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Behavioral Development of Captive Male Hybrid Cercopithecine Monkeys

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Intergeneric hybrid · Behavioral development · Sex-linked paternal effect · *Chlorocebus pygerythrus* · *Cercopithecus albogularis*

Abstract
In this study, we compare the behavioral development of captive male vervet monkeys *(Chlorocebus pygerythrus)* and Sykes' monkeys *(Cercopithecus albogularis)* to male hybrids of these species. Focal animal sampling sessions were conducted on the study subjects from birth to 90 months of age. Behavioral categories (affiliative, approach, play, sexual, tension, aggressive) were plotted for each species and the hybrids; curves were fitted using polynomial regression and were evaluated with the Wilcoxon signed ranks test. With the exception of play behaviors, the male *C. pygerythrus* × *C. albogularis* hybrids modeled the Sykes' pattern of behavioral development. We suggest that this result reflects a sex-linked paternal effect.

Introduction

Guenons (tribe Cercopithecini) are a large, diverse group of monkeys that vary greatly in features such as pelage, chromosome number, morphology, niche, diet and mating system. There is little agreement on the taxonomic classification of the cercopithecines [Thorington, 1970; Groves, 2001; Butynski, 2002; Disotell and Raaum, 2002; Tosi et al., 2004]; for example, the number of recognized genera varies from 1 to 6, with perhaps the most widely agreed upon classification includ-

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ing *Cercopithecus*, *Allenopithecus*, *Miopithecus* and *Erythrocebus* [Butynski, 2002]. Molecular data suggest that the origin of the guenon radiation occurred at least 9.5 million years ago [Disotell and Raaum, 2002]; however, there is some thought that the cercopithecines are still in an active stage of speciation, with many taxa retaining the ability to hybridize [Dutrillaux et al., 1988].

Multiple guenon taxa are often found in the same ecological communities in the wild [Gautier-Hion, 1988; Lernould, 1988; Chapman et al., 2000], and several instances of natural hybridization have been documented for parapatric populations assigned to the same, or closely related, species [Booth, 1955; Dandelot, 1959; Aldrich-Blake, 1968; Struhsaker, 1970; Kingdon, 1971; Tutin, 1999; Detwiler, 2002]. Less common is hybridization between sympatric, ecologically differentiated taxa [Jolly, 2001; Detwiler, 2002]. In this paper, we describe the behavioral development of captive male hybrids from two guenon genera: the vervet monkey (*Chlorocebus pygerythrus*, Cuvier, 1821) [Groves, 1989; Disotell, 2000] and the Sykes' monkey (*Cercopithecus albogularis*, Sykes, 1831) [Groves, 2001]. Although traditionally placed in the genus *Cercopithecus*, most taxonomists currently separate the vervet monkey into the genus *Chlorocebus* and place it in a clade with the patas monkey *(Erythrocebus patas)* [Disotell, 2000; Groves, 2000, 2001; Tosi et al., 2002]. There are no reports of intergeneric breeding for cercopithecines in the wild [Lernould, 1988].

In terms of observable characteristics, Sykes' monkeys are yellowish gray or olive in hair color with a white throat and white ear tufts [Napier, 1981]. In contrast, vervets are yellowish to olive on the back and crown with white under parts, blue abdominal skin and black facial skin encircled with a white brow band and white cheeks. Males in this species have a red penis and turquoise blue scrotum. Sykes' monkeys are sexually dimorphic, with males larger in body and canine size than females (male average 7.7 kg; female average 4.0 kg) [Bramblett and Coelho, 1987]. Growth rates of male Sykes' monkeys are slow, and apical closure of the canines and behavioral maturity are attained around the age of 84 months. Compared to Sykes' monkeys, vervets are smaller and less sexually dimorphic (male average 5.5 kg; female average 4.1 kg). Male vervets experience rapid growth, with canine apical closure and behavioral maturity reached at around 60 months of age [Bramblett, 1980; Bramblett and Coelho, 1987; Melnick and Pearl, 1987]. These species are genetically dissimilar as well: Sykes' monkeys have a diploid number of 70 while vervets have a diploid number of 60 [Dutrillaux et al., 1980].

Vervet and Sykes's monkey also differ in terms of social organization and niche. Social groups of the arboreal, forest-living Sykes' monkey are typically unimale/multifemale with 8–10 individuals [Struhsaker, 1969]. Since social interactions are somewhat rare in Sykes' monkey groups [Struhsaker, 1969], dominance hierarchies are difficult to detect [Cords, 1988, 2002; Erhart, 1993]. In comparison, vervets are more terrestrial and live in savanna woodland areas [Fedigan and Fedigan, 1988]. Social groups are multimale/multifemale and somewhat larger in size, with 20 or more animals [Struhsaker, 1969; Fedigan and Fedigan, 1988]. Vervet social organization, especially dominance [Bramblett et al., 1982] and spatial relationships [Ehardt-Seward and Bramblett, 1980], strongly reflect the long-lasting, stable hierarchies of female matrilines. Adult males are part of a group's dominance hierarchy, but their rank depends on their ability to form alliances and to intimidate other individuals [Bramblett et al., 1982], and they are not necessarily the most dominant animals in the group [Bramblett et al., 1982; Rowell, 1988]. Both Sykes' and vervet males migrate from their natal groups at adulthood [Packer and Pusey, 1987].

Differences in social organization are reflected in male mating opportunities for Sykes' and vervet monkeys. Competition between male Sykes' monkeys for access to breeding females is important since differences in reproductive success between resident and extra-group males are potentially great [Cords, 1987, 2002]. Indeed, resident males attempt to control access to their groups and are highly intolerant of male intruders and chase and threaten them [Struhsaker and Leland, 1979]. Frequent male agonistic interactions during multimale influxes reflect intense competition for mates. Sykes' females mate with multiple males if available, and between 5 and 20% of observed matings occur without the resident male's knowledge [Cords, 1988]. In contrast, because vervet social groups commonly include more than one male, male-male competition occurs within the group [Struhsaker, 1969; Rowell, 1988]. Although male-male interactions are usually aggressive [Bramblett, 1980], vervet males are known to cooperate to increase mating success [Melnick and Pearl, 1987].

In this paper, we describe the behavioral development of male vervet and Sykes' monkeys along with male *C. pygerythrus* × *C. albogularis* hybrids living in a mixed species cercopithecine colony. Based on the behavioral and ecological differences between the study species, we hypothesized that there would be typical patterns of male behavioral development for each species. We also hypothesized that the behavioral development of the *C. pygerythrus* × *C. albogularis* males would be more similar to that of vervet males than Sykes' males because the hybrids were offspring of vervet females and the majority of their behavioral interactions occurred with members of their natal group [Bramblett, unpubl. data]. Developmental trajectories of the behavior of *C. pygerythrus* × *C. albogularis* males have yet to be reported.

Materials and Methods

Study Subjects

The male study subjects (vervets n = 3; Sykes' monkeys n = 3; hybrids n = 2) were observed in a captive group setting comprised of multiple guenon species *(C. pygerythrus*, *C. albogularis* and *C. petaurista)* and their hybrids at the University of Texas at Austin. The study subjects are descended from T.E. Rowell's guenon groups formed in 1966 at Makerere University College, Kampala, Uganda [Rowell, 1970], members of which were imported to the University of Texas in 1968 and 1969 [Bramblett, unpubl. data]. Originally, the vervet and Sykes' monkeys were housed separately in large indoor/outdoor enclosures at the University's Balcones Research Center [Bramblett, 1980]. Space constraints, however, led to the introduction of a male lesser spot-nosed monkey *(C. petaurista)* to the Sykes' group in 1980, and addition of a Sykes' male to the vervet group in 1984. As a result, 3 *C. albogularis* × *C. petaurista* hybrids (1 male and 2 females) and 2 *C. pygerythrus* × *C. albogularis* hybrids (2 males) were born in the colony between 1981 and 1986 [Bramblett, unpubl. data]. We hypothesize that these cross-species matings were the result of incest avoidance by females (see Discussion). Finally, in 1986 the colony was reduced in size, and the species and hybrids were moved to an indoor room approximately 6 × 3 × 2.5 m at the University's Animal Resource Center. Therefore, the current study group is a mixed species group, which averaged 21 individuals over the study period and included individuals of both sexes and all age classes. The ratio of species members was consistent over the study period with typically

Table 1. Behavioral categories

Affiliative	Approach	Play	Sexual	Tension	Aggressive
Contact	lipsmack	false chase	ejaculate	avoid	bite
Embrace	present groom	harass	genital inspect	grimace	chase
Groom	social approach	mouth	genital muzzle	ignore	cuff
Hold		play	hip hold	mount	displace
Huddle		pull	hip touch	present	display
Muzzle		wrestle	mount	rapid glance	encircle
Touch				tail erect	forebob
				yawn	gape
					headbob
					headshake
					fight
					lid
					stare

8 vervet monkeys, 8 Sykes' monkeys, 3 *C. petaurista* × *C. albogularis* hybrids and 2 *C. pygerythrus* × *C. albogularis* hybrids.

The male hybrids in this study were offspring of *C. pygerythrus* dams and a *C. albogularis* sire. Their coat pelage and markings were more similar to vervet monkeys than Sykes' monkeys. Although darker than a typical vervet, the hybrids were olive on the back and crown, with white under parts, and white brow bands and white cheeks on their faces. At sexual maturity, both hybrid males had the conspicuous turquoise blue scrotum of adult male vervets.

Data Acquisition and Behavioral Measures

Sampling sessions were conducted on the study subjects from birth to 90 months of age. Data were collected using focal animal sampling [Altmann, 1974] and diurnal scheduling in which the behavior of a focal subject was continuously recorded during 10-min samples. Once a focal animal had been sampled, he was not re-sampled until all other study subjects were observed, and samples were balanced equally between study subjects. Data include 6,025 sampling sessions collected from January 1987 to May 1995 by multiple observers. An interobserver reliability score of at least 90% was maintained throughout the study period. Six behavioral categories (affiliative, approach, play, sexual, tension and aggressive; table 1) were selected for comparison.

Data Analyses and Statistical Treatment

Comparisons between the species and the hybrids were made using mean rates per hour of sampling for 6-month intervals beginning at birth and ending at 90 months of age. Behavioral categories were plotted for each of the study species and the hybrids, and curves were fitted using polynomial regression. The Wilicoxon signed ranks test was used to determine when curves differed from one another [Sokal and Rohlf, 1995].

Results

We found that developmental curves for the vervet and Sykes' males were significantly different for all of the behavioral categories: affiliative ($Z = -2.73$, $p = 0.006$; fig. 1), approach ($Z = -2.05$, $p = 0.04$; fig. 2), attack ($Z = -2.45$, $p = 0.01$; fig. 3), sexual ($Z = -2.84$, $p = 0.005$; fig. 4), tension ($Z = -3.35$, $p = 0.0008$; fig. 5) and play ($Z = -2.33$, $p = 0.02$; fig. 6).

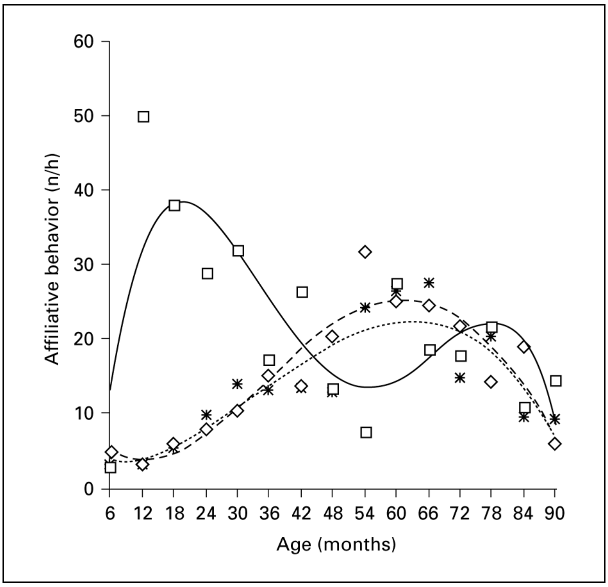

Fig. 1. Comparison of mean rates per hour for affiliative behaviors. Vervets = Squares and solid line; Sykes' monkeys = diamonds and dashed line; hybrids = stars and dotted line.

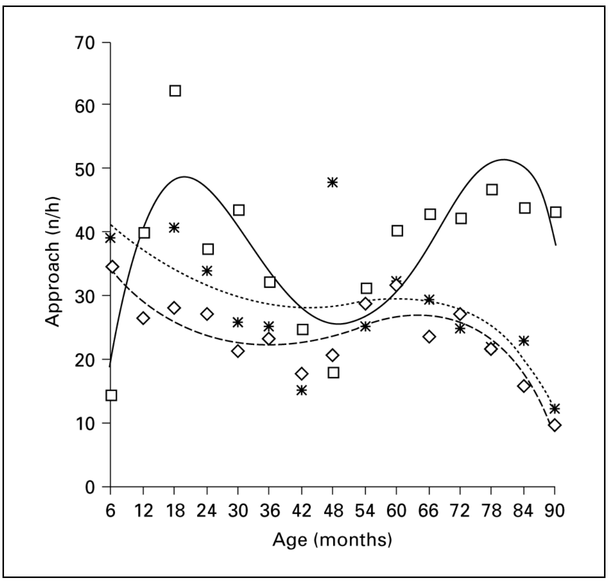

Fig. 2. Comparison of mean rates per hour for approach behaviors. Vervets = Squares and solid line; Sykes' monkeys = diamonds and dashed line; hybrids = stars and dotted line.

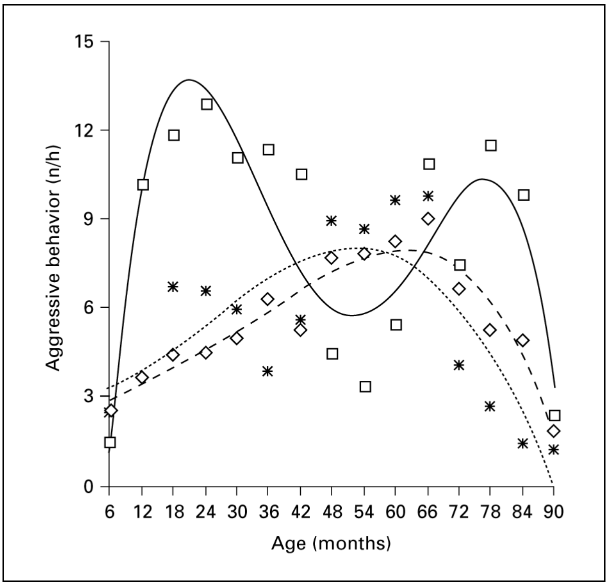

Fig. 3. Comparison of mean rates per hour for aggressive behaviors. Vervets = Squares and solid line; Sykes' monkeys = diamonds and dashed line; hybrids = stars and dotted line.

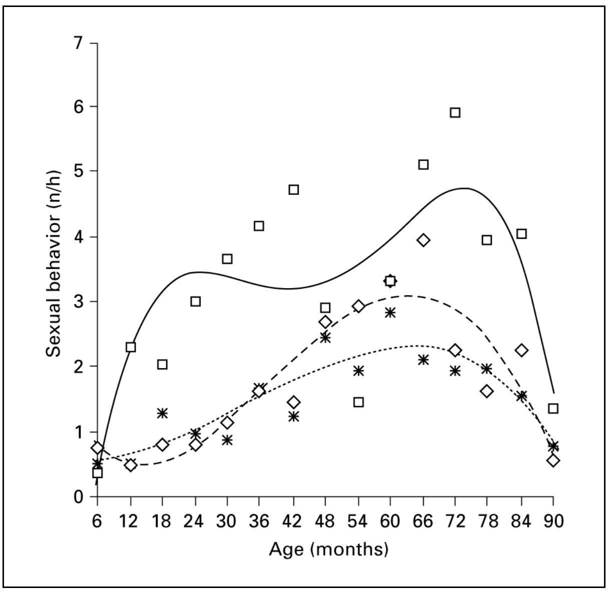

Fig. 4. Comparison of mean rates per hour for sexual behaviors. Vervets = Squares and solid line; Sykes' monkeys = diamonds and dashed line; hybrids = stars and dotted line.

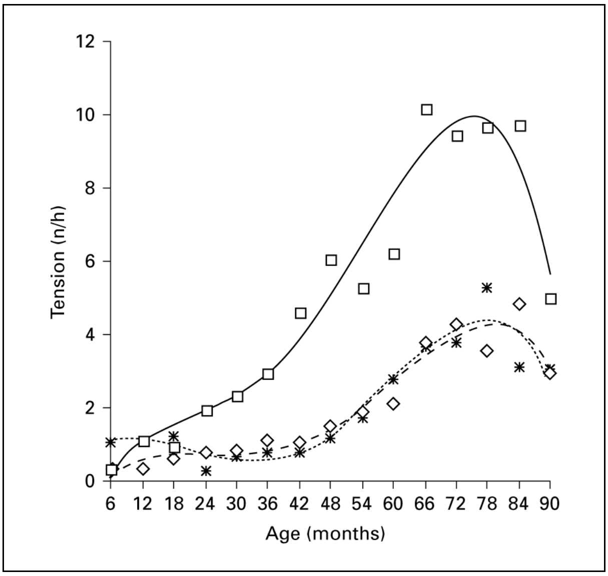

Fig. 5. Comparison of mean rates per hour for tension behaviors. Vervets = Squares and solid line; Sykes' monkeys = diamonds and dashed line; hybrids = stars and dotted line.

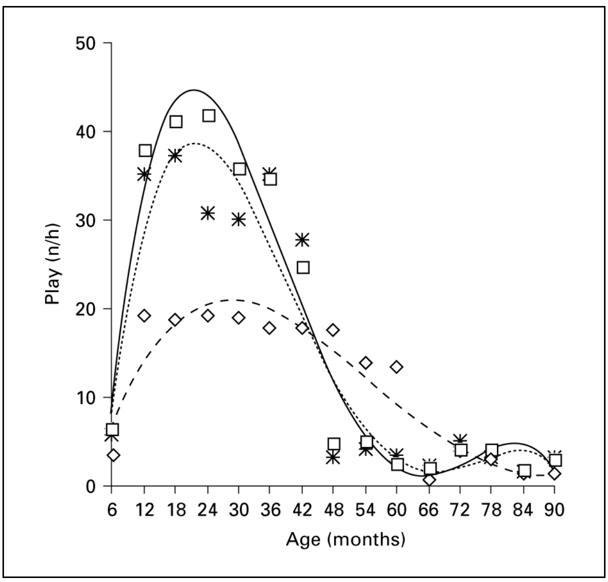

Fig. 6. Comparison of mean rates per hour for play behaviors. Vervets = Squares and solid line; Sykes' monkeys = diamonds and dashed line; hybrids = stars and dotted line.

The *C. pygerythrus* × *C. albogularis* males modeled the Sykes' pattern of development in 5 of 6 behavioral categories. Behavioral developmental curves for the hybrid males were significantly different from vervet males for the following behaviors: affiliative ($Z = -2.44$, $p = 0.01$; fig. 1), approach ($Z = -3.23$, $p = 0.001$; fig. 2), attack ($Z = -2.98$, $p = 0.003$; fig. 3), sexual ($Z = -2.86$, $p = 0.004$; fig. 4) and tension ($Z = -3.12$, $p = 0.002$; fig. 5). Play was the only behavioral category in which developmental curves were significantly different between the hybrid males and Sykes' males ($Z = -2.41$, $p = 0.02$; fig. 6).

Discussion

We found that behavioral development differed for male vervet and Sykes' monkeys. In particular, the Sykes' males had consistently lower rates of behavioral activity compared to the vervet males. This is not surprising since, like other forest guenons, Sykes' monkeys interact seldom and subtly, with relatively little use of overt contact or gestures [Struhsaker, 1969]. With the exception of approach behaviors, behavioral rates for the Sykes' males increased after infancy and decreased just before or at the time of maturation (84 months). Typically the behavioral rates of primate infants are low, probably because of their small body size, less developed motor abilities and inexperience, and vulnerability to predators and intragroup aggression [Chism, 1991]. Behavioral activity usually increases as primates enter the juvenile stage and then decreases somewhat as sexual and social maturity are attained. In contrast, with the exception of tension behaviors, behavioral rates were generally bimodal in distribution for the vervet males. They experienced a rapid increase in behavioral activity during infancy [Bramblett, 1980], a decrease near the time of maturation (60 months), followed by an increase in early adulthood and then a decrease in behavioral activity thereafter. It is unclear why behavioral rates increase in early adulthood for the vervet males.

We hypothesized that the behavioral development of the *C. pygerythrus* × *C. albogularis* hybrid males would be more similar to vervet males than Sykes' males. As offspring of vervet females, the hybrid males grew up as part of a vervet group within the mixed species *Cercopithecus* colony, and the majority of their behavioral interactions were with members of their natal group [Bramblett, unpubl. data]. Hybrid males played more with their vervet peers than with juvenile Sykes' monkeys, their grooming relationships were almost exclusively with vervets, and as they grew older the hybrids maintained proximity to, and established alliances with, adult vervet males. Similar results have been seen for wild redtail *(C. ascanius)* × blue monkey (*C. mitis*) hybrids, who were always integrated into their mother's redtail groups [Struhsaker et al., 1988]. Contrary to our expectations, however, developmental trajectories of the *C. pygerythrus* × *C. albogularis* males were more similar to Sykes' males than vervet males for all but one of the behavioral categories. We suggest that this may reflect a sex-linked paternal effect on behavioral development. Comparable studies of male hybrid behavioral development from other *Cercopithecus* species are needed to test this finding.

One benefit of hybridization is that it increases reproductive options when appropriate mates are scarce. Several researchers have suggested that cross-species matings of wild cercopithecines may reflect a shortage of conspecific mates, sex ratio biases and/or forest fragmentation [Struhsaker et al., 1988; Tutin, 1999; Detwiler, 2002]. In this study, the cross-species mating of vervet and Sykes' monkeys seems to have been the result of incest avoidance by vervet females [Bramblett, 1986]. In the 1984 mating season, mothers of the hybrids appeared to avoid mating with vervet males, who were their half-siblings, and instead copulated with a newly introduced Sykes' male. Obviously, the species-specific pelage and facial features of the Sykes' male did not function as prezygotic isolating mechanisms for vervet females.

There are also possible benefits of hybridization, such as large body size, for offspring. Struhsaker et al. [1988] proposed that the larger body size of male red × blue monkey hybrids allowed them to displace the smaller redtail monkeys from feeding sites. Although the hybrid *C. pygerythrus* × *C. albogularis* males were larger in body size compared to vervet males, they generally did not win contests over valued food sources [Bramblett, unpubl. data]. This result, however, may be an effect of captivity because both hybrid males retained their mother's low dominance ranks into adulthood, a situation that would not have happened in the wild.

Obvious disadvantages to cross-species matings may include less fertile matings compared to conspecific matings and hybrid offspring with lowered fitness. Struhsaker et al. [1988] concluded that this was the case for the wild hybrid redtail × blue monkeys they studied. They found that longer interbirth intervals resulted in lower reproductive rates for hybrid females compared to redtail and blue monkey females, and they did not document any breeding for the one hybrid male present in their study groups. Even though the *C. pygerythrus* × *C. albogularis* males in this study exhibited penile erections in the usual social contexts and experienced several mating seasons as adults before the colony was disbanded in 1995, neither hybrid male was ever seen to mate, and it is clear that neither sired any offspring. The hybrid males seem to have experienced fewer reproductive opportunities because of relatively greater rejection by females [Bramblett, unpubl. data]. Female rejection of the hybrid males may have been related to factors such as female choice, mate recognition barriers and/or incest avoidance due to the captive environment. Another possibility is that the *C. pygerythrus* × *C. albogularis* males were partially or completely infertile. In mammals, male hybrids are more likely to suffer impaired fertility compared to females [Haldane, 1922], perhaps due to sex-linked recessive genes acting epistatically in hybrids [Turelli and Orr, 1995].

It seems that the disadvantages of hybridization for cercopithecine taxa outweigh the potential benefits. However, when groups are small, isolated and have few immigrations of genetically pure animals, the only opportunity that some individuals may have to reproduce will be with members of the same or closely related species [Lernould, 1988; Struhsaker et al., 1988; Detwiler, 2002] or genus [Lernould, 1988]. This appears to be the case in this captive study, although it does not seem that hybridization had any selective advantages for the male *C. pygerythrus* × *C. albogularis* hybrids.

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