991, 1998; Dean and Beynon, 1991; Dean, 1998; Dirks, 1998, 2003; Reid et al., 1998a,b; Dean, 2000; Schwartz and Dean, 2001; Schwartz et al., 2002, 2005, 2007; Smith et al., 2004, 2007; Godfrey et al., 2006, Dirks and Bowman 2007; Bromage et al., 2009; Dirks et al., 2002,

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2009, Catlett et al., 2010; Jordana and Kohler, 2010). Dental ontogeny is of particular interest in understanding the relationships between life history and ecology among mammals for several reasons: (1) dental growth is at least partially independent of growth in the other tissues of the body (Pereira and Leigh, 2003); (2) mammalian teeth have long been recognized as a highly adaptive and important interface between individuals and their environment in terms of energy/nutrient acquisition (e.g., Cuvier, 1817); and 3) ontogeny in general "represents a series of selective compromises to a suite of environmental variables" (Wilbur et al., 1974, p. 805). Dental increments, specifically cross-striations and striae of Retzius (see Boyde, 1989; for a review), provide a powerful tool for analyzing tissue-level ontogenetic processes due to their regular periodicity.

Previous dental ontogeny research has primarily focused on the Order Primates, which is composed of two major extant suborders: the Haplorhini (tarsiers, monkeys and apes) and Strepsirhini (lemurs and lorises). Within the Haplorhini, the monkeys and apes (i.e., the anthropoids) are further subdivided into two groups: the Platyrrhini (New World monkeys) and Catarrhini (Old World monkeys and apes). Godfrey et al. (2001) contributed a landmark study of evolution in primate dental ontogeny by providing the first broad taxonomic interpretations on the interaction between body mass, brain mass, and ecological variables with tooth eruption schedules across the order (see below). However, to date, there has been a lack of similar studies examining dental microstructure growth rates and their statistical relationships with brain mass, body mass (however, see Macho, 2001), and especially ecological variables, except for a few studies on the Malagasy strepsirhines (e.g., Godfrey et al., 2006; Schwartz et al., 2007; Catlett et al., 2010). Moreover, with regard to the previous dental microstructure research, the platyrrhines have not been well-sampled as studies have focused on their catarrhine and strepsirhine relatives. This article focuses on the platyrrhine family Cebidae, since they exhibit a high degree of diversity in their body mass and ecological adaptations within a narrow phylogenetic space (i.e., a single primate family; Rosenberger, 1984, 1992; Schneider et al., 2001; Tejedor et al., 2006; Rosenberger et al., 2009). Therefore, analyses of Cebidae should reveal interesting patterns but should be less subject to the phylogenetic effects inherent in larger-scale taxonomic studies of primates (e.g., Harvey and Clutton-Brock, 1985; Godfrey et al., 2001). Because of this, the Cebidae are an ideal group to better understand the impact which body mass, brain mass, and ecology have upon dental ontogeny.

In addition to brain and body mass, we examine the influence of five additional life history variables (encephalization, age at weaning, interbirth interval, birthrate, and age at first female reproduction) on enamel growth rates in the Cebidae. The five additional life history variables are examined in the context of three ecological models: foraging independence, maternal investment, and risk aversion, which are presented as competing, but not necessarily mutually exclusive hypotheses. These variables and models have been examined with regard to their impact on somatic growth rates and tooth eruption in prior studies, but again have not been analyzed with respect to microstructural growth data (Smith, 1989; Janson and van Schaik, 1993; Leigh, 1994; Smith et al., 1994; Godfrey et al., 2001).

BRAIN AND BODY MASS

With regard to brain and body mass, primate research has repeatedly shown that they are strongly correlated with many other life history variables, such as age at weaning and somatic growth rates (e.g., Schultz, 1960; Harvey and Clutton-Brock, 1985; Harvey et al., 1987; Ross, 1991; Ford and Davis, 1992; Charnov and Berrigan, 1993) as well as the duration of dental eruption and tooth crown formation in anthropoids (e.g., Smith, 1989; Smith et al., 1994; Godfrey et al., 2001; Macho, 2001). Moreover, the different patterns of tooth eruption sequences in anthropoids have also been shown to be correlated with body mass specifically (Schultz, 1935; Smith, 2000). In other words, larger, slower-growing anthropoids seem to delay the eruption of their molars relative to their permanent premolars. It has been hypothesized that this may be due to the limited available space in the posterior aspect of anthropoid dental arcades during growth (Schultz, 1935; Smith, 2000), but this hypothesis has been countered by Boughner and Dean (2004).

Within anthropoids, the dental variables examined so far, such as tooth crown formation time, gingival emergence of teeth, and tooth eruption sequence appear to be closely correlated with one another (e.g., Smith, 1989, 2000; Smith et al., 1994; Macho, 2001; Godfrey et al., 2006). However, the Malagasy strepsirhines (lemurs) do not follow the same anthropoid pattern with regard to brain and body mass and their relationships to the duration and sequence of dental eruption or tooth crown formation times (Schwartz et al., 2002, 2005, 2007; Godfrey et al., 2004, 2005, 2006). Moreover, there are major differences between similarly-sized lemurs and anthropoids with regard to the lag time between tooth crown formation and gingival emergence (Godfrey et al., 2006). Therefore, the correlation of the dental variables within anthropoids may be circumstantial and the end result of different underlying ontogenetic needs within a specific ecological and phylogenetic context. Moreover, tooth crown formation examines dental tissue growth (e.g., enamel secretion) in the context of tooth size, which may act as a confounding variable because it is strongly tied to body size. In turn, it is still plausible that dental tissue growth rates (e.g., enamel secretion and extension; for detail, see Materials and Methods section) are evolutionarily driven or constrained by a variety of different forces than those that govern dental eruption. This difference between dental tissue growth and eruption could be a major reason why the patterns for anthropoids and strepsirhines differ (e.g., Smith, 1989, 2000; Smith et al., 1994; Schwartz et al., 2002, 2005, 2007; Godfrey et al., 2004, 2005, 2006), or strepsirhines may be an anomaly. This article attempts to provide some insight into this question by using ecological models to examine enamel secretion and extension rates within the Cebidae, a closely related, relatively unexplored, primate group with a broad range of body sizes. The Cebidae range in body size from about 100–2,500 g, and include the smallest extant anthropoids (e.g., Ford and Davis, 1992; Rosenberger, 1992).

The relationships of enamel secretion and extension rates to body mass, brain mass, and ecological variables have not been previously studied. Therefore, it is unknown whether enamel secretion and extension rates are strongly tied to body size as is tooth crown formation. In other words, smaller bodied primates will have relatively smaller teeth, have a faster eruption rate, and form their crowns in a shorter time span. However, will two smaller-bodied primate taxa in different ecological contexts exhibit comparable enamel secretion rates? Therefore, this article attempts to better understand the platyrrhines, smaller-bodied anthropoids, and how enamel growth rates are tied to life history variables in an ecological context.

ECOLOGICAL VARIABLES

With regard to particular ecological variables and their relationship with dental growth, Godfrey et al. (2001) developed and tested an array of hypotheses regarding the effects of ecological variables on the pace (absolute timing) of tooth eruption in different primate taxa, as noted above. They found that age at foraging independence was the most important predictor of eruption (see also Gibson, 1986; Dunbar, 1992, 1995; Byrne, 1995; Joffe, 1997; Ross and Jones, 1999). Other studies of subfossil strepsirhines suggest it may be important to crown formation times as well (e.g., Godfrey et al., 2006; Catlett et al., 2010). Therefore, species whose young are adapted to foraging independently at earlier ages seem to be selected to have a faster dental ontogeny relative to species with delayed independence (see below). This idea is further supported by the results of Dirks (2003), who demonstrated that among catarrhines, more folivorous species begin development of slower-growing teeth earlier relative to similarly sized frugivores/omnivores (primate folivores have been shown to have earlier ages at foraging independence; see below). Other ecological variables, such as environmental risk (*sensu* Janson and van Schaik, 1993; see below), seem to have a weaker statistical relationship with dental eruption timing (Godfrey et al., 2001; see below).

These ecological hypotheses should be tested using microstructural enamel growth rate data as well, based on the reasons discussed in the section on brain and body mass above, the influence which ecology has been shown to have on dental ontogeny (e.g., Godfrey et al., 2001, 2006; Catlett et al., 2010), as well as the fact that enamel growth rates should give us insight into tissue-level physiology and metabolism which may be obscured in gross eruption studies. Therefore, this study will use enamel growth rates to test the three main ecological hypotheses pertinent to the cebids, discussed in detail below.

FORAGING INDEPENDENCE HYPOTHESIS

Primates are assumed to vary in the cognitive and learning capabilities which underlie their foraging behavior. It has been argued that primate species whose feeding regimes require relatively low cognitive abilities (e.g., folivores) have less to learn for successful foraging, and therefore, do not need to devote as many resources to brain growth (Gibson, 1986; Dunbar, 1992, 1995; Byrne, 1995; Joffe, 1997; Ross and Jones, 1999; Godfrey et al., 2001). Since larger (i.e., more fully grown) individuals within these species should be less subject to predation pressure, these individuals should devote most of their energy to body mass growth so that they can grow more quickly (Godfrey et al., 2001). In contrast, primate species whose feeding regimes are more cognitively demanding (e.g., they require advanced mapping or problem-solving abilities), undergo selection for lengthened juvenile learning periods, delayed weaning and reproduction, as well as larger brains. In turn, they should devote relatively more energy to brain growth to facilitate the acquisition of complex foraging skills (Gibson, 1986; Dunbar, 1992, 1995; Janson and van Schaik, 1993; Byrne, 1995; Joffe, 1997; Ross and Jones, 1999; Godfrey et al., 2001). Although delayed body mass growth may put them at increased predation risk relative to their less encephalized relatives, it is hypothesized that the fitness benefits of the lengthened juvenile period (e.g., greater mapping abilities) outweigh these costs (Gibson, 1986; Dunbar, 1992, 1995; Byrne, 1995; Joffe, 1997; Ross and Jones, 1999; Godfrey et al., 2001).

Coincident with faster body mass growth, species that obtain foraging independence at relatively younger ages should exhibit faster enamel growth to process an adult diet at an earlier age (Godfrey et al., 2001). Species with a relatively delayed foraging independence age will wean later, and not require full adult dentitions as soon. In turn, they should exhibit overall slower dental ontogenies. For tooth eruption, this does seem to hold true in comparing frugivores and folivores across the primate order (Godfrey et al., 2001). Thus, we can derive the following predictions: (1) species with larger brains relative to body mass (i.e., have a higher encephalization quotient = EQ) should exhibit slower enamel growth rates than species with relatively smaller brains; and (2) species with delayed weaning should exhibit slower enamel growth rates.

RISK AVERSION HYPOTHESIS

This hypothesis, originally put forward by Janson and van Schaik (1993), suggests that species which live in a riskier environment and have a more unstable dietary supply will have slower overall growth rates to reduce the risk of starvation. That is, in environments where resource availability may fluctuate decidedly, species with lower energy expenditure in terms of metabolism and growth will be less likely to suffer from malnutrition and/or starvation (Janson and van Schaik, 1993; Leigh, 1994; Godfrey et al., 2001). Where environmental resources are relatively stable, species should be better able to afford faster growth rates and metabolism. Research has supported this hypothesis with regard to body mass growth in the anthropoids studied so far (Leigh, 1994). However, dental eruption data have not supported it; specifically, the time it takes to complete dental eruption is not significantly correlated to age at first female reproduction across primates (Godfrey et al., 2001). Moreover, Dirks and Bowman (2007) have also shown that any ecological patterns which link dental maturation to age at reproduction are highly affected by phylogenetic history. They show that cercopithecoids time their reproductive maturation differently with respect to dental eruption when to compared to the hominoids. Therefore, following Godfrey et al. (2001), we will

further test the risk aversion hypothesis by examining the relationship of enamel growth rates to age at first female reproduction and age at weaning.

MATERNAL INVESTMENT HYPOTHESIS

Based on the idea that mothers and infants may have slightly different fitness needs (e.g., Trivers, 1972, 1974; Nicolson, 1987), we hypothesize that an increase in maternal investment will result in slower infant dental growth rates. Lee (1999) has argued that increased maternal investment (reflected by prolonged interbirth intervals) is tied to greater brain growth during the period of lactation. Moreover, Leigh and Bernstein (2006) have also argued that maternal investment seems to have a major impact upon patterns of brain growth and dental eruption within papionins. Given this, it seems likely that a statistical relationship between maternal investment and enamel growth rates should exist, especially considering that the state of dental growth is important to a young primate's ability to fend for itself (e.g., Smith et al., 1994).

Therefore, we predict that when it is in the interest of both the mother and offspring to have a high maternal investment, juveniles will experience relatively slower enamel growth rates. This slower growth should result because the continued allocation of maternal resources allows the juveniles to complete dental ontogeny at a later stage of their overall development. However, for species where mothers need to conserve resources for future infants at the cost of current offspring (Trivers, 1972, 1974; Nicolson, 1987), the juveniles of that species will exhibit faster enamel growth rates due to their need to compensate for the decreased energy investment from their mothers.

Age at weaning, interbirth interval, and birth rate can serve as proxy variables for assessing maternal investment (e.g., Trivers, 1972, 1974; Nicolson, 1987; Lee, 1999; DiBitetti and Janson, 2000). Relatively higher values for these proxies (except birth rate) should reflect a relatively higher maternal investment in individual offspring. In other words, species with delayed weaning, relatively longer interbirth intervals, and lower birth rates should have relatively slower enamel growth rates.

Based on prior studies (Godfrey et al. 2001, 2004, 2006; Schwartz et al. 2007; Catlett et al. 2010), we predict that brain mass will have the strongest correlations with all three enamel growth variables measured in this study (see Materials and Methods section). Among ecological hypotheses, we predict that the foraging independence hypothesis will receive the greatest statistical support, with the enamel growth variables being strongly correlated with EQ and age at weaning (based on magnitude of r values). We also predict that risk aversion will receive the weakest statistical support, as discussed by Godfrey et al. (2001). Maternal investment, as indicated especially by interbirth interval and birth rate, is a relative unknown as it has not been explicitly assessed in prior studies.

MATERIALS AND METHODS

Systematists generally agree that Cebidae contains at least two extant subfamilies: Cebinae, which includes the genera *Cebus* and *Saimiri*; and Callitrichinae, which includes *Callithrix, Cebuella, Saguinus, Leontopithecus,* and *Callimico* (Rosenberger, 1984, 1992; Rosenberger et al., 1990; Kinzey, 1997; Schneider et al., 2001; Ray et al., 2005; Ray, 2007; Osterholtz et al., 2009; Rosenberger et al., 2009). Molecular systematists generally recognize a third subfamily, Aotinae, with its genus *Aotus.* However, the status of *Aotus* as a member of the Cebidae is still under debate (e.g., Schneider et al., 2001; Ray et al., 2005, 2007; Osterholtz et al., 2009; Rosenberger et al., 2009).

We examined mandibular premolars and molars from all eight extant cebid genera, including *Aotus*, as well as the outgroup, *Alouatta*, an ateline genus (17 species in all; Table 1). Although the phylogenetic status of *Aotus* is still under debate, we incorporated it out of a desire to favor inclusiveness and completeness. *Alouatta* spp. was included as a non-cebid outgroup because it is a large-bodied, less-encephalized platyrrhine, unlike *Cebus* which is relatively large and encephalized, and *Saimiri* and the callitrichines which are much smaller.

Teeth were extracted from their alveoli and cleaned of organic debris via incubation in a 5% enzyme detergent solution at 50°C for one week, with daily solution changes. They were then embedded in an acrylic resin (polymethyl methacrylate), sectioned, mounted to microscope slides, and polished following the protocols outlined by Hogg (2010). Teeth were imaged using a PL Fluotar 40/0.70 objective lens, mounted onto a Leica-Leitz DMRX/E Universal Microscope configured with a Marzhauser motorized stage, phase contrast, and circularly polarizing filters (CPL). All CPL images were acquired via Syncroscopy Montage Explorer (Synoptics, Ltd.), using a JVC KYF55B color video camera. See Hogg (2010) for further details on the use of CPL and enamel imaging.

We assess enamel growth rates using three component enamel growth variables: daily enamel secretion rates (DSR; for explanation, see Fig. 1), enamel extension rates (quantified by enamel formation front angles = EFF angles), and crown formation index (CFI; Hogg, 2010). Overall enamel growth rate is primarily a combination of two of these factors: DSR and enamel extension rate (Reid et al., 1998b; CFI is an index incorporating both—see below). Therefore, to appreciate overall enamel growth it is necessary to measure both of these factors, though we argue that enamel extension has the greater overall impact of the two (Fig. 1; see Discussion section).

Measurements of cross-striation breadths were taken in order to obtain mean DSRs for each species (Fig. 1). One cross-striation (i.e., 24 hr of growth; Boyde, 1989) consists of one light and one dark alternating band on an enamel prism when viewed in polarized light. Averages of cross-striation breadths were computed for nine regions within each tooth sampled. Each tooth crown was divided into three main regions: cuspal, midcrown imbricational, and cervical imbricational. Each of these three regions was subdivided into three subsets: inner (closer to dentine), middle, and outer (closer to the enamel surface). A minimum of 50 measurements was the standard for each of these nine regions for each tooth, though in a few cases only 20–30 measurements were obtained for a given region within a single tooth due to a lack of visible anatomy (for raw data and intra-observer error studies, see Hogg, 2010). For most

TABLE 1. Specimens sampled in this study

Genus	Species	Teeth	Source	Number
Alouatta	*sp.*	M_1	MNRJ	490
Alouatta	*sp.*	M_2	MNRJ	499
Alouatta	*sp.*	M_3	MNRJ	2756
Aotus	*sp.*	P_3	CSHO	
Aotus	*sp.*	P_3	CSHO	
Callimico	*goeldii*	M_1, M_3	Rose	
Callithrix	*humeralifer*	M_1, M_2	AMNH	94926
Callitrhix	*jacchus*	P_2	HTRU	
Cebuella	*pygmaea*	Premolar	AMNH	239606
Cebus	*albifrons*	P_2, P_3, M_2, M_3	AMNH	62838
Cebus	*albifrons*	P_3, P_4, M_1, M_2, M_3	AMNH	78504
Cebus	*apella*	P_2, P_4, M_1, M_2, M_3	AMNH	133091
Cebus	*apella*	P_3, P_4, M_1, M_2	Rose	Y15
Cebus	*apella*	M_1, M_3	MNRJ	445
Cebus	*apella*	M_2	MNRJ	446
Cebus	*apella*	M_3	MNRJ	448
Cebus	*capucinus*	P_2, P_3, M_2	Rose	
Cebus	*capucinus*	P_4, M_1	USNM	
Cebus	*olivaceus*	P_2, P_3, P_4, M_1, M_2, M_3	AMNH	42419
Cebus	*sp.*	P_2, M_1	Rosenberger	
Cebus	*sp.*	M_2	MNRJ	459
Cebus	*sp.*	M_1, M_2	MNRJ	460
Leontopithecus	*rosalia*	P_2, P_3, P_4, M_1	AMNH	80244
Saguinus	*fuscicollis*	P_3, P_4, M_1, M_2	AMNH	182941
Saguinus	*oedipus*	P_2, P_3, P_4	USNM	
Saguinus	*midas*	P_3, P_4	AMNH	97280
Saguinus	*nigricollis*	P_2, P_3, P_4, M_2	USNM	
Saimiri	*boliviensis*	P_2, M_1, M_3	AMNH	208075
Saimiri	*oerstedii*	P_2, M_1	AMNH	139300
Saimiri	*sciureus*	P_3, P_4, M_2, M_3	AMNH	94206
Saimiri	*sciureus*	P_2, P_4, M_1, M_2	USNM	397329

AMNH = American Museum of Natural History; CSHO = Center for the Study of Human Origins, New York University; HTRU = Hard Tissue Research Unit, New York University College of Dentistry; MNRJ = Museu Nacional do Rio de Janeiro; Rose = Rose Primate Collection, Queensborough Community College, USNM = United States National Museum of Natural History.

individuals, multiple postcanine teeth were available for sampling (Table 1). Therefore, mean cross-striation breadth for each individual (i.e., mean DSR) was calculated as the mean of all regional averages for all teeth for that individual; species means were then calculated as a grand mean of individual means. This step-by-step approach prevents a high number of measurements in any one tooth or region from skewing the final mean for each individual and species.

Enamel extension rate was quantified by measuring angles between successive EFF angles, as represented by striae of Retzius within the teeth, and the enamel–dentine junction (EDJ) (Fig 1; Beynon and Wood, 1986). EFF angles, also termed "D degrees" angle by Beynon and Wood (1986; see also Bromage et al., 1995), reflect the number of ameloblasts actively secreting enamel along the EFF at any one point in time. Since the EFF is the enamel surface throughout growth, an increase in the number of active ameloblasts will lengthen the EFF and, in turn, decrease the angle between the EFF and the EDJ (Beynon and Wood, 1986; Bromage et al., 1995). Therefore, as illustrated in Fig. 1, a more acute (smaller) EFF angle reflects a greater amount of enamel being secreted during a specific unit of time (= higher enamel extension rate). In order to limit the impact of gross anatomical differences in enamel among the different tooth types and tooth regions, all EFF angles were taken only from midcrown imbricational enamel in M_1 and M_2. EFF angles were then averaged together across individuals to create a species mean angle. As with cross-striations, all angular measurements were calibrated to the optical system used to provide the image data, and were taken in Syncroscopy Automontage (Synoptics, Ltd.).

In contrast to our methodology, a number of studies have used an approach based on the work by Shellis (1984) to directly quantify enamel extension rate in terms of an estimation of the increase in enamel height (i.e., crown height) per unit time (e.g., Risnes, 1986, 1998; Dean, 1998, 2009; Dean and Shellis, 1998; Reid et al., 1998b, Dean and Vesey, 2008; Dirks et al., 2009; Jordana and Kohler, 2010). We chose to calculate EFF angles as a proxy for extension instead due to the body size range within our sample. As has been mentioned by other authors (e.g., Shellis, 1998; Macho, 2001), there is a greater inherent difficulty in reconstructing enamel growth patterns from the teeth of very small primates such as callitrichines, which formed a major component of our sample. As smaller primates, the callitrichines not only possess less available enamel to quantify, they also have a high variability in the degree of quantifiable growth increments (Hogg, 2010). This lack of useful anatomy has greatly limited the degree to which small primates have been incorporated in previous dental increment studies (e.g., Shellis, 1998; Macho, 2001). However, since most callitrichines examined in this study did possess multiple visible striae of Retzius, mean

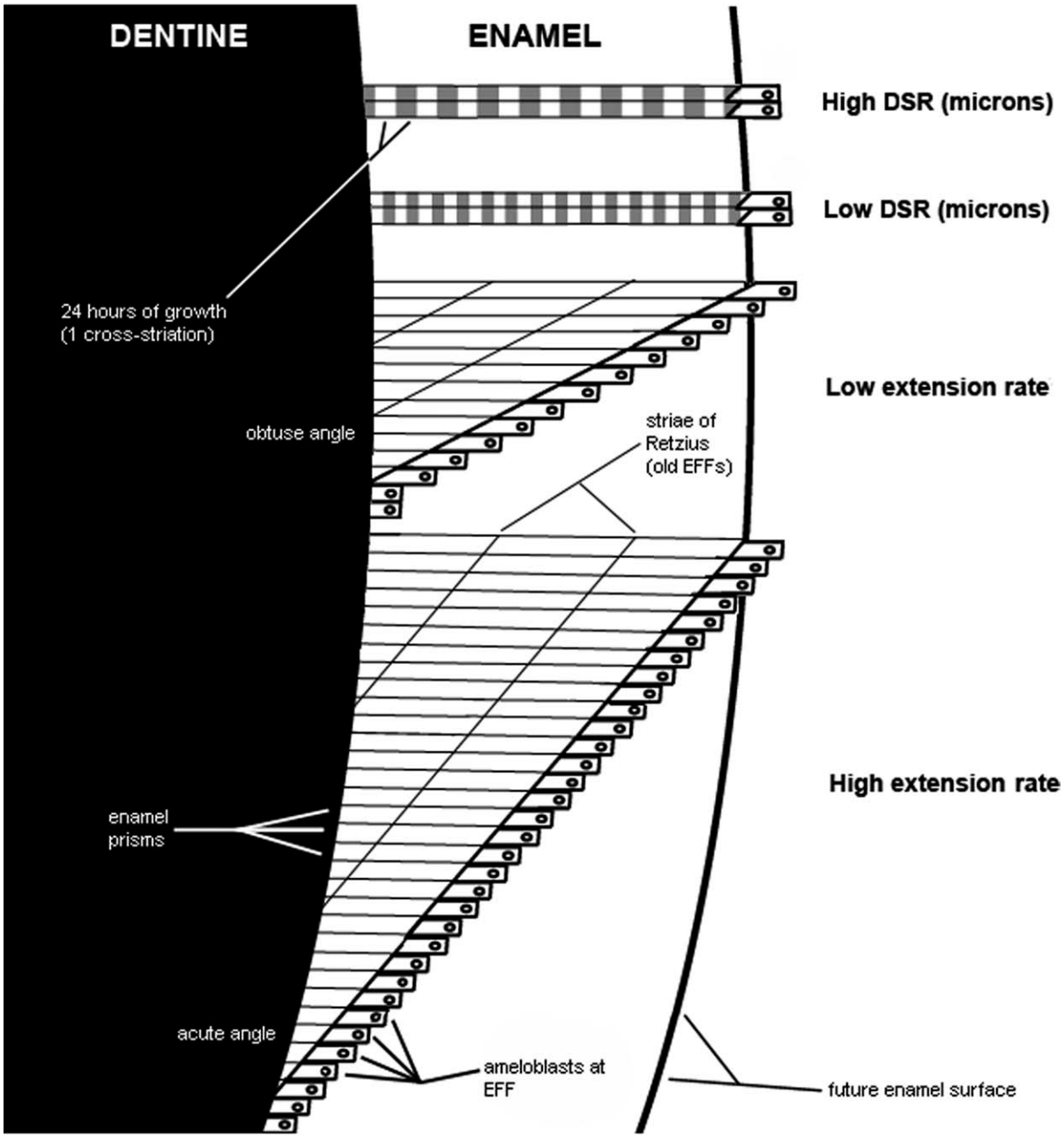

Fig. 1. The two components of enamel growth, showing ameloblasts as they progress from the EDJ as part of the EFF, which represents the change in position of the enamel surface as the enamel thickens. Top: Individual ameloblasts can increase enamel growth rate by increasing their daily enamel secretion rate (DSR) per cell, represented by thicker alternating gray-and-white bands. Below: Also, by increasing the number of ameloblasts, the same amount of work will be performed in less time. For the same final enamel thickness, an increase in the number of active ameloblasts (=high extension rate) will cause the angle between the EFF and the EDJ to become more acute. Therefore, the group of ameloblasts with the more obtuse EFF angle has deposited relatively less enamel (=low extension rate) in the same amount of time and in turn has a slower growth rate. Striae of Retzius demarcate the position of ameloblasts along the EFF at earlier growth times. The angle between striae and the EDJ is measured to compare the enamel extension rate across species.

imbricational EFF angles could be taken, providing adequate data for our correlation analyses. Based on our results and those of Hogg (2010), we propose that EFF angles are a useful substitute for direct enamel extension estimation, with the particular advantage of collecting more data from small-bodied taxa.

All data directly included in our analyses are summarized in Table 2 (raw data is in Hogg, 2010). Mean DSR (i.e., cross-striation breadth) and mean EFF angle for each species were regressed against species mean values for all seven predictor variables (i.e., body mass, brain mass, EQ, age at weaning, age at first female reproduction, interbirth

TABLE 2. Data included in statistical analyses in this study

Genus	Species	Mean EFF angle	Mean DSR	CFI	Body mass, kg	LN body mass	Brain mass, g	LN brain mass	Enceph. quotient	Weaning age, years	1st female repro., years	Interbirth interval, years	Birth rate
Aotus	spp.	16.87	4.67	0.28	0.91	−0.09	18.2	2.9	0.18	0.49	2.42	0.6	1.33
Alouatta	spp.	19.64	5.11	0.26	6.42	1.86	56	4.03	0.14	0.89	3.8	1	0.66
Callimico	*goeldii*	13.91	4.31	0.31	0.39	−0.94	10.8	2.38	0.19	0.18	1.3	0.46	2.14
Callithrix	*humeralifer*	–	4.13	–	0.32	−1.13	7.9	2.07	0.16	0.25	1.6	–	–
	jacchus	–	4.3	–	0.26	−1.36	7.9	–	0.18	0.17	1.67	0.43	4.06
Cebuella	*pygmaea*	–	4.8	–	0.12	−2.1	4.2	1.43	0.16	0.24	1.9	0.42	4.2
Cebus	*albifrons*	36.74	4.87	0.13	2.27	0.82	74.4	4.2	0.39	0.75	4	1.5	0.67
	apella	22.35	5.14	0.23	2.6	0.97	72	4.29	0.34	1.14	5.78	1.84	0.56
	capucinus	24.36	5.72	0.23	3.27	1.18	79.2	4.37	0.32	1	4	2.2	0.63
	olivaceus	–	4.467	–	2.98	1.09	80.8	4.39	0.35	1.97	6	2.17	–
Leontopithecus	*rosalia*	8.96	4.93	0.55	0.63	−0.47	12.9	2.56	0.16	0.24	2.4	0.83	4
Saguinus	*fuscicollis*	16.76	4.66	0.28	0.37	−0.99	9.3	2.23	0.17	0.25	2.33	0.66	2
	nigricollis	14.79	4.73	0.32	0.48	−0.73	8.9	2.19	0.13	0.21	2.33	0.69	–
	midas	–	4.29	–	0.52	−0.65	10.4	2.34	0.15	0.19	2	0.66	3.64
	oedipus	–	4.44	–	0.43	−0.84	9	2.2	0.15	0.22	1.89	0.77	3.26
Saimiri	*boliviensis*	–	5.7	–	0.7	−0.36	–	–	–	–	–	–	–
	oerstedii	14.18	4.78	0.34	0.71	−0.34	25.7	3.25	0.3	0.5	–	–	–
	sciureus	13.00	4.7	0.36	0.8	−0.23	25.3	3.23	0.27	0.5	2.5	1.13	0.86

EFF angle values given in degrees, DSR values given in microns.

interval, and birth rate) using BayesTraits *Continuous* software (Pagel, 1999; http://www.evolution.rdg.ac.uk/BayesTraits.html). *Continuous* analyzes continuously varying data using a phylogenetic generalized least-squares (PGLS) approach with a Brownian motion model of evolution (Pagel, 1997). We estimated lambda values (Λ), or the degree to which shared evolutionary histories produce the patterns of similarity observed in the data. Values of Λ near zero correspond to traits being less similar amongst species than expected given their phylogenetic relationships, whereas larger Λ-values imply a strong phylogenetic signal. We sampled model parameters over 1,000 Bayesian Markov chain Monte Carlo trees with rate deviance set to ensure that acceptance rates were 20%–40%. Chains were run for 2,000,000 generations sampling every 1,000 to reduce autocorrelation. The initial half of the run was removed to allow ample burn-in. Phylogenetic trees for PGLS analyses were generated from genetic data according to a Bayesian model, using 10k Trees (http://10ktrees.fas.harvard.edu/). Multivariate analyses were not performed, due to the fact that sample sizes were of a similar magnitude to the number of predictor variables.

Values for predictor variables were acquired from the literature (Table 3). To verify accuracy of body mass values, two different compilations were analyzed: Ford and Davis (1992) and Rosenberger (1992). There were no appreciable differences between them. To verify accuracy of brain mass measurements, values for all species were compared against cranial capacity estimates from Kirk (2006; see Hogg, 2010), which are all comparable. Values for encephalization quotient (EQ) were based on the standard EQ equation (Jerison, 1973) as modified for primates by Martin (1990), who gave 0.68 as the best allometric exponent in this group (EQ = observed brain mass/expected brain mass = brain mass/body mass$^{0.68}$).

Since DSR and EFF angle are not significantly correlated to one another in cebids, it is appropriate to combine the two in a common index to try and provide some further insight into an overall enamel growth rate pattern (Hogg, 2010). Accordingly, we examined CFI (Hogg, 2010) to examine the effects upon DSR and EFF angle simultaneously. The CFI for each species divides the mean DSR by the mean EFF angle. Therefore, when both DSR and enamel extension rates (as signified by low EFF angles) are high, the value of the index is high. If either of these values decreases, the value of the index decreases correspondingly. However, an increase in DSR is reflected as a corresponding increase in CFI, whereas an increase in the value of EFF angles results in a decrease of the CFI value. This decrease mathematically reflects the fact that high EFF angles are tied to slower enamel extension rates. For example, imagine two species with mean EFF angles of 10 versus 15 degrees, who share a mean DSR of 5 microns. The second species, with the 15 degree EFF angle, will have the slower enamel extension rate because it has fewer ameloblasts operating at one time (see Fig. 1). The CFI for these two species reflects this difference: CFI_1 = 5/10 = 0.5; CFI_2 = 5/15 = 0.33, respectively.

RESULTS

Table 4 provides descriptive statistics on DSR, EFF angle, and CFI for each species included in the analyses. Table 5 provides the details of regression statistics, with

TABLE 3. Specific sources of data for the variables analyzed in this study

Species	Body mass	Brain mass	Age at weaning	Age at 1st fem repr	Interbirth interval and birth rate
Alouatta spp.	Ford and Davis (1992)	Hartwig (1996)	Godfrey et al., (2001)	Godfrey et al., (2001)	Harvey and Clutton-Brock (1985)
Aotus spp.	Ford and Davis (1992)	Hartwig (1996)	Godfrey et al., (2001)	Ross (1991)	Harvey and Clutton-Brock (1985)
Callimico goeldii	Ford and Davis (1992)	Hartwig (1996)	Harvey and Clutton-Brock (1985)	Ross (1991)	Harvey and Clutton-Brock (1985)
Callithrix humeralifer	Ford and Davis (1992)	Hartwig (1996)	Lindenfors (2002)	Lindenfors (2002)	–
Callithrix jacchus	Ford and Davis (1992)	Hartwig (1996)	Harvey and Clutton-Brock (1985)	Godfrey et al., (2001)	Harvey and Clutton-Brock (1985)
Cebuella pygmaea	Ford and Davis (1992)	Hartwig (1996)	Harvey and Clutton-Brock (1985)	Ross (1991)	Harvey and Clutton-Brock (1985)
Cebus albifrons	Ford and Davis (1992)	Harvey and Clutton-Brock (1985), Hartwig (1996)	Godfrey et al., (2001)	Ross (1991)	Harvey and Clutton-Brock (1985)
Cebus apella	Ford and Davis (1992)	Hartwig (1996)	Godfrey et al., (2001)	Godfrey et al., (2001)	Harvey and Clutton-Brock (1985)
Cebus capucinus	Ford and Davis (1992)	Harvey and Clutton-Brock (1985)	Harvey and Clutton-Brock (1985)	Ross (1991)	Harvey and Clutton-Brock (1985)
Cebus olivaceus	Ford and Davis (1992)	Harvey and Clutton-Brock (1985)	Lindenfors (2002)	Lindenfors (2001)	Harvey and Clutton-Brock (1985)
Leontopithecus rosalia	Ford and Davis (1992)	Hartwig (1996)	Harvey and Clutton-Brock (1985)	Ross (1991)	Harvey and Clutton-Brock (1985)
Saguinus fuscicollis	Ford and Davis (1992)	Hartwig (1996)	Godfrey et al., (2001)	Godfrey et al., (2001)	Harvey and Clutton-Brock (1985)
Saguinus midas	Ford and Davis (1992)	Hartwig (1996)	Harvey and Clutton-Brock (1985)	Ross (1991)	Harvey and Clutton-Brock (1985)
Saguinus nigricollis	Ford and Davis (1992)	Hartwig (1996)	Godfrey et al., (2001)	Godfrey et al., (2001)	Harvey and Clutton-Brock (1985)
Saguinus oedipus	Ford and Davis (1992)	Hartwig (1996)	Harvey and Clutton-Brock (1985)	Ross (1991)	Harvey and Clutton-Brock (1985)
Saimiri boliviensis	Ford and Davis (1992)	–	–	–	–
Saimiri oerstedii	Ford and Davis (1992)	Hartwig (1996)	Godfrey et al., (2001)	–	–
Saimiri sciureus	Ford and Davis (1992)	Hartwig (1996)	Godfrey et al., (2001)	Ross (1991)	Harvey and Clutton-Brock (1985)

the predictor variables ranked in order of importance for each of the three enamel variables. Overall, our results are surprising, in that ecological variables seem to have a stronger statistical relationship with enamel growth rates than either brain or body mass, unlike a similar prior analysis of enamel eruption schedules across the primate order (Godfrey et al., 2001). However, among the three different ecological hypotheses, results are more mixed than we initially predicted. While the foraging independence hypothesis does receive more statistical support in our analyses overall, the three separate ecological hypotheses seem to have contrasting statistical relationships with the different variables of enamel growth that we analyzed.

Correlations for DSR are generally greater than those for EFF angle after phylogenetic controls are applied. Since the reverse is true in regressions for which such controls are not applied (Hogg, 2010), this suggests that EFF angle is more subject to phylogenetic effects. However, standard two-sample statistical tests performed on the Λ-values for both enamel growth variables do not support this interpretation. While the mean Λ-value is

TABLE 4. Descriptive statistics for enamel increment data obtained in this study

Genus	Species (N)	DSR mean	DSR range	DSR stand. dev.	DSR CV	EFF angle mean	EFF angle range	EFF angle stand. dev.	EFF angle CV	CFI
Alouatta	spp. (3)	5.11	6.67	1.27	0.25	19.64	6.92	2.08	0.11	0.26
Aotus	spp. (2)	4.67	6.28	1.05	0.22	16.87	5.43	3.84	0.23	0.28
Callimico	*goeldii* (1)	4.31	4.35	0.76	0.17	13.91	3.78	1.43	0.1	0.31
Callithrix	*humeralifer* (1)	4.13	2.41	0.62	0.15	–	–	–	–	–
Callithrix	*jacchus* (1)	4.3	2.73	0.53	0.12	–	–	–	–	–
Cebuella	*pygmaea* (1)	4.8	3.93	0.61	0.13	–	–	–	–	–
Cebus	*albifrons* (2)	4.87	9.07	1.4	0.29	36.74	19.63	4.61	0.13	0.13
Cebus	*apella* (5)	5.14	9	1.31	0.25	22.35	14.37	4.07	0.18	0.23
Cebus	*capucinus* (2)	5.72	8.34	1.31	0.23	24.36	14.86	3.45	0.14	0.23
Cebus	*olivaceus* (1)	4.47	6.4	0.88	0.2	–	–	–	–	–
Leontop.	*rosalia* (1)	4.93	4.49	0.83	0.91	8.96	13.83	4.3	0.5	0.55
Saguinus	*fuscicollis* (1)	4.66	5.11	0.8	0.17	16.76	7.6	2.61	0.16	0.28
Saguinus	*midas* (1)	4.29	5.08	0.86	0.2	–	–	–	–	–
Saguinus	*nigricollis* (1)	4.73	4.83	1.02	0.21	14.79	12.17	3.0	0.2	0.31
Saguinus	*oedipus* (1)	4.44	3.85	0.69	0.16	–	–	–	–	–
Saimiri	*boliviensis* (1)	5.7	4.99	0.8	0.14	–	–	–	–	–
Saimiri	*oerstedii* (1)	4.78	3.86	0.83	0.17	14.18	12.15	4.38	0.31	0.34
Saimiri	*sciureus* (2)	4.7	7.38	1.01	0.21	13.0	8.64	2.54	0.2	0.36

These mean DSR and EFF angle values (in bold) were used in the PGLS analyses (Table 5). DSR values are given in microns, EFF angle values are given in degrees. CV = coefficient of variation.

TABLE 5. PGLS regression data for the three enamel growth variables (DSR, EFF ANGLE, AND CFI) versus brain mass, body mass, and the five ecological proxies

Dependent (Y)	Predictor (X)	r^2	r	Λ	Regression slope (CI)[a]
DSR	Interbirth interval	0.598	0.773	0.426	0.684 (0.405; 0.996)
	Weaning age	0.553	0.747	0.297	1.006 (0.561; 1.465)
	Age 1st fem. repr.	0.445	0.667	0.275	0.236 (0.096; 0.3697)
	LN brain mass	0.434	0.658	0.272	0.316 (0.126; 0.499)
	LN body mass	0.367	0.606	0.297	0.235 (0.071; 0.392)
	Birth rate	0.187	0.432	0.372	−0.13 (−0.285; 0.031)
	EQ	0.084	0.289	0.700	1.279 (−2.031; 4.143)
EFF angle	EQ	0.398	0.631	0.496	56.53 (8.65–95.88)
	LN brain mass	0.335	0.579	0.366	5.465 (0.0824; 10.772)
	Birth rate	0.266	0.516	0.441	−3.861 (−8.327 to 1.823)
	Age 1st fem. repr.	0.203	0.451	0.384	2.613 (−1.35; 6.299)
	Weaning age	0.181	0.425	0.388	8.612 (−8.368; 23.429)
	LN body mass	0.175	0.419	0.420	3.04 (−1.863; 7.732)
	Interbirth interval	0.156	0.394	0.400	4.108 (−7.559; 13.614
CFI	Birth rate	0.59	0.768	0.495	0.084 (0.038; 0.131)
	EQ	0.203	0.451	0.194	−0.614 (−1.439; 0.206)
	LN brain mass	0.175	0.418	0.484	−0.056 (−0.141; 0.035)
	Weaning age	0.154	0.392	0.460	−0.119 (−0.325; 0.108)
	Age 1st fem. repr.	0.109	0.33	0.5	−0.027 (−0/081; 0.031)
	LN body mass	0.099	0.314	0.217	−0.031 (−0.1; 0.042)
	Interbirth interval	0.048	0.219	0.225	−0.016 (−0.156; 0.132)

For each enamel growth variable, predictor variables are listed in order of decreasing strength of r^2/r values. Except where noted, all values given are means for individual PGLS regressions (see Methods for explanation).
[a]CI = 95% Confidence interval of all slopes for each PGLS regression.

higher for EFF than for DSR (0.414 vs. 0.377, respectively), there is no statistically significant difference in mean Λ values between the two enamel variables in either parametric (student *t*-test: $P = 0.555$) or nonparametric analyses (Mann–Whitney test: $P = 0.141$).

It is important to note that the relationships observed for DSR and EFF angle are in fact opposite to one another in these analyses. In other words, in the cebids, DSR increases with body and brain mass (positive relationship) whereas enamel extension rates decrease (i.e., more obtuse EFF angles) for species with larger bodies and brains (negative relationship; see Fig. 2 and Table 5). Therefore, EFF angles show a relationship between dental ontogeny and body/brain mass which is similar to that of previous studies based on tooth eruption (Smith, 1989; Smith et al., 1994; Godfrey et al., 2001), whereas DSR shows the opposite pattern. These patterns apply to all variables examined in this study except for birth rate, which has a negative relationship with DSR and a positive relationship with enamel extension (i.e., as predicted, enamel extension rate decreases with higher birth rates as seen in higher EFF angle values). CFI, as the combination of these variables, shows the same directionality as enamel extension.

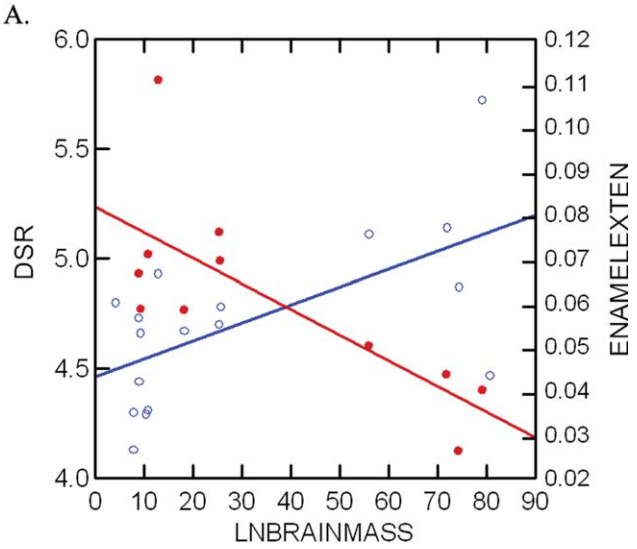

Fig. 2. Visual comparison of contrasting mean PGLS regression slopes exhibited by enamel secretion (DSR, blue) versus enamel extension (EFF angle, red), when compared against the natural logarithm (LN) of brain mass (for 95% confidence intervals of PGLS slopes, see Table 5). While the numerical value of DSR (in microns) and EFF angle (in degrees) both increase with increases in brain mass, an increase in EFF angle actually reflects a decrease in enamel extension rate. To graphically depict the fact that DSR is increasing with brain mass while enamel extension rate is decreasing, enamel extension rate data have been entered into the regression here as 1/EFF angle.

Body and Brain Mass

When analyzed with the three enamel variables, body mass only provides a strong r value when regressed against DSR; however, it is only fifth in importance for DSR among the seven predictor variables (Table 5). Brain mass is never the most important predictor for enamel growth rates in any of the analyses. Instead, brain mass is the second, third, and fourth predictor variable for EFF angle, CFI, and DSR, respectively.

Foraging Independence Hypothesis

As predicted, proxy variables linked to foraging independence exhibit a strong relationship to the enamel growth rates of cebids; however, the results are somewhat mixed across the different enamel growth variables (Table 5). Further supporting the hypothesis of Godfrey et al. (2001), EQ has the strongest relationship with EFF and is also strongly correlated with CFI, but is not strongly correlated with DSR. However, for DSR weaning age is the second-most important predictor variable. Looking beyond the strength of the correlations, for both EFF angle and DSR, regressions for EQ and age at weaning have the steepest slopes of all variables examined.

Risk Aversion Hypothesis

Unlike the results of Godfrey et al. (2001), our study provides some evidence to support the risk aversion hypothesis, but the statistical support is still not strong. In terms of statistical impact on enamel growth rates, age at first female reproduction is the third, fourth, and fifth predictor variable for DSR, EFF angle, and CFI, respectively. As stated earlier, weaning age is the second highest predictor variable for DSR but only the fourth predictor variable for EFF angle and CFI (Table 5).

Maternal Investment Hypothesis

Support for the maternal investment hypothesis is also somewhat mixed. Rather than presenting a clear pattern of association, interbirth interval, birth rate, and weaning age show highly varied relationships with the three enamel variables (Table 5). For example, interbirth interval is the number one predictor of DSR whereas birthrate is penultimate. For CFI, the situation is reversed, with birthrate as the number one predictor, and interbirth interval having the lowest correlation. EFF angle shows a similar degree of disagreement among these maternal investment variables. Lastly, while weaning age is a good predictor for DSR (only fourth in importance for EFF angle), it is difficult to interpret the significance of this since weaning age is related to other hypotheses as well.

For DSR, the maternal investment hypothesis has the strongest support, followed by risk aversion and foraging independence. However, the foraging independence variables exhibit the steepest slopes for DSR, suggesting that they may be powerful drivers of evolution in secretion rate as well (even though the relationship is positive, contrary to predictions). For EFF angle and CFI, foraging independence variables exhibit the strongest correlations, with maternal investment variables playing a lesser role and risk aversion having the least predictive power overall. However, it is important to note that all regressions of CFI exhibit slope values which are very close to zero (Table 5). This suggests that caution is warranted in making evolutionary/adaptive connections based on CFI data. Therefore, we base our interpretations primarily upon EFF angle and DSR analyses.

DISCUSSION

Our results support those of prior eruption-based analyses, indicating that brain mass has a stronger relationship with dental development than body mass (e.g., Smith, 1989; Smith et al., 1994; Godfrey et al., 2001). However, in each analysis we conducted, brain mass shows weaker relationships with enamel growth than one or more of the ecological variables. Therefore, we agree with Godfrey et al. (2001, 2003, 2006) that brain mass does not completely explain dental ontogeny on its own, and that ecology also plays an important role. In the case of enamel growth rates, in fact, our results suggest that ecological factors have a more important role in enamel growth than in tooth eruption (e.g., Godfrey et al., 2001), at least in the cebids.

The implications of this difference are not immediately clear. One possible explanation is that enamel growth rates and tooth eruption schedules are under the control of differing physiological systems and subject to different selective forces/constraints. In this case, it may be that dentine, which comprises the bulk of primate tooth crowns and roots, is a more appropriate factor to analyze. It is also possible that differences in the methods of controlling for phylogeny between our study and that of

Godfrey et al. (2001) are responsible for the disparate results between the two studies, since a similar analysis of cebids conducted without phylogenetic controls found a stronger effect for brain mass on DSR and EFF angle than all three ecological hypotheses (Hogg, 2010). Lastly, the cebids may exhibit a different pattern that is obscured when the primate order as a whole is sampled. This may be an artifact of taxonomic sampling at a lower level or an actual consequence of biological differences concerning the radiation of cebids.

With regard to the specific ecological factors, ultimately our results provide contrasting ontogenetic indications among the three enamel growth variables we examined. In turn, this contrast makes it difficult to parse out the differences among the three enamel variables. Overall, EQ is the strongest predictor variable for EFF angle and CFI (foraging independence hypothesis), whereas interbirth interval (maternal investment hypothesis) is the strongest predictor of DSR. Since enamel extension rate is biologically more important than DSR for determining the overall time it takes to form a functional tooth, we feel EFF angle is a more important indicator of overall ecological impacts upon tooth ontogeny (Shellis, 1984; see also, e.g., Godfrey et al., 2006; Dirks et al., 2009). Since our EFF angle results are also directly in line with results of prior studies based on tooth eruption and crown formation time data (Godfrey et al., 2001, 2003, 2006; Schwartz et al., 2002; Catlett et al., 2010), overall the evidence suggests that foraging independence may have a more important role than maternal investment or risk aversion. Since species should be timing their dental growth to correspond with the age at which they will need to fully rely upon their teeth (i.e., without the supplement of milk), the support for the foraging independence hypothesis makes sense. Nevertheless, since maternal investment and risk aversion do receive some statistical support in our analyses, we do not believe that they can be overlooked as contributing factors to dental ontogeny. Based on our data, we favor an overarching model in which all three ecological factors interact to drive enamel growth rates. Within this model, age at foraging independence may serve as the subcomponent which is most directly reflected in enamel growth and dental eruption.

The conflicting results among the three enamel growth variables examined here may also result from several other factors, which are not necessarily mutually exclusive. As one possibility, there may not be enough life history, ecological, or dental growth rate variability within the extant Cebidae to provide a clear resolution as to which specific ecological factors have the greatest relationship with the evolution of enamel growth, regardless of the fact that this group was specifically chosen because of its diversity. As mentioned above for brain and body mass, a second possibility is that the epigenetic mechanisms governing DSR versus enamel extension (as quantified by EFF angles) are subject to different constraints and/or selective factors, such that the activity of individual enamel-secreting cells (i.e., DSR) and the number of actively secreting cells (i.e., enamel extension rate) exhibit divergent relationships with the variables examined here. Third, the combination of enamel growth, dentine growth, and periodontal activity, as they contribute to overall tooth eruption, may exhibit different patterns than enamel examined in isolation. This may be why our moderate statistical support for the risk aversion hypothesis contrasts the lack of statistical support seen in Godfrey et al. (2001). These latter two ideas are further supported by the lack of a strong correlation between DSR and EFF angles among cebids (Hogg, 2010).

Another possible cause for the conflicting statistical relationships is that our three ecological hypotheses are too inherently interwoven to parse out any one as an obviously dominant factor affecting enamel growth rates. In other words, it is difficult to separate maternal investment entirely from foraging independence, as the two should be closely related. Foraging independence is in part a consequence of the timing of maternal resource investment, in that foraging independence occurs as maternal resources are increasingly shifted away from individual offspring (Nicolson, 1987; Garber and Leigh, 1997; Lee, 1999). Therefore, with all else being equal, species that attain foraging independence at younger ages should also exhibit relatively reduced maternal investment. Likewise, maternal investment and age at foraging independence should be somewhat correlated with the degree of malnutrition risk of juveniles, as this risk is strongly correlated to the somatic growth patterns of both platyrrhines and catarrhines (Janson and van Schaik, 1993; Leigh, 1994). This is due to the fact that mothers may be somewhat more immune to fluctuations in resource availability than infants and juveniles, and therefore prolonged maternal investment could serve as a buffer against environmental stresses. If this is true, it may be better to consider the effects of an overall, integrative ecological strategy upon evolution in dental growth, rather than attempting to isolate the effects of individual subunits within that strategy.

It is also important to reiterate that DSR and enamel extension exhibit opposite relationships to one another with respect to all variables analyzed here. The rate at which individual cells lay down enamel increases with higher values of all predictor variables except birth rate, whereas enamel extension rate decreases for these same predictor values (again, except for birth rate). The DSR patterns here are particularly surprising given that, based on prior studies, we anticipated it would have a weaker interaction with our predictor variables than EFF angles, rather than the opposite pattern which resulted. Based on DSR data for elephantoids (Dirks et al., 2010), in fact, one would predict that DSR has no important relationship with brain or body mass, as both large and small elephant species exhibit similar DSRs. Overall, this evidence suggests that the physiological and epigenetic mechanisms driving these two components of enamel growth are at least partly divergent, increasing the possibility that selection might act differently upon each of these two variables. The differences between platyrrhine and elephantoid data also suggest that DSR and its response to selection may be heavily impacted by phylogeny.

Ultimately, a much broader platyrrhine and primate sampling of DSR and EFF angle are needed to address these distinct possibilities. Larger samples would negate limitations regarding the potentially narrow diversity seen within the Cebidae, and would also allow for multivariate analyses to be conducted with confidence. Therefore, while we do find evidence that dental tissue growth may be more impacted by ecological factors and that this

may underlie differences seen between strepsirhines and anthropoids in prior studies (e.g., Schwartz et al. 2002, 2007; Godfrey et al. 2003, 2004, 2005, 2006; Catlett et al. 2010), this must remain a cautious interpretation.

Within the overarching ecological framework suggested by our data as well as that of prior studies (e.g., Godfrey et al., 2001, 2006; Catlett et al., 2010), Cebidae provides an excellent example of the interactions among brain mass, foraging independence, and maternal investment within primates, with regard to *Cebus*. *Cebus* has been identified as the third most encephalized extant primate genus after *Homo* and *Pan* (e.g., Martin, 1990). With regard to weaning age, *Cebus*, in comparison to all of its extant cebid relatives, seems to have extended its juvenile period to a pronounced degree (Table 2). As an extractive forager and omnivore which is known to use tools to access foodstuffs, *Cebus* seems to have adapted to a foraging regime that is cognitively complex (e.g., Visalberghi, 1987; Fragaszy et al., 1990, 2004; Janson and Boinski, 1992; Rosenberger, 1992; Fragaszy and Boinski, 1995; Fragaszy and Bard, 1997; Visalberghi and McGrew, 1997). The lengthened juvenile period and increased maternal investment of *Cebus*, therefore, seems to be a life history adaptation which is most likely related to this cognitive complexity and demand for prolonged learning (e.g., Gibson, 1986; Dunbar, 1992, 1995; Byrne, 1995; Joffe, 1997; Ross and Jones, 1999; Godfrey et al., 2001). Accordingly, *Cebus* juveniles seem to have not only delayed eruption relative to the smaller extant cebids (Smith, 1989; Smith et al., 1994; Godfrey et al., 2001), they also have overall "slower" physiologies underlying tooth growth as evidenced in this study.

In contrast to *Cebus*, *Alouatta,* a relatively less-encephalized (Table 2) and more folivorous platyrrhine genus (e.g. Hladik and Hladik, 1969; Milton, 1980; Rosenberger and Strier, 1989; Ford and Davis, 1992; Strier, 1992), exhibits somewhat faster dental growth rates when using EFF angle as the standard measurement. Considering the larger body size of *Alouatta* as well as its lower EQ (see Table 2; see also Ford and Davis, 1992; Rosenberger, 1992), this genus also fits well within the ecological predictions. Moreover, *Saimiri,* as a relatively encephalized sister-taxon of *Cebus,* also exhibits slower growth rates relative to its similarly sized but less-encephalized callitrichine relatives. If increased encephalization is a synapomorphy for Cebinae as postulated by Tejedor et al. (2006), this would suggest that more primitive cebines such as the fossil *Killikaike* may have also exhibited delayed foraging independence, increased maternal investment, and decreased dental growth rates relative to their less encephalized ancestors.

To summarize, our results agree with prior studies in suggesting that brain mass has a greater statistical impact upon dental ontogeny than body mass, and that foraging independence seems to have a strong correlation with dental ontogeny as well. However, unlike prior studies based on tooth eruption, we show that ecological forces seem to affect enamel growth rates even more than brain mass does. There is a complex interaction between the specific ecological variables and the components of enamel growth rates. These differences suggest that more inclusive, overarching ecological models may better explain patterns seen in the evolution of dental ontogeny within primates. Larger samples targeting more primate taxa are needed to better assess the subtle differences among the hypotheses emerging from this study. Such work is also necessary to determine whether the conflicts seen between the results of our study and those of Godfrey et al. (2001) are based more on inherent biological differences between tooth eruption and enamel growth rates, or taxonomic sampling.

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