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Effects of temporary removal and replacement of the alpha male on social behavior of the captive Sichuan snub-nosed monkey *Rhinopithecus roxellana* *

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饲养条件下川金丝猴群中主雄的移除和替换对社群行为的影响 *

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摘 要 在上海野生动物园对一群半散养的川金丝猴进行了为期一年的行为学研究。在此期间，猴群中发生了4起家庭主雄被移除和替代事件和一个雌性群因繁殖需要引入一个成年雄猴的事件，该过程在饲养条件下首次被完整记录。观察发现，繁殖群中，在家庭主雄猴的健康状况良好期间，群中各雄性成员间的社会等级关系相当稳定，很少变动。主雄猴有效地控制着群体的秩序，并严格地看护着其家庭中的雌猴免受其他雄猴的侵扰，而且它也很少对其他低序位雄猴主动攻击。全雄群中则再由一个高序位雄猴控制其他低序位雄猴。疾病、衰老、前主雄猴的存在以及被饲养人员从群中移除进行治疗等都可能引起猴群社会发生很大动荡，尤其是全雄群中各雄猴的社会等级序位发生剧烈改变，甚至发生家庭主雄的替代。在本报道中，人为因素在主雄替代过程中起着主要作用。主雄替代一旦成功，新主雄会把原主雄赶入全雄群，攻击追撵其他低序位雄猴，并彻底与全雄群完全脱离。对于每一个新主雄，家庭中的雌猴对其的接纳表现出明显的选择倾向。雌性性选择可能是野生猴群中新家庭群建立一种内在基础机制，同时提示偷配发生的可能性［动物学报 53（4）：755 – 762，2007］。

关键词 川金丝猴 主雄移除和替代 雌性性选择 人为干预

Key words Sichuan snub-nosed monkey，Removal and replacement of the alpha male，Sexual selection by females，Human interference

Relations among primate males are often characterized by antagonism and competition because their reproductive success depends upon obtaining access to receptive females. Males should therefore attempt to monopolize access to this non-shareable resource (Trivers，1972). The monopolisation potential among males is often uneven，leading to formalized dominance hierarchies，differential mating success or reproductive skew (Bercovitch，1991；Borries，1997；Johnstone et al.，1999；Cowlishaw and Dunbar，1991). Deviations

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from this basic scheme have been noted recently, especially that affiliations do occur among males as well (van Hooff and van Schaik, 1994; van Hooff, 2000) and that dominance and reproductive success are not always interrelated (Berard et al., 1993; Inoue et al., 1993).

A consistent feature of one-male-unit (OMU)-based primate societies is that the tenure of an alpha male is temporally limited. The OMU owner's monopolization (Ren et al., 2000) potential will sooner or later inevitably dwindle and the risk of being supplanted will increase. He will be confronted with challenges from newcomer males. Fights between newcomer males and the resident males in OMU societies often result in the replacement of the former resident male (*Semnopithecus* spp.: Reena and Ram, 1992; Agoramoorthy, 1994; Rajpurohit et al., 2003; *Presbytis cristata*: Wolf and Fleagle, 1977; *Presbytis thomasi*: Steenbeck et al., 2000; *Colobus vellerosus*: Saj and Sicotte, 2005; *Eyrthrocebus patas*: Enstram et al., 2002; *Theropithecus gelada*: Dunbar and Dunbar, 1975).

One way of replacing a resident male and gaining access to a group of females is via a takeover whereby one or several extra-group males invade a unit and drive out the resident. If more than one male participates in a takeover, it is often the highest-ranking of the attacking males who subsequently installs himself as the new resident of the group (Rudran, 1973; Sommer and Rajpurohit, 1989; Rajpurohit et al., 2003). Such takeovers can be accompanied by infanticide (Mori et al., 1997; Newton, 1988; Sommer, 1994; Watts, 1989), subsequent changes in female reproductive condition (Mori and Dunbar, 1985), abortion (Mori et al., 2003; Agoramoorthy et al., 1988), group splitting (Newton, 1987), and eviction of immature individuals (Rajpurohit and Sommer, 1993).

After a takeover or alpha male removal, dominance relationships among intra-group members need to be reformed. Dominance relations are essential for maintaining stability within a primate society (DeVore and Washburn, 1960). Moreover, when incursions of outside males occur, females are often not merely passive bystanders, but actively make decisions about outcomes of this transitory phase (Sugiyama, 1964; Hohmann, 1989); this is done via choices about which male to join, i.e. the current owner or the incoming one. Females thus have an influence on whether the resident male will be replaced or not.

Sichuan snub-nosed monkeys *Rhinopithecus roxellana* exhibit a multi-one-male unit or "nested" social organization with group sizes ranging from 20 to 600 individuals (Ren et al., 2000; Grüter and Zinner 2004). One-male units are not spatially isolated from each other, but habitually unite in larger semi-cohesive groups. Sexual interactions have been noted to take place beyond the OMU's boundaries (Zhao et al., 2005), implying that the mating system is not universally unimale, but also has elements of a promiscuous multimale-multifemale society (Grüter and Zinner, 2004). Behavioral data collected on individually identified animals in the wild are scarce, and not much is known about social interactions in this intriguing species in general. It has been observed that—in line with the scheme summarized above—*R. roxellana* males are intolerant of one another when in the presence of females. Moreover, a linear dominance order was found among unit males in a group (Tan et al., 2003). Life history mechanisms such as male career pathways and group ownership acquisition are poorly understood. Only one case of takeover was reported (Wang et al., 2004) whereby a solitary male penetrated an established unit at Zhouzhi and challenged the resident who had been the alpha in his unit for at least 1.5 years. During the takeover process, no escalated fights between the resident and the challenging male were witnessed, but the new resident was found with a small injury. The ousted male did not remain in the band, but all former unit members stayed. Apart from that incident, males of an all-male unit have been observed to jointly invade one-male units in another group of *R. roxellana* at Zhouzhi (ST. Guo, mentioned in Wang et al., 2004).

A colony of the Sichuan snub-nosed monkey was founded at the Shanghai Wild Animal Park in 1995, and this is still the only institution in China where bachelors and residents are kept in the same enclosure. Human removal of alpha males had been made necessary several times between April 2000 and February 2001, thus creating a resident male temporal absence that resulted in several takeovers. This unintended experimental set-up allowed us to investigate male replacements and its effect upon the social relations of the colony members. The special grouping at Shanghai allowed us to study patterns of group formation and rank reversals under captive conditions. Whether such a "natural" grouping mimicking the situation found in the wild is ideal under zoo conditions will be discussed below.

In sum, the goals of this study are 1) to summarize all the cases of artificial removal of alpha males in a captive colony of *R. roxellana* and the effects upon the social and dominance relationships among all the individuals in the colony with special emphasis placed on male rank reversals; 2) to report the process of introducing a reproductive male into an all-female group and the response of the females to the introduced male; and 3) to examine how female *R. roxellana* respond to male takeovers or artificial introductions.

1 Subjects and methods

1.1 Subjects

The study group (thereafter referred to as the "exhibition group") at the Shanghai Wild Animal Park

was composed of 13 animals which were held in a 20 m × 5 m × 2.8 m cage during the night and released on a grassy island (about 900 m^2) from 07:30 to 16:30 in the daytime. The whole enclosure was rebuilt from August to September in 2000 during which the night room was enlarged to 20 m × 5 m × 3.3 m in size. The area of the outside island was reduced to about 800 m^2, and a semicircle rockery was built around the island.

All the individuals involved at the beginning of this study are listed in Table 1. Each one in the group was individually identified, and his or her matrilineal kin relationship was known. The group consisted of two units: a one-male family and an all-male unit (Table 1).

Table 1 Composition and individual relationships of the Sichuan snub-nosed monkey "exhibition" group at the Shanghai Wild Animal Park in May 2000

	Name	Age (yr)	Sex	Relationship
Family	M0	9	♂	Father of J2, J4, J3; the first alpha male, died on July 13, 2000
	F1	13	♀	Mother of J1, J3 and M5
	F2	15	♀	Mother of J2
	F3	9	♀	Mother of J4
All-male unit				
	M1	15	♂	Father of J1
	M2	10	♂	Bachelor
	M3	8	♂	Bachelor, died on June 3, 2000.
	M4	8	♂	Bachelor
	M5	6	♂	Son of F1, subadult male
Juveniles				
	J1	3	♂	Son of F1
	J2	2	♂	Son of F2
	J3	1	♂	Son of F1
	J4	2	♀	Daughter of F3

During the study, an all-female unit of 5 females (3 adults and 2 daughters) was held in a room (7 m × 4 m × 3.3 m). One adult male named Yy was introduced into the all-female group on 09 July 2000 at 0750 hr for reproductive purposes. This was an opportunity to get to know how the females would respond to such a human-induced adult male introduction. Individuals and their relationships of this breeding group are listed in Table 2.

Table 2 Composition of the caged female band at the Shanghai Wild Animal Park in 2000

Individuals	Provenance	Relation
Xs	Shaanxi	Previous male ever introduce into this female band
Yy	Shaanxi	The introduced resident male on July 9, 2000
Qq	Shaanxi	Mothered 984 # in 1998 at the Park
Xx	Shaanxi	Adult, abortion in 2000
Tt	Shaanxi	Born 972 # in 1997
972 #	Captive	Juvenile, Xs sired in 1997
984 #	Captive	Juvenile, Xs sired in 1998

1.2 Behavioral repertoire and procedures

This study was based on a one-year observation period from May 2000 to May 2001 at the Shanghai Wild Animal Park. Most descriptive results here were extracted from several periods of consecutive observation days when the events of interest happened. Behavior definitions have been reported previously by Ren et al.(1995, 2000).

Focal animal observation sampling was employed to record the absolute frequency of occurrence of the behaviors. A social hierarchy was constructed within each sex based upon approach-retreat interactions (Rowell, 1966).

Alpha male replacement is defined as: an adult male is introduced into or takes over the target family group, and at least two of the adult females in the group sexually solicit him and others sit around him without avoiding him when he approaches.

2 Results

The following social hierarchy was prevalent before the first replacement of the resident male in the "exhibition" group: males, M0 > M1 > M3 > M2 > M4 > M5; females, F3 > F1 > F2. F1 and F3 changed their social ranks several times; only F2 kept her rank all the time. When F3 chased F1, F2 helped the former.

Case 1: M0 died and M2 became the resident male

When M0 monopolized the family, his family included the three adult females F1, F2, F3 and the four juveniles J1, J2, J3, and J4. Any member of the all-male unit (AMU) who attempted to approach the family was driven off. Only juveniles (< 2 years old) were allowed to move about freely between these two sub-units. Since April 29, 2000, two fights between M3 and M0 had been recorded, of which M3 lost both. The second confrontation between the two combatants on June 4 resulted in M3 receiving four wounds in his back from M0's canines. Veterinarians of the Park treated M3 and kept him alone in a cage. After he was released into the "exhibition" group again, M3's rank fell below M2's. On June 7, M3 died of acute pneumonia.

M2 upgraded his social position after the death of M3 and challenged M1. On July 9, M2 wounded M1 in the right leg, and the latter received two 12 cm and 14 cm deep cuts in the right hindlimb. M1 was isolated for medical treatment until July 12. When M1 was let out into the group, he had been alone most of the time since then because all the other males in the AMU avoided him. M2, M4, M5 avoided him whenever he approached. At about 14:00 on July 13, M2 moved towards the family's vicinity and tried to approach the female F3, who was feeding on the ground near the family. M0 chased and fought with M2. M2 bit M0 in the left arm and the latter got two cuts in the left forelimb: one was 7.5 cm and the other was 9 cm long in the skin. M2 was not wounded.

At 17:32, M0 died of heatstroke while being treated. M2 thereafter monopolized the harem. After the successful supplanting, all the individuals in the AMU began to stay away from M2 when he approached. The oldest male juvenile J1 was chased by M2 five times in the afternoon when he came within reach of the family. M5 and J1 then began to stay with M1. M4 stayed alone away from others in the AMU. M4's social position was degraded, leading to the following social hierarchy of the males: M1 > M5 > M4.

The immediate post-takeover phase was characterized by M2 being let alone by the three adult females. However, M2 was tolerated to feed beside the females. At 08:32 on July 14, M2 chased F3, and the latter fled. Two minutes later, F3 was caught by M2 from behind and was mounted. After 11 pelvic thrusts, they dismounted and cuddled. Because J1 was advancing at that time, M2 left F3 and chased him away. J1's mother F1 and F2 ran after M2 to attack him, and M1 also joined in and chased M2. M2 fled away and sat alone. F1, F2 and M1 subsequently withdrew and did not engage in any further conflicts. After this incident, M2 didn't stay with any of the females during the day. Up to July 15, F3 began to interact frequently with M2 and sexually prostrated to him. From then on, F3 accepted M2 as her mate, but F1 and F2 did not. Until July 26, F1 had sexually solicited and had been mounted by M2. M2 was then regarded as the alpha male of the family. The acceptance process of M2 by the females lasted 14 days.

Case 2: M4 replaced M2

During the renovation of the enclosure in August and September 2000, the monkeys were moved to another place and caged. The family was housed in one cage while the AMU was caged in another. M1 became sick on September 15 and was isolated to be treated. During that time, M4 was dominant over M5 and J1. When M1 was set free into the AMU, he began to keep out of M4's way. Treatment by man lowered M1's social rank. M4 chased J1 and M5 more often than ever. The social rank order in the AMU turned out to be: M4 > M1 > M5. On September 28, the monkeys were transferred back to the island enclosure. When the exhibition group was resettled onto the island, M4 didn't chase J1, M5 and M1 anymore. They stayed together as an AMU. The hierarchy was recorded as M4 > M1 > M5.

On November 20, the left side of the M2's face and his upper-lip were swollen, but that handicap did not influence his ability to feed and move. He was housed alone in a cage for treatment. Both M1 and M4 were observed to approach the family and to fight with each other. After defeating M1, M4 took over the family. F3 accepted M4 as her sexual partner without hesitation. F1 and F2, on the other hand, rejected M4 violently. In the afternoon of that day After M4's approached gradually, he could sit beside F1 and F2. M4 began to chase M5 and J1 as that M2 did. On November 22, F1 started sexually prostrating to M4, and the latter mounted her. The whole supplanting process only lasted two days.

When M2 was let out on November 26, M1, M4 and M5 chased M2 away. M2 lost his alpha position entirely. He began to avoid M1 when the latter approached.

Case 3: M1 monopolized the breeding family

On January 29 of 2001, M2 lost his appetite and was more quiet than usual. He was caged separately at 13:15. M1 was still the highest ranking male in the AMU. On January 30, M4 was isolated from the group because of vomiting. It was during that time M1 took over the breeding family with no apparent conflict with other males of the AMU.

When M1 came into the family, F1 accepted him as her sexual partner instantly without any evident exclusion. F2 and F3 rejected M1 strongly.

After being treated (< 30 minutes), M4 was set free into the group. M4 ran into the family, M1 attacked M4, and F1 helped M1 to chase M4. M4 was driven out into the AMU.

M5 was recorded to sit more often with M4 than J1. For most time of the day, M5 sat together with M4. M1 tolerated J1 approaching the family to a certain distance, but all females including J1's mother F1 did not. When J1 came too close, the females (especially F2) immediately drove him away.

On February 4, F3 sexually prostrated to M1 which resulted in copulation with ejaculation. F3 groomed M1 after being mounted. The supplanting process lasted six days.

M4 and M5 were caged again due to a serious cold on January 30. M4 was introduced into the exhibition group on the afternoon of February 1. When he met M1 at the gate of the doorway, M4 avoided M1 in spite of the latter showing him the friendly "open-mouth" display. M5 was let out after M4's was cured and moved normally. The three males (M5, M4 and M1) cuddled, groomed each other, and stayed together in the daytime. Over the following two days, M1 chased M4 three times and the latter fled every time. On February 2, M4 and M5 were caged again and were freed after getting injections at 15:20. M1 caught a heavy cold and was separated to be treated with penicillin. During that time, M4 and M5 sat together and did not disturb the family. When M1 was let out, he monopolized the family again without encountering any resistance from the females.

M2 was set free at 09:42 on February 3. M3 and M5 were isolated again because of a serious cold. Only J1 was healthy and moved on the periphery of the family. J1 received several attacks and chases from F1 and F2 when he approached the family. When M2 was released, J1 and M2 sat together and groomed each other. M2 was chased by M1 only once during that day. M4 and M5 were let out at 09:00 on February 4, and both M4 and

M5 began to avoid M2's approach. The dominance hierarchy in the AMU became M2 > M4 > M5. Compared with M5, M2 and M4 received more cuddling and grooming. After this change, M4 did not regain the alpha rank in AMU throughout the rest of this study.

Case 4: M2 recaptured the alpha position from M1

At 07:13 on February 23, the monkeys woke up and went to the ground to eat leaves left over from the previous night. When M2 approached F3, M1 ran after M2 and fought with him. M2 won and expelled M1 from the family. M2 was instantly accepted by F3 and F1 and controlled the family from then on. M1 once again stood up and ran towards the family, but he was attacked by F1 and F3. In the meantime, M2 approached F1 and F3. M1 gave up fighting, went back to the AMU and stayed with M5 and J1. M4 moved about by himself most time on that day. M2 chased J1 and M5 whenever they moved into his range. In this case, M2 was accepted as the alpha male shortly after defeating M1. The process of being accepted took less than 30 minutes.

Case 5: Yy was introduced into an all-female band

Yy was introduced into the captive all-female group for reproduction at 07:50 on July 9 2000. When he entered the cage, all the females avoided him. At 08:02, Yy rushed along the perch and the behavior of Yy caused the females to escape. After that, he sat alone. At 08:16, the female Xx sat down beside him and started to groom him. On July 12, Qq began to groom Yy. She left him and sat alone after finishing the grooming. After the grooming session was over, Yy tried to mount Qq when she was moving on the ground. Qq rejected his mating attempts twice. The females did not attack Yy when he approached, but avoidance of him was frequently observed. On July 15, Yy was observed moving and interacting with the females. The first voluntary sexual prostration of one of the females to him was recorded on July 16, the 7th day after the male's introduction. The female was Qq, the oldest female in the all-female group. From then on, the other females also accepted Yy as their sexual partner. The whole process lasted eight days.

3 Discussion

The circumstances of temporary male removal provided several insights into the principles and patterns that are at work in the organization of this species' social system.

3.1 Male conflicts, takeovers and social consequences

Social grouping patterns are largely unstudied in *R. roxellana*. *R. roxellana* family groups are uni-male units and only infrequently contain additional males (Ren et al., 1998). Preliminary evidence holds well with the assumption that all-male units act as a source of challengers and established OMUs act as sinks for the successful one of those rivals. Males in all-male units only achieving the dominant position in an OMU can breed. According to sexual selection theory, males should always try to exclude all other rivals from groups of females. Relationships among *R. roxellana* males are obviously dominated by reproductive competition (*sensu* Kappeler, 2000). Our observations demonstrate that there is a strong apparent conflict between the OMU and males in the AMU, and that fights between males are usually serious: They got broken tails (Qiu JH, pers. comm.), deep bite wounds etc. The turnover of the breeding male was accompanied by fighting or other forms of conflict which is in compliance with studies on other primates, e.g. Ohsawa (2003). During a takeover process in a provisioned but free-ranging population of *R. roxellana*, no escalated fights between the resident and the challenging male were witnessed, but the new resident was found with a small injury (Wang et al., 2004). It appears that the captive environment might increase the severity of male fights.

These male-male conflicts are so intense that the dominant male not only excludes all the other males from the vicinity of the family, but also the male juveniles over the age of 1.5 years. Nursing male monkeys are partly attached to family units (OMUs) and partly to all-male units. In the wild, AMUs frequently contain juveniles as well (*R. roxellana*: Ren et al., 1998; *R. bieti*: Grüter and Zinner, 2004). In Hanuman langurs, male infants are harassed (Hrdy, 1977; Mohnot, 1978) and male juveniles leave their natal troop after takeovers by a new male and join nearby all-male bands ("juvenile expulsion"; Mathur and Manohar, 1991; Rajpurohit and Mohnot, 1988; Sommer, 1988). It has been suggested that parental attacks on their sexually maturing offspring serve the function of peripheralization and incest avoidance (Tilson, 1981). In our *R. roxellana* colony, juvenile expulsion from the family unit seems to have other functions. From the perspective of a female and in line with inclusive fitness theory (Hamilon, 1964), it is in her interest to prevent her elder juvenile son from getting killed by the alpha male. The following observation furnishes evidence: In Case 1, when M2 chased J1, the mother F1 and father M1 all mobbed M2 and drove the latter away. This action also made M2 stop chasing J1 and prevented J1 from being injured. The reasons for alpha males (family owners) to chase juvenile and subadult males are thought to be the following: at a proximate level, entering the range of the OMU by juveniles triggered a stern defense by the alpha male; on a functional level, chasing them away can be seen as a tactic to avoid counterattacks from them and dispose of future possible rivals. Furthermore, the AMU appears to be a safe unit for expelled male juveniles where they are protected from being chased or wounded. This is demonstrated by the following case: when the dominant male of the family unit ran into the range of the AMU, he was usually mobbed by several male bachelors. He

presumably avoided such interactions as they might jeopardize his alpha status.

Introduction of a reproductive male into a breeding female band when the mating season is near is commonplace in captive-held primate populations (Jackle et al., 2000; Burks, 2000). In Case 5, Yy was selected as the reproductive male to be introduced into the female band (Ren et al., 2003). The process of a new male being introduced into the breeding family in captive *Gorilla gorilla gorilla* was accompanied by screaming and chasing (Jackle et al., 2000). Screaming and chasing occurred in *R. roxellana*, too. When Yy was put into the cage, he performed an exaggerated display (*sensu* Ren et al., 1990) that can cause a chain reaction and bring about group chaos. No overt juvenile chasing was observed in Case 5. Yy's approaches to the females did make the females escape and scream. So the female screaming and male chasing were *per se* different from what occurred during the process of male replacement. In our observed cases of male replacements, the new dominant male forced the juveniles out into the periphery of the family or into the AMU, while in *Gorilla g. gorilla*, the new adult male chased and even wounded the juveniles severely (Jackle et al., 2000).

There was a clear-cut hierarchy among AMU males which changed several times during the course of the study (Rajpuohit et al., 1995). A higher rank in the all-male unit implies a higher potential to achieve residency in a family unit. In Hanuman langurs, it is the highest ranking member of the all-male unit who gains control over the group (Sommer, 1988; Sugiyama, 1965). At the Shanghai Wild Animal Park, most of the supplanting processes started with a shift of rank among the males in the all-male unit (Cases 2, 3 and 4). Social rank reversal in the all-male unit can be regarded as an indicator that its social structure was not stable at that time.

Takeover in the colony ceased and social stability was re-established and maintained through active controlling of the new alpha. When M0 successfully suppressed all the challenges from M3 or other bachelor males in the all-male unit, social stability was kept. The same was evident in Case 2: After the rebuilding of the enclosure had been completed and the AMU and OMU had been re-grouped onto the island, the controlling presence of M2 made M4 stay away with the other males peacefully. Only when the male fully monopolized all the females in the family, the group became stable. The violent chasing of juveniles by the new alpha male then also eased off or stopped.

3.2 Female mate choice

Female *R. roxellana* show preference over some males as their mating partners. The process of taking over a family and being accepted by the females ranged in time from 30 minutes to 14 days in our study colony of *R. roxellana*. In Hanuman langurs for instance, replacement can be either a gradual (Newton, 1986) or a sudden event (Rajpurohit et al., 2003). Our findings would be more along the lines of a sudden takeover. However, final acceptance by the group females took even several days.

The male who took over the family unit was in all observed cases accepted by adult females as their sexual partner. Loyalty for ousted males was thus low. Female solicitation turned out to be a key event in the "acceptance process" of a new resident. Previous mating experience had an influence on the speed of the acceptance process: an unfamiliar male who had never had sexual contact with one of the family females was not so readily accepted as the new alpha as a male who had mated with one of them before. For instance, it took a relatively longer time for M2 to be accepted than M1 and M4. In the wild, females also had an influence on the outcome of group reformation: after a takeover by a solitary male, the former resident did not remain in the band. All former unit females stayed, suggesting that female preference might have played a role in the outcome of resident male replacement (Wang et al., 2004).

3.3 Captive management

Social conflicts between males-whether in captivity or in the wild-might be very brief one-time episodes, or they might be prolonged or repeated frequently (Mason and Mendoza, 1993). Such conflicts might be directly or indirectly harmful to the individual involved: Individuals might get wounded, or constant activation of stress may negatively affect their health (Weiss, 1972). In the present study, the death of M0 and M3 might have resulted from the cumulative effect of injures and stress.

Male conflicts occur more frequently in captivity than in the field (Höhn et al., 2001). Once male fights occur, escalated male fights may bring about injuries and even death (Walters and Seyfarth, 1987), and—if occurring in zoos and parks—make human intervention necessary.

Whenever males in this colony got sick or wounded, they were removed by zookeepers and were treated in isolation. Such human intervention caused takeovers and profound changes in group composition and stability. Females in the AMU were left "defenseless", and in the absence of their unit male, the females were chased by bachelor males immediately. Analogous observations of disintegration of female group integrity after removal of their harem leader have been made at the Madrid Zoo in a colony of *Papio hamadryas hamadryas* (Colmenares et al., 2006). Compared to the situation in the Shanghai Wild Animal Park, male tenures in wild *R. roxellana* are unquestionably longer (at least 1.5 yrs), and takeovers are thought to occur at much lower frequencies. Human isolation of sick males is thought to be the main factor causing recurrent aggression and fluctuations in social rank.

To keep the group stable is stopping human intervening in intermale aggressive processes. In the present study, severely wounded individuals were mainly the consequence of intentional human intervention in ritualized fights. Human interference undoubtedly enhances the tension of the fighting animals and possibly even causes unnaturally aggressive behaviors. No male got wounded in Case 4 when the zookeepers did not intervene in the monkeys' tussles. In Case 1, the wound M0 got after having been bitten by M3 was only minor and did not require treatment by the veterinary staff at all. That wound would surely have healed gradually without treatment. Furthermore, the deaths of the two resident males of the OMU happened after human capture and during medical treatment. All such evidence suggests that human intervention would in most situations be unnecessary. In most primate groups with well-established relationships, approach-retreat interactions (Rowell, 1966) serve to avoid severe aggressive behaviour (Walters and Seyfarth, 1987) including captive *R. roxellana* (Ren et al., 1990; Ren et al., 2003).

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