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Mating Strategy and Reproductive Success of Male Patas Monkeys (*Erythrocebus patas*)

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ABSTRACT. Mating behavior and paternity of offspring of wild patas monkeys were studied at Kala Maloue National Park, Cameroon. Observation of patas groups over three years revealed that multi-male situations occurred after takeover of the position of a resident male. Direct observation of behavior showed that resident males (harem males) occupied only 31% of mating in multi-male situations and 100% in one-male situations. DNA-typing revealed that resident males sired two of four of infants in the one-male situation and four of five in the multi-male situation. Under the two years cycle of the one-male situation and the multi-male situation, calculation shows that resident males sired more offspring than sneakers both in observation and paternity testing. Sneak mating occurred during both one-male and multi-male situations, and resident males performed compensatory mating, with dilution of sneaker sperm; these activities explain the discrepancy found between observation of mating and results of paternity discrimination.

Key Words: Patas monkey; Paternity test; Mating strategy; Mating system; Social evolution.

INTRODUCTION

Paternity discrimination in primates has been applied mainly to the examination of correlation between dominance rank order of males and their breeding success (INOUE et al., 1991). In non-primate species, the success of sneak mating in a polygynous breeding system has been demonstrated using DNA fingerprinting and this was indeed one of the first applications of the technique in sociobiology (HILL, 1987; WETTON et al., 1987). The present study on patas monkeys (*Erythrocebus patas*) investigates for the first time in a primate species the effect of sneak mating on reproductive success of the resident male (harem male) during a polygynous situation. Patas monkeys have a one-male/multi-female, "harem" social system which may, however, become a multi-male system as opposed to a one-male system (STRUHSAKER & GARTLAN, 1970; OLSON, 1985; HARDING & OLSON, 1986; CHISM & ROWELL, 1986; CORDS, 1987; OHSAWA, 1991); such change is known for forest *Cercopithecus* species (TSINGALIA & ROWELL, 1984; CORDS et al., 1986; CORDS, 1988). Multi-male situations occurred after a takeover of the position of the resident male (OHSAWA, 1991). Several males entered the group soon after the takeover by the new resident male and remained during the mating season, copulating with females. Such intruder males leave at the end of the mating season (Fig. 1).

To understand the above phenomenon we proposed the working hypothesis that two kinds of behavioral traits of mating are controlled by different genes. One trait is dominant-monopolizing behavior of the "resident male" (harem male), who denies access to females for other males, providing protection for both females and their offspring during and after the mating; the second trait is the subordinate-sneaking behavior of males other than the resident male, who can join a group and mate females behind or apart from the resident

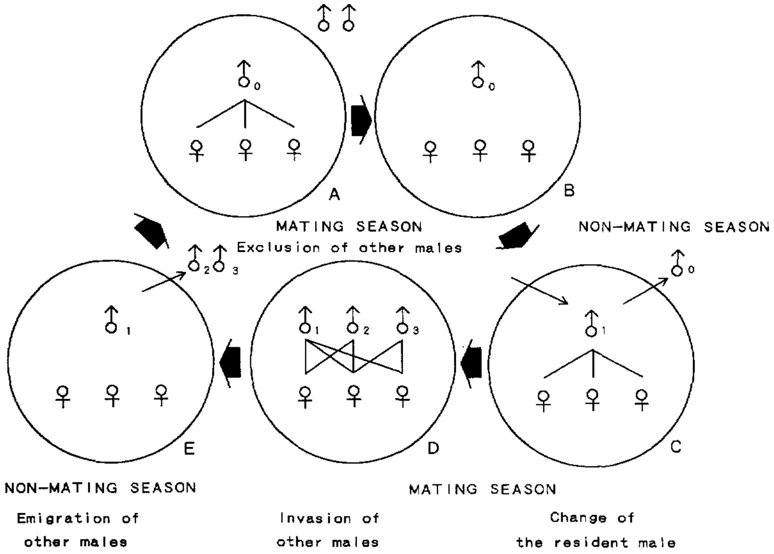


Fig. 1. The cycle of mating patterns in a group of patas monkeys. Subscript 0: The former resident male; 1: the present resident male; 2, 3: intruder males. Lines between individuals indicate mating relations. Narrow arrows indicate transfer.

male; such males leave the group before the mating season is over. If the number of non-resident (subordinate-sneaker) males increases in excess of resident males, the former monopolizing trait will decrease in a population and then as a result this one-male society may be destroyed.

The purpose of the present study is to examine the effectiveness of sneak mating and of the counter-strategy developed by resident males on reproductive success of individual patas monkeys, as determined by paternity discrimination.

The following terminology was used in the study. One-male and multi-male situations refer to the composition of group members. Polygynous and promiscuous situations refer to the combination patterns of mating based on either behavioral observation or paternity discrimination. The resident male (harem males) is the male who is the sole adult male otherwise the most dominant male in the group and stays in the group even during the non-mating season until defeated by a challenger male. Non-resident males are all adult males other than the resident males. Outsider males are adult males from outside a group who often sneak into the group or challenge the resident males in the group during the mating season.

METHODS

Groups of wild patas monkeys have been studied by the first author in the Kala Maloue National Park, northern Cameroon, since 1984. Mother-offspring relations of group members of four groups (KK, BB, KB, and PT) are known. Tenure of each resident male within these four groups has been recorded since the start of the study period. Mating frequencies of males were recorded during the multi-male mating period in the KK group in 1986

Table 1. Takeover and number of males in the group.

	Year					
Group	1986		1991		1992	
KK	T	16*	T	5	N	1
BB	N	1	N	1	T	3
KB	T	7+	T	8+	T	6
Dm	N	1	N	1	T	4
NW	N	1				

T: Takeover; N: no takeover (tenure period after takeover); * observation of KK in 1986 lasted till the end of the mating season.

(July 11 – September 6). The resident male and five non-resident males were traced as focal animals for 71 hours altogether. Total number of adult males in the group was 15 (Table 1). Mating frequencies of males during the one-male mating period were recorded for 279 hours in the BB group in 1991 (June 30 – September 8). The sampling method was ad lib. sampling, not focal sampling of the resident male, in order to avoid missing matings with the females of the BB group by non-resident outsider males. During this ad lib. sampling, three solitary males and the KK and KB groups with several males several times were observed to approach the BB group temporarily. Data on sexual behaviors other than frequency were collected throughout the study periods. Sneak matings were recorded in 1986, 1991, and 1992. The tenure of males, which allows for detection of possible fathers, was recorded throughout the study periods.

Individuals in the KK, KB, and PT groups were captured by net traps during the 1991 birth season. They were anesthetized and 10cc of blood was collected from each individual. They were released towards their group once they had regained consciousness. All individu-

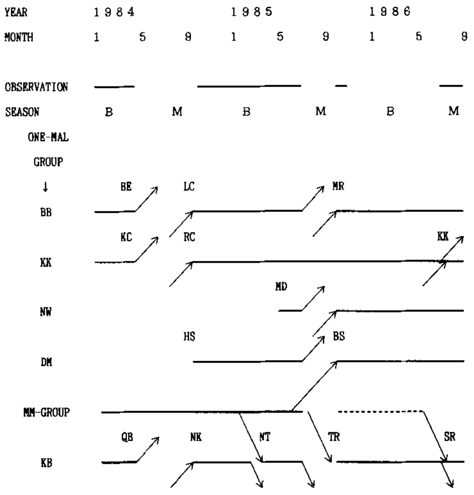


Fig. 2. Changes in resident males in several groups of patas monkeys. B: Birth season; M: mating season. MM-group is only an all-male group. Two letters beside an arrow indicate the name of males. Changes of males (takeover in one-male groups) always occurred during the mating season except one case.

als were confirmed to return to their groups without difficulty. The blood samples were centrifuged and stored with dry-ice until arrival in the laboratory in Japan.

Paternity analysis was performed using two techniques. The first was DNA fingerprinting (JEFFREYS et al., 1985) using the minisatellite probes 33.15 (JEFFREYS et al., 1985) and myo and core (KOMINAMI et al., 1988), as described by INOUE et al. (1990) (Fig. 2). The second technique involved PCR amplification of DNA using customized primers directed to the hypervariable GT-repetitive regions (INOUE & TAKENAKA, 1993).

In the present study it was not possible to allocate paternity for each infant, as blood was not collected from the exresident males in each group; hence, it was only possible to say whether the resident male was excluded as the father. Moreover, mating behavior was not recorded for the breeding season when the mothers of sampled offsprings were impregnated except in 1986 and 1991. Hence, paternity exclusion analysis can only be performed for the year of a takeover and the years of tenure following takeover. We presented a hypothesis that monopolization of females by the resident male is effective in years of tenure after takeover (one-male situation) and is not effective in the year of takeover (multi-male situation). This hypothesis was tested using both paternity discrimination and behavioral observation.

RESULTS

PROMISCUITY AND POLYGYNY

The multi-male situation was only observed just after the takeover of a group by an outsider male (OHSAWA, 1991), and takeovers always occurred during the mating season (Fig. 2) with one exception. Takeover was always followed by invasions of other males (Table 1). The frequency of mating in the multi-male situation, calculated from focal animal sampling in the KK group in 1988, was 5.1 times/10 hr for the resident male (17 times/1993 min) and 3.7/10 hr in 5 invader (non-resident) males (14 times/2266 min; 3/773; 6/732; 0/177; 5/428; 0/156, respectively). In this season the average number of males other than the resident male in the KK group was about 3. Then the frequency of copulation by males other than the resident male was 11.1/10 hr (3.7 × 3). This simple calculation shows that mating by non-resident males occupied 31% [5.1/(5.1 + 11.1)] of all copulations in the group (OHSAWA, 1991).

Data on mating in the one-male situation were collected in the BB group in 1991, during which period 64 copulations were recorded in 279 hr of observation or 2.3 copulations/10 hr. Data were simultaneously collected from all males including those who approached the group, and not just from the resident male, but all observed copulations were performed by the resident male. Table 2 shows the summary of the data. Thus a polygynous mating

Table 2. Summary of observations of mating frequency.

Mating type (Category)		Resident male	Others
Polygynous (N)*	Frequency (per 10 hr)	2.3	0
	% frequency	100	0
Promiscous (T)**	Frequency per individual (per 10 hr)	5.1	3.7
	Number of males	1	Ca. 3
	Frequency in a group	5.1	11.1
	% frequency in a group	31	69

*Data from the BB group for 279 hrs in 1991; **data from the KK group in 1986 (OHSAWA, 1991).

pattern was maintained in the one-male situation and a promiscuous mating pattern was performed in the multi-male situation.

Blood Sampling

Some of the members in three of the four intensively studied groups entered the nets. The genealogy of the KK group is shown in Figure 3, as an example, along with those members of the group from which blood samples were collected. Twelve blood samples of 23 monkeys (52%) in the KK group, 10 of 65 (15%) in the KB group, and 6 of 10 (60%) in the PT group were collected. A total of 28 monkeys were captured out of the 98 members of the three groups; amongst these, 28 were 12 mother-offspring dyads. Examples of fingerprinting are shown in Figure 4.

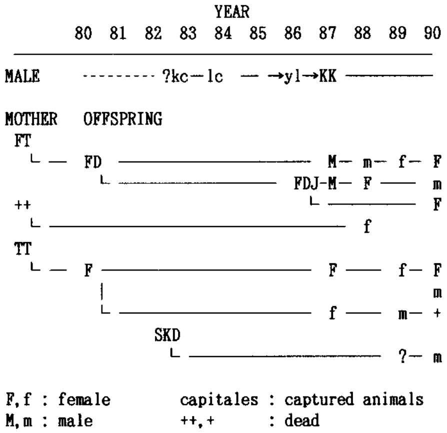


Fig. 3. The genealogy of the members of the KK group. Some animals were captured for blood sampling and paternity discrimination.

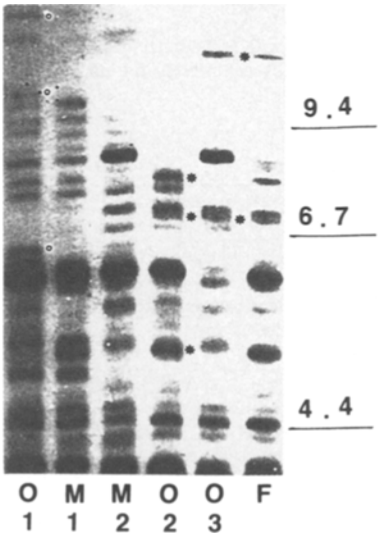


Fig. 4. DNA fingerprinting of patas monkeys, showing three sets of mother-offspring dyads: M1-O1, M2-O2 and M2-O3, and a resident male, F. (*) and (o) indicate paternally inherited bands: the band (*) is present in the resident males' fingerprint, so that the resident male is confirmed as the father of infants 02 and 03; the band (o), however, is not present in F, indicating that he can not be the father of infant 01. Numbers in the right indicate the size of DNA in kb.

Two of these 12 dyads are incomplete, as the mother, *FD*, was not caught. The paternity of her offspring (*FD*, *FD86*, and *FD88*), however, could be derived using the sample of *FD*'s mother, *FT*.

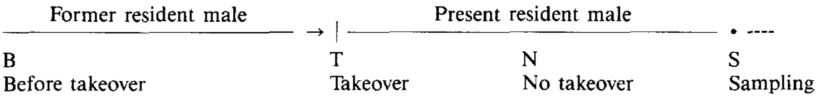
TAKEOVER, MATING PATTERN, AND PATERNITY

The 12 mother-offspring dyads were divided into three categories, before takeover (B), the year of takeover (T) and during tenure in the year following takeover (N) (Table 3). Paternity discrimination in three cases before takeover (B) showed that new harem males were not the fathers of offspring. They were not excluded as the fathers in four of five instances (80%) in the year of takeover (T). Paternity allocation to an individual was not possible in the remaining one case. We conclude that a new resident male was able to defend females against intruder males. The pattern of paternity in the year(s) following takeover

Table 3. Paternity and tenure of resident males.

			Paternity and tenure period			PCR MFGT			
Mother	Birth year	Resident male	B	T	N	17	5	2	Fingerprinting
TT	1980	KK	●			□	■	□	■
FD	1986	KK	●			□	■	■	
ONI	1989	KB	●			■	□	■	■
FT	1987	KK		○		□	□	□	□
TT	1987	KK		○		□	□	□	□
HN	1990	KB		○		□	□	□	□
AF	1990	PT		○		□	□	□	□
OZ	1990	KB		●			□	■	□
FT	1990	KK			○	□	□	□	□
TT	1990	KK			○	□	□	□	□
FD	1988	KK			●	□	□	■	
FDJ	1990	KK			●	□	■	■	■

●, ■: Denied; ○, □: not denied.



B: The infant born in the year before takeover; T: the infant born in the year in which the current harem male took over the group; N: the infant born in the year(s) following group-takeover by the present harem male.

Table 4. Comparison between behavioral data and paternity discriminated.

Mating system	Paternity discriminated	Behavioral data	Note: behaviors increasing reproductive success
Promiscuous	R = 4/5	R = 31%	Priority and compensating copulation
(T)	O = 1/5	O = 69%	Sneak mating and interference of compensating copulation
Polygynous	R = 2/4	R = 100%	Chase others away
(N)	O = 2/4	O = 0%	Sneak mating
Promiscuous (T) + Polygynous (N)			
Average in two	R = 65%	R = 66%	
years' cycle of	O = 35%	O = 34%	
takeover			

R: Resident male; O: others (intruder); Calculations: see text.

(N) showed that resident males with one or more years of tenure defended their females less effectively, as (at least) two of four infants (50%) were not sired by the resident male. Behavioral observation indicated that new resident males copulated less frequently than invader males during a takeover (and multi-male) situation, but that they were responsible for 100% of the observed copulations ($n=64$) in a non-takeover (and one-male) situation. Such observations are at odds with the results of paternity analysis. The results of paternity discrimination are summarized in Table 4.

OTHER FACTORS AFFECTING MATING SUCCESS

The behavior of individual resident males differed considerably. Some would actively chase away surrounding males, and others rejected female presentations and invitations. The results of paternity discrimination of resident males were compared with each other (Table 5). No specific conclusions about the individual differences, however, may be drawn from this result because of the very small sample size. The data do not support a hypothesis that a resident male experiences a decrease in mating success with extended tenure, because frequency of exclusion as father in resident male did not increase with extension of tenure from N1 to N3.

The role of female behavior may also be analyzed, although the sample size becomes even smaller (Table 5). Nevertheless, the age of females may affect the tendency of mating with males other than the resident male, e.g. females *FT* and *TT*, which mated with the resident male in period N were older than the other females *FD* and *FDD*, a 3-yr-old primiparous female, which mated with males other than the resident male. Presentations by young, nulliparous females were often rejected by the resident males and such females rarely mated with him. These observations support the finding that young females may mate with outsider males at the periphery of the group. A direct comparison of the number of offspring sired by resident males and others is possible, without taking the mating system (polygyny versus promiscuity) into consideration. Resident males sired more offspring (six of nine) than other males. When the mating system and the tenure of resident males (average two years) are considered (Fig. 2), resident males sired 80% [4/(4+1)] in the year of takeover and 50% [2/(2+2)] in other years. Hence, resident males sired overall 65% [(80+50)/200] of the offspring over the two-year period, whereas other males sired 35% [(20+50)/200] of the offspring. A similar calculation based on behavioral data shows that the resident males sired 66% of offspring over the two-year period, whereas other

Table 5. Paternity to each resident male.

Resident male	Tenure period and years after takeover	Paternity	Mother	
			Name	Age
KK	T0	○	*FT*	Old
	T0	○	*TT*	Old
	N1	●	*FD*	Young
	N3	○	*FT*	Old
	N3	○	*TT*	Old
	N3	●	*FDJ*	Young, primiparous
KB	T0	○	*HN*	Old
	T0	●	*OZ*	Young-middle
PT	T0	○	*AF*	Middle-old

T: Year of takeover; N: year without takeover; ●: denied; ○: not denied.

males sired 34% of offspring. These two calculations show that monopolizing females is a successful social strategy for patas monkeys, although such factors as the number of invading males or the ability of the resident male to defend his group may change with time.

SEXUAL BEHAVIOR MODIFYING MATING

Some specific events relate directly to the discrepancy found between behavioral observation and paternity discrimination.

Sneak Mating with Males Outside the Group, Initiated by Females

Case 1: July 14, 1991. 07:19. The female *WH* left her group, BB (polygynous, period N) and approached a neighboring group, KK to the east, in which there were several males at this period. The resident male of the BB group, *GZM*, followed *WH* all the time; *WH* followed a young male and presented to him and *GZM* tried to chase away the young male. *GZM* again followed *WH* when she again approached and presented to the young male. This pattern was repeated until 07:51 when they were more than 500m apart from the BB group. Then *WH* turned to the direction to her group and *GZM* followed her.

The above case shows that during the short trip of the two BB individuals, other females were left undefended, although no mating activity was observed in the remaining animals on this occasion. The *GZM* also must have overlooked the sneak mating if it happened. Thus sneak mating by females can happen when two groups approach each other. In all cases where a female approached a neighboring group, she was followed by the resident male. Success of sneak mating occurred on only one occasion, when a female of the KB group (polygynous situation) approached the KK group, followed by two stranger males on July 27, 1992. The KK resident male chased the two stranger males away and mated the KB female. Such sneak mating by females can reduce the reproductive success of resident males in his group. There was no record of this female's behavior in the multi-male situation; perhaps at this time females do not need to leave their groups to mate with non-resident males.

Compensatory Copulation by the Resident Male Against Mating by Other Males

Case 2: July 3, 1991. The new resident male was *TBI* in the KK group. Three submissive males, *HAN*, *KEG*, and *ANA*, were in the group. 15:30. *KEG* approached *TF88*, a 3-yr-old female, and mated with her 40m away from *TBI*, who rushed to *TF88* as soon as he noticed this copulation and copulated with her. *KEG* cried and grimaced at *TBI*, who once ceased to thrust and threatened *KEG*. 15:33. After completing the copulation *TF88* left *TBI* and *KEG* also left the area.

In the multi-male situation in a year of takeover, a subordinate male in the group could easily copulate with a female, who was usually responsible for initiating courtship unless the resident male was not close by. The subordinate male would quickly complete copulation, even if the resident male was visible. The resident male then rushed to the female. The resident male usually copulated with her within two or three min of the sneak mating. Whether such sperm dilution or competition decreases the possibility of the female being impregnated by the subordinate male remains to be elucidated, but such a strategy may serve to increase the reproductive success of the harem male, at the expense of the subordinate male (Fig. 5). This behavior was frequently observed, though numerical data were not collected.

Fig. 5. Compensatory copulation. A resident male (left) discovered a sneak mating, and mates the female in front of the intruder (right). The intruder male tries to disturb the resident male's conpensatory copulation.

DISCUSSION

It is easy to doubt the possibility of complete monopolization of females in a polygynous primate species such as the patas monkeys, in which the group members are widely scattered. The question remains as to whether the monopolizer has been superseded by the sneaker and as a result, the social system leans towards a multi-male one. The present study was undertaken to provide some solutions to this problem. The hypothesis was proposed that a resident male effectively excludes competitors in the year(s) of the tenure following the year of takeover, whereas his defense is not effective just after takeover. This was confirmed by behavioral data. But data on paternity discrimination using molecular biological techniques were not in agreement and in fact showed an inverse tendency to the hypothesis. Several explanations for this discrepancy may be postulated.

The first is the difference between the time point of behavioral observation and that for blood sampling for paternity discrimination; 11 of 12 blood samples of mother-offspring dyads were collected in different years from the years when behavioral data were collected. Behaviors should be recorded in the same period as blood sampled. Nor are the data on social conditions within the group, such as the number of surrounding males, number of resident females, etc. available, although the overall mating pattern (multi-male or polygynous) was known (Table 1). The second problem is related to the very small size of blood sample. This may be the probable explanation why the above hypothesis could not be confirmed. The third problem is the subjective nature of some of the sexual behaviors (sneak mating and sperm dilution) described in the last section of the results. Such behavior patterns may influence the reproductive success of the males in a group. Sneak mating by females in the one-male situation may be the most likely cause of discrepancy between behavioral observation and paternity discrimination. Sperm dilution may be effective in decreasing reproductive success of invader males in the multi-male situation.

The reproductive success of resident males could be suspected to decrease with the length of tenure of resident males. If that is the case, this tendency may possibly have been explained by a shift of female sexual interest from the resident male to intruder of non-group males (ENOMOTO, 1978; TAKAHATA, 1982; CORDS, 1984). This tendency, however, can not be seen for the year after the year of takeover and later (period N). Therefore, the idea of decrease in reproductive success along the tenure of males can not be applied in the present study.

The direct comparison of the number of offspring sired by resident males or others shows that traits of polygyny occurred in two thirds of the patas monkey groups. Systematically, the patas monkey belongs to cercopithecini (Ruvolo, 1988; Dutrillaux et al., 1988). Almost all species of this family are forest dwellers and have a one-male social structure. One may postulate that patas monkeys have emerged from the forest to populate savanna or swamp areas yet have retained their forest-type social system. There is also an opposing view that the patas monkey and three other primitive species were originally savanna or swamp inhabitants (Ruvolo, 1988), with a multi-male social structure. Results of the present study indicate that the mating behavior pattern of patas monkeys may be in the process of altering one form to another and as a result their social system may be changing.

One alternative approach to explain this behavioral dimorphism would be the evolutionary stable strategy of a mixture of resident (monopolizer) and sneaker males (Maynard Smith & Price, 1973). As is the case for the blue gills *Lepoimis macrochirus* (sneaking and paternal care: Gross & Charnov, 1980), this explanation may be more reasonable than a simple comparison of reproductive success between two behavioral traits. The present study, however, lacks data from this viewpoint. Therefore, comparison of reproductive success between two strategies was confined only in one condition (resident: sneaker = 1:3 or 1:0 and each of them is realized every two years on average). Another alternative approach would be "the assessor strategy" [an extension of the concept of the bourgeois strategy: Maynard Smith (1982)]; in which a male, on encountering a group, can choose whether to challenge the resident male or to attempt sneak matings. Such a assessing behavior would represent a realistic evolutionary strategy for patas monkeys. We actually observed such behavior on three occasions: 1) A resident male disappeared from the KK group and reappeared as a subordinate male in the KB group three years later; 2) the resident male of the KB group was defeated, yet stayed as a subordinate male of the KK group; and 3) the resident male of the KK was defeated and reappeared three days later as a subordinate male of the KB group. Moreover, many young small-sized males were observed to join the group as subordinate individuals, some of whom would surely become challengers and even residents when fully grown. Although the assessor strategy may not appear to be profitable on the basis of present findings, such a strategy would be beneficial up until a point where such subordinate males sire more offspring than resident males.

CONCLUSIONS

1) A multi-male situation developed within a patas monkey group only after the takeover of the position of the resident male.

2) Direct observation showed that 31% of matings were performed by the resident male in a multi-male situation with three subordinate males in the group. In a one-male group, the tenured resident male accounted for all matings.

3) Paternity discrimination by DNA typing revealed that 50% of infants (2/4) were sired by outsider males in a one-male situation, and that 20% (1/5) of the infants were sired by intruder males directly following takeover of a group by a new resident male. The resident males sired more infants than non-resident males in the condition of takeover cycle of two years.

4) Sneak mating by females with outsider males or subordinate males was initiated by the females. Sperm competition from compensatory mating by the resident male, following

sneak mating by females in either one-male or multi-male situation may account for some of the discrepancies between the results on sexual behavior and paternity analysis.

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