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Hormonal and Morphological Aspects of Growth and Sexual Maturation in Wild-Caught Male Vervet Monkeys (Chlorocebus aethiops pygerythrus)

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HORMONAL AND MORPHOLOGICAL ASPECTS OF GROWTH AND SEXUAL MATURATION IN WILD-CAUGHT MALE VERVET MONKEYS (CHLOROCEBUS AETHIOPS PYGERYTHRUS)

by

Tegan J. Gaetano

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ABSTRACT
ENDOCRINE AND MORPHOLOGICAL ASPECTS OF GROWTH AND SEXUAL MATURATION IN WILD-CAUGHT MALE VERVET MONKEYS (CHLOROCEBUS AETHIOPS PYGERYTHRUS)

by

Tegan J. Gaetano

The University of Wisconsin at Milwaukee, 2012
Under the Supervision of Dr. Trudy R. Turner

Knowledge of baseline changes in testosterone (T) and other androgens is central to both investigations of morphological, physiological, and behavioral correlates of inter-individual variation in the timing and shape of key events and transitions over the life course and questions of the evolution of species-specific schedules of maturation in primates. T represents an important determinant of spermatogenesis in male mammals and plays a central role in the expression of male sexual behavior and the development of secondary sex characteristics. This research integrates hormonal and morphometric methods to determine age-related changes in fecal testosterone (fT) metabolites and morphological markers of sexual maturation, including testicular volume, body mass (measured as BMI), and canine length, over the life course in a cross-sectional sample (n = 56) of wild-caught South African male vervet monkeys (*Chlorocebus aethiops pygerythrus*). Contrary to expectations of this study, T was not significantly associated with age (p = 0.1316 by ANOVA). However, BMI (p = 0.00022) and testis volume (p = 4.335e-06) were strongly related to age, corresponding to the eruption of the canine teeth at adolescence (3-4 years of age). These results

strongly suggest the existence of an adolescent growth spurt in male vervets. An interpretation of activation of the development of these maturational markers in preparation for challenges encountered at reproductive maturity, including dispersal and reproduction, is tentatively adopted here following Jolly and Phillips-Conroy (2003, 2006). However, future longitudinal observations to determine changes within individuals are necessary to provide greater confidence in this interpretation.

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I. INTRODUCTION

The concept of life history trade-offs has been instrumental to explanations of observed variation in the timing and shape of key events, transitions, and phases in the life course by providing a framework that considers all aspects of an organism. Life history theory describes differential strategies of allocation of resources among components of fitness (e.g. energy invested in survival versus reproduction) through the organizing principle of trade-offs. Trade-offs refers to the negative relationship between life history components and can be imagined as a series of facultative decisions as regards the allocation of energy to one aspect of the life course over another.

Delayed puberty and an extended period of pre-reproductive growth characteristic of the order Primates have resulted in selection for a distinct juvenile period. The juvenile period represents a trade-off between energy invested in somatic growth and survival and energy expended on reproduction. However, somatic growth and investment in the development of secondary sex characteristics (SSCs) may ultimately increase individual fitness by conferring a competitive advantage against conspecifics, either through agonistic competition or the attraction of mates (Charnov and Berrigan, 1993; Leigh and Blomquist, 2007). The transition from the pre-reproductive stage to reproductive maturity is associated with a shift in life history priorities and, accordingly, the uptake of a different fitness-maximizing strategy (reviewed in Pereira and Leigh, 2003). Thus, investigations of the timing of the expression of life history traits within an individual as well as differences in life history strategies between individuals are central to our understanding of the evolution of life history diversity.

Endocrine data have the potential to provide insight into the mechanisms regulating relationships among life history traits (Ketterson and Nolan, 1992; Whitten and Turner, 2009). Hormones act as intermediaries between the physical environment and the internal architecture of an organism, acting both at the level of genes and whole-body phenotypic traits in the regulation of transitions between life history stages (Ketterson and Nolan, 1992; Hau, 2007). Patterns of the secretion of gonadal steroid hormones, including testosterone (T), during development have been described for humans (e.g., Angsusingha *et al.*, 1974; Genazzani *et al.*, 1978; Apter, 1980; Sizonenko, 1989) and several primate taxa (e.g., McCann *et al.*, 1974; Styne and Grumbach, 1978; Castracane *et al.*, 1986; Crawford *et al.*, 1997), typically from captive populations. However, significant gaps remain in our knowledge of the mediating effects of steroid hormones on the timing and shape of life history events, particularly in ontogeny.

In male mammals, T is an important determinant of male reproductive function through its effects on the differentiation of the brain and gonads, the production of functioning gametes, the maintenance of accessory sex organs, and the expression of SSCs, such as body size and muscle mass dimorphism (reviewed in Wells, 2007), sexually-selected coloration of the pelage and dermis (e.g., Wickings and Dixson, 1992b; Setchell and Dixson, 2001; Waitt *et al.*, 2003), development of the vocal apparatus (e.g. Seyfarth and Cheney, 1997), and behaviors associated with competition for access to reproductively-viable females, including mate-guarding, aggression against conspecifics, and courtship (e.g., Bernstein *et al.*, 1979; Alberts *et al.*, 1992).

Knowledge of age-typical changes in T secretion in male primates is critical to investigations of the relationship between T and parameters of individual development, including variation in the timing of sexual maturity and patterns of SSC emergence, and questions of the evolution of species-specific schedules of growth and sexual maturation. Furthermore, the response of hormone systems to transitions in life history can be used to assess the influence of behavior and features of the external environment on the secretion of gonadal hormones.

This research integrates hormonal and morphometric methods to determine age-graded changes in T excretion and the development of morphological markers of sexual maturation body mass, testis volume, and canine length over the life course in a sample of wild-caught male South African vervet monkeys (*Chlorocebus aethiops pygerythrus*). Members of this subspecies are found throughout sub-Saharan Africa and are adapted to a wide range of environmental conditions. This adaptability decreases the likelihood that differences in the hormone profiles of sample animals are solely due to the effects of variable habitats. Fecal testosterone (fT) profiles were examined across three age classification schemas of increasing specificity in order to account for small hormonal and morphological changes that occur during puberty given the relatively rapid growth of the vervet monkey and to preserve statistical robusticity (Leigh, 1996).

The primary objective of this research was to characterize fT profiles of male vervets at each stage of the life cycle, contrasting adults and immatures to establish baseline patterns of growth and sexual maturation for the species. In this study, sexual maturation refers to changes in testicular volume, body mass (measured as BMI), and excreted levels of T and the eruption of the canine teeth that are associated with the adolescent stage of development. In male primates, these events have been interpreted to reflect a strategy of preparation for dispersal from the natal group, competition for a place in the dominance hierarchy of the adoptive troop, and ultimately, competition for reproductive opportunities (Jolly and Phillips-Conroy, 2003, 2006). In consideration of this interpretation, special attention was paid to changes occurring around the estimated age of reproductive maturity based on averages established on the basis of longitudinal behavioral studies (Horrocks, 1986; Cheney *et al.*, 1988).

To analyze fT profiles across life history stages, 56 fecal samples were collected from males of a wide age range across multiple, geographically distinct sites throughout central and southeastern South Africa and assayed for T metabolites using a method validated for vervet monkeys (Whitten *et al.*, 1998). fT profiles were compared across age classes and examined in relation to changes in testis volume, BMI, and canine length. This component was intended to provide a characterization of inter-individual differences in the relationship between excreted fT and the development of physical characteristics associated with male reproductive success. Parametric ANOVA and non-parametric Kruskal-Wallis tests were used to identify relationships among the data. Results of this research provide greater insight into how T is physiologically and morphologically expressed at different stages of the life cycle in male vervet monkeys. Knowledge of baseline changes in fT is important to both investigations of correlates of inter-individual variation in fT excretion and questions concerning the evolution of species-specific schedules of maturation in primates.

II. BACKGROUND

A. Vervet Monkey Phylogeny

Primates comprise one of 18 orders of extant placental (eutherian) mammals. With over 300 identified species (361 IUCN/SSC recognized species: Aguiar, 2010), the order Primates is one of the most speciose of the placental mammals (Groves, 2001, 2005a; Grubb *et al.*, 2003; Reeder *et al.*, 2007; Rylands and Mittermeier, 2009). The order (excluding tree-shrews) is generally acknowledged to contain six monophyletic superfamilies: Lemuroidea (Malagasy lemurs), Lorisoidea (Asian lorises, African galagos, and pottos), Tarsioidea (Indonesian and Philippine tarsiers), Ceboidea (New World monkeys), Cercopithecoidea (Old World monkeys), and Hominoidea (apes and humans) (Koop *et al.*, 1989). The group Cercopithecoidea is comprised of a single extant family, Cercopithecidae, and the extinct group Victoriapithecidae. Supported by genetic data (Zhang and Ryder, 1998) and corroborated with studies of morphology (Goodman *et al.*, 1998), the family Cercopithecidae has been determined to contain a single monophyly of two subfamilies: Colobinae (the leaf eating monkeys) and Cercopithecinae (the cheek pouch monkeys) (Page *et al.*, 1999).

Members of the diverse subfamily Cercopithecinae, also called the "omnivore" Old World monkeys, are morphologically differentiated from the colobines on the basis of the following traits: flexible buccal pouches used to store food (Fig. 3), elongated nasal bones forming a long snout, broad incisors and molars with high crowns and low cusps, and a simple, non-ruminant gut (Fleagle, 1999; Groves, 2000). Two chromosomally differentiated tribes (modified from subfamily status by Groves, 2001) characterize the subfamily: Cercopithecini and Papionini. The Papionine group, which is characterized by a diploid chromosome count of 42, includes the widely-distributed genus *Macaca* (macaques) and the African – with the exception of one species of *Papio* found in the Arabian Peninsula – papionines: *Mandrillus* (drills and mandrills), *Cercocebus* (terrestrial mangabeys), *Lophocebus* (arboreal mangabeys), *Papio* (savannah baboons), and *Theropithecus* (gelada baboons). Although some arrangements place *Lophocebus* as a subgenus of *Cercocebus* (Page *et al.*, 1999), recent chromosomal analyses of the tribe have strongly suggested a paraphyletic relationship between the two mangabey taxa, with *Cercocebus* forming a clade with *Mandrillus* and *Lophocebus* as the sister-taxon of the *Papio-Theropithecus* grouping (Disotell *et al.*, 1992; Disotell, 1996, 2000; Harris and Disotell, 1998). Further divisions of Papionini separate *Macaca* (subtribe Macacina) from all other papionines (subtribe Papionina) (Szalay and Delson, 1979).

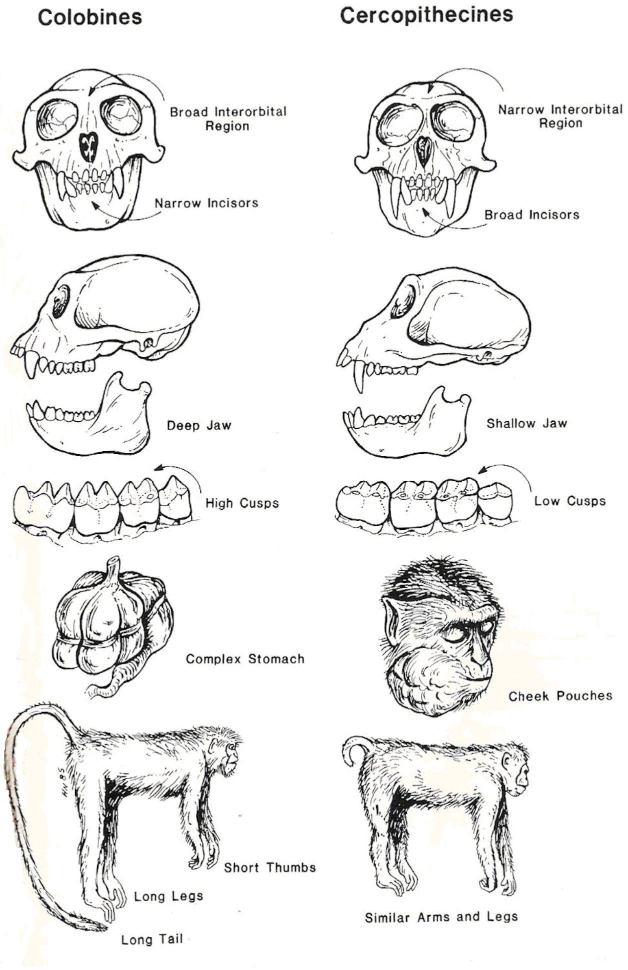


Fig. 1. Distinctive morphological traits separating the Old World monkey subfamilies Colobinae and Cercopithecinae. (Taken from Fleagle, 1999).

The tribe Cercopithecini hosts a rich diversity of morphological and behavioral forms, making defining tribe membership particularly difficult. Because of this, workers are increasingly turning to molecular characters to distinguish this group from the papionines (e.g., Dutrillaux *et al.,* 1988; Ruvolo, 1988; Turner *et al.,* 1988; Page *et al.,* 1999; Disotell and Raaum, 2002; Tosi *et al.,* 2002a; Moulin *et al.,* 2008). For example, unlike members of the tribe Papionini, the cercopithecines vary considerably in diploid chromosome count;

however, this number is always over 42 (Butynski, 2004). Morphologically, the cercopithecines are differentiated from members of Papionini by the presence of a four-cusped third, mandibular molar without a hypoconulid (Butynski, 2004).

The cercopithecines include: *Allenopithecus* (Allen's swamp monkeys), *Miopithecus* (talapoin monkeys), *Erythrocebus* (patas monkeys), *Cercopithecus* (the guenons), and the newly revived genus *Chlorocebus* (vervet or green monkeys). Although basally positioned in the tribe Cercopithecini on the basis of chromosomal (Dutrillaux *et al.,* 1988, Tosi *et al.,* 2002a) and protein DNA (Ruvolo, 1988) data, the genus-groups *Allenopithecus* and *Miopithecus* have been argued to represent members of the tribe Papionini on the basis of papionine-like cyclical sexual swellings in females, facial gestures, and social behavior (Groves, 1989, 2000; Disotell, 2000). More recent Y-chromosome and mtDNA sequence studies have indicated *Allenopithecus* as the sister-taxon of all other members of the tribe Cercopithecini (Tosi *et al.,* 2002a, 2002b; Disotell and Raaum, 2002). Furthermore, Y chromosome and karyotic studies have both suggested that the terrestrial cercopithecines – *Erythrocebus*, *Chlorocebus*, and sometimes *Cercopithecus lhoesti* – form a paraphyletic clade rooted by *Allenopithecus* and separated from the arboreal cercopithecines by a single evolutionary transition (Tosi *et al.,* 2002a, 2002b; Perelman *et al.*, 2011).

The most recent tabulations indicate between 19 (Grubb *et al.,* 2003) and 24 (Groves, 2001, 2005a) subspecies of *Cercopithecus*. Variations in the number of guenon species acknowledged in the literature are largely dependent on whether the author classifies the vervet monkey under the genus designation

Cercopithecus or *Chlorocebus*. The name *Chlorocebus* was separated from the "true *Cercopithecus*" clade by Groves (1989, 2000) on the basis of synapomorphic craniodental traits shared with *Erythrocebus*, including angular shape of the orbits, the inferior margin of the zygomata curved down rather than straight, and the upper incisors form a straight rather than sloped bite. This taxonomic distinction was further supported by Y-chromosome data in Tosi *et al.* (2002b, 2003).

Due, at least in part, to the considerable phenotypic diversity of this genus across their wide geographic distribution, the exact number of species or subspecies represented in *Chlorocebus* remains unresolved. Broadly, the number of taxonomically-distinct groups acknowledged in the literature varies according to whether the taxon is assessed according to morphological – including pelage and whisker color (see Table 1) – or genetic traits. For example, on the basis of variation in cranial morphology across ecogeographic clines, Cardini and Elton (2008) and Elton *et al.* (2010) argued the species *Cercopithecus aethiops* to contain six geographically-distinguished subspecies corresponding to the species groups recognized in Groves (2001, 2005a). By contrast, genetic studies indicate little genetic variation within the genus as a whole (Turner, 1977, 1981) and between populations inhabiting South Africa in particular (Grobler and Matlala, 2002; Grobler *et al.*, 2006; McAuliffe Dore, 2008), putting to question the robustness of species and subspecies distinctions made on the basis of color and size differences alone.

Grubb *et al.* (2003) following Napier (1981) considered the *C. aethiops* group – included in the *Cercopithecus* clade – to consist of one polytypic species, partly because Struhsaker (1970) was unable to determine differences in the vocalizations of populations of vervet (*C. aethiops*) and tantalus (*C. tantalus*) monkeys. According to Grubb *et al.* (2003) the group contains six subspecies: *C. aethiops* (grivet monkeys), *C. sabaeus* (green monkeys), *C. tantalus* (tantalus monkeys), *C. djamdjamensis* (Bale Moutains monkeys), *C. pygerythrus* (vervet monkeys), and *C. cynosuros* (Malbrouck monkeys). Each of these was elevated to species status by Groves (2001, 2005a) following Dandelot (1959, 1974). The most recent IUCN/SSC assessment of the taxa in 2008 followed Groves's (2001, 2005a) suggestion for the taxa, recognizing the genus name *Chlorocebus* as well as all six species.

This paper follows the taxonomy established by Groves (1989, 2000, 2001, 2005a) with modifications from Perelman *et al.* (2011) who sequenced 34,927 DNA base pairs to produce the most comprehensive molecular phylogenetic tree of the primates to date (see Fig. 2). Six subspecies – the six species recognized in Groves (2001, 2005a) are lowered to subspecies rank – are recognized for the species *Chlorocebus aethiops* in this paper on the basis of findings of molecular studies (Turner, 1977, 1981; Grobler and Matlala, 2002; Tosi *et al.*, 2002a, 2002b, 2003; Grobler *et al.*, 2006; Jasinska *et al.*, 2007; McAuliffe Dore, 2008; Perelman *et al.*, 2011). Collaboration of molecular and anatomical techniques may provide greater insight into the evolutionary relationship between members of *Chlorocebus* and the other primates.

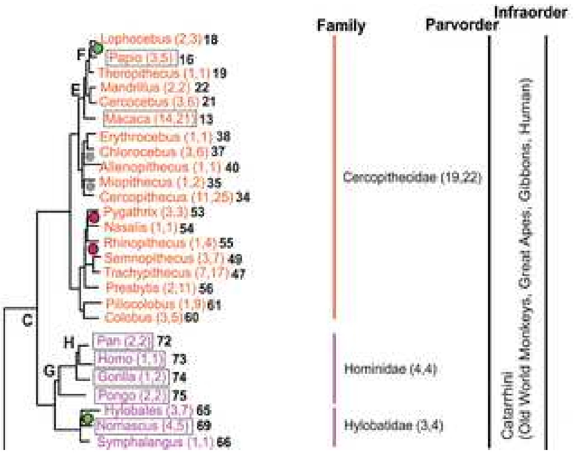


Fig. 2. Molecular phylogeny of the parvorder catarrhini based on 34,927 bp sequenced from 54 genes. (Modified from Perelman *et al.*, 2011).

Pelage color and length varies widely across the full distribution of the species, with regional patterns distinguishing the subspecies (see Fig. 4). These variations have led some authors to split the taxon into distinct species groups (e.g., Dandelot, 1959, 1974; Hill, 1966; Napier and Napier, 1967; Groves, 2001, 2005a). In particular, the distinctive features of the Bale Mountain monkey (*Ch. a. djamdjamensis*), including morphological adaptations for life at high altitudes, have propelled some authors to argue for species status (Groves, 2005a). However, because of the inability of genetics studies to detect significant variations between populations (e.g., Turner, 1977, 1981; Grobler *et al.,* 2006; McAuliffe Dore, 2008) the taxon is considered one highly polymorphic species with regional subspecies designations in this work. A full description of subspecies pelage differences is provided in Table 1.

B. Vervet Monkey Behavior and Ecology

i. Description

Table 1. Summary of pelage color variations taken to distinguish subspecies of *Chlorocebus aethiops* with notes on geographic distribution.

Subspecies	**Geographic Location**	**Pelage Color Distinctions**
Green monkey (*Ch. a. sabaeus*) *°	Distributed from Senegal and Guinea-Bissau in the west to west of the Volta River System in Ghana. The subspecies has been introduced to Barbados and St. Kitts in the Caribbean.	Sooty black framed by yellow whiskers and a bib of longer, reddish-yellow hairs. The dorsal body is bicolored, greenish-brown and yellow, with a yellow tail tip and pale feet. Unlike all other members of the species, *C. a. sabaeus* lacks the band of whitish hairs on the brow. Males have a pale blue scrotum.
Tantalus monkey (*Ch. a. tantalus*)*°	Ranges east of the Volta River system in Ghana eastwards to the Sudan, Uganda, and the Lake Turkana District of Kenya.	Black face rimmed by long whitish hairs brushed up to conceal the ears. A white brow band is separated from whiskers by a band of black hairs on the temporal bar. An olive dorsal body with a white caudal tuft, pale feet and a white tail tip. Males have a sky blue scrotum.
Vervet monkey (*Ch. a. pygerythrus)*†§*°	Distributed from the Ethiopian Rift Valley, highlands east of the rift, and southern Somalia in the north to the eastern lowlands of Ethiopia Kenya, Tanzania, Uganda, Zambia, Malawi, Mozambique, Botswana, and South Africa in the south.	Grayish-yellow hairs on the dorsal body, extending to the tail, with a black tail tip. Short black hairs cover the face, framed by a bonnet of long, white hairs extending down the throat and along the belly. Members of this subspecies are distinguished by a red subcaudal patch. Males have a turquoise blue scrotum.
Grivet monkey (*Ch. a. aethiops*)‡*°	Distributed in the Sudan from Khartoum in the north to Mongalla in the south and in Djibouti, Ethiopia, and Eritrea as far south as the south Banks of the River Omo and as far east as the Ethiopian Rift Valley.	Pale grayish-olive hairs dorsally, with elongated white whiskers and a white moustache framing a sooty black face. A white frontal brow band separates the shorter shairs of the face from the longer hairs of the head and body. Members of this subspecies have a white caudal tuft and a tan tail tip. Males have a sky blue scrotum.
Malbrouk monkey (*Ch. a. cynosuros*)*°	Ranges from southern Democratic Republic of the Congo southwards to northern Namibia and to the Luangwa River Valley, Zambia, west of the Luangwa River.	Short white hairs form a bonnet around a slightly depigmented face with bald rings around the eyes and extend down the breast and ventral body. Short grayish-olive hairs cover the dorsal body and the head, leaving the ears exposed. Members of this subspecies have a red subcaudal patch and sooty hands and feet. Males have an azure blue scrotum.
Bale Mountains monkey (*Ch. a. djamdjamensis*)‡¤°	Distributed throughout the highlands of Ethiopia, east of the Ethiopian Rift Valley in the Bale Mountains.	Members of this subspecies have longer, brownish-russet hairs covering the dorsal body with shorter whiskers and a shorter, black-tipped tail. A beard of long white hairs rims a black face with only a faint, white brow band separating the face from the dorsal hairs. Males have a pale blue scrotum.

* Turner, 1977 (based on Hill, 1966); † Kingdon, 1988; ‡ Lernould, 1988; § Skinner and Chimimba, 2005; ¤ Cawthon Lang, 2006; ° Groves, 2005b

Compared with other semi-terrestrial members of Cercopithecinae occupying open habitats (e.g., *Papio*, *Mandrillus*, *Theropithecus*, *Erythrocebus*), vervet monkeys are small and only moderately sexually dimorphic in body size, with an average adult female weight of 3.55 kg to the male's 5.19 kg (calculated as the average of nine mean body weights from captive and wild studies reviewed in Turner *et al.*, 1994). Members of both sexes have a yellow to greenish-brown dorsal coat with long, white hair on the ventral body and a band of white hair on the brow and along the cheeks, framing a sooty black face (with the exception of the pale-faced *Ch. a. cynosuros*) (Groves, 2001; Cawthon Lang, 2006). The skin of the hands and feet is black or mottled black and pale. Infants are born with a black natal coat and pinkish skin on the face, hands and feet. Adult coloration is gradually acquired by 12 weeks of age (Lee, 1984a). Both males and females of the species have eggshell blue abdominal skin, which is most visible in the adult male scrotum (Chiarelli, 1972). Males have colorful genitalia consisting of a sky blue scrotum and a red penis and perianus surrounded by long, white hairs. These sexually-selected features are exposed during male-male dominance displays and are commonly referred to in the literature as the "red, white and blue display" (Struhsaker, 1967a; Durham, 1969).

Experimental manipulations of male scrotal color in captive populations have demonstrated a link between color saturation and male-male aggression. In a series of studies, Gerald (1999, 2001) found that males with similar scrotal color exhibited greater aggression towards one another than males with different scrotal color. Furthermore, male scrotal color has been shown to be positively related to testes volume in *Ch. a. pygerythrus*, suggesting that this trait may be related to sperm competition (Danzy *et al.*, 2011, *in prep.*). Recent reports of increasing scrotal albinism among island populations of *Ch. a. sabaeus*, however, suggest a reduction in the sexual significance of these traits in this subspecies (Gerald *et al.*, 2010). The cause of this variation between subspecies is unknown.

Vervets are primarily quadrupedal and are specialized for terrestrial running, which accounts for approximately 20% of locomotion, and arboreal climbing and jumping (Chiarelli, 1972; Fleagle, 1999). Compared with the almost exclusively arboreal guenons, the vervet monkey has developed anatomical adaptations (e.g., greater forearm, hand [males only], foot and tail lengths) suited for mosaic habitats requiring terrestrial as well as arboreal locomotion (Anapol *et al.*, 2005). These adaptations are argued to have, at least in part, permitted the vervet monkey to survive, and even thrive, in heavily human-disturbed habitats, such as those characteristic of the Cape Verde and Caribbean islands (Boulton *et al.*, 1996).

The maximum lifespan of vervet monkeys in the wild is unknown due to high incidence of predation but they are known to live between 11 and 13 years in captivity (Fairbanks and McGuire, 1986; Cawthon Lang, 2006). Vervets are preyed upon by a number of species in the wild, including baboons (*Papio spp*.); leopards (*Panthera pardus*) and other felids, including caracals (*Caracal melanotis*), servals (*Felis serval*), lions (*Panthera leo*), and African wild cats (*Felis silvestris*); hyenas (*Crocuta spp.*); jackals (*Canis mesomelas* and *C. adustus*); and raptors, including Verreaux's eagle owl (*Bubo lacteus*), martial eagles (*Polemaetus bellicosus*), and crowned hawk-eagles (*Stephanoaetus coronatus*) (Struhsaker, 1967a; Isbell, 1990; Cawthon Lang, 2006). Venomous snakes, including Egyptian cobras (*Naja haje*) and puff-adders (*Bitis arietans*), are also a source of potential harm to unwary vervets (Struhsaker, 1967a). On the islands of Barbados and St. Kitts and Nevis dogs, first introduced to the islands as pets, account for a considerable proportion of vervet injuries and deaths (Isbell and Enstam, 2002). However, of all of these, humans are perhaps their greatest threat. Vervets are actively hunted and eaten by non-Muslim human populations throughout their African distribution (Wolfheim, 1983). In other areas, vervets are considered agricultural pests and are exterminated both by private landowners and by government programs (Hey, 1967; Lee *et al.*, 1986).

ii. Diet and Distribution

Geographic Distribution and Habitat

Vervets are the most abundant of the cercopithecine monkeys and are widely distributed across the savannas and riverine forests of sub-Saharan Africa, from Senegal in the west to Somalia in the east and from the southern border of the Sahara Desert to the southernmost point of South Africa, with the notable exceptions of the Namib Desert of southern Africa and the dense rain forests of the West African countries of Nigeria, Cameroon, Gabon, Congo and the Democratic Republic of the Congo (Table 1, Fig. 3) (Struhsaker, 1967a; Fedigan and Fedigan, 1988; Enstam and Isbell, 2007). In the mid-17th century populations of *Ch. a. sabaeus* from West Africa were introduced to the islands of the

Republic of Cape Verde off the coast of Senegal and the Caribbean islands of Barbados and St. Kitts and Nevis (Horrocks, 1986).

Persistent zones of hybridization exist between most subspecies of *Ch. aethiops* (see Detwiler *et al.*, 2005 for a comprehensive survey of hybrid zones) (e.g., *Ch. a. tantalus* x *Ch. a. pygerythrus* along the western shores of Lake Abaya, Ethiopia and parts of Congo-Kinshasa [Dandelot, 1959; Dandelot and Prevost, 1972; Lernould, 1988; Groves, 2001], *Ch. a. aethiops* x *Ch. a. pygerythrus* in Ethiopia [Dandelot and Prevost, 1972; Grubb *et al.*, 2003], and *Ch. a. djamdjamensis* x *Ch. a. aethiops* x *Ch. a. pygerythrus* x *Ch. a. tantalus* from southwest Uganda to western Ethiopia [Napier, 1981; Kingdon, 1997]), with the exception of island populations of *Ch. a. sabaeus* on the Cape Verde and Caribbean islands, *Ch. a. sabaeus* x *Ch. a. tantalus* (Turner, 1977), and *Ch. a. cynosuros*. Additionally, hybrids of *Ch. a. pygerythrus* and the guenon species *Cercopithecus mitis* have been recorded at Ngong Forest Sanctuary and Diani Forest in southern Kenya (De Jong and Butynski, 2010).

Although vervet monkeys have a relatively broad environmental tolerance, inhabiting such disparate biotic zones as tropical rain forest, lowland evergreen forest, montane evergreen forest, thorn forest, scrub and the Mediterranean evergreen vegetation of parts of South Africa (Gartlan and Brain, 1968) and able to tolerate temperature lows from -4°C at the tip of South Africa to highs up to 33.7°C in Cameroon, 40°C in Senegal and 50°C in Ethiopia (Nakagawa, 1999), they typically prefer drier habitats than their guenon relatives and primarily woodland savannas and gallery forests along rivers and other water courses

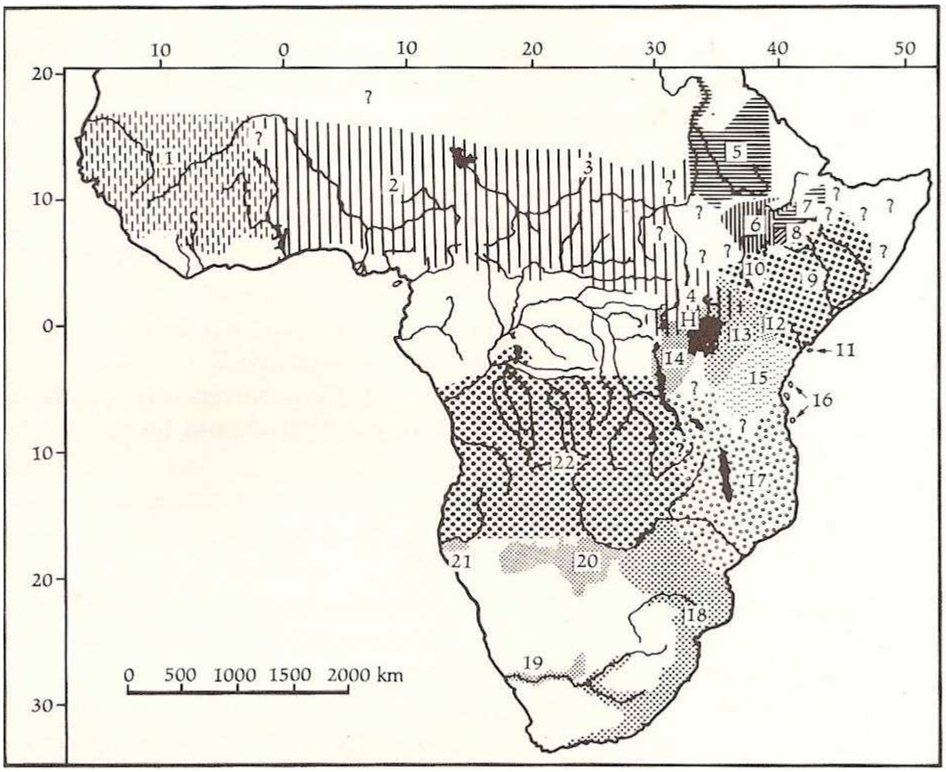


Fig. 3. Continental map of Africa with known distribution of *Ch. aethiops* subspecies: (1) *Ch. a. sabaeus*, (2) *Ch. a. tantalus tantalus*, (3) *Ch. a. t. marrensis*, (4) *Ch. a. t. dugetti*, (5) *Ch. a. aethiops*, (6) *Ch. a. a. matschiei*, (7) *Ch. a. a. hilgerti*, (8) *Ch. a. djamdjamensis*, (9) *Ch. a. pygerythrus arenarius*, (10) *Ch. a. p. zavattarii*, (11) *Ch. a. p. excubitor*, (12) *Ch. a. p. rubella*, (13) *Ch. a. p. callidus*, (14) *Ch. a. p. centralis*, (15) *Ch. a. p. johnstoni*, (16) *Ch. a. p. nesiotes*, (17) *Ch. a. p. rufoviridis*, (18) *Ch. a. p. pygerythrus*, (19) *Ch. a. p. marjoriae*, (20) *Ch. a. p. ngamiensis*, (21) *Ch. a. p. helvescens*, (22) *Ch. a. cynoruos*, zone of hybridization (H). (Taken from Lernould, 1988).

(Fleagle, 1999; Skinner and Chimimba, 2005). Also unlike the guenons, vervets do not occupy forests homogenously; rather, they maximize fringe resources between dense forests and open savanna grasslands (Gartlan and Brain, 1968). Vervets have also been observed to colonize resource-poor habitats, such as the mangrove swamps of West Africa (Zinner *et al.,* 2002) and those disturbed by human activity (Lee *et al.*, 1986).

Diet

Like all other members of the subfamily Cercopithecinae, vervets are distinguished from the African Colobinae by morphological adaptations for a predominantly frugivorous diet (e.g., flexible cheek pouches; molars with high crowns and low, rounded cusps; and a simple, non-ruminant gut) (Fleagle, 1999; Groves, 2000; Enstam and Isbell, 2007). Like the forest guenons, vervets regularly consume invertebrates, flowers, fruit, seeds, leaves and tree gum and are known to eat bark, grass and the stems, pith and swollen thorns of the angiosperm *Acacia* spp. (Kavanagh, 1978; Wrangham and Waterman, 1981; Whitten, 1983; Isbell *et al.*, 1998; Enstam and Isbell, 2007). However, unlike the guenons, flowers (up to 50%) and even tree gum (up to 60%) have been demonstrated to constitute greater proportions of the annual diet of the vervet monkey than fruit (see Table 2), leading some writers to suggest that vervets are more accurately described as nectivores or florivores (Whitten, 1988).

However, as illustrated in Table 2, the reliance of vervets on particular food items fluctuates greatly across study sites and seasons. For example, Barrett (2009) found that the variable climate of northern South Africa produced markedly different vervet diet profiles between the wet and dry seasons (see Table 2). Moreover, during the lean months of the dry season vervets have been observed to engage in more crop and food-raiding foraging strategies (Saj *et al.*, 1999). The search for easily accessible food and water during the dry season has led vervets to utilize human-occupied areas and has resulted in considerable conflict between humans and vervets (e.g., Brennan *et al.,* 1985; Boulton *et al.,* 1996; Saj *et al.,* 2001; McDougall, *et al.*, 2010; McAuliffe Dore, *in prep.*).

The ability of vervets to modify their diet to maximize the resources of the various habitats they occupy, including disturbed areas of secondary growth, has earned them such titles as “opportunistic omnivore” and “eclectic feeder” and is partly responsible for the widespread success of the species (Struhsaker, 1969; Kavanagh, 1978; Lee *et al.,* 1986; Gautier-Hion, 1988; Estes, 1991). Much like the macaques of India, Japan, Singapore, and elsewhere (e.g., Fuentes *et al.,* 2007, 2008; Hsu and Kao, 2009), vervets successfully exploit heavily human-modified habitats such as tourist centers and urban parks (Fedigan and Fedigan, 1988). Human foods tend to be easily digested and energy-rich compared with the protein-rich and fibrous mature leaves available during the dry season (Quick, 1986) and regular intake of human foods has been shown to be associated with higher average BMIs in vervets (Pampush, 2010). The ability of vervets to adapt to a wide range of environments is perhaps best illustrated by the overwhelming success of vervets on the Caribbean islands of Barbados and St. Kitts and Nevis compared with the failed introduction of the arboreal guenon *Cercopithecus mona* to the island of Grenada, West Indies, 200-300 years ago (Fedigan and Fedigan, 1988; Glenn, 1997). Moreover, prolonged contact with humans has been demonstrated to have a profound effect on the acquisition of technical skills by vervets, such as operating door and window latches (e.g. Van De Waal and Bshary, 2010).

Vervets forage for food in small groups during the day, exploiting open savanna and human-populated areas, and retreat to designated sleeping trees at the edges of riparian forest at night (Harrison, 1983; Fedigan and Fedigan, 1988). In response to periods of resource scarcity and temperature extremes during the annual dry season, vervets modify foraging behaviors, spending more time foraging in groups for uncommon foods; ranging patterns, conserving energy when food is sparse and expending energy when greater returns are expected; and defense of home ranges (i.e. degree of territoriality) (Kavanagh, 1978; Harrison, 1983, 1984; Fedigan and Fedigan, 1988; Lee and Hauser, 1998). Priority of access to clumped food resources (e.g. the new leaves, gum and flowers of *Acacia tortilis*, *A. xanthophloea*, and *A. elatior*) is awarded according to hierarchical rank, with high ranking females spending greater amounts of time eating these foods than low ranking females (Whitten, 1983). It has been suggested that the consumption of these foods is positively correlated with reproductive success in female vervets (Whitten, 1983), perhaps due to antibiotic properties (including condensed tannins) of *Acacia spp*. (Wrangham and Waterman, 1981).

iii. Social Organization

Group Composition, Ranging, and Territoriality

Vervets live in relatively stable multi-male, multi-female social groups varying in size from as few as two adults and accompanying dependents (Isbell *et al.*, 1991) to up to 140 individuals (Kavanagh, 1981; Isbell and Young, 1993), with a mean

Table 2. Summary of average group sizes, home range sizes and proportion of food items in the vervet diet provided in a sample of long-term studies.

Average Group Size	**Home Range Size (HA)**	**Diet***						
		% Leaves	**% Inverts**	**% Fruit**	**% Flowers**	**% Seeds**	**% Gum**	**Source**
18	102.5	5.1	28.7	26.83	4.3	1.0	2.2	Buffle Noir, Cameroon: Kavanagh, 1978, 1981
76	56.25	16.8	7.2	61.0	11.2	2.0	1.3	Kalamaloue National Park, Cameroon: Kavanagh, 1978, 1981
N/A	N/A	26.6	7.7	11.11	4.3	2.6	30.0	Amboseli National Park, Kenya: Wrangham and Waterman, 1981
37	N/A	0.0	N/A	5.18	41.17	22.25	N/A	Samburu-Isiolo Reserve, Kenya: Whitten, 1983, 1988
40	N/A	0.0	N/A	6.34	48.28	16.46	N/A	Samburu-Isiolo Reserve, Kenya: Whitten, 1983, 1988
18-28	178.0	7.0	11.0	50.0	14.0	13.0	2.5	Parc National du Niokolo-Koba, Senegal: Harrison, 1983, 1984
26-30	N/A	1.6-6.3	0.8-1.8	3.4-11.8	4.0-9.2	6.6-8.3	7.0-38.6	Segera Ranch, Kenya: Isbell *et al.*, 1998
8-10	N/A	0.0	0.6-8.3	2.2	0.6-5.9	6.6-12.1	56.8-62	Segera Ranch, Kenya: Isbell *et al.*, 1998
N/A	N/A	11	5	44	N/A	N/A	N/A	Palmiet Valley, KZN, South Africa: Harrison and Byrne, 2000†
N/A	37-76	1-2	2-3	20-35	2	2-6	0.5	Blydeberg Conservancy, South Africa: Barrett, 2009‡

* Percentages of total diet may not add up to 100% given omissions of other trace food items. Note that data may not be directly comparable given different methods used by the authors. N/A indicates that the author did not provide data for that value.

† This study also reported that 23% of the vervet diet comprised of sugarcane

‡ Differences between averages reported for home range size and diet composition in this study reflects seasonal variability. During the dry season vervets ranged an average of 76 ha in comparison to wet season average distance of 37 ha.

size of 25 (Struhsaker, 1967b; Fedigan and Fedigan, 1988). Although group sizes fluctuate greatly across habitats and seasons (Table 2), adult mean sex ratios remain fairly consistent at between 1.0 and 1.5 females to every male (Hall and Gartlan, 1965; Struhsaker, 1967a, 1967b; Horrocks, 1986; Fedigan and Fedigan, 1988). Unusual among most primates (and mammals in general), vervet males tolerate the presence of other, reproductively-active males year-round. Several explanations for this residence pattern have been proposed, including cooperative defense of food (Isbell *et al.*, 1991) or females (Wrangham, 1980; Andelman, 1986; Altmann, 1990; Mitani *et al.*, 1996), defense against predation threat (Van Schaik and Van Noordwijk, 1989; Baldellou and Henzi, 1992; Hill and Lee, 1998), and the size of the neocortex, which has been proposed to constrain group size by limiting the number of social relationships an individual is able to monitor (Dunbar, 1992, 1995; Dunbar and Schultz, 2007). However, the most convincing explanation, called the "limited dispersal hypothesis," suggests that the high costs of male dispersal across a highly variable landscape may favor the formation of multi-male groups (Isbell *et al.*, 2002; see *Dispersal*).

Following the hypothesis that primate group sizes and ranging patterns are determined by the intensity and type of exploitation competition (i.e. scramble or contest), it is expected that terrestrial species primarily reliant on a frugivorous diet will tend to live in larger groups and occupy larger home ranges than smaller, arboreal and predominantly folivorous species (Van Schaik and Van Hooff, 1983; Dunbar, 1998; Wrangham *et al.*, 1993). Accordingly, both vervet group and home range sizes are predicted to fall somewhere between those characteristic of *Papio* spp. (average group size: 55; average home range size: 1,352 ha; reviewed in Melnick and Pearl, 1987) and *Cercopithecus* spp. (average group size: 20; average home range size: 40 ha; reviewed in Enstam and Isbell, 2007) (Chapman and Chapman, 2000).

However, comparisons show that while the average vervet group (25) and home range (42 ha) sizes follow predictions of the hypothesis (Struhsaker, 1967b; Wolfheim, 1983; Fedigan and Fedigan, 1988; Enstam and Isbell, 2007), the species exhibits variation in group size and ranging behavior substantial enough both between and within populations to obscure interspecific differences. Indeed, depending on social group size and seasonal resource availability, home ranges can vary in size from as small as 9.4 ha to up to 518 ha (Wolfheim, 1983), and day range lengths can far exceed these figures (see Table 2) (Enstam and Isbell, 2007).

For vervet monkeys, the most reliable predictor of group size and activity patterns, including ranging, is access to high-quality food resources. As demonstrated by Isbell and Young (1993), although time spent feeding does not significantly increase in resource-poor areas, group sizes tend to be smaller and population densities higher, suggesting that less energy is expended in expanding and defending home ranges during periods of resource scarcity (Kavanagh, 1981). Other aspects of animal activity have also been shown to be influenced by poor ecological conditions. For example, Isbell and Young (1993) found that individuals in smaller groups tended to allogroom at lower rates than individuals in larger groups.

Vervet monkeys are more territorial than members of *Cercopithecus* and fiercely defend small, semi-permanent territories against invasions from other troops (Struhsaker, 1967b; Cheney *et al.*, 1981; Isbell *et al.*, 1990). Encounters between conspecific groups of vervet monkeys typically involve three different aggressive vocalizations – intergroup *wrr*s, grunts, and *long aar*s (Struhsaker, 1967c) – as well as agonistic chases and physical attacks (Hauser, 1989; Enstam and Isbell, 2007). However, individuals of different sexes, ages, and ranks behave differently in response to intergroup encounters. Perhaps predictably, Cheney *et al.* (1981) found that individuals with the most to lose from intergroup incursions, namely high-ranking females and adult males with the greatest access to receptive females, engaged the most in intergroup encounters, whereas juvenile males that have not yet dispersed from their natal groups tended to behave affiliatively towards individuals, especially females, from other groups.

Dispersal

Like the females of many Old World Monkey species (e.g., *Macaca*, *Papio*, *Cercopithecus*), female vervet monkeys remain in their natal groups their entire lives where they form linear rank hierarchies organized along stable matrilines and according to which priority of access to food, water, and social and sexual partners is organized (Cheney *et al.*, 1981; Cheney and Seyfarth, 1987). Although females rarely leave their natal groups, extreme droughts resulting in population decreases and extinctions among the well-studied vervet troops of Amboseli

National Park, Kenya, in the late 1970s and 1980s propelled several juvenile females to join other troops (Hauser *et al.*, 1986; Isbell *et al.*, 1990, 1991).

By contrast, males disperse to neighboring groups at sexual maturity (reached at approximately 3 years of age) and establish dominance hierarchies through contest competition with resident males (Whitten and Turner, 2009). Inter-troop male migration peaks at the onset of the mating season (roughly April through October; Andelman, 1987) and is associated with increases in male-male aggression (Henzi and Lucas, 1980). The outcomes of male dominance interactions are determined by an array of factors, including age, length of group tenure, availability of male relatives or other allies, and fighting ability (Struhsaker, 1967b; Cheney *et al.*, 1981). Males may migrate multiple times over the course of their lives (Cheney and Seyfarth, 1983; Isbell *et al.*, 2002).

Dispersal has been shown to be highly correlated with increases in the secretion of both testosterone and the mammalian stress hormone cortisol in a number of female-philopatric species (e.g., *Cebus apella*: Lynch *et al.*, 2002; *Chlorocebus aethiops*: McGuire *et al.*, 1986; Whitten and Turner, 2004; *Crocuta crocuta*: Holekamp and Smale, 1998; *Macaca* spp.: Muehlenbein *et al.*, 2004; *Papio hamadryas*: Beehner *et al.*, 2006; *Propithecus verreauxi*: Brockman *et al.*, 2001). During dispersal, individuals experience higher rates of mortality from predation and starvation compared with resident male conspecifics and lose opportunities to mate while alone (Isbell *et al.*, 1993; Wolff, 1994; Alberts and Altmann, 1995). Thus, dispersal represents a cost to individual fitness.

Unlike the forest guenons, vervet troops are restricted to sleeping trees located along narrow strips of riverine forest, with troops lined up one after another rather than scattered homogenously throughout the habitat (Enstam and Isbell, 2007). This arrangement severely reduces dispersal options for males (i.e. only two directions). Under the limited dispersal hypothesis, limited choices for dispersing males as well as the relatively high costs associated with migration were significant enough in vervet evolution to facilitate selection for a facultative multi-male social system (Isbell *et al.,* 2002). However, because vervet males do not often disperse across long distances and do not have an extensive "non-group phase," the costs of dispersal may be negligible (Cheney and Seyfarth, 1983). Thus, lack of dispersal choices is the more robust explanation for multimale residence.

A consequence of few dispersal options, parallel dispersal, in which males emigrate from their natal groups with related males or join troops containing older relatives, is vervets. Patterns of parallel dispersal result in a high probability of genetic relatedness between resident and immigrant males (Cheney *et al.*, 1981; Isbell *et al.,* 2002). According to the rule of inclusive fitness, vervets are thus expected to have reduced male-male aggression and low rates of infanticidal behavior (Hrdy, 1979; Isbell *et al.,* 2002). Few instances of infanticide have been recorded for *Ch. aethiops*, and all cases of suspected infanticide (Fairbanks and McGuire, 1987) and aggression towards immigrant males (Steklis *et al.,* 1985) have occurred under captive conditions or in unimale troops or troops with a low relatedness quotient due to greater dispersal options (Isbell *et al.* 2002).

Additionally, in contrast to females of other savanna-dwelling Cercopithecines (e.g., *Cercocebus*, *Papio*, *Theropithecus*), the evolution of concealed ovulation in female vervets can be understood in connection with selection pressures acting in favor of the co-residence of related males and accordingly, against infanticide and male-male aggression (Andelman, 1987). Although high-ranking vervet males tend to have higher reproductive success than low-ranking males (Struhsaker, 1967b), there is no evidence for monopolization of copulations by males or the formation of aggressive male coalitions (Andelman, 1987). Given concealed ovulation and male co-residence characteristic of the species, the reproductive payoff of these efforts would be small. This suggests that females may selectively choose to mate with high-ranking males during estrous (Keddy, 1986).

Intragroup Relationships

As a consequence of sex-biased dispersal in vervets, relations between females constitute the majority of all adult social interactions in the species (Rowell, 1988). Conversely, interactions between females and resident males are primarily restricted to the mating season (Enstam and Isbell, 2007). Female rank is inherited maternally and is supported through coalitions of female kin against unrelated individuals including resident males (Struhsaker, 1967a). Both male and female rank hierarchies are linear and rank is demonstrated through priority of access to spatial positions (Struhsaker, 1967b), food (Whitten, 1983), and grooming and mating partners (Seyfarth and Cheney, 1984), as well as through agonistic interactions (Isbell and Pruetz, 1998). Female rank hierarchies remain relatively stable over time and rank reversals are rare (Melnick and Pearl, 1987). Following predictions of the social model hypothesis, which predicts that in primate societies with female philopatry and stable female dominance hierarchies, older, high-ranking females will be the principal shapers of social learning (Kendal *et al.*, 2010), vervet matriarchs direct the transmission of social traditions across generations (Van De Waal *et al.*, 2010).

The strength of female dominance hierarchies in primates is strongly influenced by access to resources (Sterck *et al.*, 1997). Reliance on clumped, monopolizable resources such as fruit and meat is commonly associated with formalized nepotistic or despotic linear hierarchies and higher rates of agonistic behavior between and within social groups while abundant or dispersed resources, such as plant material, are correlated with egalitarian or individualistic relationships among females (Clutton-Brock and Harvey, 1977; Whitten, 1983; Van Schaik, 1989; Isbell, 1991; Pruetz and Isbell, 2000; Sterck and Steenbeek, 1997; Isbell and Young, 2002). Although the omnivorous vervets tend to follow general patterns of the socioecological model, the ability of vervets to exploit a diverse range of foods (see Table 2) and form temporary subgroups during seasonal periods of resource scarcity suggest that resource competition may not be the primary determinant of female dominance interactions for this species (Altmann, 2009; Koenig, 2002; Sussman and Garber, 2007). Others have suggested predation threat (Sussman and Garber, 2007) and group size and spread (Koenig and Borries, 2006) as potential influences on the dynamics of female social interactions in vervets.

Vervet monkeys have an extensive repertoire of vocalizations, including, but not limited to, affiliative grunts, alarm calls, and intergroup trills (Struhsaker, 1967b). Using playback experiments, Cheney and Seyfarth (1980, 1981, 1982a, 1986, 1988) demonstrated that these vocalizations contain discrete, context-dependent messages relating to the external world. For example, predator alarm calls produced by vervets were found to vary according to predator threat (e.g., Cheney and Seyfarth, 1981, 1985a; Seyfarth *et al.*, 1980a, 1980b; Seyfarth and Cheney, 1990; Owren, 1990; Brown *et al.*, 1992); that is, alarm calls for one class of predators were structurally unique from all other predator calls and were recognized as such by all adult members of the group.

The specificity of these calls to particular predators has been suggested to have evolved as a response to the 3-D predator landscape (Makin *et al.*, 2012). Vervets commonly utilize habitats characterized by both aerial and terrestrial predator threats. Thus, predator alarm calls are expected to confer a survival advantage that outweighs the costs of evolving such a sophisticated system. A variety of other primate groups have been observed to produce referential predator alarm calls (e.g., *Cebus capuchinus*: Digweed *et al.*, 2005; *Cercopithecus campbelli*: Zuberbühler, 2001; *Cercopithecus diana*: Zuberbühler *et al.*, 1997, 1999; Zuberbühler, 2000; *Colobus badius*: Standford, 1995; *Eulemur fulvus*: Fichtel and Kappeler, 2002; *Propithecus verreauxi*: Fichtel and Kappeler, 2002; *Pan troglodytes*: Crockford and Boesch, 2003), however, these calls may not always communicate response urgency (Pereira and Macedonia, 1991).

Competency in the production and recognition of these vocalizations was found to be gradually acquired during juvenescence, suggesting that, to some extent, this represents a learned behavior (Seyfarth and Cheney, 1980, 1986, 1997; Hauser, 1989). Further study revealed that vocalizations are involved in the formation and maintenance of vervet social relationships. In a series of papers, Cheney and Seyfarth (1980, 1982a, 1982b, 1985b, 1986) demonstrated that vervets are able to recognize both kin and nonkin individuals based on their vocalizations and classify individuals according to dominance relations, rank hierarchies, and matrilineal kinship based on these vocalizations. Furthermore, it was found that individuals are able to remember who behaved affiliatively or agonistically toward them in the past and modify their behavior to reflect these relationships. This ability to simultaneously monitor many relationships has been suggested to exert a constraint on social group size (see *Group Composition, Ranging, and Territoriality*).

vi. Life History

Notable among Old World monkeys, vervet females do not exhibit a defined estrus period of perineal swelling within menstrual cycles (Rowell, 1970; Eley *et al.,* 1989). Instead, female vervets are characterized by concealed ovulation and prolonged sexual receptivity extending beyond the period of maximum fertility (Andelman, 1987). Mean menstrual cycle and menses lengths have been reported at between 30 and 33 days and 2.5 and 5.0 days, respectively (Johnson *et al.*, 1973; Else *et al.*, 1986; Eley *et al.*, 1989; Seier *et al.*, 1991). Menstruation generally begins between 6 and 14 days before peak circulating estradiol concentrations (Hess *et al.*, 1979).

In the wild, vervet monkey scheduling of reproduction follows a marginally seasonal pattern for both males and females (Eley *et al.*, 1986; Else *et al.*, 1986; Kudolo *et al.*, 1986). Females generally give birth to a single infant at the beginning of the annual wet season (November through May for South Africa) when food is generally most abundant (Struhsaker, 1967a; Gartlan, 1969; Lancaster, 1971); however, in vervet populations inhabiting Barbados births peak in the dry season (Horrocks, 1986). In captivity vervets reproduce throughout the year (Seier, 2005). Twinning has been observed in a wild population; however, both twins were not successfully raised to adulthood (Pollack and Raleigh, 1994).

Mean gestation period lengths have been reported for captive populations at 165 days by Rowell (1970) and 163 days by Johnson *et al.* (1973). Bramblett *et al.* (1975) reported a mean interbirth interval for female vervets of 337.9 days, but intervals commonly range from 183 to over 800 days (Fairbanks and McGuire, 1984; Lee, 1984a; Caro *et al.*, 1995). Female rank is the most robust predictor of female reproductive success in vervets, with higher-ranking females reproducing earlier and having shorter interbirth intervals, more births per year, and higher rates of infant survivorship than lower-ranking females (Whitten, 1983; Fairbanks and McGuire, 1984; Cheney *et al.*, 1988).

Male reproductive success is influenced by a number of factors, including male-male competition, female rank, and female preference for higher-ranking males (Keddy, 1986). Males do not establish courtships or associate with females outside of the breeding season (Keddy, 1985). However, a recent study demonstrated that when the number of receptive females in a population is few males associate with females more than when receptive females are abundant, conforming to biological market theory (Fruteau *et al.*, 2009).

Average birth weights are about 343-364 g for males and 318-352 g for females (Seier, 1986; Cho *et al.*, 2002). Infants generally remain dependent on their mothers for 12 months (Lee, 1987); however, vervet mothers typically initiate weaning when the infant is about 3-6 months old (Fairbanks and McGuire, 1987). The timing of weaning is dependent on a number of factors, including availability of high-quality nutrition (Lee, 1984b; Hauser and Fairbanks, 1988), the mother's reproductive experience (Whitten, 1982; Fairbanks and McGuire, 1987; Fairbanks, 1988a), and maternal condition (Lee *et al.* 1991). In some wild populations it has been estimated that the abortion rate is about 26% (Turner *et al.*, 1987) and 30-57% of infants die in their first year of life (Cheney *et al.*, 1988; Eley, 1992).

In her review of alloparenting in primates, Hrdy (1976) observed that alloparenting often involves the kidnapping and exploitation of an infant by the 'caretaker' and sometimes results in harm or fatality of the infant, causing a reproductive cost to the mother. Infant kidnapping and abuse has been documented in a number of primate species (e.g., *Macaca fuscata*: Schino *et al.*, 1993; *Papio cynocephalus*: Shopland and Altmann, 1987; Kleindorfer and Wasser, 2004; *Semnopithecus entellus*: Hrdy, 1978).

However, in vervets, alloparental care does not appear to be abusive (Struhsaker, 1971; Lancaster, 1971; Lee, 1984a). Instead, allomothering is suggested to benefit the mother by reducing the amount of time and energy invested in infant care and the alloparent by providing parental experience (Fairbanks, 1990). Supporting this reciprocal benefits hypothesis, reports of vervet allomothering suggest that nulliparous females related to the mother are the most frequent caretakers (e.g., Struhsaker, 1971; Johnson *et al.*, 1980; Lee, 1984a; Meaney *et al.*, 1990). However, unrelated juvenile males and adult, reproductively-active females, have also been observed to care for infants (Krige and Lucas, 1974; Fairbanks, 1988b). Adult males do not generally engage in parental care (Gartlan, 1969); however, lower-ranking males have been observed to associate with groups of infants (Danzy, *pers. obs*.).

Compared with six other Old World monkeys, Rowell and Richards (1979) classified vervets, along with Sykes' monkeys, as a fast-maturing, quick-breeding species. Infants are nutritionally independent at 12 months of age although adult dentition is not fully emerged until about 40-67 months (Turner *et al.*, 1998; Bolter and Zihlman, 2003). In their analysis of patterns of physical development in wild vervets, Bolter and Zihlman (2003) found that vervet body systems develop in a mosaic fashion, with the brain maturing first, followed by the skeletal and dental framework, and finally muscle mass. Moreover, they observed pronounced sexual dimorphism in the rate and timing of physical development, with females attaining adult proportions earlier than males (Bolter and Zihlman, 2003). Age of first reproduction is about 36-41 months for females (Fairbanks and McGuire, 1984). Males reach sexual maturity considerably later, at about 46 months of age (Hiyaoka *et al.*, 1990; Bolter and Zihlman, 2003); however, they may not successfully reproduce until later in life (Keddy, 1986).

Like in many other Old World monkey species, play constitutes a considerable part of infant and juvenile vervet activity (Fedigan, 1972; Rose, 1977; Fairbanks, 1993; Govindarajulu *et al.*, 1993). Fairbanks (1993) has argued that play in vervets encourages physical fitness and facilitates learning about the outside world. A similar argument has been made for a number of animal, including primate, taxa (e.g., Poirier and Smith, 1974; Smith, 1982; Caro, 1988; Burghardt, 1998; Byers, 1998; Spinka *et al.*, 2001). Although play is not estimated to be a significant energetic cost (Martin, 1984), Lee (1984b) found that juvenile vervets typically engage in more high-intensity play behaviors when food densities are higher. This suggests that seasonality may have some influence on the behavior of infant and juvenile vervets. However, ecological stress does not appear to inhibit the ability of vervets to successfully reproduce (Lee, 1984a citing long-term data from Cheney and Seyfarth).

Predation accounts for up to 70% of adult vervet monkey deaths in the wild (Isbell 1990). While reproductive senescence has been demonstrated for only a small number of nonhuman primates (e.g. Bowden, 1979), in a comparative study of several primate species, Caro *et al.* (1995) found that while some females continue to reproduce their entire adult lives, others stop well before death. This pattern parallels but does not approximate human menopause. Whether or not a menopause-like postreproductive period exists for nonhuman primate females is still debated. Altmann (1987) argued that nonhuman primate females do not consistently exhibit a complete cessation of reproductive potential and therefore cannot be considered to have a menopausal period.

C. Life History Theory

Life history theory describes all components of the life of an organism – how big it will be at birth, how fast it will grow, when it will start reproducing, how many offspring it will have, how long it will live – in order to arrive at an understanding of the evolutionary forces that shaped it (Stearns, 1976, 1989, 1992; Van Noordwijk and De Jong, 1986; Hill, 1993; Hill and Kaplan, 1999; Leigh and Blomquist, 2007). Evolutionary theory predicts that selection will favor phenotypic traits that confer a fitness advantage measured as reproductive output (Darwin, 1871). Drawing from this basic tenet, life history theory attends to the very simple question: Why not have more offspring? An answer is approached through the notion of trade-offs.

“Trade-offs” refers to the negative correlation between life history traits; that is, the fitness costs associated with the allocation of energy, a limited resource, to one aspect of the life course over another (Clutton-Brock *et al.*, 1982; Rose, 1983; Reznick, 1985; Stearns, 1989, 1992). For example, early sexual maturation is often associated with early termination of the life span (see for example Miyatake, 1997; Leroi *et al.*, 1994; Djawdan *et al.*, 1996). Life history theory predicts that selection will favor suites of traits that code for the most efficient allocation of time and energy resources given constraints of the environment to four competing events in the life course: growth, storage, and reproduction (Gadgil and Bossert, 1970; Stearns, 1976, 1992, 2000; Partridge and Harvey, 1988; Hill and Kaplan, 1999). However, optimal schedules of resource allocation vary widely across taxa (see *Comparative Life Histories*). The concept of life history trade-offs has been instrumental to explanations of observed variation in the timing and shape of key events, transitions, and phases in the life course both between and within species by providing a framework that considers all aspects of an organism. Although heuristic to a certain extent, imagining life as a sequence of facultative “decisions” inextricably linked to a fitness value has drawn attention to the mechanisms underlying patterns of phenotype expression.

The focus of life history theory on the variables time and energy follows from the principle that fitness is constrained by the ability of an individual to harvest energy from the environment and convert that energy into reproductive output over unit time (Hill, 1993; Hill and Kaplan, 1999). Specifically, natural selection is expected to act on life events related to age-schedules of reproduction and mortality, such as age at first reproduction, interbirth interval, and lifespan, given that fitness is calculated as intrinsic rate of increase and is derived from the sum of reproductive output of each year lived (Aiello and Wheeler, 1995). Although much of the language of life history theory emphasizes selection at the level of the individual, trade-offs ultimately function to shape the evolution of taxon-specific ‘norms of reaction’ – the array of possible life history features produced by the genotype across a range of environments (Gomulkiewicz and Kirkpatrick, 1992; Worley *et al.*, 2003).

i. Comparative Primate Life Histories

Body and brain size have long been recognized to predict mammalian metabolic rates according to the law of surface area (Kleiber, 1947; McMahon, 1973; Gould, 1975a; Martin, 1981; McNab and Eisenberg, 1989; White and Seymour, 2003), and have been proposed to account for much of the variation in mammalian life histories (Western, 1979; Western and Ssemakula, 1982; Harvey and Clutton-Brock, 1985; Smith, 1992). The study of proportion as a function of scale, 'allometry' is concerned with how life history traits scale to size measures, such as limb length (e.g., Aiello, 1981, 1984), cranial capacity (e.g. Pilbeam and Gould, 1974), and tooth size (e.g., Gould, 1975b; Gingerich and Smith, 1985).

Size effects have been proposed to influence the diversity of structural forms among related taxa (Gingerich *et al.*, 1982; Shea, 1992; West *et al.*, 1997; Leigh *et al.,* 2003; Purvis *et al.*, 2003) and have been used to predict such life history parameters as reproductive rate (e.g., Fenchel, 1974; Reiss, 1991; Ross and Jones, 1999), growth rate (e.g., Gould, 1966; Millar, 1977; Pontier *et al.*, 1989), and lifespan (e.g., Sacher, 1959; Promislow, 1993). However, size alone does not provide a complete explanation for differences in mammalian life history components, which have been found to systematically co-vary across taxa independent of size effects (e.g. brain, body, and neonatal weights: Harvey and Clutton-Brock, 1985; Promislow and Harvey, 1990). For example, although the dental complement has a strong allometric effect, the indriid primates of Madagascar show accelerated dental development but delayed growth of the skeletal framework and delayed sexual maturation (Godfrey *et al.*, 2003).

An alternative explanation suggests that taxon-specific life history strategies are the result of selection acting on a combination of life history variables adapted to rates of adult extrinsic mortality and are only marginally constrained by size effects (Partridge and Harvey, 1988; Promislow and Harvey, 1990; Harvey and Purvis, 1991; Janson and Van Schaik, 1993; Kappeler, 1996; Janson, 2003; Johnson, 2003; Purvis *et al.,* 2003; Rubenstein, 2003). Supporting this hypothesis, a growing number of studies have shown that when phylogenetic effects are removed, variation in mammalian life history traits does not significantly correlate with allometric scaling measures (e.g. brain size and metabolic rate: Read and Harvey, 1989; Harvey *et al.,* 1991; Harvey and Keymer, 1991). Following from this hypothesis, the expression of “timed” phenotypes, such as weaning, dispersal, and reproduction, which are direct components of lifespan, may provide particular insight into the causes of variation in energy production and allocation in the life histories of mammals (McNab, 1988; Smith, 1992; Enquist *et al.,* 1999; Hill and Kaplan, 1999).

Drawing on techniques of allometric scaling, the ‘allochronic’ model scales life history traits to life span or other timed events in the life course (Smith, 1992; Glazier and Newcomer, 1999). Rates (analogous to size) and patterns (analogous to shape) of life events are scaled to taxon-specific age schedules of reproduction and mortality, providing a link between the timing and pattern of events in life history and dynamics of energy production and allocation. For example, early age at first reproduction tends to coincide with other stereotypically “fast” traits, such as relatively high mortality rates, large litters, short interbirth intervals, and short life spans (Mangel and Stamps, 2001; Bielby *et al.*, 2007). Although few empirical studies have made use of it (see for exception Smith, 1992; Glazier and Newcomer, 1999), the allochronic model has the unique potential to reveal interrelations of life history traits and explain how suites of traits correspond to constraints of the lifespan, and therefore conditions of the environment.

Introduced to ecology by MacArthur and Wilson (1967), *r*- and *K*-selection, in which *r* refers to the maximum intrinsic rate of increase and *K* is the carrying capacity of the environment, has since been broadened by Pianka (1970, 1972), Gadgil and Solbrig (1972), and Stearns (1976, 1977, 1989) to describe variation in the “pace” of mammalian life histories. Whereas *r*-selected taxa are opportunistic, characterized by early maturation, the production of many, “cheap” offspring, and early termination of life, *K*-selected taxa exist at or near the carrying capacity of the environment and gain a reproductive advantage by increasing the competitive ability of each offspring (see for review Parry, 1981). The *r*- and *K*-selection model produces a fast-slow continuum of mammalian life histories, in which most mammals exist somewhere between the extremes. Although it has been the subject of criticism (e.g. Hairston *et al.*, 1970), taken heuristically, the *r*- and *K*-selection model contributes elements of density-dependent regulation, resource availability, and environmental variability to more widely accepted density-independent demographic models (Boyce, 1984; Reznick *et al.*, 2002).

Compared with those of most other mammals of similar body size, primate life histories tend towards the “long-and-slow” end of the continuum. Primates are characterized by relatively low rates of production and growth, long gestation periods, long interbirth intervals, the production of few, large neonates, low juvenile and adult rates of extrinsic mortality, long lifespans, and delayed reproductive maturity (e.g., Harvey and Clutton-Brock, 1985; Promislow and Harvey, 1990; Pereira, 1993; Ross, 1998; Ross and Jones, 1999; Mace 2000; Leigh and Blomquist, 2007). Reprinted from Charnov and Berrigan (1993), Figure 4 describes the average adult life span and average age at first reproduction of two primate taxa compared against a sample of other mammals. The primate averages are well above those of the other mammals sampled, suggesting that primates have considerably slower life histories than other mammals of similar body size.

Variation in life history variables between primate grades is such that the fast-slow continuum can also be found within the primate order (Kappeler *et al.*, 2003). Differences in the pace of primate life histories are most pronounced between the phylogenetically primitive strepsirhine primates and the anthropoids. For example, the gray mouse lemur, a small prosimian primate, reaches reproductive maturity within a year of birth and produces two or more litters of two offspring each per season (Wrogemann *et al.*, 2001; Andrès and Solignac, 2003; Génin, 2008), whereas relatively long-lived gorilla females give birth to singleton infants at intervals of four to six years after transferring from their natal groups at seven to ten years of age (Watts, 1990; Doran and McNeilage, 1998; Stokes *et al.*, 2003; Robbins *et al.*, 2004).

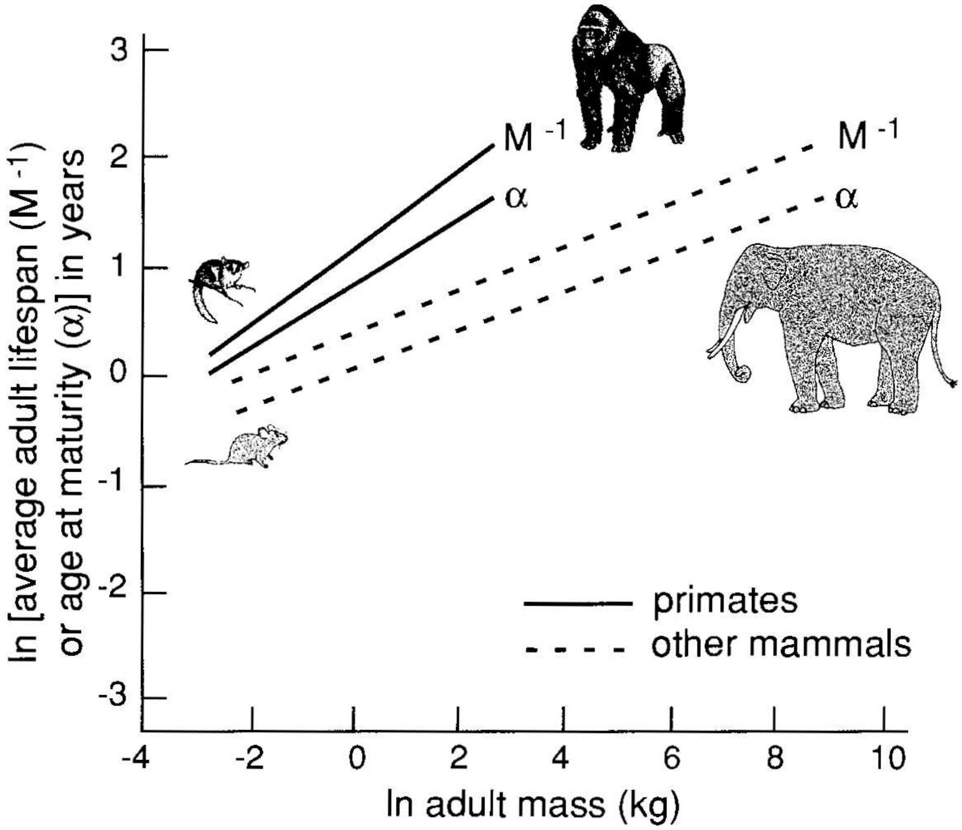


Fig. 4. Average values for age at reproductive maturity (α, measured from weaning to age at first reproduction) and adult life span (measured as the inverse of the average adult instantaneous mortality rate, M) for a sample of primates and other mammals. (Taken from Charnov and Berrigan, 1993).

ii. Male Life History Strategies

Life history parameters of most male mammals are shaped by the organizing principle that male reproductive success is limited by access to reproductively viable females (Darwin, 1871; Wade, 1979; Andersson, 1994). Conversely, female reproductive success is shaped by conditions of menstruation, gestation, birth, and lactation, and does not appear to be limited by the ability to attract mates (for exceptions see Johnson, 1988; Rosenqvist, 1990; Owens *et al.*, 1994). While males also invest in reproduction through spermatogenesis, the development of secondary sexual attributes, mate competition, and even parental care, reduced male investment in gametes and parental care increases their potential rate of reproduction, resulting in an operational sex bias in favor of males (Trivers, 1972; Clutton-Brock and Vincent, 1991; Clutton-Brock and Parker, 1992; Kvarnemo and Ahnesjo, 1996; Kokko and Monaghan, 2001; Clutton-Brock, 2007). Although metabolic costs associated with spermatogenesis can reduce survivorship in some animals (e.g., *Austropotamobius italicus*: Rubolini *et al.*, 2007; *Caenorhabditis elegans*: Van Voorhies, 1992; *Notophthalmus viridescens*: Takahashi and Parris, 2009; *Vipera berus*: Olsson *et al.*, 1997), competition for access to reproducing females represents the limiting factor of primate male reproductive success.

In consideration of sex differences in energy investment in gametes, males are expected to have a higher potential reproductive rate than females (Parker *et al.*, 1972; Clutton-Brock and Vincent, 1991; Clutton-Brock and Parker, 1992). Sexual dimorphism in reproductive success was first demonstrated in the common fruitfly (*Drosophila melanogaster*) by Bateman (1948) and has since been substantiated for a number of animal taxa (e.g., *D. melanogaster*: Partridge and Farquhar, 1983; *Enallagma hageni*: Fincke, 1986; *Gryllus bimaculatus*: Simmons, 1988; *Mirounga augustirostris*: Le Boeuf, 1974; *Papio* spp.: DeVore, 1965; *Rana sylvatica*: Howard, 1980). However, a recent replication of

Bateman’s classic experiment with *D. melanogaster* reported little evidence to support the claim that the sexes differ in fitness potential as a consequence of disproportionate investment in gametes (Gowaty *et al.*, 2012). Moreover, reproductive output of males cannot exceed that of females (Queller, 1997). Thus, it is perhaps more accurate to say that males are expected to have higher rates of *variation* in reproductive success than females (see Kokko *et al.*, 2006 for review).

In his oft-cited treatise on sexual selection, Trivers (1972) argued that sexual dimorphism in behavior and the expression of such secondary sexual traits as size, color, and the development of the vocal apparatus is a product of differential investment in parental care. Among primates, species with polygynous social systems, wherein males engage in intense competition for access to females, exhibit greater sexual dimorphism in canine length and body size than monogamous or polyandrous species (Clutton-Brock, 1977; Harvey *et al.*, 1978; Plavcan, 1999). However, the strength of this argument has been called to question (Wade, 1979), and factors including phylogeny (e.g. Cheverud *et al.*, 1985), allometric effects (e.g., Leutenegger and Cheverud, 1982; Fairbairn, 1997), predation pressure (e.g., Leutenegger and Kelly, 1977; Harvey *et al.*, 1978; Anderson, 1986), and diet (e.g. Ford, 1994) have been proposed to influence sexual size dimorphism.

Male reproductive competition represents a central determinant of taxon-specific patterns of social group organization and adult sex ratios. For example, differences between single-male and multi-male taxa in testes size are such that relative testis size has been used to predict the mating system of taxa for which only anatomical data exists (Dixson, 1995). A number of explanations have been proposed to account for different mating systems in the order primates.

Harcourt *et al.* (1981) suggested that breeding season length may determine mating system. In taxa with a short breeding season, a single male may not be able to monopolize access to all reproductively-receptive females given that frequent copulations reduce sperm quality and output (Harcourt, 1991; Harcourt *et al.,* 1995), thus resulting in a multi-male system; whereas an extended breeding season may enable a single male to competitively exclude all other males.

Shorter breeding seasons are also expected to be associated with selection for increased investment in sperm-producing tissue (Harcourt *et al.,* 1981). This hypothesis was substantiated by Ridley (1986). Altmann (1990) called to question Ridley's categorization of breeding season lengths and instead suggested the number of adult females in a group as predicted by resource abundance to represent the most important determinant of mating system (see also Emlen and Oring, 1977). This hypothesis was supported by Andelman (1986), who demonstrated that cercopithecine groups with less than five females tend to be single-male and groups with more than ten females are multi-male.

Predation (Clutton-Brock, 1989; Van Schaik and Hörstermann, 1994) and infanticide risk (Van Schaik, 1996; Van Schaik and Kappeler, 1997) have also been offered as possible explanations for patterns of social group organization. Although interspecific patterning of social group organization and mating system may be determined by one or a combination of these factors, it is important to note that considerable variation exists within species that may be influenced by conditions of the environment, such as seasonal fluctuations in temperature and rainfall or anthropogenic modification of primate habitats (Fuentes, 2007; Thierry, 2007, 2008; Chapman and Rothman, 2009).

Although traditionally approached from a reproductive or evolutionary ecology perspective, infanticide is ultimately a subject of life history as both frameworks attempt to explain the evolution of phenotypes, particularly those relating to individual reproductive success (Chisholm *et al.*, 1993; Stearns, 2000; Kaplan and Gangestad, 2004). Infanticide has been well-documented in primates (e.g., *Cercopithecus mitis*: Butynski, 1982; *Macaca* spp.: Soltis *et al.*, 2000; *Papio* spp.: Palombit *et al.*, 2000; Weingrill, 2000; *Presbytis entellus*: Hrdy, 1974; Hausfater, 1982; Newton, 1986) and other mammals (e.g., *Mus musculus*: Huck *et al.*, 1982; Brooks and Schwarzkopf, 1983; *Panthera leo*: Pusey and Packer, 1994; *Rattus* spp.: Mennella and Moltz, 1988; *Ursus arctos*: Bellemain *et al.*, 2006) and is generally considered to be a product of sexual conflict (Smuts and Smuts, 1993; Van Schaik and Kappeler, 1997; Van Schaik *et al.*, 2004). Hrdy (1974) was the first to suggest that the killing of infants by recently immigrated or dominant males may confer a reproductive advantage by hastening the mother's return to estrus and increasing the male's probability of successfully siring offspring due to his new social status. In response, females have evolved a number of counter-strategies, including sexual signaling through genital swelling (e.g., Zinner *et al.*, 2004; Engelhardt *et al.*, 2005), promiscuous mating (e.g., Agrell *et al.*, 1998; Wolff and Macdonald, 2004; Kowalewski and Garber, 2010), and developing “friendships” with resident males (e.g., Van Schaik and Kappeler, 1997; Palombit, 2000; Weingrill, 2000; Nguyen *et al.*, 2009). Although hotly debated (e.g., Dolhinow, 1977; Bartlett *et al.*, 1993; Sussman *et al.*, 1995), Hrdy’s explanation remains the best supported explanation for infanticide in primates.

iii. Life History Variables in Ontogeny

As a consequence of their slow growth rate, primates spend an extended amount of their lives as juveniles. Investment in this life stage represents a central trade-off between energy expended on growth and survival and energy expended on reproduction (Stearns, 1989, 1992). However, the allocation of energy to growth may ultimately increase individual fitness by reducing predation risk through increased size or by enhancing intrasexual competitive ability (Nylin and Gotthard, 1998; Hill and Kaplan, 1999; Mace, 2000). For example, following from predictions of sexual selection theory, investment in the development of SSCs, such as the vocal apparatus required for the production of characteristic long calls of orangutan males (Mitani, 1985; Schürmann and Van Hooff, 1986; Delgado, 2006) and the bright pelage and sexual skin coloration of male drills and mandrills (Setchell and Dixson, 2001; Marty *et al.*, 2009; Setchell *et al.*, 2005, 2006), confers a reproductive advantage for males of primate groups in which male fitness is defined through competition with conspecifics and female choice (West-Eberhard, 1979; Small, 1989; Setchell and Kappeler, 2003).

In the model proposed by Charnov and Berrigan (1993), patterns of juvenile development set the pace of adult lives because energy allocated to growth during the juvenile period is converted into reproductive effort following growth cessation at adulthood. Thus, increased investment in growth ultimately results in an increase in the net energy available for reproduction over the life course (reviewed in Leigh and Blomquist, 2007). In terms of metabolic expenditure, Charnov and Berrigan (1993) divide the developmental period into three distinct stages, each characterized by a different growth function (Fig. 5). First, the costs of growth of an individual from the time of conception until weaning are almost entirely absorbed maternally through lactation and food-sharing (Altmann and Samuels, 1992), but may also be supplemented by alternate caregivers (e.g. Callitrichidae: Garber and Leigh, 1997). From weaning until adulthood, which is commonly taken as age at first reproduction (Pereira, 1993), the energy costs of further growth as well as the development of secondary sex characteristics are taken up by the individual with minimal provisioning by the mother or other related individuals (e.g., Schessler and Nash, 1977; De Waal, 1989; De Waal *et al.*, 1993). At growth cessation, energy gained during the growth period is converted into reproductive effort.

The timing of life stage transitions is mediated by aspects of the physical, biotic, and social environment, most notably by rates of extrinsic mortality. Theories of the evolution of aging predict that organisms that experience high rates of mortality attributable to extrinsic factors, such as predation, starvation, or disease, will evolve high intrinsic rates of mortality, i.e. early senescence and a short lifespan (Williams, 1957; Hamilton, 1966; Abrams, 1993; Holliday, 2006). Following from the principle of trade-offs, the limiting effects of rates of extrinsic mortality on the lifespan are expected to determine species-specific dynamics of growth, maturation, body size, and reproduction (Promislow and Harvey, 1990; Stearns *et al.*, 2000). As mentioned earlier, the juvenile period represents an important determinant of lifetime reproductive success. Because juvenescence is characterized by nutritional independence from the mother and entrance into an adult ecological niche, juveniles are particularly vulnerable to starvation and foraging-related predation. In their 'juvenile risks' model, Janson and Van Schaik (1993) propose that this risk is minimized in primates through the adoption of a slow-growth strategy, prolonging the juvenile period but lowering the risk of death per unit time. Additionally, a prolonged juvenile period may confer a fitness advantage by allowing an individual sufficient time to attain the ecological and social skills necessary to successfully exploit the adult foraging niche and navigate social life.

The transition from one developmental stage to the next is associated with a shift in life history priorities and, accordingly, the uptake of a different fitness-maximizing strategy (reviewed in Pereira and Leigh, 2003). Given that it is under directional selection, inter-individual differences in resource-acquisition ability more than allocation strategy may better predict fitness (Hunt *et al.*, 2004). However, the timing of changes in energy allocation from somatic growth to reproduction reflects a fundamental trade-off between reproductive rate and reproductive span (Johnson, 2003), and consequently, represents an important determinant of individual fitness (e.g. Kappeler, 1996). Moreover, the timing of this life history event affects both the rate and direction of changes in population size (Stearns, 1992; Pereira and Leigh, 1993; Alberts and Altmann, 1995). For example, in populations characterized by a positive net growth, individuals favoring a strategy of early sexual maturation are expected to have a higher fitness value because each current offspring produced represents a higher proportion of the population than each future offspring relative to mortality risk (Hill, 1993). The opposite pattern is expected for populations of decreasing size.

Although species-specific generalities are often used in life history research, variation in life history traits exists between individuals of a single species which shape individual reproductive success and fitness. Variability in life history traits within a species may arise in one of two ways. First, phenotypic plasticity can occur when the norms of reaction for an individual interact with a variable environment to produce the most efficient allocation of resources, often corresponding to a change in form or activity (Nylin and Gotthard, 1998; West-Eberhard, 2003). Over time, such changes may become fixed in the population as alternative strategies.

For example, orangutan males lacking the pronounced sexually selected features characteristic of the species, termed “Peter Pan” or “sneaker” males, contribute to the gene pool through sexual coercion. Second, variability in a population may reflect a maladaptation. Some individuals are of higher quality than others (Kokko, 1998). Thus, examinations of variation in the force of selection operating at different times in the life course of an individual as well as differences in life history strategies among individuals are central to our understanding of the evolution of diversity among primate life histories.

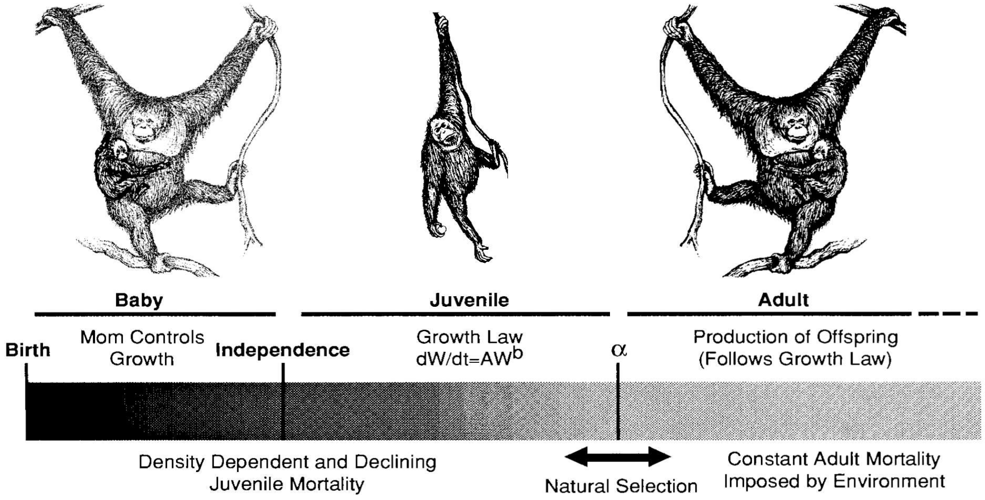


Fig. 5. Representation of the life history model proposed by Charnov and Berrigan (1993) which diagrams three life history transitions defined in terms of energetics: (1) infancy, taken as the period from birth to weaning during which individual costs of growth are met by the mother; (2) juvenescence, from weaning until reproductive maturity growth is a condition of individual metabolic expenditure and (3) adulthood, at which time growth is converted into reproductive effort. (Taken from Charnov and Berrigan, 1993).

D. Hormones and Life Histories

i. Testosterone and the Endocrine System

Sex-specific hormones, most notably T in males and estrogens (estradiol-17β and estrone) in females, are important determinants of mammalian reproductive function. Their roles include controlling differentiation of the brain and gonads, maturation of reproductive organs, control of energy investment in gametes, development of secondary sex characteristics, and stimulation of sexual behavior (Selcer and Leavitt, 1991). Hormones control reproductive function by means of a series of feedback loops along the hypothalamic-pituitary-gonad (HPG) axis. This system acts in an episodic or pulsatile fashion, with hypothalamic pulses of gonadotropin-releasing hormone (GnRH) or GnRH-like molecules regulating the release of the gonadotropic hormones (GtHs) follicle-stimulating hormone (FSH) and luteinizing hormone (LH) from the anterior pituitary gland (King and Millar, 1991). The HPG axis also plays a role in the regulation of other pituitary hormones, effects on the placenta, gonads, and adrenal gland, and activity in the central and peripheral nervous systems (Cameron, 1990; Lavy *et al.*, 1991; Finn *et al.*, 1998). GnRH along with the other releasing hormones (e.g., corticotropin-releasing hormone, thyrotropin-releasing hormone, somatocrinin) are secreted by peptidergic neurons of the hypothalamic median eminence and transported to the anterior pituitary by means of veins of the hypothalamo-hypophyseal portal (HHP) system (Nelson, 2000). GnRH exists in two forms in mammals, GnRH I, which regulates GtH release, and GnRH II, which has been suggested to act as a neuromodulator and has been demonstrated to stimulate sexual behavior (Neill *et al*., 2001; Millar, 2003, 2005). GnRH activity is moderated by a number of neuronal systems within the central nervous system (CNS), including those that regulate the release of such neurotransmitters as norepinephrine, serotonin, and endogenous opiate peptides (Zheng, 2009). Binding sites for GnRH analogs have been demonstrated in the testicular Leydig cells and ovarian granulosa cells of mammals and GnRH-like peptides have been found in testicular extracts and follicular fluid (e.g., Hsueh and Schaeffer, 1985; Millar and King, 1987; King and Millar, 1992; Okubo and Nagahama, 2008). Although interspecies differences exist in the control of the GnRH system by the CNS, most structural and chemical aspects of reproduction, particularly the hypothalamic-pituitary axis (HPA) and the HHP system, are identical among vertebrates (Lavy *et al.*, 1991).

The hypophyseal GtHs LH and FSH directly affect the gonads in the control of the development, maturation, and release of mammalian gametes (Licht, 1979; Ishii, 1991). In females, FSH and LH control the development and function of ovarian follicles. FSH binds to membrane receptors of the granulosa cells of immature ovarian follicles to stimulate LH receptor activity and the release of aromatase (Erickson and Hsueh, 1978; Erickson *et al.*, 1979). LH, in turn, stimulates the production of androgens, principally T and 5α-dihydrotestosterone (DHT) (Nelson, 2000). These are secreted by thecal cells and stored in the follicular cavity until they can be converted to the female sex steroid estrogen by the granulosa cells (Baird *et al.*, 1981). In the testis of males, FSH and LH play different roles. FSH targets Sertoli cells in the seminiferous tubule to activate spermatogenesis and increase the synthesis of proteins such as androgen-binding protein, plasminogen activator, protein kinase inhibitor, and gamma glutamyl transpeptidase, and LH targets the Leydig cells in the interstitial tissue to stimulate the secretion of androgens, including T (Steinberger, 1971; Bremner *et al.*, 1981; DiZerega and Sherins, 1981; Swerdloff and Heber, 1981; Ishii, 1991). T secreted by the Leydig cells acts in conjunction with FSH on Sertoli cells in the activation of spermatogenesis (Tähkä, 1986). Although Leydig cells do not have FSH receptors, FSH directly increases sensitivity of the testis to LH at puberty (Fakunding *et al.*, 1976). Gonadal hormones have an inhibitory effect on GnRH activity, mediating the secretion of the GtHs, possibly through the suppression of GnRH secretion and the suppression of pituitary responsiveness to GnRHs (Clayton and Catt, 1981; Matsumoto and Bremner, 1984; Singh *et al.*, 1995).

ii. Testosterone and Male Life Histories

T and the other androgens (i.e. androstenedione and DHT) act on the accessory ducts and glands of the male reproductive tract, the secretory products of which are critical to the production of functional sperm, and maintain the accessory sex organs, including the prostate, seminal vesicles, and bulba urethra glands (Knorr *et al.*, 1970; Nelson, 2000). Androgens also support the expression of SSCs, such as the development of the vocal apparatus used in the long-calls of many primate species (e.g., Wich *et al.*, 2003; Fischer *et al.*, 2004), vibrant coloration of the pelage and dermis of mandrills, vervet monkeys, and others (e.g., Wickings and Dixson, 1992a, 1992b; Setchell and Dixson, 2001; Waitt *et al.*, 2003; Danzy, 2012) and sex dimorphism in body size and muscle mass (reviewed in Wells, 2007). Although primarily associated with the initiation of spermatogenesis and the maintenance of the reproductive tract, androgens play a prominent role in regulating respiratory metabolism and are linked to many diseases, such as prostate cancer, endometrial cancer, breast cancer, osteoporosis, and loss of libido (Chang, 2002).

Hormones act as intermediaries between the physical environment and the internal architecture of an organism, acting both at the level of genes and whole-body phenotypic traits, including behavior, in transitions between life history stages, such as maturation and reproduction (Ketterson and Nolan, 1992; Hau, 2007). T has been a focus of male life history traits due to its effects the expression of SSCs, courtship and mating behaviors (e.g., vocalizations and presentations, copulatory behavior), and aggression (e.g. mate guarding, male-male competition, territorial behavior), and suppressing immune function (Folstad and Karter, 1992; Owen-Ashley *et al.*, 2004; Muehlenbein and Bribiescas, 2005) and parental care (Marler and Moore, 1988) (see Table 3 for summary). Interconnections between patterns of T secretion and reproductive behavior are supported by experimental manipulation studies (e.g., Moore, 1984; Hegner and Wingfield, 1987; Ketterson *et al.*, 1992; De Ridder *et al.*, 2000).

In primates, the correlation between circulating levels of T and aggressive behavior is tenuous. An almost equal number of studies support (e.g., Bernstein *et al.*, 1979; Alberts *et al.*, 1992) and refute (e.g., Steklis *et al.*, 1985, 1986; Nieuwenhuijsen *et al.*, 1987; Lynch *et al.*, 2002) the association. More recent studies (e.g., Cavigelli and Pereira, 2000; Muller and Wrangham, 2004; Whitten and Turner, 2004; Archer, 2006; Cristóbal-Azkarate *et al.*, 2006; Gould and Ziegler, 2007) have looked at seasonal or event-driven variability in the relationship between T and aggressive and reproductive behavior using the challenge hypothesis as a theoretical starting point. Proposed by Wingfield *et al.* (1990), the ‘challenge hypothesis’ suggests that sexually selected behaviors in males of species that compete for reproductive access to females, the expression of which are a function of circulating androgens, should fluctuate in response to challenges of the social environment (see also Wingfield, 1984; Wingfield *et al.*, 1987, 2001, 2006). While expectations of this hypothesis suggest that circulating levels of T should increase in preparation for critical moments in the life course, empirical evidence in primates is mixed. A number of studies have shown compelling evidence for increases in circulating T in preparation for critical events such as dispersal (e.g., Brockman *et al.*, 2001; Gesquiere *et al.*, 2005; Beehner *et al.*, 2006) and seasonal competition for mating opportunities (e.g., Cavigelli and Pereira, 2000; Ostner *et al.*, 2002; Teichroeb and Sicotte, 2008; Girard-Buttoz *et al.*, 2009), whereas other studies have not found significant support for these patterns (e.g. Beehner *et al.*, 2009). However, by positing a link between elevated T levels and conditions specific to male life histories, specifically the need to compete for access to reproductively viable females, the challenge hypothesis provides an explanation for patterns of T secretion and the expression of behaviors and SSCs associated with reproductive effort.

Social factors, such as sex ratio (e.g., Cristóbal-Azkarate *et al.,* 2006; Rangel-Negrín *et al.*, 2011) and social structure, may also exert an influence on patterns of expression of male T (see Hirschenhauser and Oliveira, 2006 for a full review). The strength of the relationship between T and the expression of male reproductive behaviors is expected to vary according to mating system and degree of paternal care. Males of species with monogamous mating and paternal care of offspring (e.g., gibbons, siamangs, muriquis, owl monkeys) should exhibit more aggression and a corresponding increase in T in response to social challenges, such as the initial formation of pair bonds and territorial encroachment by conspecifics, than males of species with polygynous mating and little or no paternal investment. Although few of these species have been the subjects of studies evaluating the challenge hypothesis, Strier *et al.* (1999) did not find evidence for differences in T between breeding and nonbreeding seasons in male muriquis (*Brachyteles arachnoides*).

Alternatively, males of species with strict hierarchical (e.g. gorillas) or promiscuous hierarchical (e.g. chimpanzees) multimale-multifemale mating systems are expected to exhibit many elevations in circulating T over the life course, corresponding to rank reversals, seasonal competition for mates, and migration between social groups. Although few studies have been conducted, these predictions are generally upheld by empirical evidence. For example, preliminary data on urinary T levels from three mountain gorilla groups at Karisoke, Rwanda, indicated slightly higher levels of T and greater aggression in silverback males during intergroup encounters (Robbins and Czekala, 1997). In, perhaps a more convincing example, Muller and Wrangham (2004) demonstrated a clear connection between male T levels and periods of maximum female tumescence (an index of female receptivity) in a population of chimpanzees at Kibale National Park, Uganda. However Muehlenbein *et al.* (2004) pointed out that fission-fusion sociality characteristic of chimpanzees may result in a level of unpredictability too high for the anticipation of challenges necessary to the hypothesis.

iii. Testosterone Secretion over the Life Cycle

Table 3. Summary of evidence for and against a positive correlation between circulating T and the expression of male behavioral and morphological SSCs.

Trait	Support Positive Relationship	Refute Positive Relationship	Incomplete Evidence for Relationship
Body Size Dimorphism	Bardin and Catterall, 1981; Ford and Klindt, 1989; Fennel and Scanes, 1992b; Wehrenberg and Giustina, 1992; Borski *et al.*, 1996; Wells, 2007; Cox *et al.*, 2009	*Fennel and Scanes, 1992a; Abell, 1998; Cox *et al.*, 2005	*Cox and John-Alder, 2005
Aggression	Selinger and Bermant, 1967; Rose *et al.*, 1975; Selmanoff *et al.*, 1977; Bernstein *et al.*, 1979; Wingfield *et al.*, 1987; Alberts *et al.*, 1992	Steklis *et al.*, 1985, 1986; Nieuenhuijsen *et al.*, 1987; Lynch *et al.*, 2002; Wiley and Goldizen, 2003	Cavigelli and Pereira, 2000; Muller and Wrangham, 2004; Whitten and Turner, 2004; Archer, 1991, 2006; Cristóbal-Azkarate *et al.*, 2006; Gould and Ziegler, 2007
Vocalizations†	Andrew, 1969; Wada and Gorbman, 1977; Fusani *et al.*, 1994; Nespor *et al.*, 1996; Wich *et al.*, 2003; Fischer *et al.*, 2004		
Coloration	Vandenbergh, 1965; Wickings and Dixson, 1992b; Rhodes *et al.*, 1997; Setchell and Dixson, 2001; Setchell *et al.*, 2008		Danzy, 2012; Danzy *et al.*, *in prep.*
Mating/Courtship Behavior	Alsum and Goy, 1974; Phoenix, 1974; Crews *et al.*, 1978;	Camazine *et al.*, 1980; Crews *et al.*,1984	Lincoln *et al.*, 1972; Hutchison, 1978
Social Rank	Rose *et al.*, 1971; Eberhart *et al.*, 1980; Anestis, 2006; Beehner *et al.*, 2006	Eaton and Resko, 1974; Bernstein *et al.*, 1979; Gordon *et al.*, 1976; Barrett *et al.*, 2002	Dixson, 1977; Czoty *et al.*, 2009
Paternal Behavior	Wang and De Vries, 1993; Trainor and Marler, 2001, 2002	Hegner and Wingfield, 1987; Saino and Møller, 1995; Schoech *et al.*, 1998; Nunes *et al.*, 2000, 2001	Ketterson *et al.*, 1992; Lynn, 2008

*Negative relationships between T and body size were found for reptiles with female-larger sexual size dimorphism.

†Development of the vocal apparatus used in the production of long calls has been demonstrated to co-vary with body size dimorphism (Green, 1981; Fischer *et al.*, 2002; Harris *et al.*, 2006).

The classic view of mammalian sexual differentiation is that masculinization of the gonads is activated by the presence of the sex-determining region of the Y (*Sry*) gene on the paternally-contributed Y chromosome (Ohno, 1967). The expression of this chromosome starts a chain reaction starting with the promotion of the Leydig cells to secrete androgenic hormones, including T (Wachtel *et al.*, 1991). The secretion of T then triggers the development of the testes from the undifferentiated gonads within the urogenital ridge (Davidoff *et al.*, 2009). In the absence of the Y chromosome, the secretion of estrogen is stimulated and the Mullerian duct develops into the Fallopian tubes, uterus, and vagina. However, while the Y chromosome may be primarily responsible for initiating processes of sexual differentiation, genes coding for sexually dimorphic traits have been disproportionately identified on the X chromosome (Templeton, 1977; Grula and Taylor, 1980a, 1980b; Rice, 1984).

The relative roles of genetics and hormones in shaping processes of sexual differentiation and dimorphism in mammals are unclear. Because the presence or absence of the Y chromosome only triggers the release of sex-specific hormones it has been argued that sexual differentiation of the internal and external genitalia is primarily under hormonal control (Sanders and Reinisch, 1990; Menke *et al.*, 2003). The 'androgen theory of sexual differentiation' goes so far as to suggest that most, if not all, sex differences in the neural structures that influence behavior, including differentiation of neural connections, the volume of cell nuclei, dendritic distribution patterns, serotonin levels, RNA metabolism, and cholinesterase activity, can been attributed to the secretion of T (Jost *et al.*, 1970;

Gorski, 1978; MacLusky and Naftolin, 1981; De Vries *et al.*, 1984; Morris *et al.*, 2004). However, several studies have documented morphological and functional sexual dimorphism prior to differentiation of the gonads, suggesting "direct genetic" control of some sex-specific traits (Wai-Sum *et al.*, 1988; Reisert and Pilgrim, 1991; Arnold, 1996, 2002).

The early postnatal period has been identified as a critical phase of sexual differentiation and development, during which T is biologically active and available to gonadal tissues (Mann *et al.*, 1989; Mann and Fraser, 1996). Activation of the hypothalamic-pituitary-T axis in human infants has been shown to be associated with a "surge" in the gonadotropins LH and FSH and T secretion beginning in the second postnatal week, peaking in months two through four, and returning to baseline concentrations at approximately six months of age (Forest *et al.*, 1973, 1974; Forest, 1990). A similar surge has been demonstrated for male macaques (Steiner and Bremner, 1981; Fuller *et al.*, 1982; Dixson *et al.*, 1998), chimpanzees (Fuller *et al.*, 1982), and marmosets (Abbott and Hearn, 1978a). Experimental manipulation of circulating T levels in male and female rhesus macaques and marmosets during this period resulted in abnormal penile and clitoral development, supporting the argument that this period represents a critical stage of physio-sexual development during which T is biologically active and available to gonadal tissues (Dixson *et al.*, 1998; Brown *et al.*, 1999). Artificial manipulation of circulating T during this period has also been shown to affect sexual behavior at adulthood (Abbott and Hearn, 1978b); however, treatment of macaques with LHRH analogues used to mediate T fluctuations in adulthood had no effect (Eisler *et al.*, 1993; Lunn *et al.*, 1994). Thus, prenatal androgenization more than the postnatal T surge is primarily responsible in organizing the neural substrates involved in sexual differentiation (Goy and McEwan, 1980).

Delayed puberty and an extended period of pre-reproductive growth are two of several key characteristics that distinguish primates apart from other mammals (Tanner, 1955; Schultz, 1956; Watts, 1985). Puberty is most often defined as the period of sexual maturation during which an organism attains the ability to produce mature gametes, taking place roughly between weaning or nutritional independence and age at first reproduction (Wilson, 1992; Pereira, 2002; Bronson and Rissman, 2008). It is a period of reproductive readiness that is most obviously characterized by maturation of the gonads and the development of SSCs (Schreibman *et al.,* 1991). During the pre-reproductive period, circulating concentrations of LH, FSH, and gonadal hormones are low, however at puberty, the HPG axis is activated, an event which stimulates the synthesis and pulsatile release of GnRH and increases mean circulating levels of LH and FSH (Cameron *et al.*, 1985; Schreibman *et al.*, 1991). Increases in the amplitude of GtH pulses are particularly evident during sleep (Kapen *et al.*, 1974). This phenomenon was first demonstrated in humans (Boyar *et al.*, 1974) and has since been observed for a number of mammalian taxa, including sheep (Lee *et al.*, 1976) and chimpanzees (Hobson *et al.*, 1980).

Activation of the HPG axis at puberty involves the following events as demonstrated by Wray and Hoffman (1986) in laboratory rats: (1) the establishment of synaptic connections and neuronal remodeling to facilitate the synchronization of GnRH neurons, (2) stimulation of GnRH release by the extrahypothalamic neurotransmitter system, and (3) a change in the number of receptors on GnRH-secreting neurons. The relationship between increases in GnRH secretion and increases in the secretion of GtHs was further demonstrated by Marshall and Kelch (1986) and Marshall *et al.* (1993) in a series of experiments that artificially administered GnRH to prepubertal male and female rhesus macaques. The result of these studies was premature secretion of T and spermatogenesis in males and ovarian follicular development in females.

The timing of transitions in life history, and between the prepubertal and postpubertal stages of development in particular, and the rhythm of reproductive events are shaped by a combination of factors, including seasonal ecological variables, such as photoperiod (e.g., Lincoln, 1981; Tähkä *et al.*, 1983), temperature (e.g., Licht, 1984; Bourne *et al.*, 1986; Huf, 1989), and rainfall, and environmental stressors, such as predation, anthropogenic stress, and social stress (reviewed in Bourne, 1991; Wingfield and Kenagy, 1991). Many primate species exhibit a seasonal patterning of reproductive activity (Walker *et al.*, 1984). Thus, perhaps unsurprisingly, puberty in these species may be activated by seasonal cues such as photoperiods and temperature (Ishii, 1991). Other influencing factors include physiological factors associated with nutrition, adiposity, and metabolic rate (Bronson and Rissman, 1986; Schwartz *et al.*, 1988; Cameron, 1990, 1996; Cameron *et al.*, 1993; Foster and Nagatani, 1999) and conditions of the social environment such as sex ratio and pheromones (e.g., Bartlett *et al.*, 1993; Kraus *et al.*, 1999; Abbott *et al.*, 2009).

Social control of puberty is particularly evident in species with social regulation of reproduction (e.g., gorillas, tamarins, marmosets). For example, in a study by Epple and Katz (1980), juvenile female saddle-back tamarins (*Saguinus fuscicollis*) exposed to adult males conceived an average of 233 days earlier than juvenile females reared in same-sex peer groups. Inversely, the presence of adult, reproductively active females appears to suppress the onset of puberty in subordinate females (e.g., *Callithrix jacchus*: Abbott and Hearn, 1978; Barrett *et al.*, 1990; *Saguinus* spp.: Epple and Katz, 1984; Ziegler *et al.*, 1987).

Prenatal exposure to hormones has also been shown to affect the timing of puberty, the expression of reproductive phenotypes, and fertility. For example, exposure of prenatal female rhesus macaques (*Macaca mulatta*) and humans to androgens has been shown to delay menstruation (Goy *et al.*, 1988; Zehr *et al.*, 2005; Abbott *et al.*, 2009). Exposure of prenatal female rhesus macaques to T has also been shown to cause pseudohermaphroditism (Thornton and Goy, 1986).

Before attaining adult body proportion and composition, individuals undergo rapid and pronounced morphological and physiological changes. Although an adolescent growth spurt in weight and skeletal dimensions is best documented in humans (e.g., Leigh and Park, 1998; Bogin, 1999a, 1999b; Leigh, 2001), evidence of a growth spurt exists for a number of primates, including chimpanzees (e.g., Spence and Yerkes, 1937; Grether and Yerkes, 1940; Gavan, 1953) and some Old World monkey (e.g., *Macaca* spp.: Van Wagenen and

Catchpole, 1956; Castracane *et al.,* 1986; Turnquist and Kessler, 1989; Hamada *et al.*, 1999; *Mandrillus sphinx*: Setchell *et al.*, 2001; Setchell and Dixson, 2002; *Papio* spp.: Copeland *et al.,* 1982; Altmann and Alberts, 1987) and New World monkey (e.g. *Cebus albifrons*: Wylin and Naftolin, 1978) species. Factors such as seasonality and nutrition may affect growth spurt onset and duration. In Japanese macaques, the spurt follows a seasonal pattern, with animals exhibiting higher rates of growth during the spring and summer months when resources are abundant (Hamada *et al.*, 1999). Seasonality has also been demonstrated to affect rates of adolescent growth in humans (Bogin 1978; Mirwald and Bailey, 1997).

Table 4. Timing of the acquisition of SSCs in male vervet monkeys.

Trait	**Age Class**	**Source**
Cranial Capacity	Two	Bolter and Zihlman, 2003
Scrotal Pigmentation	Six	Gerald, 2001; Danzy, 2012; Danzy *et al., in prep.*
Eruption of Canines	Six	Turner *et al.*, 1998; Bolter and Zihlman, 2003; Danzy, 2012
Descent of the Testes	Six to Seven	Bolter and Zihlman, 2003; Whitten and Turner, 2009
Dispersal	Six to Seven	Struhsaker, 1967a
Reproductive Maturity*	Seven	Horrocks, 1986; Cheney *et al.*, 1988
Skeletal Framework	Seven	Bolter and Zihlman, 2003
Dental Complement	Seven	Turner *et al.*, 1998; Bolter and Zihlman, 2003; Danzy, 2012
Muscle Mass†	Eight	Bolter and Zihlman, 2003

*Based on behavioral data
†Includes development of the masticatory musculature

III. OBJECTIVES/HYPOTHESES

Knowledge of baseline changes in fT in males is central to both investigations of the morphological, physiological, and behavioral correlates of inter-individual variation in fT excretion at each stage of the life course and questions concerning the evolution of species-specific schedules of maturation in primates. In view of this, the primary objective of this research was to characterize fT profiles of wild, male vervet monkeys, contrasting individuals within and between age groups to establish baseline patterns of growth and sexual maturation for the species. Based on results obtained for vervets (Bolter and Zihlman, 2003, Whitten and Turner, 2009) and other primates (e.g., *Aotus trivirgatus*: Dixson *et al.*, 1980; *Callithrix jacchus*: Abbott and Hearn, 1978a; *Macaca mulatta*: Rose *et al.*, 1978; Dixson and Nevison, 1997; *Mandrillus sphinx*: Wickings and Dixson, 1992a, 1992b; *Papio* spp.: Castracane *et al.*, 1986; Crawford *et al.*, 1997; Gesquiere *et al.*, 2005; Beehner *et al.*, 2009; *Pongo pygmaeus*: Kingsley, 1988; *Saguinus mystax*: Huck *et al.*, 2005; *Theropithecus gelada*: Beehner *et al.*, 2009), it was expected that patterns of fT excretion would strongly correlate with age. Moreover, fT was expected to be more sensitive to relative age of reproductive maturity than any other stage of life history.

Secondly, this study sought to explore the relationship between T and parameters of individual development, including variation in the timing of sexual maturity and patterns of SSC emergence. Changes in testicular volume and body mass and the eruption of the canine teeth associated with the adolescent stage of development have been shown to have fitness consequences (e.g. Leigh *et al.*, 2008). Although age of first reproduction for male vervets can only be established with behavioral observations, changes in the expression of these traits during adolescence have been used as an approximate marker of reproductive maturity in many mammals (reviewed in Kunz *et al.*, 1996). Jolly and Phillips-

Conroy (2003, 2006) interpreted the attainment of these SSCs and changes in excreted T in baboons to reflect a strategy of preparation for challenges associated with attaining reproductive maturity, including dispersal from the natal group, competition for a place in the dominance hierarchy of the adoptive troop, and competition for reproductive opportunities. If this interpretation is supported in vervets, maturational changes in fT excretion are expected to coincide with the emergence and development of SSCs. Furthermore, inter-individual variation in the expression of fT and the morphological SSCs is expected to be greater for subadults than for any other age group. Approaching these objectives from a life history perspective, this study specifically looks at relative age of reproductive maturity as a life stage transition, or “maturational milestone”, of particular importance to lifetime reproductive output and individual fitness (Stearns, 1992).

IV. METHODS

Over the past ten years, a broad survey of the genetic, morphological, and endocrinological variation of vervet monkeys across their South African distribution has been conducted (Grobler and Matlala, 2002; Anapol *et al.*, 2005; Grobler *et al.*, 2006; Freimer *et al.*, 2007; Jasinska *et al.*, 2007; Whitten and Turner, 2008; McAuliffe Dore *et al.*, 2009). Variation within and between populations of vervets was evaluated by sample procedures that emphasized sampling breadth (over 800 individuals have been sampled to date) and depth (procedures targeted vervet troops in their entirety at over 30 locations). The subjects of this study represent a small subset of this undertaking.

Research presented here is compliant with protocols approved by the University of Wisconsin at Milwaukee IACUC, the University of California at Los Angeles IACUC, and the University of the Free State, South Africa. This research also adheres to the legal requirements of South Africa. Trapping and collection of materials follows both provincial and CITES regulations. This research was supported in part by NIH R01RR016300. Ethical clearance to trap and sample vervets was obtained from the University of the Free State (13/2010) and the University of Wisconsin at Milwaukee. All vervets sampled were collected under permit IEB 0002 issued by the South African National Department of Water and Environmental Affairs and associated Provincial permits.

A. Study Sites and Populations

The fieldwork for this project was conducted at multiple, geographically distinct sites throughout central and southeastern South Africa from mid-April to mid-November, 2010 (Fig. 6). The sites reflect a wide range of habitat types, altitudes, and microclimates and differ in mean values for precipitation, temperature, and humidity (Table 5). Rainfall is highly variable across sites and drought conditions fluctuate greatly from year to year. The annual dry season (roughly June through August) is characterized by a decline in the availability of food and clean drinking water and, as a consequence, vervet monkey mortality rates rise during this period as individuals enter areas of high human population density in search of easily-accessible food (see Lee and Hauser, 1998). The sites range from protected bushveld in regional and private nature and game reserves to highly cultivated farmland and differ greatly in size, characteristic vegetation, and relative predation pressure. Although the South African Problem Animal Control Ordinance ("Ordinance 26, 1957"), which allowed the extermination of pest animals including vervets, has been repealed, in much of the country vervets are still considered agricultural pests and are frequently persecuted by private landowners (Lee *et al.,* 1986; Grobler *et al.*, 2006). Human population pressures vary greatly among sites but are generally lowest for reserves and highest for privately owned lodges and farms (Meiring, *pers. obs.*). All vervet monkeys used in this study belonged to the subspecies *Chlorocebus aethiops pygerythrus*. This is the predominant subspecies found in South Africa (Turner, 1977; Kingdon, 1988; Skinner and Chimimba, 2005; Cawthon Lang, 2006).

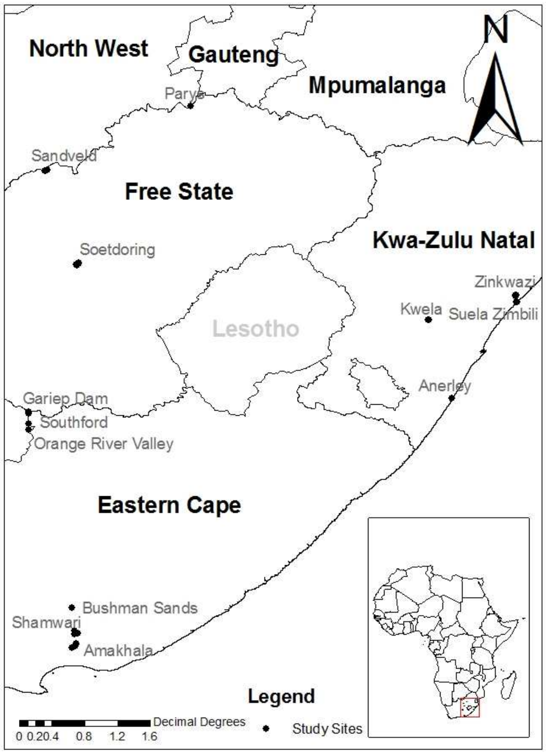


Fig. 6. Provincial map of South Africa with distribution of trapping sites indicated as black dots.

Table 5. Description of vervet trapping sites. Rainfall is reported as an average annual range.

Site	Province	GPS Coordinates*	Elevation (m)	Rainfall (mm)
Soetdoring Reserve	Free State	26.0590, -28.8220	1395-1400	400-600
Orange Valley Farm	Free State	25.1580, -30.6390	950-1125	400-600
Southford Stud Farm	Free State	25.4722, -30.8327	950-1125	400-600
Gariep Dam Fishery	Free State	25.4760, -30.6180	950-1125	400-600
Sandveld Reserve	Free State	25.6700, -27.6830	1200-1325	400-600
Parys Golf Estate	Free State	27.4580, -26.8940	1350-1460	400-600
Zinkwazi Lodge	KZN†	31.4400, -29.2770	25-550	600-1200
Suela Zimbili	KZN	31.4240, -29.2080	25-550	600-1200
Kwela Lodge	KZN	30.3610, -29.4940	700-850	600-1200
Camp Anerley	KZN	30.6510, -30.4560	25-550	600-1200
Shamwari Reserve	East Cape	26.0332, -33.3211	450-700	550-700
Bushman Sands	East Cape	26.0772, -33.3180	450-700	550-700
Amakhala Reserve	East Cape	26.0070, -33.4930	450-700	550-700

* GPS coordinates are provided in decimal degrees
† Kwa-Zulu Natal

B. Sampling Procedures

Animals were trapped following procedures described in Brett *et al.* (1982), Whitten and Turner (2004), and Grobler and Turner (2010). Although animals were sampled opportunistically, natural troops were targeted in their entirety. Areas near known sleeping sites or in close proximity to areas where vervet troops had been visually documented were pre-baited with maize, orange sections, and/or apple slices given regional preferences before traps (n=28) were introduced. After one to three days of comfortable feeding, during which animals would commonly sit, forage, and play on or around the collapsed traps, the traps were set with orange segments. Traps were set before dawn (*ca.* 05:30 h) and were checked at intervals of 30 minutes. The traps consisted of a wooden frame covered by a strong wire mesh. The trap was sprung when the loaded trigger stick was disturbed by an animal. Once sprung, the trap provided a barrier, allowing the animal to be sedated without direct contact by passing a syringe through the wire mesh. Animals in traps were sedated by intramuscular injections of zoletil (also known as telazol) or ketamine (1.0mg/kg) by a certified veterinarian and immediately transported to the processing area. Both zoletil and ketamine have been shown to have only mild effects on cortisol levels in Old World monkeys (Bentson *et al.*, 2003; Suleman *et al.*, 2004), and, although repeated sedation with ketamine is associated with reduced animal appetite (Springer and Baker, 2007), both of these agents have been judged safe for short-term anesthesia of vervet monkeys (Vercruysse and Mortelmans, 1978). Reports of the effects of repeated chemical immobilization on plasma testosterone are contradictory. While some studies suggest that chronic immobilization stress decreases plasma testosterone levels (Demura *et al.*, 1989; Almeida *et al.*, 1998) others have observed the opposite reaction (Almeida *et al.*, 2000). Still others have reported no effect (Hayashi and Moberg, 1987). Regardless, chemical immobilization with zoletil or ketamine is not expected to affect single measure fecal androgens given gut passage delay (Whitten *et al.*, 1998; Beehner and Whitten, 2004; Palme, 2005). Body temperatures were monitored for all animals throughout the processing procedure. Processed animals were transferred to a secure recovery area and closely monitored until they rejoined their troops.

A large quantity of both invasive and non-invasive cross-sectional data was collected from each animal for analysis. Biological samples, including blood serum, tissue samples from ear punches, fecal samples, genital and rectal swabs, and hair, as well as sex (visual assessment), dental age, whole-body morphological measurements in accordance with Anapol *et al.* (2005), pelage photographs, and behavioral footage were collected. For the purposes of this research sex, dental age, morphological measurements used to calculate body mass index (BMI), canine length, testis volume, and cross-sectional hormone profiles using fecal steroid assays were collected from 59 animals from 17 troops. All samples were collected during periods of low or no precipitation to reduce hormone degradation (see Beehner and Whitten, 2004).

Fecal samples were collected either immediately after defecation in a trap or were manually obtained from sedated animals using a sterile finger probe to avoid contamination. All samples represent individuals. To prevent breakdown of the steroid hormones by exogenous microbes, samples were processed within a few hours of defecation. A portion of approximately 5 g feces was mixed thoroughly with a wooden spatula to reduce the presence of hormone "hot spots". The sample was then stored in a polyethylene twist-off BD Falcon tube (BD Biosciences, San Jose, California) labeled with the date and sample number at -30º C. Samples were stored in a portable -30º C freezer in the field until they could be transferred to a permanent -30º C freezer located at the University of the Free State in Bloemfontein, SA, for longer-term storage. Frozen storage of fecal samples has been shown to minimize bacterial metabolism of the steroids and is the recommended method of preservation (Beehner and Whitten, 2004).

C. Data Collection and Analysis

i. Age Classifications

Establishing a standard procedure for determining age is critical for both describing the growth of individuals and comparing patterns of development between and within species (Schultz, 1935; Smith, 1989; Smith *et al.*, 1994). Patterns of dental eruption were used as a relative measure of age in this study (Fig. 7). Eruption sequences and long bone lengths are generally considered to be the most accurate external identifiers of age in primates (e.g., *Alouatta* spp.: Balcells and Veà Baró, 2009; *Chlorocebus aethiops*: Bolter and Zihlman, 2003; *Erythrocebus patas*: Jogahara and Natori, 2012; *Papio* spp.: Phillips-Conroy and Jolly, 1988, Kahumbu and Eley, 1991). Although inter-individual variations exist, particularly among immature individuals, mean age of tooth eruption is highly correlated with mean body weight and mean brain weight (Smith *et al.*, 1994). Each animal was assigned an age class based on the presence and condition of permanent dentition following recent consensus for age classification in the field (Turner *et al.*, 1998; Bolter and Zihlman, 2003; Danzy, 2012; Danzy *et al.*, *in prep.*) (see Table 4). Non-deciduous canine length was measured using digital calipers to the nearest 0.001 inch from the tooth tip to where the tooth emerged from the gum.

When exact age is not known, narrow age classes are preferred for age estimations (Altmann *et al.*, 1981). However, narrow age class divisions often result in sample sizes far below statistical significance. For this reason, and for the sake of convenience, broad age classes that loosely correspond to life history stages (e.g., infant, juvenile, adult) are commonly used in the literature. Rather than based on dentition, broad age classes are typically assigned based on visual documentation of physical, including scrotal color, descent of the testes, and body size for males, and behavioral maturational markers, such as nutritional independence. However, visual documentation provides only a rough estimate of age and may or may not produce biologically meaningful age categories. Taking into account the benefits and drawbacks of both approaches to establishing age, this study assessed individuals according to three classification schemas of increasing specificity. First, animals were grouped into three classes: Infants (age classes one and two: from birth to 20 months of age), Juveniles (age classes three through six: roughly corresponding to 22 through 40 months), and Adults (age classes seven and eight: 40 months and after). This is the only breakdown that satisfies requirements of statistical significance for all age classes. Second, because juveniles undergo considerable changes between the events weaning and reproduction, the juvenile class defined in Schema 1 was split into Juveniles (age classes three and four: 22 through 31 months) and Subadults (age classes five and six: 32 through 40 months). The third schema included all eight age classes described in Table 6. Overlap and gaps in this breakdown are due to inter-individual variation in patterns of dental eruption. A complete breakdown of the three classification schemas used in this study is provided in Table 7.

ii. Morphological Measurements

Morphological measurements used in this study as an index of maturation include canine length, testes volume, and body length and weight used to calculate BMI.

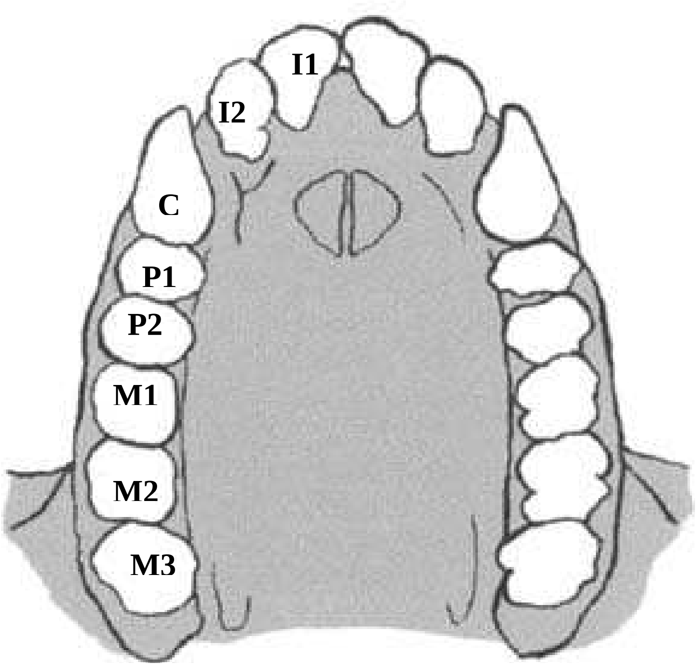


Fig. 7. Dental patterns in catarrhini (Taken from Bolter and Zihlman, 2003).

Table 6. Age categories defined according to dental eruption*

Age Category	Age Class	Eruption Sequence†	Age (Months)§
Infant	One	All deciduous	0 - 8
	Two	**M1**	12 - 20
Juvenile	Three	M1, **I1**, **I2**	22 - 27
	Four	M1, I1, I2, **M2**	26 - 31
Subadult	Five	M1, I1, I2, M2, **P3**, **P4**	32 - 49
	Six	M1, I1, I2, M2, P3, P4, **C**	38 - 40
Adult	Seven	All permanent dentition	40 – 67
	Eight	Worn dentition	> 67

*Turner *et al.*, 1998; Bolter and Zihlman, 2003; Danzy, 2012; Danzy *et al., in prep.*
†I = Incisor, C = Canine, P = Premolar, M = Molar
§Overlap and gaps in age are present due to inter-individual variation

Body weights were obtained to the nearest 0.01 kg using a cloth weigh bag attached to a digital scale. Osteological markers were used to obtain linear measurements after Schultz (1929), Turner *et al.* (1997), and Anapol *et al.* (2005) using a standard tape measure to the nearest mm. Although body length, chest girth, and lengths of the tail, right foot, right hand, and right upper and forelimbs were collected as part of a survey of the genetic and morphological variability of South African vervet monkeys (Grobler and Matlala, 2002; Anapol *et al.*, 2005; Grobler *et al.*, 2006; McAuliffe Dore *et al.*, 2009), only body length was used for the purposes of this study. A description of these measurements is provided in Figure 8.

Along with canine size and testis volume, BMI was calculated for each individual as a measure of male sexual maturation. Following Groves and Harding (2003), Primate Body Mass Index was calculated as weight over body length squared (Fig. 9). Although this formula is less precise than the Human Body Mass Index, which includes head and leg lengths, it has been validated for use as a measure of primate body condition (Pampush, 2010). Testis volume was measured using a scaled orchidometer, which estimates volume by comparing the testis with a series of ellipsoid beads (Karaman *et al.*, 2005).

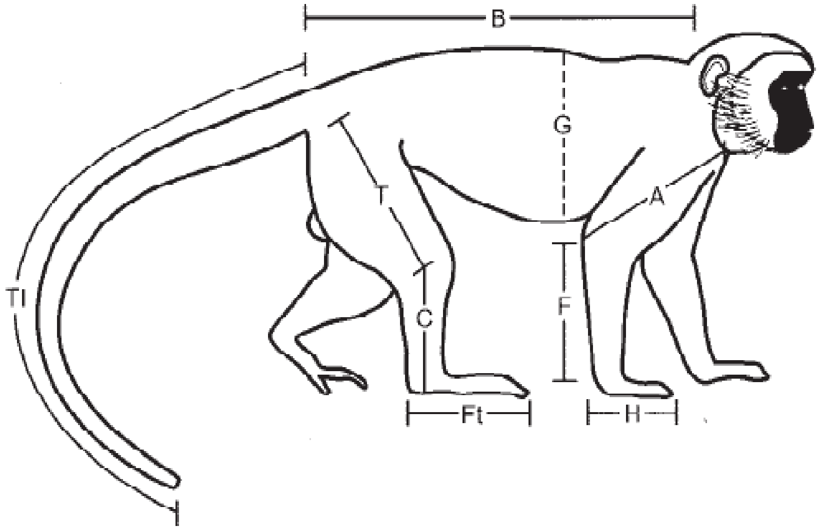


Fig. 8. Description of morphological measurements: (B) body length, (G) chest girth, (A) arm length, (F) forearm length, (H) hand length, (T) thigh length, (C) crus or foreleg length, (Ft) foot length, and (Tl) tail length. (Taken from Anapol *et al.*, 2005).

Table 7. Age breakdown of vervet sample according to three classification schemas.

						Age Classification											
			Schema 1			**Schema 2**				**Schema 3**							
Site	**Troop**	**Samples**	Infant	Juvenile	Adult	Infant	Juvenile	Subadult	Adult	One	Two	Three	Four	Five	Six	Seven	Eight
Soetdoring Reserve	A	6	1	4	1	1	1	3	1	1	0	0	1	1	2	0	1
	B	4	1	1	2	1	1	0	2	0	1	0	1	0	0	2	0
Orange Valley Farm	A	2	0	1	1	0	1	0	1	0	0	0	1	0	0	0	1
Southford Stud Farm	A	6	0	3	3	0	2	1	3	0	0	1	1	0	1	3	0
Gariep Dam Fishery	A	3	0	2	1	0	0	2	1	0	0	0	0	2	0	1	0
Sandveld Reserve	A	4	0	2	2	0	1	1	2	0	0	0	1	0	1	1	1
	B	4	2	0	2	2	0	0	2	0	2	0	0	0	0	2	0
Parys Golf Estate	A	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0
Zinkwazi Lodge	A	2	0	1	1	2	0	0	1	2	0	0	0	0	0	1	0
Suela Zimbili	A	3	2	0	1	2	0	0	1	2	0	0	0	0	0	0	1
Kwela Lodge	A	5	1	0	4	1	0	0	4	0	1	0	0	0	0	4	0
	B	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0
Camp Anerley	A	2	1	0	1	1	0	0	1	0	1	0	0	0	0	1	0
Shamwari Reserve	A	8	1	2	5	1	1	1	5	1	0	0	1	0	1	5	0
Bushman Sands	A	3	0	1	2	0	1	0	2	0	0	0	1	0	0	1	1
Amakhala Reserve	A	2	0	0	2	0	0	0	2	0	0	0	0	0	0	2	0
Total		56	9	18	29	9	9	9	29	4	5	1	8	4	5	24	5

A.

$$\text{Human Body Mass Index} = \frac{\text{Weight (kg)}}{(\text{Head} + \text{Body Length} + \text{Leg Length (m)})^2}$$

B.

$$\text{Primate Body Mass Index} = \frac{\text{Weight (kg)}}{(\text{Body Length (m)})^2}$$

Fig. 9. A. Formula used for calculating human body mass index (BMI) following Groves and Harding (2003). **B.** Formula used to calculate vervet BMI derived from A.

iii. Hormonal Analysis

The procedure for preservation, extraction, and radioimmunoassay of excreted T from fecal samples used in this study generally follows Whitten *et al*. (1998) and Beehner and Whitten (2004). Fecal samples frozen at -40° C at the genetics lab of the University of the Free State, South Africa, were thawed and homogenized in a 10.0 ml methanol:acetone solution (100% methanol; 4:1) using a electric homogenizer. After 7-10 hours, 4.0 ml of the sample solution was filtered through a 0.2-µm polytetrafluoroethylene (PTFE) syringeless filter (Whatman, Clifton, NJ) to remove particulate matter. The filtrate was diluted 1:1:1.75, filtrate: 100% methanol:distilled water. Solid-phase extraction cartridges (Sep-Pak Plus, Waters Associates, Milford, Massachusetts) were then primed following the manufacturer’s instructions by passing 2.0 ml of 100% methanol and then 15.0 ml of distilled water through the cartridge. The filtrate was loaded onto the primed cartridge and set with 2.0 ml sodium azide solution (0.1%). The loaded cartridges were then stored in a Whirl-Pak bags (Nasco, Fort Atkinson, Wisconsin) with 10-20 desiccate beads at -10° C at the University of the Free State, SA, until they could be transported for analysis.

Samples were carried by hand to the anthropology laboratory at the University of Wisconsin at Milwaukee for storage at -80º C. They were then transferred to the University of Illinois Animal Science Lab for processing. The cartridges were flushed with 2.0 mls of 100% methanol, dried down, and reconstituted in a phosphate-buffered saline solution containing gelatin buffer (PBS-gel). Radioactive immunoassay (RIA) kits incorporating a tritium tracer (Perkin Elmer, Waltham, Massachusetts, USA) and antibody were used to analyze concentrations of excreted T for all samples. Samples were set up in an assay with 3H-steroid, PBS-gel, and the antibody, and counted on the scintillation counter to determine the bound hormone (following Bahr *et al.*, 1983). Dry rather than wet weights of the samples were used to express T in order to control for differences in moisture content and were reported as pg/g (weight of empty falcon tubes was subtracted from the weights of the tubes plus dry sample) (Wasser *et al.*, 1993). This protocol has been shown to reliably reflect testicular and adrenal function in a sample of primate species (e.g., *Macaca fuscata*: Barrett *et al.*, 2002; *Propithecus verreauxi*: Brockman *et al.*, 1998). Although an antibody against testosterone was used in the assay, it is important to note that fecal steroid hormones exist as a mixture of metabolites (Bosacker, 2008). Parameters used to check assay quality were inter- and intra-assay variation. The

%CV for fT intraassay variation was 2.29+/-1.33 (n = 59) and the average interassay variation was 8.6.

iv. Data Analysis

The numeric data collected for this study did not meet assumptions of parametric statistical tests. To normalize distributions and equalize variances, thereby enabling parametric analyses, fT and BMI were log-transformed (base 10). Because testis mass and canine length have been shown to scale allometrically with body mass and body length, respectively, relative values were calculated to control for this association (Gingerich *et al.*, 1982; Kenagy and Trombulak, 1986). Relative testis volume was calculated by dividing total testicular volume by body weight (cc/kg) and relative non-deciduous canine length was calculated by dividing canine length by body length (inches/cm). Outliers (defined at the 95% confidence interval or greater than two standard deviations above the mean) were removed from the sample using Grubbs' second test to reduce sampling error. This test has been authenticated for use with ordinal and continuous numeric data (Grubbs, 1950).

One-way analysis of variance (ANOVA) tests were used to determine if the categorical variable age predicted the continuous numeric variables log fT and log BMI. Because relative testis volume and relative canine length were non-normal after transformation, the relationship between these variables and animal age was assessed using the nonparametric Kruskal-Wallis test, followed by a post Kruskal-Wallis test for multiple comparisons. Since canine teeth erupt late in development, relative canine length could not be compared between individuals of all age categories. Instead, canine length was compared between subadult and adult individuals (age classes six and seven and eight, respectively) and inter-individual variation in canine length was examined among fully adult animals (age classes seven and eight). Within-subjects correlation was used to identify significant relationships among the continuous numeric variables.

Statistical tests were performed using R (R Foundation for Statistical Computing, Vienna, Austria), and the threshold for all analyses was set at $p < 0.05$. The data were modeled in ANOVA using a model I analysis for planned comparisons. Boxplots and beanplots were generated to provide an illustration of the relationship between the categorical variable age and the numeric dependent variables. Beanplots are particularly useful for visual comparisons because of their ability to illustrate densities of the sample distributions (Kampstra, 2008). Relationships among the numeric variables were illustrated with regression plots. Regression lines were fitted to the data using a model I (least-squares) regression analysis.

V. RESULTS

Grubbs' second test for outliers identified and removed three individuals from the dataset, giving the study a final sample size of 56 animals. Because the dependent variables assessed were not normally distributed, medians were calculated and compared instead of means. The descriptive statistics median and inter-quartile range (IQR) were calculated for the untransformed variables fT, BMI, testis volume, and canine length and are presented by age group for each age classification schema in Table 8.

Table 8.
Descriptive statistics median (IQR) for untransformed fT (pg/g), BMI (kg/m^2), testis volume (cc), and canine length (inches) for each age schema (n = number of samples).

Variable	**n**	**fT**	**BMI**	**Testis Vol.***	**Canine Length†**
Schema 1:					
Infant	9	25.36 (8.655)	21.07 (3.94)	1 (0.5)	N/A
Juvenile	18	30.11 (27.21)	24.05 (6.09)	1.5 (2.75)	0.45 (0.18)
Adult	29	34.71 (33.54)	31.23 (4.41)	15 (13)	0.72 (0.09)
Total:	56	30.56 (22.28)	27.17 (9.19)	10 (14)	0.7 (0.11)
Schema 2:					
Infant	9	25.36 (8.655)	21.07 (3.94)	1 (0.5)	N/A
Juvenile	8	21.25 (8.03)	22.76 (5.35)	1.5 (1.25)	N/A
Subadult	10	41.37 (23.41)	25.08 (9.69)	1.5 (7)	0.45 (0.18)
Adult	29	34.71 (33.54)	31.23 (4.41)	15 (13)	0.72 (0.09)
Total:	56	30.56 (22.28)	27.17 (9.19)	10 (14)	0.7 (0.11)
Schema 3:					
One	4	24.3 (9.23)	20.07 (3.8)	0.5 (0.13)	N/A
Two	5	25.36 (5.8)	21.8 (3.76)	1 (0)	N/A
Three	1	18.4 (N/A)	20.79 (N/A)	4 (N/A)	N/A
Four	8	24.22 (17.31)	24.05 (4.91)	1 (1.13)	N/A
Five	4	26.68 (13.47)	22.34 (3.64)	1.5 (4.38)	N/A
Six	5	44.94 (12.63)	26.72 (9)	8 (7)	0.45 (0.18)
Seven	24	33.582 (18.5)	30.642 (6.75)	15 (8)	0.705 (0.1)
Eight	5	58.32 (5.348)	32 (1.12)	25 (0)	0.758 (0.07)
Total:	56	30.56 (22.28)	27.17 (9.19)	10 (14)	0.7 (0.11)

* Total sample size for the variable testis volume is 55. Testis volume was not collected for an individual from the juvenile category (age class two).

† Sample sizes for the variable canine length are 3 for the subadult category (age class six) and 27 for the adult category (age classes seven and eight).

Do patterns of fT excretion correlate with age?

Results of ANOVA tests describing the effects of age on patterns of fT excretion and the expression of the secondary sexual characteristic BMI for each age schema are presented in Table 9. Significant results (*p*-value) of pair-wise comparisons between age categories are provided in Table 10. Both testis volume and canine length had bimodal distributions across age categories after transformation and were therefore analyzed using the Kruskal-Wallis test. Results of this test for each age schema are presented in Table 11. Post Kruskal-Wallis multiple comparisons test results are provided in Table 12. Because information on testis volume was not collected for one animal from the juvenile age category (age class two), this sample was removed from the dataset prior to analysis. Analysis of the relationship between relative canine length and age was restricted to subadult (age class six) and adult (age classes seven and eight) animals. Boxplots and beanplots illustrating the relationship between age and the transformed dependent variables log fT, log BMI, and relative testis volume are presented for each age schema in Figures 10, 11, and 12, and are presented for age and relative canine length in Figure 12.

Table 9.
ANOVA summary of results for log fT (pg/g) and log BMI (kg/m²) for each age schema. Significant results indicated in bold type.

Variable	**ANOVA Summary**				
Schema 1:	**F**	**Sum Sq.**	**Mean Sq.**	**(*df*1, *df*2)**	**Sig. (*p*-value)**
log Testosterone	1.39	0.1423	0.0711	(2, 53)	0.258
log BMI	18.53	0.2286	0.1143	(2, 53)	**7.928e-07**
Schema 2:	**F**	**Sum Sq.**	**Mean Sq.**	**(*df*1, *df*2)**	**Sig. (*p*-value)**
log Testosterone	1.53	0.2255	0.0752	(3, 52)	0.2177
log BMI	11.81	0.2251	0.0750	(3, 52)	**5.176e-06**
Schema 3:	**F**	**Sum Sq.**	**Mean Sq.**	**(*df*1, *df*2)**	**Sig. (p-value)**
log Testosterone	1.7	0.5634	0.0804	(7, 48)	0.1316
log BMI	5.094	0.2421	0.0346	(7, 48)	**0.00022**

Table 10.
Summary of pair-wise comparisons (*p*-value) of ANOVA tests between age and the dependent variables log fT (pg/g) and log BMI (kg/m²) for each age schema. Significant results are indicated with bold type

	Log fT(pg/g)		**Log BMI (kg/m²)**	
Age Category	**F**	**Sig. (p-value)**	**F**	**Sig. (p-value)**
Schema 1				
Infant to Juvenile	1.077	0.286	2.778	**0.0076**
Juvenile to Adult	1.665	0.102	5.851	**3.13e-07**
Schema 2				
Infant to Juvenile	0.044	0.965	1.717	0.0920
Juvenile to Subadult	1.611	0.113	2.591	**0.0124**
Subadult to Adult	1.456	0.151	5.515	**1.11e-06**
Schema 3				
One to Two	-0.027	0.9784	0.054	0.9572
Two to Three	-0.624	0.5359	-0.069	0.9449
Three to Four	-0.129	0.8982	1.52	0.1352
Four to Five	0.353	0.7259	1.096	0.2787
Five to Six	1.743	0.0877	2.363	**0.0222**
Six to Seven	0.730	0.4691	3.804	**0.0004**
Seven to Eight	1.965	0.0552	3.422	**0.0013**

Table 11.
Kruskal-Wallis summary of results for relative canine length (inches/cm) and relative testis volume (cc/kg) for each age schema. Significant results indicated in bold type.

Variable	**H**	***df***	**Sig. (*p*-value)**
Canine Length*			
Schema 2	3.4885	1	0.0618
Schema 3	4.3417	2	0.1141
Relative Testis Volume			
Schema 1	34.2661	2	**3.624e-08**
Schema 2	34.6300	3	**1.458e-07**
Schema 3	37.1806	7	**4.335e-06**

* Values for relative canine length were not available for Schema 1

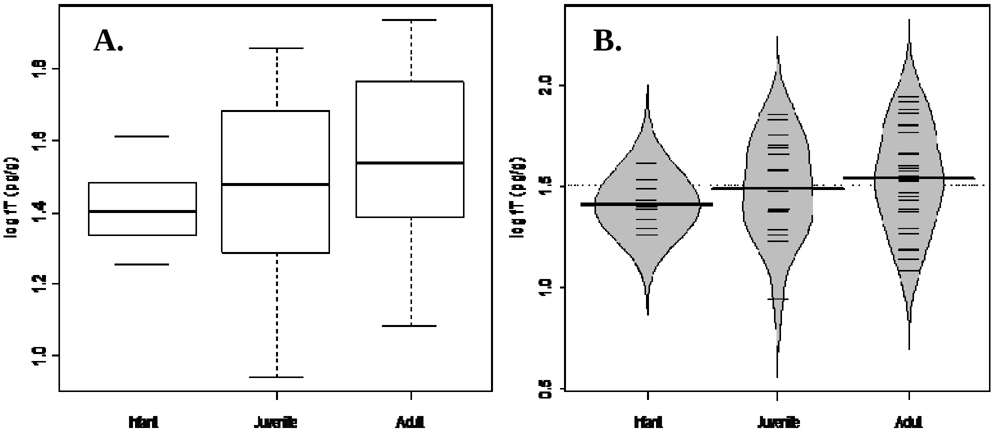
Table 12. Summary of results for post Kruskal-Wallis multiple comparison test between age and the dependent variables relative testis volume (cc/kg) and relative canine length (inches/cm) for each age schema. False indicates that observed differences between age categories did not meet the threshold of critical difference. True indicates that significance was met.

	Relative Testis Volume			**Relative Canine Length**		
Age Category	**Obs. Dif.**	**Crit. Dif.**	**Difference**	**Obs. Dif.**	**Crit.Dif.**	**Difference**
Schema 1						
Infant to Juvenile	3.3472	16.2971	FALSE	N/A	N/A	N/A
Juvenile to Adult	24.2088	11.5085	TRUE	N/A	N/A	N/A
Schema 2						
Infant to Juvenile	1.0694	20.5381	FALSE	N/A	N/A	N/A
Juvenile to Subadult	4.5556	19.9249	FALSE	N/A	N/A	N/A
Subadult to Adult	21.9310	16.1277	TRUE	10.0000	10.5007	FALSE
Schema 3						
One to Two	3.7500	35.3870	FALSE	N/A	N/A	N/A
Two to Three	17.7500	55.9518	FALSE	N/A	N/A	N/A
Three to Four	20.8750	53.0805	FALSE	N/A	N/A	N/A
Four to Five	4.3750	30.6461	FALSE	N/A	N/A	N/A
Five to Six	4.5000	33.5711	FALSE			
Six to Seven	18.7500	24.6018	FALSE	9.3478	12.9370	FALSE
Seven to Eight	6.8500	24.6018	FALSE	4.4022	11.4172	FALSE

Schema 1

Significant differences between age categories for the variable log fT were not found (F(2,53) = 1.39, *p* = 0.258). Log BMI (F(2,53) = 18.53, *p* = 7.928e-07) and relative testis volume (H(2) = 34.2661, *p* = 3.624e-08), two of the three morphological measures of sexual maturation used in this study, were found to be significantly predicted by age category. Juveniles had significantly higher values for log BMI (*p* = 0.0076) than infants, and adults had significantly higher values for log BMI (*p* = 3.13e-07) and testis volume than juveniles (difference = 24.2088). Juveniles and infants did not significantly differ in testis volume (difference = 3.3472).

(a)



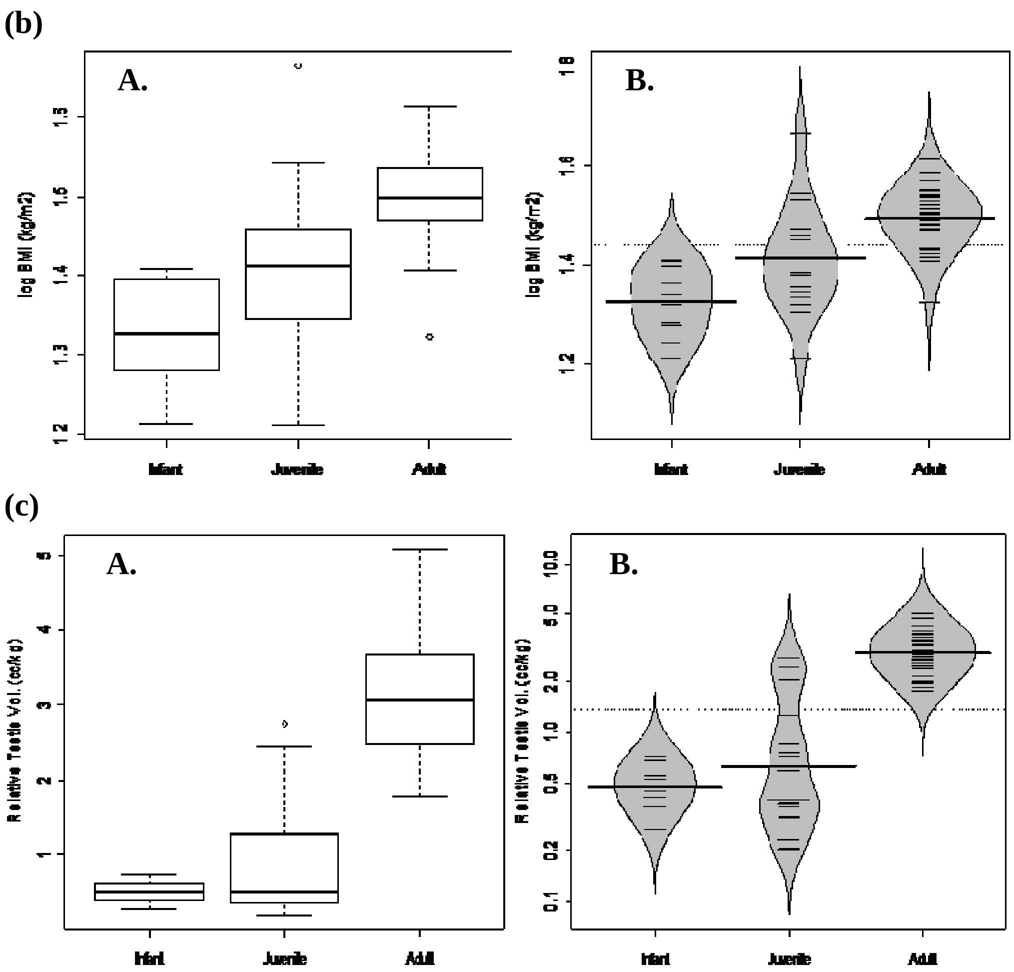


Fig. 10. A. Boxplots and **B.** beanplots of **(a)** log fT, **(b)** log BMI, and **(c)** relative testis volume of vervet males according to age category (Schema 1).

Schema 2

When the age class 'Juvenile' used in Schema 1 was further divided into 'Juvenile' and 'Subadult' categories, significance for the variable log fT was not met (F(3,52) = 1.53, *p* = 0.2177). Juveniles did not have significantly different values for log fT (*p* = 0.113) or relative testis volume (difference = 4.5556) than subadults. However, subadult animals had significantly higher values of log BMI (*p* = 0.0124) than juvenile animals. While differences between juveniles and subadults did not reach significance for two variables, the removal of subadults from the lumped category ‘Juvenile’ revealed a greater degree of variation among the dependent variables of this age group as demonstrated by the IQR. Subadults had considerably larger IQRs than juveniles for fT (23.41 versus 8.03), BMI (9.69 versus 5.35), and testis volume (7 versus 1.25). This observation suggests that the subadult stage, more than any other stage of development, is characterized by a high degree inter-individual variation in the attainment of the maturational markers BMI, testis volume, and perhaps even fT.

Moreover, the separation of subadult animals from the lumped juvenile category revealed a significant difference in values for log BMI (p = 1.11e-06) and relative testis volume (difference = 21.9310) between subadults and adults. Overall, age group membership was a significant predictor of log BMI (F(3, 52) = 11.81, p = 5.176e-06) and relative testis volume (H(3) = 34.63, p = 1.458e07). Although significance was not met, infants tended to have lower values for log BMI than juveniles (p = 0.092), but they were not found to have significantly different values for relative testis volume than juveniles (difference = 1.0694). Differences between subadults and adults in the variable relative canine length neared statistical significance (difference = 10).

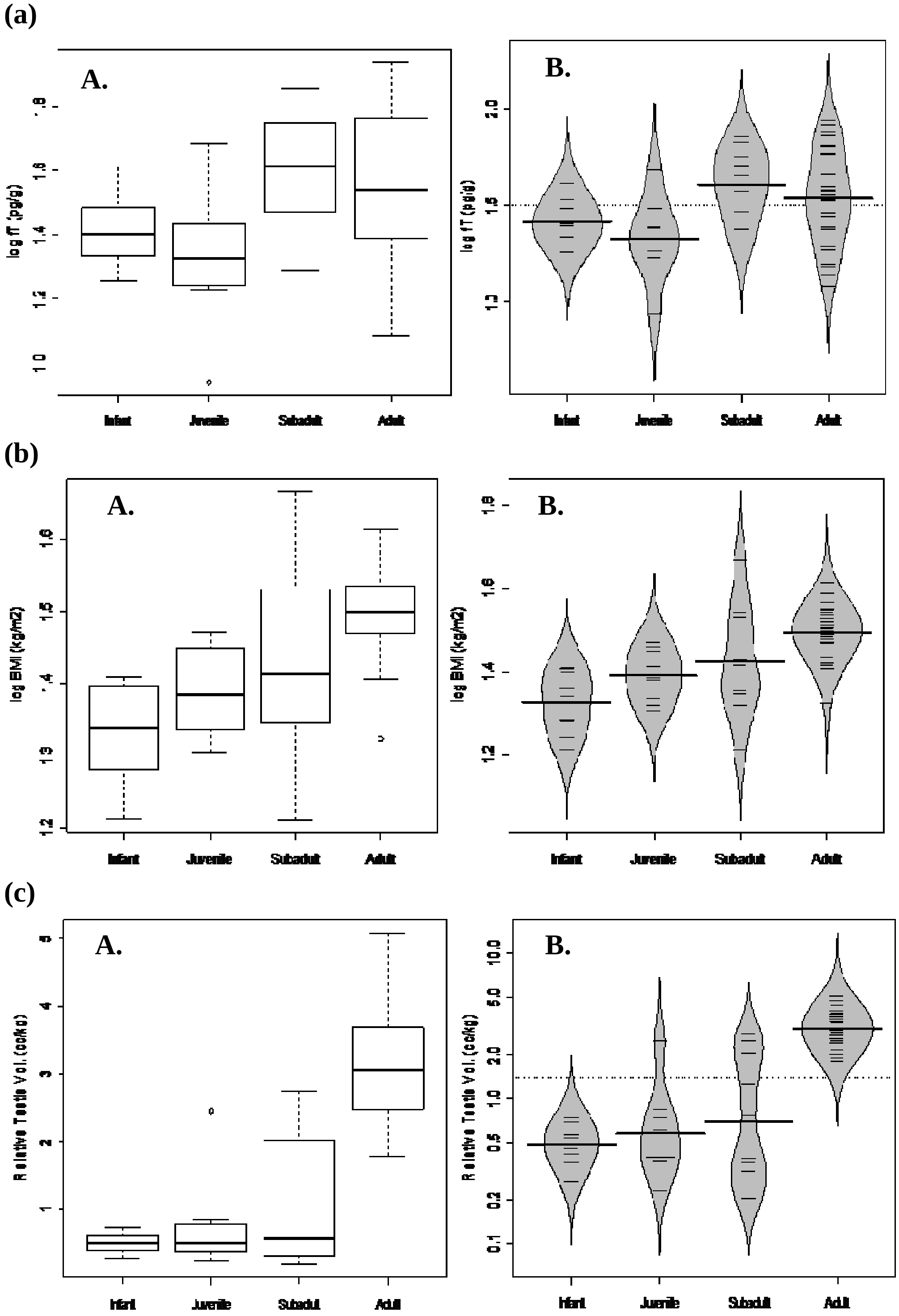
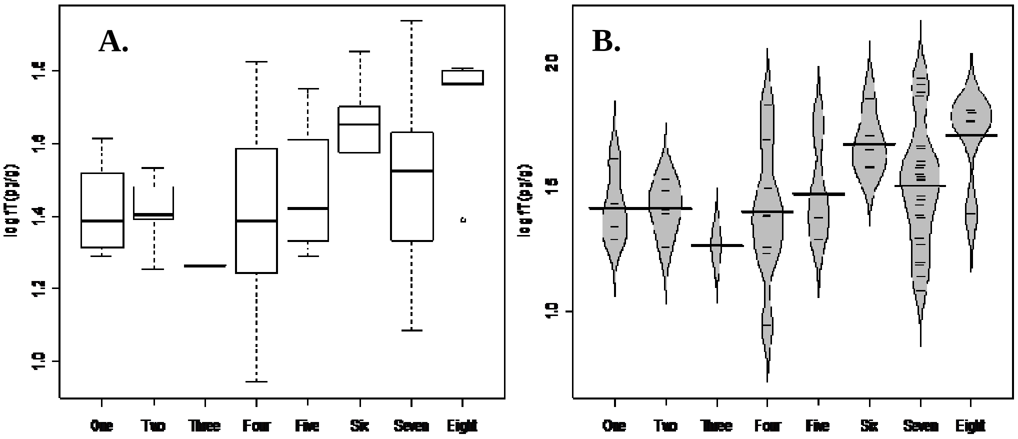


Fig. 11. A. Boxplots and **B.** beanplots for **(a)** log fT, **(b)** log BMI, and **(c)** relative testis volume of vervet males according to expanded age categories (Schema 2).

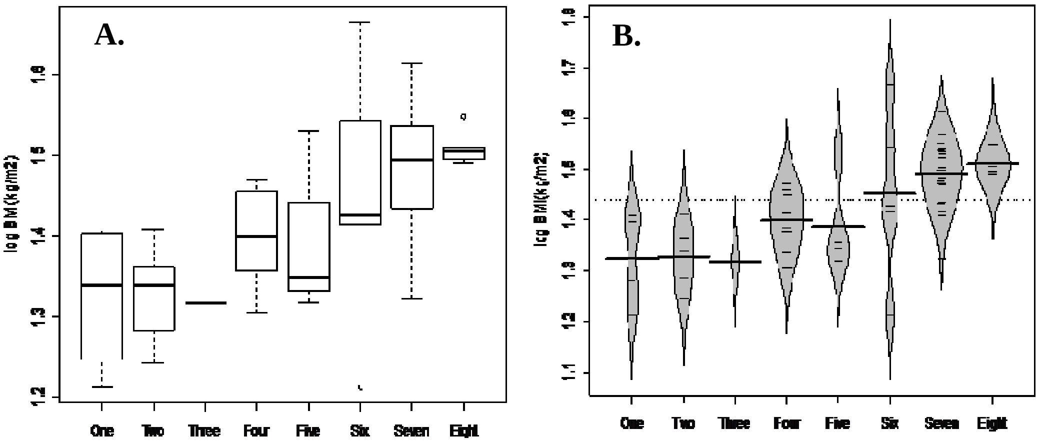
Schema 3

Log fT did not significantly differ across age classes (F(7,48) = 1.686, *p* = 0.1349), however, age class six animals tended to have higher T values than age class five animals (p = 0.0877) and the difference between age class seven and eight animals neared significance (*p* = 0.0552). Age was found to significantly predict log BMI (F(7, 48) = 5.094, *p* = 0.00016). Age class eight animals had significantly higher values for BMI than age class seven animals (*p* = 0.00128), which had significantly higher values than age class six animals (*p* = 0.0004), which had significantly higher values than age class five animals (*p* = 0.0222). Relative testis volume was found to be significantly correlated with age (H(7) = 37.1806, *p* = 4.335e-06), but values did not significantly differ between age classes. It is important to note that differences between age classes of this schema may be due to small sample sizes. Age class three in particular is only represented by a single animal. Finally, relative canine length did not significantly correlate with age (H(2) = 4.3417, *p* = 0.1141) either between age classes six and seven (difference = 9.3478) or seven and eight (difference = 4.4022). Although this breakdown highlights the small differences between age classes, general trends among the data are more difficult to isolate. Consistent with predictions, expression of the dependent variables showed age-typical patterns, with trajectories of fT, BMI, testis volume, and canine volume increasing with age (see Fig. 12).

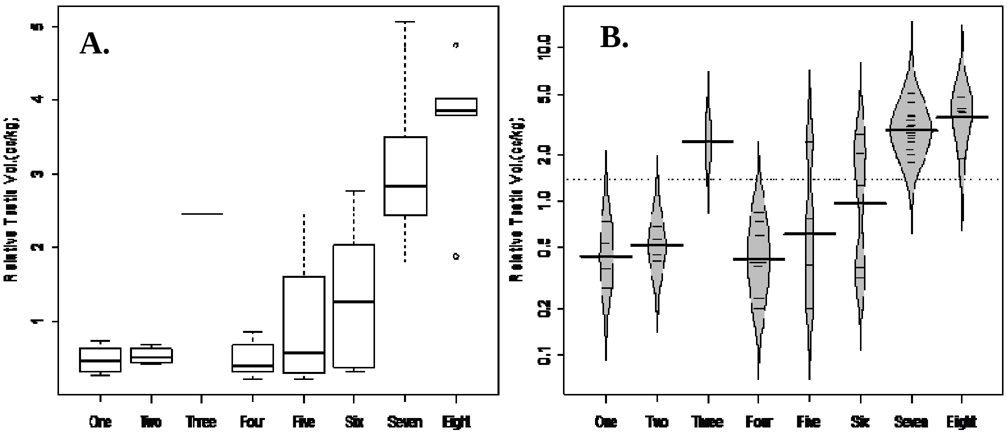
(a)


A.
log fT(pg/g)
1.0
1.2
1.4
1.6
1.8
One
Two
Three
Four
Five
Six
Seven
Eight
B.
log fT(pg/g)
1.0
1.5
2.0
One
Two
Three
Four
Five
Six
Seven
Eight

(b)


A.
log BMI(kg/m2)
1.2
1.3
1.4
1.5
1.6
One
Two
Three
Four
Five
Six
Seven
Eight
B.
log BMI(kg/m2)
1.1
1.2
1.3
1.4
1.5
1.6
1.7
1.8
One
Two
Three
Four
Five
Six
Seven
Eight

(c)


A.
Relative Testis Vol.(cc/kg)
1
2
3
4
5
One
Two
Three
Four
Five
Six
Seven
Eight
B.
Relative Testis Vol.(cc/kg)
0.1
0.2
0.5
1.0
2.0
5.0
10.0
One
Two
Three
Four
Five
Six
Seven
Eight

(d)

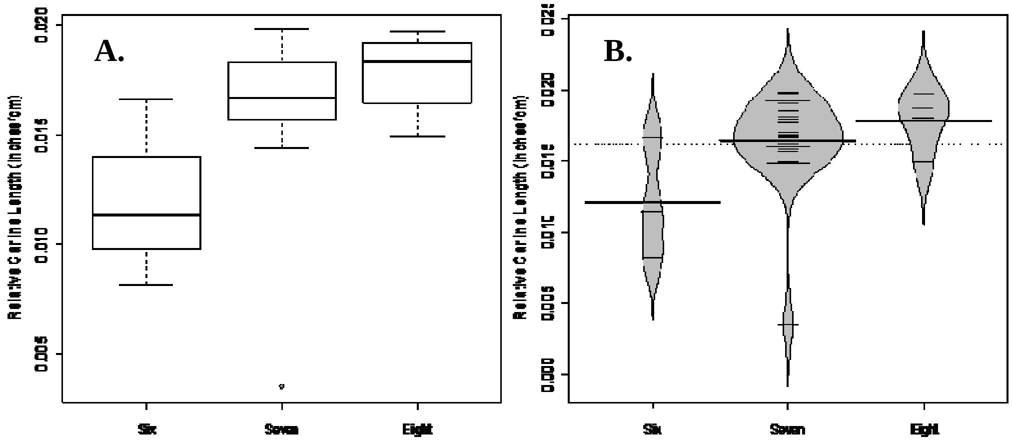


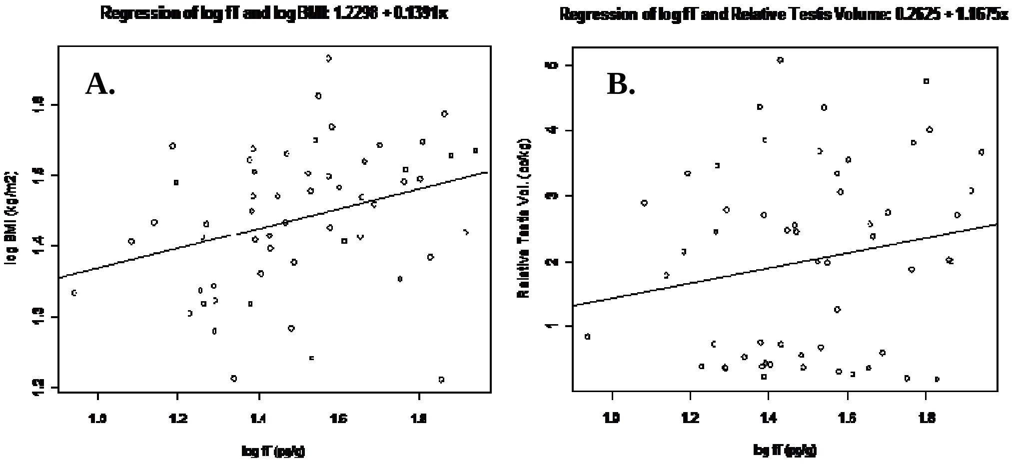
Fig. 12. A. Boxplots and **B.** beanplots for **(a)** log fT, **(b)** log BMI, **(c)** relative testis volume, and **(d)** relative canine length of vervet males according to age class (Schema 3).

Is fT more sensitive to relative age of reproductive maturity than any other transition in the life course?

Although concentrations of fT correlated generally with age, with older animals having higher log fT values than younger animals, a significant increase in fT was not evident in animals estimated to be at or near the age of reproductive maturity (age class six to seven) based on dental records for the species. This result is in direct contradiction to predictions of the study. However, significance was neared both between age classes five and six ($p = 0.0877$) and seven and eight ($p = 0.0552$). Although statistically insignificant, animals appeared to exhibit an increase in relative testis volume (Fig. 12c) and relative canine length (Fig. 12d) between age classes six and seven. A significant increase in log BMI was observed in animals at reproductive maturity (age class six: $p = 0.0222$) that continued well into adulthood (age classes seven: $p = 0.0004$, and eight: $p = 0.0013$).

Do maturational changes in fT excretion coincide with the development of secondary sexual characteristics, including enlargement of the testes and increased body mass and canine length?

The relationship between fT and the SSCs testis volume, canine length, and BMI is somewhat tenuous. While log fT was found to be significantly related to log BMI (F(1, 54) = 5.965, *p* = 0.0179), it was not a reliable predictor of relative testis volume (F(1, 53) = 1.892, *p* = 0.1748) or relative canine length (F(1, 28) = 0.0406, *p* = 0.8418). Log BMI was a better predictor of relative testis volume (F(1, 53) = 17.57, *p* = 0.0001057) but not of relative canine length (F(1, 28) = 1.346, *p* = 0.2558). Relative testis volume was the only variable that was significantly correlated with relative canine length (F(1, 28) = 4.863, *p* = 0.03582). These relationships are illustrated with scatter plots with least-squares lines of regression in Fig. 13.



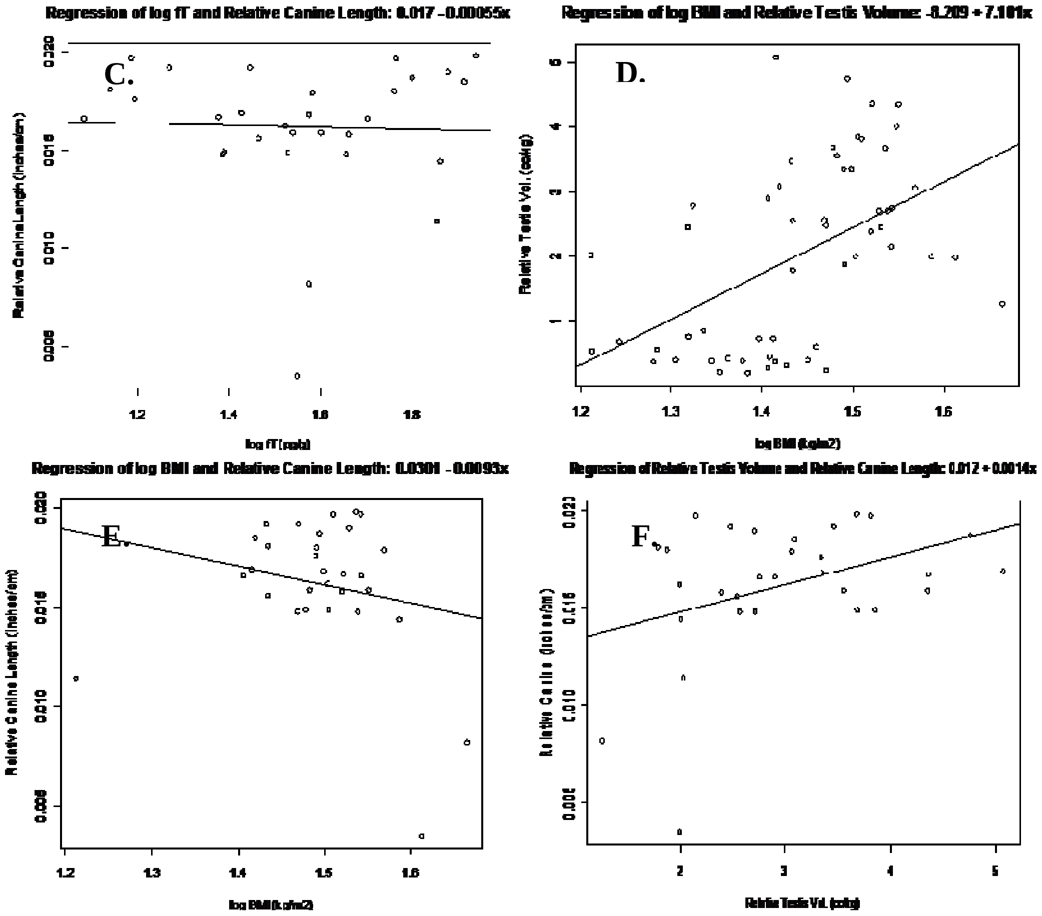


Fig. 13. Scatterplots with least-squares regression lines for the log-transformed or relative values of **A.** fT and BMI, **B.** fT and testis volume, **C.** fT and canine length, **D.** BMI and testis volume, **E.** BMI and canine length, and **F.** testis volume and canine length.

Is inter-individual variation in fT and the development of SSCs greatest for individuals approaching age at reproductive maturity?

Variation in the dependent variables was evident for individuals of all age categories; however, inter-individual variation was generally greatest for subadult and adult animals as demonstrated by the IQR. Using the age classification of Schema 2, subadults and adults were found to have considerably larger IQRs than juveniles and infants for fT (Infant: 8.665; Juvenile: 8.03; Subadult: 23.41; Adult:

33.54) and testis volume (Infant: 0.5; Juvenile: 1.25; Subadult: 7; Adult: 13), although not for BMI (Infant: 3.94; Juvenile: 5.35; Subadult: 9.69; Adult: 4.41). Although not collected for infant and juvenile animals, inter-individual variation in canine length was greater for subadults (0.18) than adults (0.09). While small sample sizes may have contributed to these results, particularly for adults, they can also be interpreted to reflect different pathways of maturation.

VI. DISCUSSION

Although several significant findings emerge from the data, all results must be regarded as preliminary until they can be corroborated with further observations, both cross-sectional and longitudinal, from a larger sample population. The sequence of events that characterize male vervet monkey growth and sexual maturation is summarized in Figures 10, 11, and 12, and parallels findings from other works summarized in Table 4. Excretion of T and maturation of the male SSCs body mass, testis volume, and canine length followed markedly different trajectories. Significant results are summarized in Tables 11 and 12. While fT did not undergo a significant spurt at the onset of reproductive maturity as expected, age class six animals tended to have higher values for fT than age class five animals and differences in fT between age classes seven and eight neared statistical significance, suggesting a possible role of T later in adulthood. Body mass showed significant increases at age classes six, seven, and eight, suggesting that body mass is strongly correlated with an adolescent growth spurt. Although relative testis volume correlated with age, significant differences were not found between age classes. However, visual comparison of the beanplots showed modest increases in testis volume at age classes five, seven, and eight. The spike in body mass corresponds roughly to the eruption of the canine teeth between age classes six and seven and parallels findings for vervets by Whitten and Turner (2009). Similar growth spurt patterns have been demonstrated for baboons, (Jolly and Phillips-Conroy, 2003, 2006), mandrills (Setchell and Dixson, 2002), and mangabeys (Deputte, 1992), and are reportedly greater for males than for females (Glassman *et al.*, 1984).

Jolly and Phillips-Conroy (2003, 2006) interpreted this pattern as a reproductive strategy of preparation prior to emigration from the natal group and competition for a place in the dominance hierarchy of the adoptive troop. Traits that contribute to male reproductive functioning (i.e. spermatogenesis) and the ability of males to compete for or attract reproductively-viable mates, including the endocrine mechanisms underlying the development of these traits, are expected to emerge in preparation for critical life history events. Trajectories of T secretion in many animals follow such a pattern of preparation for and activation of reproduction, with spikes directly preceding and following reproductive events (Alberts and Altmann, 1995). Changes in T excretion and the emergence of male SSCs reported here appear to follow a mosaic pattern, beginning with significant increases in body mass at age class six and continuing well into adulthood, the eruption of the canine teeth between age classes six and seven, followed by descent and enlargement of the testes beginning around age class seven, and rounded off by a near-significant increase in fT at age class eight. It is uncertain whether these results can be interpreted as following a pattern of developmental preparation for reproduction. Documentation of the timing of first reproduction of individuals is necessary to support the application of this interpretation to the data.

As discussed earlier, the expectation of this study, that fT levels would increase as age of reproductive maturity was approached, with subadult males exhibiting higher concentrations of fT than any other age group in preparation for dispersal and reproduction, was not upheld statistically. Furthermore, fT was expected to positively correlate with the emergence of the SSCs body mass, testis volume, and canine length. Although fT positively correlated with body mass, the descent and enlargement of the testes and increases in canine length could not be significantly attributed to differences in fT concentrations. This result is consistent with previous findings for baboons (Castracane *et al.*, 1981; Muehlenbein *et al.*, 2001) but not for humans (Prader, 1984). Body mass, testis volume, and canine size tended to co-vary, although BMI did not significantly predict canine size independent of the effects of testis volume.

In a recent study, Gesquiere *et al.* (2005) found that early-maturing baboon males had consistently higher fT concentrations than late-maturing males. In some mammals, such as the Mongolian gerbil (*Meriones unguiculatus*), patterns of sexual maturation are strongly bimodal, with animals characterized as either early-maturing or late-maturing strategists (Clarke *et al.*, 1986). Among primates, divergent developmental patterns have been reported by Watts (1985, 1990) for rhesus macaques and Tanner (1978, 1981) and Bielicki *et al.* (1984) for humans. Vervet males represented in this study exhibited considerable variation both within and between age classes. Adult (age classes seven and eight) animals generally had the greatest variation in values for fT and testis volume and subadults (age classes five and six) had the greatest inter-individual variability for body mass and canine length. Although animals could not easily be classified as early-maturing and late-maturing morphs, future longitudinal studies will provide another dimension to this work by determining if divergent developmental strategies exist for vervets. Moreover, longitudinal records would establish whether individual fT concentrations are stable throughout the vervet life course as reported in baboons (Gesquiere *et al.*, 2005) and rhesus macaques (Bercovitch and Clarke, 1995) or whether they fluctuate in response to life stage transitions or challenges of the environment.

The secretion of T and the development of body systems have been shown to be sensitive to a variety of factors in vervets and other primate species, including maternal rank (e.g., *Ch. aethiops*: Lee, 1984a; *Macaca mulatta*: Dixson and Nevison, 1997; *Papio* spp.: Bercovitch and Strum, 1993; Altmann and Alberts, 2003, 2005; Johnson, 2003), dominance rank (e.g., *Macaca mulatta*: Bercovitch, 1993; Bercovitch and Clarke, 1995; *Mandrillus sphinx*: Setchell and Dixson, 2001; *Pan troglodytes*: Muehlenbein *et al.*, 2004; Muller and Wrangham, 2004; Anestis, 2006; *Papio ursinus*: Beehner *et al.*, 2006), and ecological variables (e.g., *Macaca mulatta*: Bernstein *et al.*, 1974; Robinson *et al.*, 1975; Gordon *et al.*, 1976). Although these components were not included in this study, it is interesting to note that at most sites one or two adult males had considerably higher fT concentrations than all others. The high variability in fT excretion among adult animals (age classes seven and eight) observed here further suggests that these males may be repressing the T levels of other males. This conclusion was also made in Whitten and Turner (2004). Future behavioral analysis is required to determine if this variability in patterns of fT excretion is associated with dominance rank.

A neonatal surge in T within the first few months of life has been well documented in mammals (e.g., *Callithrix jacchus*: Lunn *et al.*, 1994; *Homo sapiens*: Forest *et al.*, 1974; Winter *et al.*, 1975, 1976; Andersson *et al.*, 1988; *Macaca mulatta*: Dixson, 1986; Mann *et al.*, 1989; Nevison *et al.*, 1997; *Pan troglodytes*: Winter *et al.*, 1975; *Rattus* spp.: Corbier *et al.*, 1978, 1992; Baum *et al.*, 1988). However, this surge could not be demonstrated in this work because invasive sampling techniques prohibited the collection of fecal samples from infants within the first 2-3 months of life. In females, menarche marks the onset of reproductive maturity, which may be identified through visual observation of perineal swelling or menstrual bleeding (Resko *et al.*, 1982), ultrasonographic assessment of ovarian and uterine volume (Rockett *et al.*, 2004), or by monitoring reproductive hormones (e.g., LH, FSH, 17β-estradiol, inhibin A and B) (Ross and Lipsett, 1978; Buck Louis *et al.*, 2008). However, there is no obvious criterion of male reproductive readiness (Gesquiere *et al.*, 2005). This study follows much of the primate literature in estimating reproductive maturity on the basis of the descent and enlargement of the testes (e.g., Castracane *et al.*, 1986; Nieuwenhuijsen *et al.*, 1987; Crawford *et al.*, 1997; Muehlenbein *et al.*, 2001, 2002; Jolly and Phillips-Conroy, 2003; Charpentier *et al.*, 2008; Luetjens and Weinbauer, 2012). However, testicular development occurs at a gradual rate and is subject to inter-individual variability.

Above all else, the results presented here highlight the considerable variation present in patterns of male vervet monkey growth and sexual maturation. Although individual variation in phenotypic traits is a necessary condition of differential fitness and natural selection (Darwin, 1871; Endler, 1986), variation in life history components between individuals as opposed to aggregates, including species, has only recently become a subject of serious inquiry (Cam *et al.*, 2002; Kappeler *et al.*, 2003; Pereira and Leigh, 2003; Figueredo *et al.*, 2005). Inter-individual variation in the ontogenetic trajectory of a trait in particular has been argued to represent an important resource for investigations of the underlying mechanisms of life history evolution (Wright and McConnaughay, 2002; Leigh and Blomquist, 2007). Although this cross-sectional examination provided a description of age-graded trajectories of T excretion and the development of SSCs in wild male South African vervet monkeys, longitudinal data are necessary to identify causes of intra- and inter-individual variation in the expression of these traits. Factors affecting the timing and shape of individual life histories are complex and many. Longitudinal data are better able to account for ecological and social conditions that may exert an influence on individual schedules of somatic growth and sexual maturation.

VII. CONCLUSION

Knowledge of baseline patterns of somatic growth and sexual maturation is critical to determining species-specific parameters of development, including the timing of sexual maturity and correlates of reproductive success, as well as mapping individual trajectories (Leigh, 1992). Cross-sectional data of 56 vervet monkeys indicate that fT is not a reliable predictor of patterns of somatic growth and sexual maturation in male vervet monkeys. Like baboons and several other primate taxa, male vervets exhibited an adolescent growth spurt in body mass and testis volume corresponding to the eruption of the canine teeth. This spurt can tentatively be interpreted to reflect a strategy of preparation for dispersal and competition for reproduction. However, future longitudinal observations are necessary to support this interpretation.

Although general trends in patterns of T secretion and the development of male SSCs emerge for the species, considerable inter-individual variation existed for these traits within age classes. However, given that cross-sectional techniques were used, this variation may simply reflect day-to-day variability in circulating T (see Morley *et al.*, 2002). While reducing the identification of ‘false’ phenomena (Muehlenbein *et al.*, 2001), the use of cross-sectional data to study patterns of growth and development is associated with certain limitations, including the inability to detect all physiological and hormonal changes associated with puberty given the rapid growth period of many nonhuman primates, including vervets (Castracane *et al.*, 1986; Leigh, 1996). Thus, longitudinal data would provide greater confidence that small changes in individual trajectories of growth and maturation are accounted for. Further research on other possible correlates of patterns of T secretion and the maturation of SSCs would provide additional insight into the forces regulating male vervet monkey growth and reproductive functioning.

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