

## **Male Demography, Female Mating Behavior, and Infanticide in Wild Patas Monkeys (*Erythrocebus patas*)**

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*Infanticide by males has been hypothesized to be a naturally selected behavioral strategy that increases the infanticidal male's reproductive success. The sexual selection hypothesis has been challenged via alternative, nonadaptive hypotheses that dispute its empirical and theoretical bases. Two of the most widely recognized alternatives are the social pathology hypothesis, in which infanticide results from overcrowding or recent human disturbance, and the generalized aggression hypothesis, in which infanticide is an epiphenomenon of increased male aggression. We report the first case of infanticide in wild, seasonally breeding patas monkeys (*Erythrocebus patas*) living at a low population density in a stable habitat, conditions which do not support the social pathology hypothesis. Its exceptional occurrence is consistent with the sexual selection hypothesis: over a 7-year period the infanticidal male was the only one of 13 resident males that was not present during the actual conception season but was present during the following birth season. Also consistent with this hypothesis, mothers were differentially targeted for male aggression, which increased sevenfold during the days surrounding the infanticide and then decreased to baseline levels after the infanticide. Aggression targeted at mothers does not support the generalized aggression hypothesis. As predicted by the sexual selection hypothesis, females began soliciting mating immediately after the infanticide, despite its occurrence in the nonconceptive season.*

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**KEY WORDS:** *Erythrocebus patas*; infanticide; patas monkeys; seasonal breeding; sexual selection hypothesis.

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## INTRODUCTION

Infant-killing by males was first reported by Herodotus in 625 B.C. for domestic cats (de Selincourt, 1982; Grene, 1987: Book 2:66). Since then, male infanticide has been reported in many other mammals ranging from rodents to primates to carnivores (Hausfater and Hrdy, 1984; Parmigiani and vom Saal, 1994) and several hypotheses have been proposed to explain this behavior. The sexual selection hypothesis provides an adaptive explanation by hypothesizing that infanticide by males is a naturally selected behavioral strategy to increase the infanticidal male's reproductive success because the death of preweaned infants brings females into estrus earlier than were the infants to survive until weaning (Hrdy, 1974, 1977). However, an infanticidal male could employ infanticide as a form of intrasexual competition regardless of its effects on the timing of estrus because killing unrelated infants reduces competitors' genes in the gene pool (Hrdy, 1974, 1977). Infanticide could still be effective in such species as long as the infanticidal male mates with and sires the females' subsequent offspring.

Alternative hypotheses comprise nonadaptive explanations. The social pathology hypothesis proposes that infanticide is an abnormal behavior that results from overcrowding or stress from anthropogenic habitat disturbance (Boggess, 1979; Curtin and Dolhinow, 1978). The generalized aggression hypothesis argues that infants are killed simply because they are not as successful as older individuals in avoiding aggression of adult males: an epiphenomenon of heightened male aggression directed at all group members (Bartlett *et al.*, 1993; Dagg, 1998; Sussman *et al.*, 1995).

Infanticide by males occurs in several primate species, most of which breed year-round (*Papio* spp.: Collins *et al.*, 1984; Palombit *et al.*, 1997; *Cercopithecus mitis*: Butynski, 1982; Fairgrieve, 1995; *Alouatta seniculus*: Crockett and Sekulic, 1984; *Semnopithecus entellus*: Hrdy, 1974; Mohnot, 1971; Ross, 1993; Sommer, 1987, 1994; Sugiyama, 1965; *Gorilla gorilla beringei*: Fossey, 1984; Watts, 1989; *Ptilocolobus badius*: Struhsaker and Leland, 1985, 1987). Male infanticide also occurs in seasonally breeding species (*Propithecus diadema*: Erhart and Overdorff, 1998; Wright, 1995; seasonally breeding populations of Hanuman langurs: Borries, 1997; Newton, 1986; *Lemur catta*: Hood, 1994; Pereira and Weiss, 1991; *Cebus olivaceus*: Valderrama *et al.*, 1990). In seasonally breeding species with an interbirth interval of 2 years, infanticidal males may benefit by reducing the interbirth interval, causing females whose infants have been killed to come into estrus the following breeding season, when the infanticidal male may still be in the group to mate with them (Borries, 1997; Erhart and Overdorff, 1998). Even in species wherein the interbirth interval is not reduced by loss of an infant,

infanticide functions as a form of intrasexual competition. Effective intrasexual competition includes many ways to prevent reproduction by other males, from winning fights to maintaining exclusive access to females to infanticide, and the ability to perform these behaviors will be selected if the males exhibiting such behaviors reproduce.

We report the first suspected case of infanticide in seasonally breeding patas monkeys (*Erythrocebus patas*) living at a low population density in a stable habitat. Behavioral and morphological evidence surrounding the infant's death, demographic data on births and male residency patterns over a 7-year period, and the rarity of infanticide in patas monkeys are all consistent with the predictions of the sexual selection hypothesis for infanticide and are inconsistent with alternative explanations.

## METHODS

### Study Site and Animals

The study site is Segera Ranch (36° 50' E, 0° 15' N; elevation 1800 m), on the Laikipia Plateau in central Kenya. Segera is a privately-owned conservation area and cattle ranch of 17,000 ha with stable populations of  $\geq 30$  species of large mammals (Isbell *et al.*, 1998). The only potentially anthropogenic disturbance to the monkeys is from movements of cattle by herders and their dogs. The intensity of cattle herding has remained stable since before 1992, with cattle densities at *ca.* 20 individuals/km<sup>2</sup> (G. Prettijohn and J. Ruggieri, personal communication).

Climatological data have been kept at one of three locations, all within 10 km of the study site, since October 1992. The 7-year average annual rainfall is 700 mm. Although rainfall varies considerably, on average the wettest months are April and May and the driest February and September. The habitat in the study area is primarily open acacia woodland, with *Acacia drepanolobium* accounting for >98% of all woody vegetation (Young *et al.*, 1997; Enstam and Isbell, submitted).

Patas monkeys on Segera are similar to ones studied elsewhere. They occur at the lowest densities for their body weight of all primates (Clutton-Brock and Harvey, 1977) and typically live in uni-male groups with about 15 adult females (Chism and Rowell, 1986; Cords, 1987). Females remain in their natal groups throughout life whereas males disperse at maturity and live either as extragroup males or as residents of other female groups (Chism *et al.*, 1984; Chism and Rowell, 1986). Extragroup males are sometimes seen with female groups during the breeding season (Chism and Rowell, 1986). Patas monkeys have well-defined breeding and birth seasons, with a mean

interbirth interval of 11.8 months (Chism *et al.*, 1984; L. A. Isbell, unpublished data).

We have observed one group of Segera patas monkeys continuously since August 1992. They live within a home range of approximately 4,000 ha. Home range overlap with other groups is minimal. Intergroup encounters have been rare; we witnessed only 6 intergroup encounters since 1992 and none since 1995. The estimated density of patas monkeys at the study site ranges from 0.5 to 1.2 individuals/km<sup>2</sup>. Group size has varied from 20 to 51 individuals, including 6–15 adult females, one resident adult male outside the breeding season, and  $\leq 3$  males during the breeding season. These minimum and maximum group sizes spanned the period of intensive behavioral sampling by Enstam reported here (October 1997 to September 1999). We identified adults individually either by natural markings and characteristics or by temporary dye marks (black Nyanzol D powder: Belmar Inc.) sprayed onto the pelage from a SuperSoaker water gun (Larami Corp.) or syringe. Since the long-term study began, we have records on seven full breeding seasons (1993–99). The resident male at the beginning of the breeding season was replaced by another male during six breeding seasons (1993–98). During the 7 months before the attack on the infant (October 1998 to April 1999), the male that attacked the infant and is suspected of committing infanticide was the only male in the group.

### Data Collection and Analysis

We have demographic data—births, deaths, disappearances, immigrations, and adult male replacements—for each observer day (range: 0–22 days/month) since August 1992. We calculated adult male tenure and replacements from these records. In cases where in the actual entry date of a male is unknown, we used the midpoint between earliest and latest possible arrival to estimate his entry date. When a new male joined the group, the resident male, if still present in the group, invariably became solitary or disappeared. This is a replacement. Males are residents if present in the group for  $\geq 10$  days and transients when they are present for  $< 10$  days. We estimated conception dates by backdating 167 days (Sly *et al.*, 1983) the birthdates of 74 infants born between 1993 and 2000. In cases where in the actual birthdate is unknown, we used the midpoint between earliest and latest possible birthdates to estimate birthdate.

We recorded all occurrences of adult agonistic interactions and matings since 1992. We determined relative dominance by responses of individuals to other individuals. Cringing, cowering, running away, or being supplanted

are performed by losers of agonistic interactions. We used agonistic interactions between the adult male and individual adult females to determine rates of agonism (Isbell and Pruettz, 1998). Male agonism toward females includes him approaching a female and she avoiding or leaving or her being supplanted or chased. Mating behavior included both completed matings with an ejaculatory pause, and attempted matings. In addition, as part of the intensive behavioral study from October 1997 to September 1999 (except September 1998) Enstam recorded all occurrences of solicitation of mating by females during 20–30 min focal samples of all adults in the group. She recorded solicitation of mating when a female crouched and curled her tail over her back while running in front of, and often stopping to sit near, the adult male. This behavior could also be accompanied by the female drooling (Chism *et al.*, 1984). After a resident male, RPH, attacked an infant, Enstam increased the length of focal samples on him to document potential changes in the nature of interactions between RPH and individual adult females.

Although data on matings, solicitations, and agonistic interactions are routinely collected by all members of the research team, analyses of matings, solicitation of matings, and male agonism toward females are taken from focal data collected only by Enstam on RPH and the previous resident male to avoid possible bias due to differences in interobserver reliability ( $n = 1,494$  focal minutes on RPH,  $n = 480$  focal minutes on the previous resident male). We divided rates of the behaviors into five time periods: the previous resident male's tenure (March 1998 to September 1998), the actual non-conceptive season with RPH as resident male (16 December 1998 to 16 May 1999), the period when the infant was attacked until it died (17–20 May 1999), the period immediately following the infant's death (21–23 May 1999), and the general conceptive season (1 July to 15 September 1999, when Enstam's study ended). We performed two-tailed statistical tests on agonism data by comparing the number of focal minutes involving agonistic interactions with the number of focal minutes involving no agonistic interaction for four sets of two time periods. Mothers and non-mothers refer only to cycling adult females, and do not include juvenile females. The general conceptive season is based on the 74 births that occurred since 1993 backdated by 167 days. Actual conceptive seasons are restricted to a given year and are based on backdated births for that year.

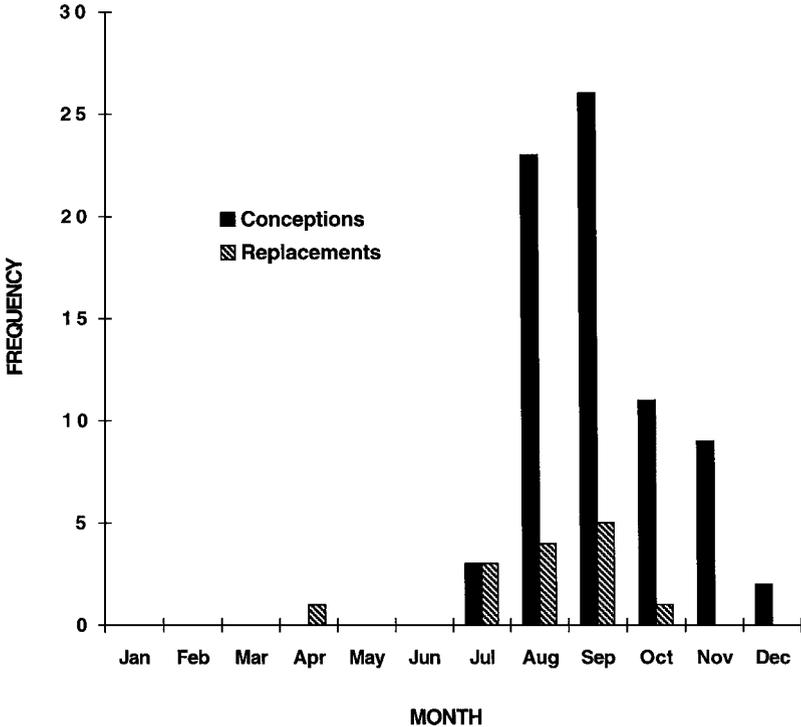
The 3-month-old infant that was attacked by RPH on 17 May and found dead 4 days later was placed in a plastic bag and frozen until we performed a necropsy on 29 May. A 4-month-old infant vervet (*Cercopithecus aethiops*) that we found dead 2 days after its mother died was treated similarly for comparison.

## RESULTS

### Male Demography Relative to Conceptions

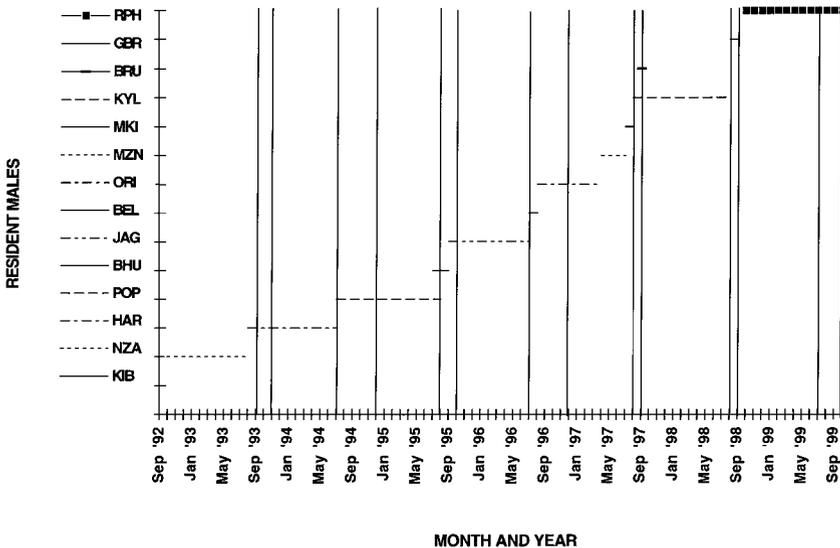
Over a 7-year period, 14 different males established residency in the study group; their tenures ranged from 22 to 373 days ( $\bar{x} = 177$  days). Replacement of resident males was seasonal, with 12 of 14 replacements occurring between July and September (Fig. 1; Chism and Rowell, 1986). The other two occurred in April and in October. RPH, the male that attacked the infant, became resident in the group in October 1998, later in the year than any other male.

RPH's entry into the group was well within the general conceptive season of July to mid-December (Fig. 1). Sixty of the 74 (81%) births were conceived between August and October, and 11 of 74 (15%) were conceived in



**Fig. 1.** Conceptions relative to male replacements: Frequency of conceptions (black bars) and male replacements (striped bars) per month between September 1992 and October 1999. Male replacements occur most often between July and September. The majority of conceptions occur between August and October.

November and December (three infants were conceived in July). The majority of male replacements occurred between July and September. RPH was not present in time to sire that particular year's infants, however. RPH was first observed with the group on 10 October 1998 (the midpoint of possible entry dates was 4 October). Backdating the three births that occurred in 1999 reveals a conception window from 9 August to 8 September 1998, a minimum of 33 days before we saw RPH with the group (or, a minimum of 27 days from the midpoint of possible entry dates). RPH was the only one of 14 resident males in 7 years to have been absent during the actual conception season but present during the following birth season. MZN, the male that became resident in May 1997, was not present in the group during the breeding or the birth season. The other 12 resident males were present in the group at the estimated time of conception for 11–100% of all infants born the following birth season (Fig. 2). After 7 months in the group as the only resident male, RPH attacked a male infant. Although he survived the attack, he was dead 4 days later.



**Fig. 2.** Male residency patterns over 85 months. Three letter codes on the vertical axis represent individual males. All males except RPH were present in the group during the actual conceptive season during their year of residency (Fig. 1). Vertical lines highlight the actual conceptive season for each year.

## Observations of Suspected Infanticide and Subsequent Behavioral Changes

### *Attack on and Subsequent Death of the Infant: 17–21 May 1999*

At 1712 h on 17 May, RPH approached JAD, one of two lactating females in the group, and her 3-month-old infant, which was 1 m away from her. RPH picked him up and bit him on the right arm, distal to the shoulder. Both the infant and mother screamed during the attack. JAD, another adult female, and several juveniles chased RPH, who ran away, dropping the infant. Blood was visible on his upper right arm and elbow. In the days immediately following the attack, the infant appeared weak and listless. Dried blood was still visible on his right arm. He was able to cling to JAD, but was not observed to suckle. He remained within arm's reach of his mother during the next 3 days.

At 1303 h on 21 May, JAD was without her infant. At 1530 h, another adult female and a juvenile stood bipedally and scanned the ground. Closer inspection revealed that they were looking at the infant's body. Gross examination of the body revealed two puncture wounds to the right of his spine in addition to the wound on the right arm. One puncture was near the right shoulder with the second puncture several mm directly posterior to the first (Fig. 3). The two puncture wounds are conservatively estimated to be 23.5–32.3 mm apart with each puncture being 2.9–4.6 mm wide based on measurements from photographic slides. Necropsy revealed four more punctures on the left dorsal surface of the thorax. Two were adjacent to the spine, the other two were more lateral. All six punctures to the thorax are assumed to have been inflicted during a fatal attack on 21 May since we did not see the male bite the infant on the back during the attack on 17 May.

We measured the four punctures on the infant's left side after the skin had been removed. All four punctures formed a rectangle of maximally 30 mm (anterior–posterior) by 40 mm (medial–lateral). In addition to the punctures, there was severe bruising of the skin and muscle along the entire dorsal surface of the thorax, intrathoracic hemorrhaging, bruising on the stomach, lesions on the liver, and blood in the pericardial sac, the latter indicating trauma to the heart. The intervertebral disk between the 9th and 10th thoracic vertebrae had been severed. Cause of death was probably pneumothorax, deflation of the lungs, and suffocation. Although the infant was not observed to suckle during the 3 days following the attack, it is not likely that he died of dehydration or starvation. An infant vervet that apparently died of dehydration or starvation 2 days after its mother died showed no sign of trauma.



**Fig. 3.** Puncture wounds on the right side of the thorax of a 3-month-old infant patas monkey that was attacked by the resident male. (Photo by R. Chancellor)

#### *Comparison of Intercanine Distance and Canine Width*

The puncture wounds on the left side of the infant's thorax measured 30 mm apart (medially–laterally). On the right side, the punctures were between 23.5 and 32.3 mm apart. To determine the source of the fatal wounds, we matched intercanine distances and canine widths of adult male patas monkeys, adult female patas monkeys (provided by the Caribbean Primate Research Center Museum and J. Loy), male black-backed jackals (*Canis mesomelas*), and female black-backed jackals (provided by L. Frank) with the puncture wounds on the infant. Although it is unlikely that a predator would drop a patas monkey as small as an infant, even if it was being chased, we examined jackals because they are confirmed predators of juvenile patas monkeys at the study site. The range of intercanine distances on the infant were far greater than all intercanine distances for jackals in this sample, enabling us to exclude jackals as the cause of the fatal wounds (Table I).

The intercanine distances of the maxillae of catarrhine primates are always greater than the intercanine distances of the mandible (Fleagle, 1999). If the interpuncture distance of 30 mm on the infant's left side were mandibular, then the puncture wounds on his right side would have come

**Table I.** Comparison of Intercanine Distances and Canine Widths. Percentages are the percentage of samples that fit within the range measured on the infant

	Distance between wounds <sup>a</sup>	Male patas ( <i>n</i> = 9)	Female patas ( <i>n</i> = 9)	Male jackals ( <i>n</i> = 5)	Female jackals ( <i>n</i> = 5)
<b>Maxilla</b>					
Measurement 1 <sup>b</sup>		13% (1/8)	0% (0/9)	0% (0/5)	0% (0/5)
Range (mm)	30.1–32.3	31.5–36.5	23.5–30.0	26.1–26.93	22.53–26.72
Measurement 2 <sup>c</sup>		11% (1/9)	0% (0/6)	0% (0/5)	0% (0/5)
Range (mm)	30.1–32.3	23.0–30.2	21.5–25.5	18.59–19.83	19.32–19.65
Measurement 3 <sup>d</sup>		0% (0/9)	0% (0/6)	0% (0/5)	0% (0/5)
Range (mm)	30.1–32.3	35.0–43.2	25.0–30.0	25.29–25.84	23.74–25.7
<b>Mandible</b>					
Measurement 1 <sup>b</sup>		33% (3/9)	25% (2/8)	0% (0/5)	0% (0/5)
Range (mm)	23.5–29.9	28.9–3.4	19.5–24.3	22.23–23.19	21.36–22.81
Measurement 2 <sup>c</sup>		33% (3/9)	0% (0/6)	0% (0/5)	0% (0/5)
Range (mm)	23.5–29.9	21.5–28.0	17.5–20.5	14.08–15.05	13.04–15.7
Measurement 3 <sup>d</sup>		33% (3/9)	17% (1/6)	0% (0/5)	0% (0/5)
Range (mm)	23.5–29.9	27.9–3.4	21.0–25.0	17.86–20.65	18.48–20.9
<b>Canine width</b>					
Upper <sup>e</sup>		0% (0/9)	17% (1/6)	80% (4/5)	20% (1/5)
Range (mm)	2.9–4	5.5–6.5	1.75–3.9	2.9–3.54	2.08–2.97
Lower <sup>e</sup>		63% (5/8)	0% (0/5)	40% (2/5)	0% (0/5)
Range (mm)	2.9–4	2.5–5.0	1.5–2.5	1.4–3.29	1.93–2.81
Rank of overall fit		1.3	3	2.5	3.2

Note: Sample sizes are sometimes different from the total *n* because some teeth were broken.

<sup>a</sup>The puncture wounds on the infant's right side were between 23.5 and 32.3 mm apart. See text for methodology in dividing the range into maxillary and mandibular ranges.

<sup>b</sup>Tip-to-tip distance between canines.

<sup>c</sup>Distance between buccal surfaces of canines at the incisor level.

<sup>d</sup>Distance between lingual surfaces of canines at the incisor level.

<sup>e</sup>Canine widths were obtained by subtracting measurement 2 from measurement 3 and dividing by 2.

from a maxilla with an intercanine distance >30 mm, but not >32.3 mm (the maximum possible measurement). If, however, the wounds on his left side were from a maxilla, the puncture wounds on the right side would have come from a mandible with an intercanine distance not <23.5 mm (the minimum possible measurement), but not >30 mm.

Assuming the puncture wounds on his right side were from a maxilla, our range of maxillary measurements match no adult female patas, but instead 11–13% of adult male patas (Table I). Assuming the puncture wounds on his right side were from a mandible, our range of mandibular measurements match 17–25% of all adult female and 33% of all adult male patas. Finally, our estimated width of the punctures matches, at best, 17% of upper canine width measurements for adult female patas, and 63% of lower canine width measurements for adult male patas. Since the degree of sexual dimorphism in the canines of patas monkeys is greatest in canine width, it

is not surprising that the greatest difference between adult male and female patas in degree of fit with the actual puncture wounds is in canine width (Table I).

Based on these percentages we ranked the male patas, female patas, male jackals and female jackals with regard to degree of overlap with the range of wounds on the infant, with 1 indicating the highest degree of overlap and 4 indicating the lowest degree of overlap (Table I). Taken together, the puncture wounds on the infant are more consistent with canine measurements of adult male patas monkeys than with adult female patas monkeys.

#### *Agonism Directed Toward Adult Females by the Resident Male*

In the 4 days between the attack and the infant's death, the rate of agonistic interactions between RPH and adult females during focal samples increased >7 times over his rate of agonism during the general nonconceptive season (16 December 1998 to 16 May 1999). This is 21 times greater than that shown by the previous resident male (Fig. 4). After the infant died, however, agonism returned to a rate similar to those before the attack (Fig. 4). Between the observed attack and the infant's death, the number of focal minutes involving agonistic interactions between RPH and adult females compared with the number of focal minutes involving no agonistic interaction are significantly greater than during the general nonconceptive season (16 December 1998 to 16 May 1999) (two-tailed Fisher's exact test:  $p < 0.01$ ) and the previous resident male's tenure (two-tailed Fisher's exact test:  $p < 0.0001$ ). Almost immediately following the death of JAD's infant, the number of focal minutes involving agonism compared to the number of focal minutes involving no agonism did not differ significantly from the general nonconceptive season (two-tailed Fisher's exact test:  $p > 0.90$ ) or during the tenure of previous male (two-tailed Fisher's exact test:  $p > 0.45$ ). RPH's agonistic behavior during the height of his aggressive interactions was directed primarily toward lactating females. He directed 15 of 16 aggressive interactions toward JAD and RBY, the only two lactating females. After the attack on JAD's infant, both infants were always within a meter of their mothers. Whenever RPH approached either JAD or RBY, she would immediately pick up her infant if it was not already in contact with her. Of the 15 interactions with JAD and RBY, nine (60%) involved JAD. The agonism shown by RPH toward JAD was most often of high intensity, i.e., chasing. On three of the nine occasions, RPH pursued JAD for > 45 s. These chases were noticeably longer than chases involving other animals, which typically last <15 s.

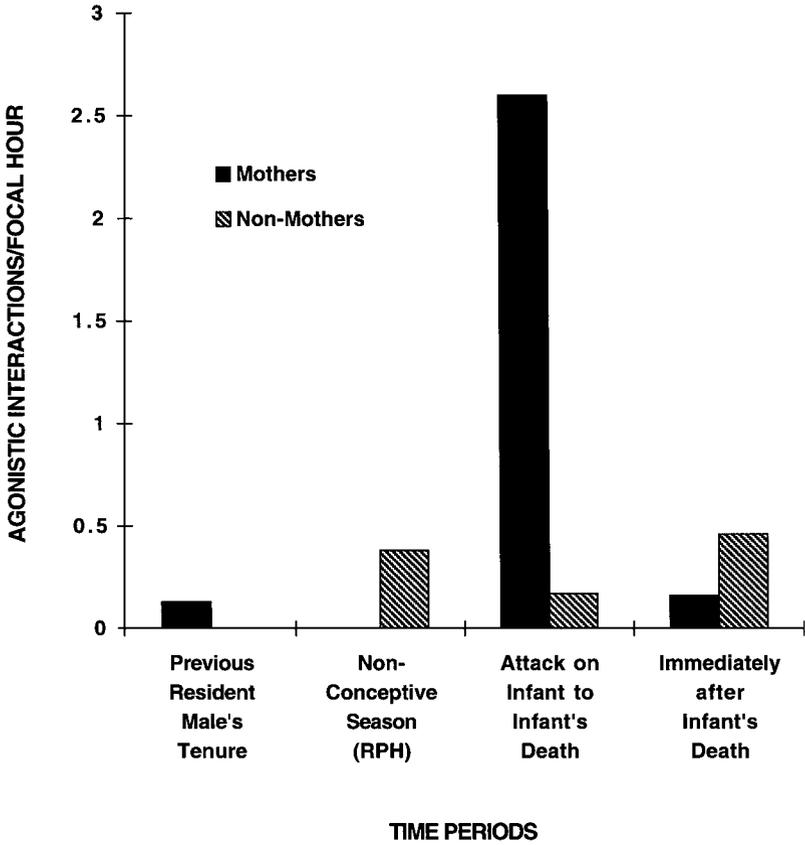
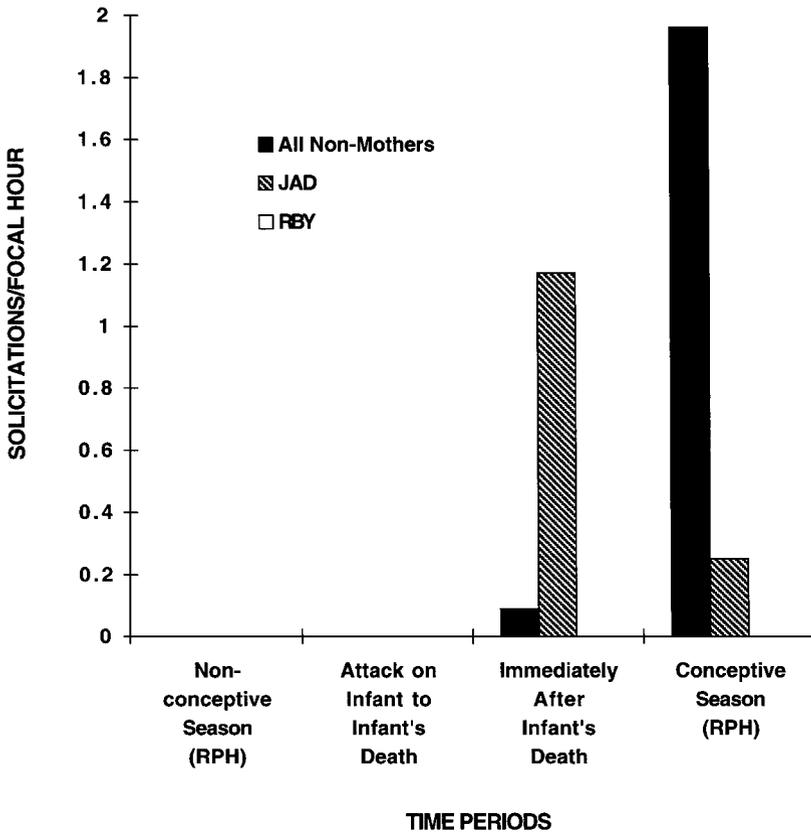


Fig. 4. Rates of Agonism by RPH, the Resident Male: Frequency of the male's agonistic interactions toward mothers (black bars) and non-mothers (striped bars) per focal hour.

*Mating Behavior Immediately Following the Death of the Infant*

Although May is within the general nonconceptive season, after the infant's death two of eight females solicited RPH during focal samples conducted by Enstam. Thirteen of 14 (93%) solicitations were by JAD (Fig. 5). Mating behavior also increased after the infant's death, and during focal samples, RPH mated 11 times in May, all of which were with JAD after her infant died. The first mating occurred at 1433 h on 22 May, 23 h after we found the infant's body. Outside of focal samples, one additional mating occurred in May, on 27 May, not with JAD. In the previous 6 years, we observed only one mating in May.



**Fig. 5.** Rates of solicitations of matings: Frequency of solicitations of matings by non-mothers (black bars), JAD, mother of the infant that was not killed (striped bars), and RBY, the mother of the infant that was killed (white bars). While JAD solicited RPH immediately after her infant died, RBY did not solicit matings in either the general nonconceptive or general conceptive seasons.

Male aggression toward mothers or infants and solicitation of mating have not accompanied the loss of other infants. Since the long-term study began, two other infants died  $\leq 3$  months of birth. The resident male did not target the infants or their mothers with aggression, nor did the mothers solicit or mate with the resident male before the general conceptive season began.

#### *Mating Behavior and Agonism in the Following Conceptive Season*

RPH was the only male in the group (including transients) during the actual conceptive season following the infanticide. He mated 19 times with

8 females (including JAD) between July and October 1999. Six of the females also solicited matings from RPH 20 times during this period. We saw no mating behavior during November or December 1999. Eight infants were born in 2000, all between 12 January and 3 April. Five of them died within 1 month of birth. RPH has been the group's only resident male since October 1998, and we never saw him attack or behave aggressively toward the infants. Their deaths are attributable to factors other than the adult male (S. Robbins, personal communication). JAD's new infant is one of three surviving infants of the eight born in 2000, and all survivors are 5–6 months old.

## DISCUSSION

The behavioral and physical evidence suggest that the resident male patas monkey killed the infant. Demographic evidence indicates that he could not have been the infant's sire. By killing the infant, he effectively lowered a competitor's reproductive success. Sometime before 1303 h on 21 May 1999, RPH picked up the infant so that its back was in RPH's mouth. In this position, RPH's upper canines penetrated one side of the infant's thorax, near the spine, while his lower canines penetrated the other side. The two pairs of punctures (one pair more laterally located) on the left side of the infant's thorax may have been caused by one pair of canines biting into the body twice with the other pair remaining implanted. During one of the bites, one pair of RPH's upper and lower canines likely penetrated between the 9th and 10th thoracic vertebrae, cutting into the intervertebral space.

Our results are not consistent with overcrowding/human disturbance and generalized aggression, two alternative hypotheses for infanticide. Patas monkeys are not overcrowded at Segera. Like patas monkeys elsewhere, their density at Segera is very low relative to other primates of similar body size (Chism and Rowell, 1988; Clutton-Brock and Harvey, 1977), and at the time of the attack, the estimated density was 0.5 individuals/km<sup>2</sup>, the lowest since the study began in 1992. The low density was not an obvious result of stress, but instead appeared to be a result of illness following unusually heavy rains during the 1997 El Niño event (L. A. Isbell, in preparation) and other natural causes, such as predation. Nor was the population subjected to increased human disturbance around the time of the infant's death. Cattle herding, the only potential source of human disturbance, has not changed in intensity in the 7 years of the study. If human disturbance caused the infanticide, then we are left to explain why it has occurred only once in 7 years.

The male's behavior is also not consistent with the generalized aggression hypothesis. His behavior was not directed toward all members of the group but instead was focused specifically on the infants and lactating

mothers. He attacked and wounded the infant 4 days before it died, and he increased his rate of aggression in the days between the attack and the infant's death. After the infant died, his aggression returned to a rate comparable to that before his attack and to that of the previous (non-infanticidal) male.

Conversely, the male's behavior is consistent with the sexual selection hypothesis. He directed aggression toward mothers, was observed to attack the infant and stopped directing aggression toward mothers after the infant died, and mated with the female whose infant died. Female behavior is also consistent with sexual selection hypothesis. The death of the infant led to an abrupt increase in solicitations and matings within the group in the general nonconceptive season. The fact that solicitations and matings have never occurred after females lost their infants through miscarriage, predation, or illness suggests that reproductive behavior of females is not triggered simply by the termination of pregnancy or the loss of an infant. Active solicitation of mating by females, and matings that (1) occur even during pregnancy, (2) increase when a male becomes resident late in the general conceptive season, and (3) increase after infanticide, are all consistent with the sexual selection hypothesis, and they suggest that solicitation of mating is a strategy of female patas monkeys to avoid infanticide by confusing paternity (Hrdy, 1977).

Infanticidal behavior may be rare in patas monkeys because the timing of replacements and the mating behavior of females maximize the chance that most males will have the opportunity to mate during the actual conceptive season during which they are resident and thus potentially father infants born the following birth season. Of the 13 resident male patas monkeys that were there during the 1993–98 general conceptive seasons, 12 were potential fathers of  $>1$ , and as many as all, of the infants born during the subsequent birth season, based on presence in the group (MZN became resident in April 1997, after the end of the birth season, and left in July 1997, before the start of the breeding season). RPH was not present during the actual 1998 conceptive season and thus was the only male that could not have been a potential father to any of the infants born during his residence in the group the following birth season. RPH was, however, the only male in the group during the actual 1999 conceptive season (Fig. 2), and the only one observed to mate with resident females. We have never seen him attack infants conceived while he was the sole male mating with females. Both of these observations are consistent with the prediction of the sexual selection hypothesis that only males that are not possibly fathers will commit infanticide.

Although RPH was in the group at the time of the infant's birth, he did not attack it until it was 3 months old. This contrasts with many other cases of observed or suspected infanticide, wherein males attacked very young infants after recently emigrating into a group (diademed sifakas: Erhart and Overdorff, 1998; Hanuman langurs: Borries, 1997; Hrdy, 1974; Mohnot, 1971;

mountain gorillas: Fossey, 1984; red colobus; Struhsaker and Leland, 1985), though infants as old as 16 months have been attacked by adult males (Borries, 1997). There are several possible reasons for RPH's delayed attack on the infant. As with many other primates, in the first few months of life infant patas monkeys spend virtually all of their time in contact with the mother or other females (Chism, 1978, 1986; Chism *et al.*, 1984), and an adult male patas monkey has very limited opportunity to interact with young infants (Chism, 1986). Studies of patas monkeys in captivity show that the percent of time infants spend out of contact with their mothers increases steadily during the first 3 months of life (Chism, 1978, 1986). By the end of their third month, infants spend *ca.* 45% of time out of contact with their mothers, compared with *ca.* 25% at the end of the second month (Chism, 1978). Unlike Hanuman langur females, which are largely ineffective in countering male aggression (Hrdy, 1977), patas females, either alone or in coalition with other females and juveniles, can defend themselves successfully against unwanted harassment by the resident male (Rowell and Chism, 1986). Under such circumstances, it may be safer for a male to postpone attacking an infant until it is at an age when it is more easily approached and therefore not as easily defended by its mother.

That males attack infants when they are easy targets has also been suggested for Hanuman langurs by Borries (1997). Three infant langurs were attacked by adult males only after they were handicapped by injuries. In addition, 64% of infants attacked by adult males were not in contact with another langur at the time of the attack (Borries, 1997). Although the patas infant was not physically handicapped at the time of the first attack, he was a meter away from his mother. Perhaps he was further away from her during the second attack.

The dominance rank of mothers may also determine the ease with which an infant can be attacked. Although patas monkeys do not have stable, linear dominance hierarchies over long periods of time (Isbell and Pruettz, 1998), RBY was the highest-ranking female in the group, while JAD was the lowest-ranking (L. A. Isbell, unpublished data). Thirty-seven min before RPH was attacked JAD's infant he was chased out of the group by RBY and another adult female. Although we did not witness the stimulus that evoked the aggression on the part of the two females, RBY was the only other lactating female in the group then, and it is possible that RPH had attempted to attack her infant, but was deterred. The fact that subsequently RPH did not attack RBY's infant (despite his attempts to approach her and her infant) may have been due to RBY's high status in the group and her ability to obtain support from other adult females against RPH, thus making her infant more difficult to attack than JAD's. Perhaps RPH waited until JAD's infant was 3 months old before he attacked it and refrained from

attacking RBY's infant because his access to the infants differed with time and relative status of the mothers.

One of the expectations of the sexual selection hypothesis for male infanticide is that the subsequent interbirth interval of the victim's mother is shortened, thus allowing the infanticidal male to mate with females with which he might not otherwise have access (Hrdy, 1974). A decrease in the interbirth interval is unlikely in seasonally breeding species since the timing of matings is temporally fixed. This is presumably why infanticide is so rare in seasonal breeders (Hrdy and Hausfater, 1984). Indeed, the majority of the seasonally breeding primate species in which infanticide occurs have interbirth intervals that are  $\geq 2$  years in length if the infant survives: (diademed sifakas:  $>2$  years (Erhart and Overdorff, 1995); Hanuman langurs: mean: 2.4 years (Borries, 1997); ring-tailed lemurs: 2 years (Richard, 1987)). Interbirth intervals of this length may still be shortened because rather than conceiving every 24 months if the infant survives, the victim's mother may conceive in the following breeding season, possibly when the infanticidal male is still with the group (Borries, 1997; Erhart and Overdorff, 1998).

Patas monkeys differ from other seasonally breeding primates by breeding annually. With an interbirth interval of 11.8 months (Chism *et al.*, 1984; L.A. Isbell, unpublished data), they have one of the shortest interbirth intervals of any primate of similar body size. Patas monkeys reproduce at the upper limit of their reproductive potential. Thus, it is probably not possible for a female that loses her infant to have a significantly shortened interbirth interval.

A shorter interbirth interval is not a necessary component of the sexual selection hypothesis, though it was integral to the original formulation of the hypothesis. What is necessary is that the infanticidal male eliminates the offspring of other males only and subsequently sires offspring of his own. RPH was not the father of either of the infants born in 1999 since he entered the group  $>1$  month after the last conception occurred, and he attacked one of the infants on 17 May 1999. In contrast, all of the infants born in 2000 (the first birth season following the infanticide) were conceived when RPH was the only male in the group. RPH has not attacked any of the infants and is most likely the father of all of them.

Although rare, sexually selected infanticide can happen even in an annually breeding species such as the patas monkey. The majority of adult male replacements in patas monkeys occur during the breeding season and individual males seldom stay in a group for more than one breeding season (Fig. 2). Under rare circumstances when a male enters a group too late, i.e., after all the females have conceived, infanticide benefits him by costing his rivals. A male that cannot possibly be the father of any of the infants loses nothing by committing infanticide and gains by eliminating the offspring of

his rivals as long as he later mates with the females and sires their offspring the next season.

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